# The multicolored Asian lady beetle, Harmonia axyridis: A review of its biology, uses in biological control, and non-target impacts

Author: Koch, R L.

Source: Journal of Insect Science, 3(32) : 1-16

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.003.3201

Koch RL. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. 16pp. *Journal of Insect Science*, 3:32, Available online: insectscience.org/3.32

Journal of Insect Science

insectscience.org

# The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts

**R L Koch**

*Department of Entomology, 219 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, Minnesota, 55108, USA*
koch0125@umn.edu

Received 16 May 2003, Accepted 22 August 2003, Published 13 October 2003

## Abstract

Throughout the last century, the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) has been studied quite extensively, with topics ranging from genetics and evolution to population dynamics and applied biological control being covered. Much of the early work on *H. axyridis* was conducted in the native Asian range. From the 1980's to the present, numerous European and North American studies have added to the body of literature on *H. axyridis*. *H. axyridis* has recently gained attention in North America both as a biological control agent and as a pest. This literature review was compiled for two reasons. First, to assist other researchers as a reference, summarizing most of the voluminous body of literature on *H. axyridis* pertaining to its biology, life history, uses in biological control, and potential non-target impacts. Secondly, to be a case study on the impacts of an exotic generalist predator.

*Keywords: Harmonia axyridis*, classical biological control, augmentative biological control, conservation biological control, non-target effects

## Introduction

The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), is a well-known aphid predator in its native Asian range (e.g., Hukusima and Kamei, 1970, Hukusima and Ohwaki, 1972, Yasumatsu and Watanabe, 1964). The presumed native distribution of *H. axyridis* extends from the Altai Mountains in the west to the Pacific Coast in the east, and from southern Siberia in the north to southern China in the south (e.g., Chapin, 1965, Dobzhansky, 1933, Korschefsky, 1932, Kuznetsov, 1997, Sasaji, 1971). Numerous releases of *H. axyridis* as a classical biological control agent were made in North America, dating back to 1916 (Gordon, 1985). The first established population was documented in 1988 in North America (Chapin and Brou, 1991). After this initial detection, it spread rapidly across North America (Colunga-Garcia and Gage, 1998, Dreistadt et al., 1995, Hesler et al., 2001, Smith et al., 1996, Tedders and Schaefer, 1994). Currently, it occurs throughout much of the continental United States, except for Montana, Wyoming, and parts of the southwestern United States (RLK, unpublished data). This exotic coccinellid adds to the approximately 475 species of Coccinellidae in North America north of Mexico (Gordon, 1985). *H. axyridis* has also been released in Europe (Iperti and Bertand, 2001, Katsoyannos et al., 1997) and was recently recorded in South America (de Almeida and da Silva, 2002).


Photo Credit: R.C. Venette, University of Minnesota

## Taxonomic History

*H. axyridis* is currently placed in the tribe Coccinellini of the family Coccinellidae (Kovar, 1996). The taxonomic history of *H. axyridis* is rather complicated, and the following taxonomic treatment is primarily derived from Sasaji (1971) and Chapin (1965). In 1773, this coccinellid was initially described as *Coccinella axyridis* Pallas. Eight junior synonyms were also proposed for this species (*Coccinella bisex-notata* Herbst 1793, *Coccinella 19-sinata* Faldermann 1835, *Coccinella conspicua* Faldermann 1835, *Coccinella aulica* Faldermann 1835, *Harmonia spectabilis* Falderman 1835, *Coccinella succinea* Hop 1845, *Anatis circe*

Mulsant 1850, and *Ptychanatis yedoensis* Takizawa 1917). The generic placement was changed to *Leis* by Mulsant in 1850 and then to *Ptychanatis* by Crotch in 1874. In 1885, Weise proposed that this coccinellid be transferred to the subgenus *Harmonia* in *Coccinella*. In 1915 and 1943, Jacobson and Timberlake, respectively, raised *Harmonia* to generic status. Numerous subspecies and aberrations have been described for this polymorphic species (Korschefsky, 1932). *H. axyridis* is often referred to by its Entomological Society of America accepted common name, the multicolored Asian lady beetle. Another common name for this species is the Halloween beetle (Mahr, 1996). This name likely comes from the massive fall migrations of *H. axyridis*, which occur around Halloween (i.e., late October in North America).

**Stage Specific Descriptions**

Shortly after *H. axyridis* was detected in North America, descriptions and taxonomic keys were published (e.g., Chapin and Brou, 1991, Gordon and Vandenberg, 1991). These New World descriptions differ little from the Old World descriptions (e.g., Chapin, 1965, Kuznetsov, 1997, Sasaji, 1971). Adults are 4.9-8.2 mm in length and 4.0-6.6 mm in width (Kuznetsov, 1997). The body is a moderately convex, shortened oval, approximately 4/5 wide as long (Kuznetsov, 1997, Sasaji, 1971). Coloration and maculation is highly variable (e.g., Korschefsky, 1932). The head can be black, yellow, or black with yellow markings (Kuznetsov, 1997, Sasaji, 1971). The pronotum is yellowish with black markings in the center. These markings can be four black spots, two curved lines, a black M-shaped mark, or a solid black trapezoid (Chapin and Brou, 1991). The lateral edges of the pronotum have a yellowish oval-shaped spot (Chapin, 1965). In general, elytra can range from being yellow-orange to red with zero to 19 black spots, or may be black with red spots. The reader is referred to Korschefsky (1932) for citations to descriptions of various color morphs. A transverse plica is usually present above the apex of the elytra (Chapin, 1965, Chapin and Brou, 1991). The ventral surface can be yellow-orange to black (Chapin and Brou, 1991, Kuznetsov, 1997).

The color polymorphism of *H. axyridis* appears hereditary and likely associated with a series of multiple alleles (Honek, 1996). Komai (1956) reviewed the genetics behind the phenotypic variability of Coccinellidae. Larval diet (Grill and Moore, 1998) and temperatures to which pupae are exposed (Sakai et al., 1974) may also influence the coloration and maculation of adults. Over 40 years, the frequency of the various color morphs was shown to go through relatively long periods of both stability and change (Komai, 1956). Color polymorphism was also shown to vary seasonally within a year (Komai, 1956, Osawa and Nishida, 1992). Spatial variation in the frequency of the various color morphs has also been documented (Dobzhansky, 1933). It is interesting to note that the dark color morphs are rare in North America (e.g., LaMana and Miller, 1996), whereas in Asia, the dark morphs can be common (e.g., Dobzhansky, 1933).

Eggs are oval shaped and about 1.2 mm long (El-Sebaey and El-Gantiry, 1999). Freshly oviposited eggs are pale yellow in color and with time turn to a darker yellow (El-Sebaey and El-Gantiry, 1999, He et al., 1994). Approximately 24 hours prior to hatching, the eggs become gray-black (El-Sebaey and El-Gantiry, 1999, He et al., 1994). Larvae range in size from 1.9 to 2.1 mm in the first instar to 7.5 to 10.7 mm in the fourth instar (Sasaji, 1977). However, El-Sebaey and El-Gantiry (1999) reported larval lengths somewhat shorter than those reported by Sasaji (1977). Larvae are covered with many scoli (Savoiskaya and Klausnitzer, 1973). On the abdomen, the dorsal scoli are three pronged and the dorsal-lateral scoli are two pronged (Sasaji, 1977, Rhoades, 1996). Instars can be relatively easily distinguished from one another based on coloration. First instars generally have a dark blackish coloration (Sasaji, 1977, Rhoades, 1996). However, El-Sebaey and El-Gantiry (1999) reported a red spot located medially on the sixth abdominal segment of the first instar. Second instars are similar in color to the first instar, except for orange coloration of the dorsal-lateral areas of the first (Rhoades, 1996) or first and second abdominal segments (Sasaji, 1977). In the third instar, the orange coloration covers the dorsal and dorsal lateral areas of the first abdominal segment and dorsal lateral areas of the second to fifth abdominal segments (Sasaji, 1977, El-Sebaey and El-Gantiry, 1999). The fourth instar has the same orange markings on a blackish background as the third instar, however the scoli of the dorsal areas of the fourth and fifth abdominal segments are also orange (Sasaji, 1977). Like other members of the subfamily Coccinellinae, pupae are exposed, and the fourth instar exuvium remains attached to the posterior end of the pupa, where the pupa is attached to the substrate (Savoiskaya and Klausnitzer, 1973).

**Biology**

*Life History*

The holometabolous life cycle is similar to that of other aphidophagous coccinellids, proceeding through the egg, four instars, pupal, and adult stages (e.g., Hodek, 1973). At 26º C on a diet of *Acyrthosiphon pisum*, the mean duration of each stage is as follows: egg 2.8 days, first instar 2.5 days, second instar 1.5 days, third instar 1.8 days, fourth instar 4.4 days, pupa 4.5 days (LaMana and Miller, 1998). Development from egg to adult was shown to require 267.3 degree days above a lower developmental threshold of 11.2º C in the United States (LaMana and Miller, 1998), and 231.3 degree days above a lower developmental threshold of 10.5º C in France (Schanderl et al., 1985). Temperature not only influences the rate of development, but also adult weight. Larvae reared at higher temperatures produce smaller adults than larvae reared at lower temperatures (Kawauchi, 1979). Diet has also been shown to impact larval development. Hukusima and Ohwaki (1972) found that developmental time decreased with an increase in aphid consumption. The species of aphid preyed upon and the species of plant the aphids develop on can effect larval developmental time, adult longevity, and fecundity (Hukusima and Kamei, 1970). Adults typically live 30 to 90 days depending on temperature (El-Sebaey and El-Gantiry, 1999, He et al., 1994, Soares et al., 2001). However, adults may live up to three years (Savoiskaya, 1970a, Savoiskaya, 1970b). Pre-mating and pre-oviposition periods were shown to decrease with increasing temperature (He et al., 1994, Stathas et al., 2001). Under laboratory conditions, females can produce up to 3,819 eggs at a rate of 25.1 eggs per day (Hukusima and Kamei, 1970). However, Stathas et al. (2001) reported a lower maximum total fecundity of 1,642 eggs. Females typically will oviposit batches of approximately 20 to 30 eggs (Takahashi, 1987).

*H. axyridis* generally is considered bivoltine in much of Asia (e.g., Osawa, 2000, Sakurai et al., 1992), North America (Koch and Hutchison, 2003, LaMana and Miller, 1996), and Europe (Ongagna et al., 1993). However, up to four to five generations per year have been observed (Wang, 1986, Katsoyannos et al., 1997). During the summer, beetles may become quiescent (Sakurai et al., 1992). In the United States, adults migrate to overwintering sites in late October (Kidd et al., 1995, LaMana and Miller, 1996). In Ohio, migrations began on the first day with temperatures exceeding 18º C after temperatures had dropped to near freezing (Huelsman et al., 2002). Length of the photoperiod triggers the physiological readiness of some insects to initiate migratory flights (Danks, 1991). However, for *H. axyridis*, the impact of photoperiod has not been examined. In Asia, the start of migratory flights ranges from mid-October (Liu and Qin, 1989) to late November (Sakurai et al., 1993). Hodek et al. (1993) reviewed long-distance migratory fights of Coccinellidae. *H. axyridis* expresses a hypsotactic behavior, meaning that it migrates towards prominent, isolated objects on the horizon (Obata, 1986a). During the fall migrations, they preferentially choose to land on white or light-colored objects (Obata, 1986a, Tanagishi, 1976). Upon arrival at an aggregation site, they form mass aggregations (Liu and Qin, 1989, Tanagishi, 1976) in dark, concealed locations (Sakurai et al., 1993). In mountainous areas, aggregations are often formed under south facing rocks mid-way up a mountain (Liu and Qin, 1989). In other areas, aggregations may be formed on buildings, often on walls with a southern or western exposure (Kidd et al., 1995). It seems unlikely that volatile chemical cues are used for formation of overwintering aggregations (Nalepa et al., 2000).

In Japan, *H. axyridis* acclimates to winter by decreasing its supercooling point and lower lethal temperature to approximately –19º C and –16º C, respectively (Watanabe, 2002). The decrease in supercooling point was significantly correlated with an increase in myo-inositol content (Watanabe, 2002). Most of the winter is passed in a state of diapause that appears to be regulated by the corpus allatum (Sakurai et al., 1992). Diapause is entered with an empty digestive tract, enlarged fat body (Iperti and Bertand, 2001), and most females overwinter unmated (Iperti and Bertand, 2001, Nalepa et al., 1996). In late-winter or early-spring, they switch from diapause to a quiescent state (Iperti and Bertand, 2001). Upon arrival of warm temperatures in spring, they mate and disperse from overwintering sites (LaMana and Miller, 1996). Sexual activity of *H. axyridis* and other Coccinellidae was reviewed by Hodek and Ceryngier (2000).

*Population dynamics*

Cannibalism appears to play an important role in the population dynamics of *H. axyridis* (Osawa, 1993). Wagner et al. (1999) showed that cannibalism is heritable and that variability exists between lineages. The intensity of cannibalism seems to be inversely related to aphid density (Burgio et al., 2002, Hironori and Katsuhiro, 1997). Across multiple habitats and years, Osawa (1993) reported approximately 50 percent cannibalism on eggs. The intensity of sibling cannibalism on eggs was density independent, while non-sibling cannibalism on eggs was density dependent (Osawa, 1993) and most intense near aphid colonies (Osawa, 1989). Larval cannibalism increased as a function of conspecific larval density (Michaud, 2003a). Cannibalism by one larva on another was shown to provide nutritional benefits when other prey were scarce (Wagner et al., 1999), nutrient deficient, or toxic (Snyder et al., 2000). However, *H. axyridis* displays kin recognition, and is less likely to cannibalize a sibling than a non-sibling (Joseph et al., 1999, Michaud, 2003a). Mortality within the fourth instar (93.3 percent) was the highest of all stages, due to food shortages after aphid densities crash (Osawa, 1992b). Larval (first to fourth instar) mortality (95 to 97 percent) appears to be a key factor in population dynamics (Osawa, 1993). Later, Kindlmann et al. (2000) identified the first and fourth instars as key factors. Osawa (1993) found that larval and pupal mortality were density dependent. Osawa (1992a) showed that cannibalism on pupae decreased as a function of distance away from aphid colonies. Overall survival from egg to adult may range from 0 to 16 percent (Hironori and Katsuhiro, 1997, Osawa, 1992b, Osawa, 1993).

Male-killing bacteria can influence the demography of coccinellids. The male killing bacterium infecting some populations of *H. axyridis* has been identified as a member of the genus *Spiroplasma* (Majerus et al., 1999). This vertically transmitted bacterium causes female biased sex ratios by killing males early in embryogenesis (Majerus et al., 1998). The inviability of male eggs results in a reduction in the likelihood of a female being cannibalized by a sibling (Majerus, 1994). Resource reallocation through the consumption of inviable male eggs by neonate female siblings decreases the likelihood of starvation of female offspring of infected females (Hurst et al., 1992). Despite the prevalence of the male-killing bacteria in some Asian populations (Majerus et al., 1998), there is no evidence for female biased sex ratios in North American populations of *H. axyridis* (e.g., Heimpel and Lundgren, 2000).

*Prey searching and predation*

*H. axyridis* appears to have a high ability to track aphid populations in space and time (Osawa, 2000, With et al., 2002). Prey searching and oviposition behavior of *H. axyridis* and other Coccinellidae was reviewed by Evans (2003). Peak arrival and oviposition generally occurs before or at the peak of the aphid population (Hironori and Katsuhiro, 1997, Osawa, 2000). If a coccinellid oviposits when an aphid colony is waning, it is likely that the offspring of that coccinellid will die due to starvation (Dixon, 2000). It appears that ovipositing females use semiochemicals to assess if an aphid colony is too old for her offspring to survive. The presence of conspecific larval tracks, containing oviposition-deterring pheromone, inhibited oviposition (Yasuda et al., 2000). Conspecific feces also inhibits oviposition, and decreases feeding rates (Agarwala et al., 2003).

Larvae and adults tend to show an aggregated distribution (Johki et al., 1988, Kawai, 1976, Ren et al., 2000). Aggregations may result from a “trapping effect” when individuals switch from an extensive to intensive search (Kawai, 1976). While searching for prey, larvae are reported to use random movements (Kawai, 1976) but switch from extensive search to intensive search after contact with prey (e.g., Ettifouri and Ferran, 1993). Despite being considered random, the movements of larvae are guided by positive phototaxis and negative geotaxis, generally resulting in larvae climbing up plants (Kawai, 1976). Contrary to the idea of random search, data are accumulating to indicate that vision and olfaction may be used for prey detection. Harmon et al. (1998) found that more aphids are consumed in the light than in the dark. Larvae and adults showed long and short distance visual perception (Lambin et al. 1996), with adults exhibiting better visual perception than larvae. Mondor and Warren (2000) showed that adults were attracted to the color yellow more than to the color green. However, if they were conditioned to receiving food with one of the colors, then females tended to spend more time on the color associated with food. Conversely, males tended to spend more time on the color not associated with food (Mondor and Warren, 2000). Adults were attracted to green leaves and the odor of aphids over short distances (Obata, 1986b, Obata, 1997). Han and Chen (2000, 2002) showed that *H. axyridis* could respond to volatiles from aphids and aphid-damaged tea shoots. Unlike *Adalia bipunctata* (Hemptinne et al., 2000), adult *H. axyridis* were not attracted to the aphid alarm pheromone (Mondor and Roitberg, 2000).

*H. axyridis* is a predator of numerous aphid species (Hodek, 1996, Tedders and Schaefer, 1994, Yasumatsu and Watanabe, 1964). They will also feed on Tetranichidae (Lucas et al., 1997), Psyllidae (Michaud, 2001b, Michaud, 2002a), Coccoidea (McClure, 1986, Yasumatsu and Watanabe, 1964), immature stages of Chrysomelidae (Yasumatsu and Watanabe, 1964), Curculionidae (Kalaskar and Evans, 2001, Stuart et al., 2002), and Lepidoptera (Koch et al., 2003, Hoogendoorn and Heimpel, 2003 *in press,* Shu and Yu, 1985), and on pollen and nectar (Hukusima and Itoh, 1976, Lamana and Miller, 1996). Tedders and Schaefer (1994), Yasumatsu and Watanabe (1964), and Hodek (1996) provide more detailed reviews of the diversity of species consumed. Some prey appear to be chemically protected from predation. A diterpene from the eggs of the slug, *Arion* sp., (Schroder et al., 1999) and an alkaloid from the pupae of the Mexican bean beetle, *Epilachna varivestis*, (Rossini et al., 2000) both act as antifeedants to *H. axyridis*.

The total number of aphids consumed through the larval stages can vary from about 90 to 370 aphids, depending on the species of aphids consumed (Hukusima and Kamei, 1970). Aphid consumption increased for each successive instar (Hukusima and Kamei, 1970, Miura and Nishimura, 1980). Averaged across larval instars, 23.3 aphids were consumed per day (He et al., 1994). Mean daily aphid consumption by *H. axyridis* adults typically ranges from 15 to 65 aphids per day (Hu et al., 1989, Hukusima and Kamei, 1970, Lou, 1987, Lucas et al., 1997), with females consuming more than males (Hukusima and Kamei, 1970, Lucas et al., 1997). The foraging efficiency of *H. axyridis* increased (i.e., more prey consumed) with prey density and degree of aggregation, however variability in prey consumption also increased with increasing prey aggregation (Yasuda and Ishikawa, 1999).

A variety of functional responses to prey density have been reported. Lou (1987) reported a linear increase in the number of prey consumed (i.e., Type I functional response) for predation by adults on *Rhopalosiphum prunifoliae* (=*padi*) . He et al. (1994) reported a Type II functional response for predation by larvae on *Lipaphis erysimi*. Lin et al. (1999) fit models for Type II functional responses to compare the predation of adults on two different aphid species. Type II functional responses were also documented for adults and larvae preying on eggs and larvae of the monarch butterfly, *Danaus plexippus* (Koch et al., 2003). A Type III functional response was reported for *H. axyridis* adult predation of *Cinara* spp. (Hu et al., 1989), however the data presented by the authors lacked the characteristic sigmoidal shape of a Type III functional response.

*Natural enemies*

Despite having aposematic coloration and reflex bleeding (Grill and Moore, 1998) of alkaloid laden secretions (Alam et al., 2002), *H. axyridis* does have natural enemies. From a biological control perspective, natural enemies may be important for two reasons. For biological control practitioners looking to utilize *H. axyridis* as a control agent, the impact of natural enemies should be minimized in order to maximize its effectiveness. Conversely, some biological control practitioners may be considering the use of natural enemies of *H. axyridis* as a means to mitigate its potential adverse impacts.

Several parasitoids attack *H. axyridis*. A phorid, *Phalacrotophora* sp., was reported to parasitize *H. axyridis* pupae in Asia (Maeta, 1969, Osawa, 1992a, Park et al., 1996). Disney (1997) described this phorid as *Phalacrotophora philaxyridis* sp. nov., and suggested that *P. philaxyridis* may have followed *H. axyridis* to North America or that native *Phalacrotophora* spp. in North America may begin to attack *H. axyridis*. Two tachinids parasitize *H. axyridis* adults: *Degeria lutuosa* in Korea (Park et al., 1996) and *Strongygaster triangulifera* in the United States (Nalepa and Kidd, 2002, Nalepa et al., 1996). *Harmonia axyridis* is also parasitized by a braconid, *Dinocampus* (=*Perilitus*) *coccinellae* in Korea (Park et al., 1996) and in the United States (Hoogendoorn and Heimpel, 2002).

*H. axyridis* may fall victim to predation. Eight species of birds preyed on *H. axyridis* in Russia (Nechayev and Kuznetsov, 1973). De Clercq et al. (2003) showed that the results of intraguild predation between *H. axyridis* and the pentatomid, *Podisus maculiventris*, strongly favored *P. maculiventris*. However, Hough-Goldstein et al. (1996) concluded that *H. axyridis* was not a preferred prey for *P. maculiventris*. *H. axyridis* generally is preyed upon by other coccinellids, only if *H. axyridis* is smaller than the other coccinellid (e.g., Cottrell and Yeargan, 1998). Dutcher et al. (1999) reported higher densities of *H. axyridis* on trees with ants excluded compared to trees with ants. However, *H. axyridis* was more successful than *C. septempunctata* at fending off attacking red imported fire ants, *Solanopsis invicta* (Dutcher et al., 1999). Yasuda and Kimura (2001) found that a crab spider, *Misumenops trucuspidatus*, preyed on *C. septempunctata* and *Propylea japonica*, but not on *H. axyridis*.

## Biological Control

*Classical Biological Control*

Classical biological control is the use of exotic natural enemies to control exotic pests (e.g., Caltagirone and Doutt, 1989). In North America, *H. axyridis* has been released extensively for classical biological control: California in 1916, 1964 and 1965; Washington in 1978-1982; Nova Scotia, Connecticut, Georgia, Louisiana, Maryland, Washington D.C., Delaware, Maine, Mississippi, Ohio, Pennsylvania, and North Carolina in 1978-1981 (Gordon, 1985). Despite the numerous intentional releases of *H. axyridis* into North America, Day et al. (1994) suggested that the current populations of *H. axyridis* in the North America stemmed from accidental seaport introductions. Based on a gene flow analysis, Krafsur et al. (1997) suggested that populations of *H. axyridis* in North America may have come from a single source, but the authors could not determine whether the source was part of an intentional or accidental introduction.

*H. axyridis* was released for biological control in pecans (Tedders and Schaefer, 1994) and red pines (McClure, 1987). In pecans, *H. axyridis* appears to be contributing more to biological control of the pecan aphid complex in the southeastern United States than in the southwestern United States (Rice et al., 1998, Tedders and Schaefer, 1994). Besides offering effective control of target pests, *H. axyridis* is also providing control of pests in other systems. In apple orchards, *H. axyridis* provides effective biological control of *Aphis spiraecola* (Brown and Miller, 1998). The biological control of several citrus pests may also be benefiting from the establishment of *H. axyridis* (Michaud, 1999, Michaud, 2000, Michaud, 2001a, Michaud, 2001b, Michaud, 2002a, Stuart et al., 2002). In Asia , and in the United States, *H. axyridis* has been identified an important natural enemy of *Aphis glycines* in soybeans (Rutledge CE, personal communication). In sweet corn, *H. axyridis* may be contributing to biological control of *Ostrinia nubilalis* and *Rhopalosiphum maidis* (Hoogendoorn and Heimpel, *in press,* Musser and Shelton, 2003). *Harmonia axyridis* has also been documented in alfalfa (Buntin and Bouton, 1997, Colunga-Garcia and Gage, 1998), cotton (Wells et al., 2001), tobacco (Wells and McPherson, 1999), and winter wheat (Colunga-Garcia and Gage, 1998), where it may be contributing to biological control. However, on hemlock trees, the impact of *H. axyridis* and other predators on *Adelges tsungae* is considered negligible (Wallace and Hain, 2000).

*Augmentative Biological Control*

Augmentative biological control is comprised of inundative and inoculative releases of natural enemies. With inundative releases, control is expected solely from the agents released. With inoculative releases, control is expected from the progeny of the agents (Elzen and King, 1999). *H. axyridis* has been utilized in augmentative biological control in Asia (e.g., Seo and Youn, 2000), Europe (e.g., Trouve et al., 1997), and North America (e.g., LaRock and Ellington, 1996). *H. axyridis* is commercially available in North America (Heimpel and Lundgren, 2000). However, the number of commercial insectaries rearing *H. axyridis* is decreasing, due to its potential pest status (RLK unpublished data).

Liu and Qin (1989) suggested that *H. axyridis* should be a promising candidate for augmentative biological control. It effectively suppressed *Chaetosiphon fragaefolii* on strawberry (Sun et al., 1996) and *Macrosiphum rosae* on roses (Ferran et al., 1996). However, it did not improve biological control of *Aphis gossypii* on cucumbers beyond the control offered by *Aphidius colemani* (Fischer and Leger, 1997). Under field conditions, LaRock and Ellington (1996) reported an effective integrated pest management program, incorporating inoculative releases of *H. axyridis* and other predators, for the pecan aphid complex. Mass releases of *H. axyridis* provided effective control of scale insects in pine forests (Wang, 1986). *H. axyridis* was also effective when released against *Phorodon humuli* on hops (Trouve et al., 1997).

Trouve et al. (1997) and Sidlyarevich and Voronin (1973) suggested that control would only be provided by the larval stages, because adults tended to disperse from plants. To improve their efficacy in augmentative biological control, a flightless strain was developed. The biology of the flightless strain is similar to the wild type, except for the inability to fly and a slightly longer prey handling time (Tourniaire et al., 1999, Tourniaire et al., 2000). Weissenberger et al. (1999) showed that a flightless strain of *H. axyridis* can be effectively used for augmentative biological control of *P. humuli* in hops.

The relative ease of rearing *H. axyridis* makes it particularly attractive for augmentative biological control. Matsuka and Niijima (1985) describe a system for mass rearing *H. axyridis*. It can be reared on a variety of aphid species (Hodek, 1996). Non-aphid diets, such as the eggs of various Lepidoptera (Abdel-Salam and Abdel-Baky, 2001, Schanderl et al., 1988), pulverized drone bee brood (Okada and Matsuka, 1973), eggs of brine shrimp (Hongo and Obayashi, 1997), and various artificial diets (Dong et al., 2001), can also be used. Nutritional analyses of various diets and their impact on fitness parameters of *H. axyridis* have been examined in detail (Matsuka and Takahashi, 1977, Niijima et al., 1986, Specty et al., 2003). One caveat for the use of factitious prey or diets is that foraging efficiency may be reduced, due to changes in search patterns, when *H. axyridis* is released on a target prey (Ettifouri and Ferran, 1993).

Rearing conditions other than diet have also been examined for *H. axyridis*. Fecundity can be increased by prolonging the amount of time females spend with males (Pando et al., 2001). Ongagna and Iperti (1994) reported how temperature and photoperiod can be altered to promote or deter diapause during rearing. Finally, the influence of temperature on development was described in the biology section of this review.

*Conservation Biological Control*

Conservation biological control encompasses techniques used to increase the activity or density of natural enemies already present in a system (e.g., Giles and Obrycki, 1997). The impact of insecticides on *H. axyridis* has been examined under field and laboratory conditions for application to several systems, such as grapefruit (Michaud, 2002d), apples (Cho et al., 1997), peaches (Sauphanor et al., 1993), sweet corn (Musser and Shelton, 2003), cotton (Wells et al., 2001), hops (Weissenberger et al., 1997), and alfalfa (Buntin and Bouton, 1997) (Table 1). Most of these studies relied on mortality as an indicator of susceptibility, but some also examined sublethal effects (e.g., Michaud, 2002d, Weissenberger et al., 1997) or behavioral effects (e.g., Provost et al., 2003, Michaud, 2002c, Vincent et al., 2000). Cho et al. (1997) concluded that synthetic pyrethroids were less toxic to *H. axyridis* than to aphids. In more recent studies, new pesticide formulations, such as spinosad, indoxacarb, and pyriproxyfen showed minimal toxic effects to *H. axyridis* (Michaud, 2002d, Michaud, 2003b, Musser and Shelton, 2003) (Table 1). Biorational pesticides, such as soap, oil, azadiractin, and *Beauvaria bassiana*, were also shown to be much less toxic than a conventional insecticide, carbaryl, to *H. axyridis* (Smith and Krischik, 2000) (Table 1). Non-target impacts of acaricides on *H. axyridis* have also been examined (Cho et al., 1996, James, 2002, Michaud, 2002c) (Table 1). Relatively little work has been done on the ovicidal activity of insecticides and acaricides to *H. axyridis* (except: Cho et al., 1996, Ying, 1982).

The impacts of pesticides other than insecticides and

**Table 1.** Known susceptibility of *Harmonia axyridis* to various insecticides and acaricides.

| Product | Rate* or units for LC50 | Method[1] | Relative acute susceptibility[2] or LC50 | | Citation |
|---|---|---|---|---|---|
| | | | Larvae | Adults | |
| Abamectin + petroleum oil | 0.0015 + 1.0 % AI | L:R(s) | High | — | (Michaud, 2002c) |
| Alphamethrin | ppm(AI) | L:D(t) | 87.93 | 100.04 | (Cho et al., 1997) |
| Azadiractin | 1.25 ml/l | L:DR(s) | — | Low | (Smith and Krischik, 2000) |
| Azocyclotin | ppm(AI) | L:D(t) | >40,000 | >40,000 | (Cho et al., 1996) |
| Beauvaria bassiana, strain GHA | 7.5 ml/l | L:DR(s) | — | Low | (Smith and Krischik, 2000) |
| Bifenzate | 0.001% (AI) | L:DR(s) | Moderate | — | (James, 2002) |
| Carbaryl | 5.21 ml/l | L:DR(s) | — | High | (Smith and Krischik, 2000) |
| Chlorpyrifos | 0.45% AI | L:D(s) | High | — | (Michaud, 2002d) |
| Chlorpyrifos | 0.45% AI | L:R(s) | High | — | (Michaud, 2002d) |
| Deltamethrin | ppm(AI) | L:D(t) | 19.65 | 89.35 | (Cho et al., 1997) |
| Dicofol | 0.03% AI | L:D(s) | Low | — | (Michaud, 2002c) |
| Dicofol | ppm(AI) | L:D(t) | >80,000 | >80,000 | (Cho et al., 1996) |
| Dicofol | 0.03% AI | L:R(s) | Low | — | (Michaud, 2002c) |
| Dichlorbenzuron | 62.5 ml/l | L:D(s) | Low | — | (Sun et al., 1999) |
| Dichlorbenzuron | 62.5 ml/l | L:O | Low | — | (Sun et al., 1999) |
| Diflubenzuron | 0.03% AI | L:D(s) | Low | — | (Michaud, 2002c) |
| Diflubenzuron | 0.03% AI | L:R(s) | Low | — | (Michaud, 2002c) |
| Esfenvalerate | ppm(AI) | L:D(t) | 30.53 | 8.09 | (Cho et al., 1997) |
| Ethion + petroleum oil | 0.003% AI | L:D(s) | Low | — | (Michaud, 2002d) |
| Ethion + petroleum oil | 0.003% AI | L:R(s) | Moderate | — | (Michaud, 2002d) |
| Fenbutatin oxide | 0.24% AI | L:D(s) | Low | — | (Michaud, 2002c) |
| Fenbutatin oxide | 0.24% AI | L:R(s) | Low | — | (Michaud, 2002c) |
| Fenpropathrin | ppm(AI) | L:D(t) | 22.81 | 263.42 | (Cho et al., 1997) |
| Fenpropathrin | ppm(AI) | L:D(t) | 22.81 | 263.42 | (Cho et al., 1996) |
| Fenpropathrin | 0.5% AI | L:R(s) | High | — | (Michaud, 2002d) |
| Fenpropathrin | 100 mg/l | L:D(s) | High | — | (Sun et al., 1999) |
| Fenpyroximate | ppm(AI) | L:D(t) | >12,000 | 1811.04 | (Cho et al., 1996) |
| Halofenozide | mg/l | L:O | — | 67.1 | (Carton et al., 2003) |
| Imidacloprid | 0.053 kg(AI)/ha | F:(s) | Low | Low | (Wells et al., 2001) |
| Imidacloprid | 0.005% AI | L:D(s) | Low | — | (Michaud, 2002d) |
| Imidacloprid | 0.15 g/l | L:D(t) | 0.085 | — | (Vincent et al., 2000) |
| Imidacloprid | 0.005% AI | L:R(s) | Moderate | — | (Michaud, 2002d) |
| Imidacloprid | 0.15 g/l | L:R(s) | Low | — | (Vincent et al., 2000) |
| Indoxacarb | 0.0616 kg(AI)/ha | F:(s) | Moderate | Low | (Musser and Shelton, 2003) |
| Methomyl | ppm(AI) | L:D(t) | 148.26 | 34.95 | (Cho et al., 1997) |
| Methoxyfenozide | mg/l | L:O | — | 71.3 | (Carton et al., 2003) |
| Monocrotophos | ppm(AI) | L:D(t) | 208.64 | 366.7 | (Cho et al., 1997) |
| Parrafinic oil | 20 ml/l | L:DR(s) | — | Low | (Smith and Krischik, 2000) |
| Phospamidon | ppm(AI) | L:D(t) | 61.31 | 44.02 | (Cho et al., 1997) |
| Pymetrozine | 0.00022% AI | L:DR(s) | Low | — | (James, 2002) |
| Pyridaben | 0.038% AI | L:D(s) | Moderate | — | (Michaud, 2002c) |
| Pyridaben | ppm(AI) | L:D(t) | >25,000 | >25,000 | (Cho et al., 1996) |
| Pyridaben | 0.038% AI | L:R(s) | Low | — | (Michaud, 2002c) |
| Pyridaphenthion | ppm(AI) | L:D(t) | 186.7 | 341.65 | (Cho et al., 1997) |
| Pyriproxyfen | 0.0013% AI | L:D(s) | Low | Low | (Michaud, 2002d) |
| Pyriproxyfen | 0.0013% AI | L:R(s) | Low | Low | (Michaud, 2002d) |
| Soap, potassium salts, and fatty acids | 20 ml/l | L:DR(s) | — | Low | (Smith and Krischik, 2000) |
| Spinosad | 0.0790 kg(AI)/ha | F:(s) | Moderate | Moderate | (Musser and Shelton, 2003) |
| Spinosad | 0.05% AI | L:D(s) | Low | Low | (Michaud, 2002d) |
| Spinosad | 0.05% AI | L:R(s) | Low | Low | (Michaud, 2002d) |
| λ-cyhalothrin | 0.0262 kg(AI)/ha | F:(s) | High | High | (Musser and Shelton, 2003) |

* If data on multiple rates were presented in the original manuscripts, the recommended field is presented here.

[1] Methods: Upper case letters to the left of the colon indicate whether it was a laboratory study (L) or field study (F). Upper case letters to the right of the colon indicate whether the pesticide was applied directly to the insect (D), the insect was exposed to residue (R), or the insect was exposed orally through consumption of treated food (O). Lower case letters in parentheses indicate whether the pesticide was applied as a spray (s), as a topical application of drops (t), or as a dip (d).

[2] Relative acute susceptibility ratings: Low = 0-33% mortality, Moderate=34-66% mortality, High = 67-100% mortality

acaricides have also received attention. Fungicides appear to be relatively benign to *H. axyridis* (Michaud, 2001c, Michaud and Grant, 2003). Under field conditions, Wells et al. (2001) found that application of a fungicide, chlorothalonil, resulted in greater abundance of coccinellids, including *H. axyridis*. The herbicide, glufosinate-ammonium, was shown to be toxic to *H. axyridis* (Ahn et al., 2001).

The susceptibility of *H. axyridis* to various pesticides varies depending on the developmental stage. Adult*s* were often less susceptible than immature stages (e.g., Ahn et al., 2001, Michaud, 2002c, Michaud, 2002d) (Table 1). Cho et al. (2002) suggest that the differential susceptibility between larval and adults is due to enzyme activity and target-site sensitivity.

Concern has been raised about the potential adverse impact of insect-resistant transgenic crops on natural enemies (e.g., Hilbeck et al., 1998). Natural enemies may be exposed to the toxins of the transgenic plant through consumption of plant tissues (e.g., Lundgren and Wiedenmann, 2002) or through consumption of prey that have previously fed on transgenic plants (e.g., Head et al., 2001). Densities of *H. axyridis* on corn modified to express toxins from *Bacillus thuringiensis* (*Bt*) specific to Lepidoptera were not significantly different from densities on non-*Bt* isolines of corn (Musser and Shelton, 2003, Wold et al., 2001). Ferry et al. (2003) examined the impact of oilseed rape, genetically modified to express a cysteine protease inhibitor, on *H. axyridis*. In vitro studies showed that the protease inhibitor inhibited digestive enzymes of *H. axyridis*. However, in vivo studies showed no adverse effects when *H. axyridis* consumed prey reared on transgenic oilseed rape (Ferry et al., 2003). These rather limited data suggest that insect-resistant transgenic crops can be compatible with biological control in an integrated pest management program.

Little work has been done on other aspects of conservation biological control with *H. axyridis*. To promote the abundance of *H. axyridis*, Hukusima and Kamei (1970) suggested that overwintering shelters should be created by wrapping tree trunks and branches with cloth. However, Nalepa et al. (2000) found that artificial shelters were not attractive to *H. axyridis*. Hukusima and Kamei (1970) also suggested that alternate foods should be provided when aphids are scarce, but the authors did not say how to provide the alternate foods. Dong (1988) reported greater densities of *H. axyridis* in cotton fields interplanted with corn compared to cotton alone.

*Non-target impacts*

The history of classical biological control contains numerous success stories (e.g., Caltagirone and Doutt, 1989, McEvoy and Cox, 1991, Radcliffe and Flanders, 1998). Unfortunately, exotic natural enemies may impact organisms other than the targeted pests (e.g., Howarth, 1991, Louda et al., 2003, Simberloff and Stiling, 1996). Adverse effects of *H. axyridis* on insects, humans, and crops are beginning to be identified.

Displacement of native natural enemies may result from the establishment of an exotic natural enemy. An inventory of Coccinellidae in North Dakota was recently conducted, and may be used to provide baseline data for examination of the displacement of native Coccinellidae by exotic Coccinellidae (Fauske et al., 2003). In South Dakota, the abundance of *Coccinella transversoguttata richardsoni* and *Adalia bipunctata* was approximately 20 times lower after the establishment of an exotic coccinellid, *C. septempunctata* (Elliott et al., 1996). Evidence is building to indicate that *H. axyridis* may be having similar adverse effects on native Coccinellidae. Over a 13-year period Brown and Miller (1998) monitored the abundance various species of Coccinellidae in apple orchards. The abundance of native coccinellids decreased after the establishment and rapid rise to dominance of the exotics, *C. septempunctata* and *H. axyridis* (Brown and Miller, 1998). A nine-year study of the abundance of various Coccinellidae in an agricultural landscape showed a decrease in the abundance of *Brachiacantha ursina*, *Cycloneda munda*, and *Chilocorus stigma* after the establishment *H. axyridis* (Colunga-Garcia and Gage, 1998). Similarly, observations made over five years in citrus groves show an increase in the abundance of *H. axyridis* and a decrease in the abundance of the formerly dominant predator, *Cycloneda sanguinea* (Michaud, 2002b). Conversely, Brown (2003) suggested that *H. axyridis* may be competitively suppressing another exotic, *C. septempunctata*, in apple orchards allowing native predators to increase in abundance. Through predation studies, Lucas et al. (2002) showed that the addition of *H. axyridis* to the predator guild on apple trees did not hinder the suppression of *Aphis citricola* and *Tetranychus urticae*.

Intraguild predation has been examined as a mechanism leading to displacement of native species by *H. axyridis,* which appears to be a top predator in the guild of aphidophagous insects. In other words, *H. axyridis* may also use other aphidophagous species as a food source (Dixon, 2000). Numerous studies indicate that *H. axyridis* can effectively utilize other members of the aphidophagous guild as a food source (Table 2). In many cases, *H. axyridis* had a greater ability than the other guild members did to utilize heterospecifics for food. This ability may be due to the higher attack and escape rates for *H. axyridis* than those of *C. septempunctata* during interspecific interactions (Yasuda et al., 2001). The intensity of predation by *H. axyridis* on other guild members appears to be inversely related to aphid density (Burgio et al., 2002, Hironori and Katsuhiro, 1997). Others have suggested that high predation rates of *H. axyridis* on its own eggs compared to eggs of other coccinellid species, may mitigate the displacement of native coccinellids (Burgio et al., 2002, Lynch et al., 2001).

The displacement of native coccinellids by *H. axyridis* might also be driven by indirect mechanisms. One potential mechanism of displacement is resource competition. In citrus groves, Michaud (2002b) showed that *H. axyridis* was a more voracious predator and had higher fecundity and fertility than *C. sanguinea*. Alternatively, Hoogendoorn and Heimpel (2002) examined an indirect interaction between *H. axyridis* and *C. maculata* mediated by the parasitoid, *Dinocampus coccinella*. The presence of *H. axyridis* actually benefited *C. maculata* by diverting some of the parasitoid eggs away from the *C. maculata* population (Hoogendoorn and Heimpel, 2002).

*Harmonia axyridis* may inadvertently feed on parasitoids of aphids. Nakata (1995) noted that the predator guild, including *H. axyridis,* in potato fields, feeds on parasitized aphids that have not yet mummified. In a more thorough study of *H. axyridis* feeding on parasitized aphids, Takizawa et al. (2000b) found that survival, developmental time and weight were not affected by feeding on aphids containing parasitoid larvae. However, when feeding on

**Table 2.** Known non-pest insect prey of *Harmonia axyridis*

| Order | Family | Species | Stage Consumed* | Citation |
|---|---|---|---|---|
| Coleoptera | Coccinellidae | *Adalia bipunctata* | PP, P | (Sakuratani et al., 2000) |
| | | | L | (Kajita et al., 2000) |
| | | | E | (Lynch et al., 2001) |
| | | | E | (Burgio et al., 2002) |
| | | *Adonia variegata* | E | (Lynch et al., 2001) |
| | | *Coleomegilla maculata* | E, L | (Cottrell and Yeargan, 1998) |
| | | *Coccinella septempunctata* | L | (Hironori and Katsuhiro, 1997) |
| | | | L | (Yasuda and Ohnuma, 1999) |
| | | | L | (Yasuda et al., 2001) |
| | | *C. septempunctata brucki* | P | (Takahashi, 1989) |
| | | | L | (Dixon, 2000) |
| | | *Cycloneda sanguinea* | E, L | (Michaud, 2002b) |
| | | *Propylea japonica* | L | (Dixon, 2000) |
| | | *P. quatuordecimpunctata* | E | (Lynch et al., 2001) |
| Lepidoptera | Nymphalidae | *Danaus plexippus* | E, L | (Koch et al., 2003) |
| Neuroptera | Chrysopidae | *Chrysoperla carnea* | E | (Phoofolo and Obrycki, 1998) |

* E=egg, L=larva, PP=prepupa, P=pupa

aphids containing parasitoid pupae, developmental time and weight were adversely affected (Takizawa et al., 2000b). Snyder and Ives (2003) present evidence that *H. axyridis* preferentially preyed on aphids rather than mummies. Beyond the direct impact of *H. axyridis* feeding on parasitized aphids, the presence of *H. axyridis* near an aphid colony may decrease the oviposition rate of parasitoids (Takizawa et al., 2000a).

There is a paucity of literature on the potential adverse effects of *H. axyridis* on other non-pest insects (Table 2). Boettner et al. (2000) suggested that there is a need to examine the potential adverse impact of *H. axyridis* on native aphids and the insects that depend on the aphids. Koch et al. recently identified *H. axyridis* as a potential hazard to immature monarch butterflies, *Danaus plexippus* (Table 2). In laboratory and field-cage studies, eggs and larvae of *D. plexippus* incurred significant predation by *H. axyridis* adults and larvae.

Harris (1990) stated, “most biological control agents that become extremely abundant are a nuisance.” *H. axyridis* is a prime example of a biological control agent becoming a nuisance to humans. In late autumn, *H. axyridis* is known to migrate and form aggregations at overwintering sites (Huelsman et al., 2002, Obata, 1986a, Obata et al., 1986, Tanagishi, 1976). In North America, aggregation sites are often homes or other buildings (Huelsman et al., 2002, Kidd et al., 1995). Details on migration and overwintering aggregations were given in the biology section of this review. Many people become annoyed by the swarms of *H. axyridis* flying toward their homes (Kidd et al., 1995). Adult *H. axyridis* often make their way inside the buildings, where they will overwinter. Throughout the winter and especially in the spring as temperatures begin to increase, homeowners contend with *H. axyridis* crawling and flying about the inside of their homes (Huelsman et al., 2002). Researchers are also considering the use of pyrethroids (Huelsman et al., 2002) and plant-derived products, such as camphor and menthol (Riddick et al., 2000) for use on the exterior of homes to prevent beetles from entering the home. The presence, alone, of *H. axyridis* is not the only annoying factor to homeowners. Some people have developed an allergic rhinoconjunctivitis to *H. axyridis* (Huelsman et al., 2002, Magnan et al., 2002, Yarbrough et al., 1999). Surprisingly to many people, *H. axyridis* has been reported to bite humans (Huelsman et al., 2002). *Adalia bipunctata* is also known to occasionally bite humans (Svihla, 1952). *H. axyridis* sometimes forms overwintering aggregations in beehives. They are a nuisance to the beekeepers, but are apparently not harmful to the bees (Caron, 1996).

*H. axyridis* has recently attained status as a potential pest of fruit production and processing. In autumn, adult *H. axyridis* have been reported aggregating on, and in some cases feeding on, fruits such as apples, pears, and grapes (J. Kovach, personal communication). This is a particularly important problem in vineyards that grow grapes for wine production (Ejbich, 2003, Ratcliffe, 2002). *H. axyridis* is apparently difficult to remove from clusters of grapes during harvest, so some get crushed with the grapes during processing. Alkaloids in *H. axyridis* taint the flavor of the resulting wine (Ejbich, 2003). Similar fruit feeding behavior has been reported in Europe for *C. septempunctata* on pears and peaches, and *A. bipunctata* on cherries and plums (Hodek, 1996).

## Summary and Future Work

*H. axyridis* has rapidly spread across the United States since its initial detection in 1988. The impacts of the establishment of this exotic predator are already being felt. Biological control of aphids and other small soft-bodied pests in some systems appears to be benefiting from the voracious appetite of *H. axyridis*. Use of *H. axyridis* in classical and augmentative biological control has been successful in a variety of systems, such as pecans (Tedders and Schaefer, 1994), strawberry (Sun et al., 1996), and roses (Ferran et al., 1996). In regards to conservation biological control, there is some evidence that *H. axyridis* is not very sensitive to some insecticides used for pest control. Unfortunately, a suite of potential adverse impacts accompanies the potential benefits offered by *H. axyridis* as a biological control agent. The lack of dietary specificity for *H. axyridis* may lead to unintended adverse ecological effects through predation on native beneficial insects and other non-pest insects. The emerging status of *H. axyridis* as a pest to fruit production and processing in autumn is a novel adverse impact for an exotic predator imported for biological control of insect pests. Direct impacts of *H. axyridis* on humans as a household pest and allergen add to the list of its adverse impacts. Like other exotic organisms *H. axyridis* will likely become a permanent member of the fauna in regions that it has invaded or will invade. Because of the likely permanence of *H. axyridis*, we need to continue working to determine how to better utilize this voracious predator in insect pest management, and to examine the adverse impacts as a case study for future releases of exotic generalist predators.

Despite the relatively large body of knowledge on *H. axyridis*, much work is needed to further evaluate (i.e., beneficial versus adverse impacts) and utilize (e.g., insect pest management) the establishment of *H. axyridis*. More work is needed to evaluate the impact of *H. axyridis* on pest suppression in the various cropping systems. In systems were *H. axyridis* has become a dominant predator, work is needed to improve the compatibility of existing integrated pest management tactics with the biological control offered by *H. axyridis*. For example, the impact of coleopteran specific Cry3Bb toxins expressed by genetically modified, corn rootworm resistant corn have been examined for *C. maculata* (Lundgren and Wiedenmann, 2002), but not for *H. axyridis*. Also, with *H. axyridis* becoming a dominant predator of *A. glycines* in North American soybeans (Rutledge et al., 2003 *in review*), the toxicity of a commonly used herbicide in soybeans, glyphosphate, needs to be examined. Continued study on the foraging behavior and predation by *H. axyridis* may lead to methods for modifying habitats to promote the efficacy of pest suppression offered by *H. axyridis*.

Our knowledge of the adverse impacts of *H. axyridis* also needs to be improved. The problem of *H. axyridis* as a household pest needs further attention. We need to determine ways to reliably predict the autumn migration of *H. axyridis* to homes and buildings (e.g., Huelsman et al., 2002). Tactics to prevent the entry of *H. axyridis* into homes and to mitigate the problem if it does enter homes need further examination. The economic impact of *H. axyridis* as a pest to fruit production and processing needs to be quantified, and integrated pest management programs need to be developed in these systems. From an ecological viewpoint, the establishment of *H. axyridis* provides a model system for examining the impacts of an exotic predator on native organisms (e.g., Koch et al., 2003 *in press*).

To determine if the introduction of *H. axyridis* into the United States was a biological control success or disaster, the beneficial impacts of *H. axyridis* must be weighed against its adverse impacts. Risk analysis (e.g., Lonsdale et al., 2001) could be used as a tool to weigh the beneficial impacts against the adverse impacts. I hope that biological control practitioners in countries where *H. axyridis* is not yet established can use the information presented here to determine if introductions of *H. axyridis,* or other generalist predators, are justified.

## Acknowledgements

I thank G. Heimpel, W.D. Hutchison, R.C. Venette, C. Cannon, E. Hodgson, J. Kovach and J. Luhman for reviewing parts or all of earlier versions of this manuscript. I am also grateful to Z. Wu for translating the Chinese literature.

## References Cited

Abdel-Salam AH, Abdel-Baky HF. 2001. Life table and biological studies of *Harmonia axyridis* Pallas (Col., Coccinellidae) reared on the grain moth eggs of *Sitotroga cerealella*. Journal of Applied Entomology 125: 455-462.

Agarwala BK, Yasuda H, Kajita Y. 2003. Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predation avoidance. Journal of Chemical Ecology 29: 357-376.

Ahn Y, Kim Y, Yoo J. 2001. Toxicity of herbicide glufosinate-ammonium to predatory insects and mites of *Tetranychus urticae* (Acari: Tetranychidae) under laboratory conditions. Journal of Economic Entomology 94: 157-161.

Alam N, Choi IS, Song KS, Hong J, Lee CO, Jung JH. 2002. A new alkaloid from two coccinellid beetles *Harmonia axyridis* and *Aiolocaria haexaspilota*. Bulletin of the Korean Chemical Society 23: 497-499.

Boettner GH, Elkinton JS, Boettner CJ. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conservation Biology 14: 1798-1806.

Brown MW. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. BioControl 48: 141-153.

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

Buntin GD, Bouton JH. 1997. Aphid (Homoptera: Aphididae) management in alfalfa by spring grazing cattle. Journal of Entomological Science 32: 332-342.

Burgio G, Santi F, Maini S. 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Biological Control 24: 110-116.

Caltagirone LE, Doutt RL. 1989. The history of the vedalia beetle importation to California and its impact on the development of biological control. Annual Review of Entomology 34: 1-16.

Caron DM. 1996. Multicolored Asian lady beetles: a "new" honey bee pest. American Bee Journal 136: 728-729.

Carton B, Smagghe G, Tirry L. 2003. Toxicity of two ecdysone agonists, halofenozide and methoxyfenozide, against the multicolored Asian lady beetle *Harmonia axyridis* (Col., Coccinellidae). Journal of Applied Entomology 127: 240-242.

Chapin EA. 1965. Coccinellidae. Insects of Micronesia. Coleoptera, 189-254. Honolulu, Hawaii: Bernice P. Bishop Museum.

Chapin JB, Brou VA. 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proceedings of the Entomological Society Washington 93: 630-635.

Cho J, .Hong KJ, Yoo JK, Bang JR, Lee JO. 1997. Comparative toxicity of selected insecticides to *Aphis citricola*, *Myzus malisuctus* (Homoptera: Aphididae), and the predator

*Harmonia axyridis* (Coleoptera: Coccinellidae). Journal of Economic Entomology 90: 11-14.

Cho JR, Hong KJ, Lee GS, Choi BR, Yoo JK, Lee JO. 1996. Selection of the acaricides selective to *Harmonia axyridis* and effect of their application on phytophagous mites and natural enemies. Korean Journal of Applied Entomology. 35: 243-248.

Cho JR, Kim YJ, Kim HS, Yoo JK. 2002. Some biochemical evidence on the selective insecticide toxicity between the two aphids, *Aphis citricola* and *Myzus malisuctus* (Homoptera: Aphididae), and their predator, *Harmonia axyridis* (Coleoptera: Coccinellidae). Journal of Asia-Pacific Entomology 5: 49-53.

Colunga-Garcia M, Gage SH. 1998. Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environmental Entomology 27: 1574-1580.

Cottrell TE, Yeargan KV. 1998. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). Journal of the Kansas Entomological Society 71: 159-163.

Danks HV. 1991. Winter habitats and ecological adaptations for winter survival. In: Lee RE Jr, Denlinger DL, editors. Insects at Low Temperatures, 231-259. New York, NY: Chapman and Hall.

Day WH, Prokrym DR, Ellis DR, Chianese RJ. 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. Entomological News 105: 224-256.

de Almeida LM, da Silva VB. 2002. First record of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): a lady beetle native to the Palaearctic region. Revista Brasileira de Zoologia 19: 941-944.

De Clercq P, Peeters I, Vergauwe G, Thas O. 2003. Interactions between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. BioControl 48: 39-55.

Disney RHL. 1997. A new species of Phoridae (Diptera) that parasitises a wide-spread Asian ladybird beetle (Coleoptera: Coccinellidae). The Entomologist 116: 163-168.

Dixon AFG. 2000. Insect Predator-Prey Dynamics: Ladybird beetles and Biological Control. Cambridge, United Kingdom: Cambridge University Press.

Dobzhansky T. 1933. Geographical variation in ladybeetles. The American Naturalist 67: 97-126.

Dong H, Ellington JJ, Remmenga MD. 2001. An artificial diet for the lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Southwestern Entomologist 26: 205-213.

Dong YG. 1988. Trials of the control of *Aphis gossypii* Glover with *Coccinella axyridis* Pallas. Zhejiang Agricultural Science no. 3: 135-139.

Dreistadt SH, Hagen KS, Bezark LG. 1995. *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), first western United States record for this Asiatic lady beetle. Pan-Pacific Entomologist 71: 135-136.

Dutcher JD, Estes PM, Dutcher MJ. 1999. Interactions in entomology: aphids, aphidophaga and ants in pecan orchards. Journal of Entomological Science 34: 40-56.

Ejbich K. 2003. Producers in Ontario and northern U.S. bugged by bad odors in wine. Wine Spectator 15 May: 16.

Elliott N, Kieckhefer R, Kauffman W. 1996. Effects of an invading coccinellid on native cocccinellids in an agricultural landscape. Oecologia 105: 537-544.

El-Sebaey IIA, El-Gantiry AM. 1999. Biological aspects and description of different stages of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Bulletin of the Faculty of Agriculture, Cairo University. 50: 87-97.

Elzen GW, King EG. 1999. Periodic release and manipulation of natural enemies. In: Bellows TS , Fisher TW, editors. Handbook of Biological Control, 253-270. San Diego, CA: Academic Press.

Ettifouri M, Ferran A. 1993. Influence of larval rearing diet on the intensive searching behavior of *Harmonia axyridis* [Col.: Coccinelidae] larvae. Entomophaga 38: 51-59.

Evans EW. 2003. Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. European Journal of Entomology 100: 1-10.

Fauske GM, Tinerella PP, Rider DA. 2003. A list of the lady beetles (Coleoptera: Coccinellidae) of North Dakota with new records from North Dakota and Minnesota. Journal of the Kansas Entomological Society 76: 38-46.

Ferran A, Niknam H, Kabiri F, Picart JL, Herce Cd, Brun J, Iperti G, Lapchin L. 1996. The use of *Harmonia axyridis* larvae (Coleoptera: Coccinellidae) against *Macrosiphum rosae* (Hemiptera: Sternorrhyncha: Aphididae) on rose bushes. European Journal of Entomology 93: 59-67.

Ferry N, Raemaekers JM, Majerus MEN, Jouanin L, Port G, Gatehouse JA, Gatehouse AMR. 2003. Impact of oilseed rape expressing the insecticidal cysteine protease inhibitor oryzacystatin on the beneficial predator *Harmonia axyridis* (multicolored Asian ladybeetle). Molecular Ecology 12: 493-504.

Fischer S, Leger A. 1997. Biological control of aphids on cucumbers grown in greenhouses using banker plants. Revue Suisse de Viticulture, Arborculture and Horticulture 29: 119-126.

Giles K, Obrycki J. 1997. Reduced insecticide rates and strip-harvest: effects on arthropod predator abundance in first-growth alfalfa. Journal of the Kansas Entomological Society 70: 160-168.

Gordon RD. 1985. The Coleoptera (Coccinellidae) of America north of Mexico. Journal of the New York Entomological Society 93: 1-912.

Gordon RD, Vandenberg N. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington 93: 845-864.

Grill CP, Moore AJ. 1998. Effects of a larval antipredator response and larval diet on adult phenotype in an aposematic ladybird beetle. Oecologia 114: 274-282.

Han B, Chen Z. 2000. Behavior response of four *Leis axyridis* varieties to volatiles from tea and *Toxoptera aurantii*. Chinese Journal of Applied Ecology 11: 413-416.

Han BY, Chen ZM. 2002. Composition of the volatiles from intact and tea aphid-damaged tea shoots and their allurement to several natural enemies of the tea aphid. Journal of Applied Entomology 126: 497-500.

Han X. 1997. Population dynamics of soybean aphid *Aphis glycines* and its natural enemies in the field. Hubei Agricultural Sciences 2: 22-24.

Harmon JP, Losey JE, Ives AR. 1998. The role of vision and color in the close proximity foraging behavior of four coccinellid species. Oecologia 115: 287-292.

Harris P. 1990. Environmental impact of introduced biological control agents. In: Mackauer M, Ehler LE, Roland J, editors. Critical Issues in Biological Control, 289-300. Andover: Intercept, Ltd.

He JL, Ma EP, Shen YC, Chen WL, Sun XQ. 1994. Observations of the biological characteristics of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Journal of the Shanghai Agricultural College 12: 119-124.

Head G, Brown CR, Groth ME, Duan JJ. 2001. Cry1Ab protein levels in phytophagous insects feeding on transgenic corn: implications for secondary exposure risk assessment. Entomologia Experimentalis et Applicata 99: 37-45.

Heimpel GE, Lundgren JG. 2000. Sex ratios of commercially reared biological control agents. Biological Control 19: 77-93.

Hemptinne JL, Gaudin M, Dixon AFG, Lognay G. 2000. Social feeding in ladybird beetles: adaptive significance and mechanism. Chemoecology 10: 149-152.

Hesler LS, Keickhefer RW, Beck DA. 2001. First record of *Harmonia axyridis* (Coleoptera: Coccinellidae) in South Dakota and notes on its activity there and in Minnesota. Entomological News 112: 264-270.

Hilbeck A, Moar WJ, Pusztai-Carey M, Filippini A, Bigler F. 1998. Toxicity of *Bacillus thuringiensis* Cry1Ab toxin ot the predator *Chrysoperla carnea* (Neuroptera: Chrysopidae). Environmental Entomology 27: 1255-1263.

Hironori Y, Katsuhiro S. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga 42: 153-163.

Hodek I. 1973. Life history and biological properties. In: Hodek I, editor. Biology of Coccinellidae, 70-76. The Hauge, Holland: Dr. W. Junk N. V., Publishers.

Hodek I. 1996. Food relationships. In: Hodek I, Honek A, editors. Ecology of Coccinellidae. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Hodek I, Ceryngier P. 2000. Sexual activity in Coccinellidae (Coleoptera): A review. European Journal of Entomology 97: 449-456.

Hodek I, Iperti G, Hodkova M. 1993. Long-distance flights in Coccinellidae (Coleoptera). European Journal of Entomology 90: 403-414.

Honek A. 1996. Variability and genetic studies In: Hodek I, Honek A, editors. Ecology of Coccinellidae. Dordrecht, The Netherlands: Kluwer Academic Press.

Hongo T, Obayashi N. 1997. Use of diapause eggs of brine shrimp, *Artemia salina* (Linne) for artificial diet of coccinellid beetle, *Harmonia axyridis* (Pallas). Japanese Journal of Applied Entomology and Zoology 41: 101-105.

Hoogendoorn M, Heimpel GE. 2002. Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. Biological Control 25: 224-230.

Hoogendoorn M, Heimpel GE. *in press*. PCR-based gut content analysis of insect predators: use in field- caught predators. Proceedings of the 1st International Symposium on Biological Control of Arthropods, Honolulu, Hawaii.

Hough-Goldstein J, Cox J, Armstrong A. 1996. *Podisus maculiventris* (Hemiptera: Pentatomidae) predation on ladybird beetles (Coleoptera: Coccinellidae). Florida Entomologist 79: 64-68.

Howarth FG. 1991. Environmental impacts of classical biological control. Annual Review of Entomology 36: 485-509.

Hu YS, Wang ZM, Ning CL, Pi ZQ, Gao GQ. 1989. The functional response of *Harmonia* (*Leis*) *axyridis* to their prey of *Cinara* sp. Natural Enemies of Insects 11: 164-168.

Huelsman MF, Kovach J, Jasinski J, Young C, Eisley B. 2002. Multicolored Asian lady beetle (*Harmonia axyridis*) as a nuisance pest in housholds in Ohio. In: Jones SC, Zhai J, Robinson WH, editors. Proceedings of 4th International Conference on Urban Pests, 243-250.

Hukusima S, Itoh K. 1976. Pollen and fungus as food for some Coccinellid beetles. Research Bulletin of the Faculty of Agriculture, Gifu University 39: 31-37.

Hukusima S, Kamei M. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Research Bulletin of the Faculty of Agriculture, Gifu University 29: 53-66.

Hukusima S, Ohwaki T. 1972. Further notes on feeding biology of *Harmonia axyridis* (Coleoptera: Coccinellidae). Research Bulletin of the Faculty of Agriculture, Gifu University 33: 75-82.

Hurst GDD, Majerus MEN, Walker LE. 1992. Cytoplasmic male killing elements in *Adalia bipunctata* (Linnaeus) (Coleoptera: Coccinellidae). Heredity 69: 84-91.

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

James DG. 2002. Selectivity of the acaracide, bifenazate, and aphicide, pymetrozine, to spider mite predators in Washington hops. Internat. J. Acarol. 28: 175-179.

Johki Y, Obata S, Matsui M. 1988. Distribution and behaviour of five species of aphidophagous ladybirds (Coleoptera) around aphid colonies. In: Niemczyk E , Dixon AFG, editors. Ecology and Effectiveness of Aphidophaga, 35-38. The Hague, The Netherlands: SPB Academic Publishing.

Joseph SB, Snyder WE, Moore AJ. 1999. Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. Journal of Evolutionary Biology 12: 792-797.

Kajita Y, Takano F, Yasuda H, Agarwala BK. 2000. Effects of indigenous ladybird species (Coleoptera : Coccinellidae) on the survival of an species in relation to prey abundance. Applied Entomology and Zoology 35: 473-479.

Kalaskar A, Evans EW. 2001. Larval responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to weevil larvae versus aphids as prey. Annals of the Entomological Society of America 94: 76-81.

Katsoyannos P, Kontodimas DC, Stathas GJ, Tsartsalis CT. 1997. Establishment of *Harmonia axyridis* on citrus and some data on its phenology in Greece. Phytoparasitica 25: 183-191.

Kawai A. 1976. Analysis of the aggregation behavior in the larve of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to prey colony. Researches on Population Ecology 18: 123-134.

Kawauchi S. 1979. Effects of temperatures on the aphidophagous Coccinellids. Kurume University Journal 28: 47-52.

Kidd KA, Nalepa CA, Day ER, Waldvogel MG. 1995. Distribution of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in North Carolina and Virginia. Proceedings of the Entomological Society of Washington 97: 729-731.

Kindlmann P, Yasuda H, Sato S, Shinya K. 2000. Key life stages of two predatory ladybird species (Coleoptera: Coccinellidae). European Journal of Entomology 97: 495-499.

Koch RL, Hutchison WD. 2003. Phenology and blacklight trapping of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Minnesota agricultural landscape. Journal of Entomological Science 38: 477-480.

Koch RL, Hutchison WD, Venette RC, Heimpel GE. 2003. Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). Biological Control. 28:265-270.

Komai T. 1956. Genetics of ladybeetles. Advances in Genetics 8: 155-188.

Korschefsky R. 1932. Coccinellidae. Pages In: Schenkling S, editor. Coleopterorum Catalogus, 439-447. Berlin.

Kovar I. 1996. Phylogeny. In: Hodek I , Honek A, editors. Ecology of Coccinellidae, 19-31. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Krafsur ES, Kring TJ, Miller JC, Nariboli P, Obrycki JJ, Ruerson JR, Schaefer PW. 1997. Gene flow in the exotic colonizing ladybeetle *Harmonia axyridis* in North America. Biological Control 8: 207-214.

Kuznetsov VN. 1997. Lady beetles of Russian Far East. Gainesville, FL: Memoir Seis Editor, CSE.

LaMana ML, Miller JC. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biological Control 6: 232-237.

LaMana ML, Miller JC. 1998. Temperature-dependent development in an Oregon population of *Harmonia axyridis* (Coleoptera: Coccinellidae). Environmental Entomology 27: 1001-1005.

Lambin M, Ferran A, Maugan K. 1996. Perception of visual information in the ladybird *Harmonia axyridis* Pallas. Entomologia Experimentalis et Applicata 79: 121-130.

LaRock DR, Ellington JJ. 1996. An integrated pest management approach, emphasizing biological control, for pecan aphids. Southwestern Entomologist 21: 153-167.

Lin Z, Wang L, Sun Q, Nan S. 1999. Preliminary study on predation of *Leis axyridis* on two aphid species. Journal of Heilonjiang August First Land Reclamation University 11: 26-28.

Liu H, Qin L. 1989. The population fluctuations of some dominant species of ladybird beetles in Eastern Hebei Province. Chinese Journal of Biological Control 5: 92.

Lonsdale WM, Briese DT, Cullen JM. 2001. Risk analysis and weed biological control In: Wajnberg E, Scott JK, Quimby PA, editors. Evaluating Indirect Ecological Effects of Biological Control. New York, NY: CABI Publishing.

Lou HH. 1987. Functional response of *Harmonia axyridis* to the density of *Rhopalosiphum prunifoiae*. Natural Enemies of Insects 9: 84-87.

Louda SM, Pemberton RW, Johnson MT, Follett PA. 2003. Nontarget Effects-the Achilles' heel of biological control? Annual Review of Entomology 48: 365-396.

Lucas E, Coderre D, Vincent C. 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. Entomologia Experimentalis et Applicata 85: 151-159.

Lucas E, Gagne I, Coderre D. 2002. Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempuntata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). European Journal of Entomology 99: 457-463.

Lundgren J, Wiedenmann RN. 2002. Coleopteran-specific Cry3Bb toxin from transgenic corn pollen does not affect the fitness of a nontarget species, *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae). Environmental Entomology 31: 1231-1218.

Lynch LD, Hokkanen HMT, Babendreier D, Bigler F, Burgio G, Gao ZH, Kuske S, Loomans A, Menzler-Hokkanen I, Thomas MB, Tommasini G, Waage JK, Lenteren JCv, Zeng QQ. 2001. Insect biological control and non-target effects: a European perspective. In: Wajnberg E, Scott JK, Quinby PC, editors. Evaluating Indirect Ecological Effects of Biological Control, 99-125. Wallingford, Oxon, UK: CABI Publishing.

Maeta Y. 1969. Some biological studies on the natural enemies of some coccinellid beetles. Tohoku Konchu Kenyu 4: 1-6.

Magnan EM, Sanchez H, Luskin AT, Bush RK. 2002. Multicolored Asian lady beetle (*Harmonia axyridis*) sensitivity. Journal of Allergy and Clinical Immunology 109: 205.

Mahr S. 1996. Know your friends: multcolored Asian ladybeetle. Midwest Biological Control News, Online. 2.

Majerus MEN. 1994. Ladybirds. London: Harper Collins.

Majerus TMO, Majerus MEN, Knowles B, Wheeler J, Bertrand D, Kuznetzov VN, Ueno H, Hurst GDD. 1998. Extreme variation in the prevalence of inherited male-killing microorganisms between three populations of *Harmonia axyridis* (Coleoptera: Coccinellidae). Heredity 81: 683-691.

Majerus TMO, Graf von der Schulenberg JH, Majerus MEN, Hurst GDD. 1999. Molecular identification of a male-killing agent in the ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Insect Molecular Biology 8: 551-555.

Matsuka M, Niijima K. 1985. *Harmonia axyridis*. In: Singh P , Moore RF, editors. Handbook of Insect Rearing, 265-268. Amsterdam: Elsevier.

Matsuka M, Takahashi S. 1977. Nutritional studies of an aphidophagous coccinellid *Harmonia axyridis* II.

Significance of minerals for larval growth. Applied Entomology and Zoology 12: 325-329.

McClure MS. 1986. Role of predators in regulation of endemic populations of *Matsucoccus matsumarae* (Homoptera: Margarodidae) in Japan. Environmental Entomology 15: 976-983.

McClure MS. 1987. Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean and Godwin (Homoptera: Margarodidae) in the Unted States. Environmental Entomology 16: 224-230.

McEvoy P, Cox C. 1991. Successful bilogical control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. Ecological Applications 1: 430-442.

Michaud JP. 1999. Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. BioControl 44: 347-367.

Michaud JP. 2000. Development and reproduction of ladybeetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphidae). Biological Control 18: 287-297.

Michaud JP. 2001a. Evaluation of green lacewings, *Chrysoperla plorabunda* (Fitch) (Neurop., Chrysopidae), for augmentative release against *Toxoptera citricida* (Hom., Aphididae) in citrus. Journal of Applied Entomology 125: 383-388.

Michaud JP. 2001b. Numerical response of Olla V-Nigrum (Coleoptera: Coccinellidae) to infestations of Asian Citrus Psyllid, (Hemiptera: Psyllidae) in Florida. Florida Entomologist 84: 608-612.

Michaud JP. 2001c. Response of two ladybeetles to eight fungicides used in Florida citrus: Implications for bological control. Journal of Insect Science 1: 1-6.

Michaud JP. 2002a. Biological control of Asian citrus psyllid, *Diaphorina citri* (Hemiptera: Psyllidae) in Florida: a preliminary report. Entomological News 113: 216-222.

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

Michaud JP. 2002c. Non-targets impacts of acaricides on ladybeetles in citrus: a laboratory study. Florida Entomologist 85: 191-196.

Michaud JP. 2002d. Relative toxicity of six insecticides to *Cycloneda sanguinea* and *Harmonia axyridis* (Coleoptera: Coccinellidae). Journal of Entomological Science 37: 83-93.

Michaud JP. 2003a. A comparative sudy of larval cannibalism in three species of ladybird. Ecological Entomology 28: 92-101.

Michaud JP. 2003b. Toxicity of fruit fly baits to beneficial insects in citrus. Journal of Insect Science 3: 1-9.

Michaud JP, Grant AK. 2003. Sub-lethal effects of a copper sulfate fungicide on development and reproduction in three coccinellid species. Journal of Insect Science 3: 1-6.

Miura T, Nishimura S. 1980. The larval period and predacious activity of an aphidophagous coccinellid, *Harmonia axyridis* Pallas. Bulletin of the Faculty of Agriculture, Shimane University 14: 144-148.

Mondor EB, Roitberg BD. 2000. Has the attraction of predatory coccinellids to cornicle droplets constrained aphid alarm signaling behavior? Journal of Insect Behavior 13: 321-328.

Mondor EB, Warren JL. 2000. Unconditioned and conditioned responses to color in the predatory coccinellid, *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology 97: 463-467.

Musser FR, Shelton AM. 2003. Bt sweet corn and selective insecticides: impacts on pests and predators. Journal of Economic Entomology 96: 71-80.

Nakata T. 1995. Population fluctuations of aphids and their natural enemies on potato in Hokkaido, Japanese Journal of Applied Entomology and Zoology 30: 129-138.

Nalepa CA, Kidd KA. 2002. Parasitism of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) by *Strongygaster triangulifera* (Diptera: Tachinidae) in North Carolina. Journal of Entomological Science 37: 124-127.

Nalepa CA, Kidd KA, Ahlstrom KR. 1996. Biology of *Harmonia axyridis* (Coleoptera: Coccinellidae) in winter aggregations. Annals of the Entomological Society America 89: 681-685.

Nalepa CA, Kidd KA, Hopkins DI. 2000. The multicolored Asian ladybeetle (Coleoptera: Coccinellidae): Orientation to aggregation sites. Journal of Entomological Science 35: 150-157.

Nechayev VA, Kuznetsov VN. 1973. Avian predation on coccinellids in Primorie Region. Pages 97-99. Entomofauna Sovetskogo Dalnego Vostoka. Vladivostok: Tr. Biol.-pochv. Inst.

Niijima K, Matsuka M, Okada I. 1986. Artificial diets for an aphidophagous coccinellid, *Harmonia axyridis*, and its nutrition (minireview). In: Hodek I, editor. Ecology of Aphidophaga, 37-50. Prague: Academia, Dr. W. Junk, Dordrecht.

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

Obata S. 1986b. Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Entomophaga 31: 303-311.

Obata S. 1997. The influence of aphids on the behaviour of adults of the ladybird beetle, *Harmonia axyridis* (Col.: Coccinellidae). Entomophaga 24: 103-106.

Obata S, Johki Y, Hidaka T. 1986. Location of hibernation sites in the ladybird beetle, *Harmonia axyridis* In: Hodek I, editor. Ecology of Aphidophaga. Dordrecht: Academia, Prague and Dr. W. Junk.

Okada I, Matsuka M. 1973. Artificial rearing of *Harmonia axyridis* on pulverized drone honey bee brood. Environmental Entomology 2: 301-302.

Ongagna P, Giuge L, Iperti G, Ferran A. 1993. Cycle de développment d'*Harmonia axyridis* (Col. Coccinellidae) dans son aire d'introduction: le sud-est de la France. Entomophaga 38: 125-128.

Ongagna P, Iperti G. 1994. Influence de la température et de la photopériode chez *Harmonia axyridis* Pall. (Col., Coccinellidae): obtention d'adultes rapidement féconds ou en dormance. Journal of Applied Entomology 117: 314-317.

Osawa N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. Researches on Population Ecology 31: 153-160.

Osawa N. 1992a. Effect of pupation site on pupal cannibalism and parasitism in the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). Japanese Journal of Entomology 60: 131-135.

Osawa N. 1992b. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) in relation to the aphid abundance. Japanese Journal of Entomology 60: 575-579.

Osawa N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. Researches on Population Ecology 35: 335-348.

Osawa N. 2000. Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. Populuation Ecology 42: 115-127.

Osawa N, Nishida T. 1992. Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. Heredity 69: 297-307.

Pando FJQ, Sánchez NC, Rivero SHT. 2001. Effecto del tiempo de disponibilidad del macho en la fecundidad de *Harmonia axyridis* Pallas (Coleoptera: Coccinelidae). Folia Entomologica Mexicana 40: 49-52.

Park H, Park YC, Hong OK, Cho SY. 1996. Parasitoids of the aphidophagous ladybeetles, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in Chuncheon areas, Korea. Korean Journal of Entomology 26: 143-147.

Phoofolo MW, Obrycki JJ. 1998. Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. Entomologia Experimentalis et Applicata 89: 47-55.

Provost C, Coderre D, Lucas E, Bostanian NJ. 2003. Impact of lambda-cyhalothrin on intraguild predation among three mite predators. Environmental Entomology 32: 256-263.

Radcliffe EB, Flanders KL. 1998. Biological control of alfalfa weevil in North America. Integrated Pest Management Reviews 3: 225-242.

Ratcliffe S. 2002. National pest alert: Multicolored Asian lady beetle. USDA CSREES Regional Integrated Pest Management Program and the Pest Mangement Centers.

Rice NR, Smith MW, Eikenbary RD, Arnold D, Tedders WL, Wood B, Landgraf BS, Taylor GG, Barlow GE. 1998. Assessment of legume and nonlegume ground covers on Coleoptera: Coccinellidae density for low-input pecan management. American Journal of Alternative Agriculture 13: 111-123.

Ren GW, Shen WP, Ma JG. 2000. The spatial distribution pattern and sampling method of the larvae of *Leis axyridis* in tobacco fields. Entomological Knowledge 37: 164-165.

Rhoades, M.H. 1996. Key to first and second instars of six species of Coccinellidae (Coleoptera) from alfalfa in Southwest Virginia. Journal of the New York Entomological Society, 104: 83-88.

Riddick EW, Aldrich JR, Milo AD, Davis JC. 2000. Potential for modifying the behavior of the multicolored Asian ladybeetle (Coleoptera: Coccinellidae) with plant-derived natural products. Ann. Entomol. Soc. Am. 93: 1314-1321.

Rossini C, Gonzalez A, Farmer J, Meinwald J, Eisner T. 2000. Antiinsectan activity of epilachnene, a defensive alkaloid from pupae of Mexican bean beetles (*Epilachna varivestis*). Journal of Chemical Ecology 26: 391-397.

Sakai T, Uehara Y, Matsuka M. 1974. The effect of temperature and other factors on the expression of elytral pattern in lady beetle, *Harmonia axyridis* Pallas. Bulletin of the Faculty of Agriculture, Tamagawa University 14: 33-39.

Sakurai H, Kawai T, Takeda S. 1992. Physiological changes related to diapause of the lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Applied Entomology and Zoology 27: 479-487.

Sakurai H, Kumada Y, Takeda S. 1993. Seasonal prevalence and hibernating-diapause behavior in the lady beetle, *Harmonia axiridis*. Research Bulletin of the Faculty of Agriculture, Gifu University. 58: 51-55.

Sakuratani Y, Marsumoto Y, Oka M, Kubo T, Fuji A, Uotani M, Teraguchi T. 2000. Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. European Journal of Entomology. 97: 555-558.

Sasaji H. 1971. Fauna Japonica, Coccinellidae (Insecta: Coleoptera). Tokyo: Academic Press Japan.

Sasaji H. 1977. Larval characters of Asian Species of the Genus *Harmonia* Mulsant. Memoir of the Faculty of Education Fukui University Series II Natural Science. 27: 1-17

Sauphanor B, Lenfant C, Chen X, Sureau F, Eisenlohr U, Domange AL. 1993. Possibilites d'utilisation et actions secondaires d'un extrait de neem (Azadirachta indica) en verger de pecher. Bulletin-OILB-SROP 16: 10-13.

Savoiskaya GI. 1970a. Coccinellids of the Alma-Ata reserve. Trudy Alma Atinskogo Gosudarstvennogo Zapovednika. 9: 163-187.

Savoiskaya GI. 1970b. Introduction and acclimatisation of some coccinellids in the Alma-Ata reserve. Trudy Alma Atinskogo Gosudarstvennogo Zapovednika 9: 138-162.

Savoiskaya GI, Klausnitzer B. 1973. Morphology and taxonomy of the larvae with keys for their identification. In: Hodek I, editor. Biology of Coccinellidae, 36-55. The Hauge, Holland: Dr. W. Junk N. V., Publishers.

Schanderl H, Ferran A, Garcia V. 1988. L'élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecimnotata* à l'aide d'oefs d'*Anagasta kuehniella* tué aux rayons ultraviolets. Entomologia Experimentalis et Applicata 49: 235-244.

Schanderl H, Ferran A, Larroque M. 1985. Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. Agronomie 5: 417-421.

Schroder FC, Gonzalez A, Eisner T, Meinwald J. 1999. Miriamin, a defensive diterpene from the eggs of a land slug (*Arion* sp.). Proceedings of the National Academy of Sciences 96: 13620-13625.

Seo MJ, Youn YN. 2000. The asian ladybird, *Harmonia axyridis*, as biological control agents: I. Predacious behavior and feeding ability. Korean Journal of Applied Entomology 39: 59-71.

Shu CR, Yu CY. 1985. An investigation on the natural enemies of *Hyphantria cunea*. Natural Enemies of Insects 7: 91-94.

Sidlyarevich VI, Voronin KE. 1973. Trials on using *Leis axyridis* under glass. Zashchita Rastenii 6: 24.

Simberloff D, Stiling P. 1996. How risky is biological control. Ecology 77: 1965-1974.

Smith SF, Krischik VA. 2000. Effects of biorational pesticides on four coccinellid species (Coleoptera: Coccinellidae) having potential a biological control agents in interiorscapes. Journal Economic Entomology 93: 732-736.

Smith WM, Arnold DC, Eikenbary RD, Rice NR, Shiferaw A, Cheary BS, Carroll BL. 1996. Influence of ground cover on beneficial arthropods in pecan. Biological Control 6: 164-176.

Snyder WE, Ives AR. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biological control. Ecology 84: 91-107.

Snyder WE, Joseph SB, Preziosi RF, Moore AJ. 2000. Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. Environmental Entomology 29: 1173-1179.

Soares AO, Coderre D, Schanderl H. 2001. Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology 98: 287-293.

Specty O, Febvay G, Grenier S, Delobel B, Piotte C, Pageaux J, Ferran A, Guillaud J. 2003. Nutritional plasticity of the predatory ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): Comparison between natural and substitution prey. Archives of Insect Biochemistry and Physiology 52: 81-91.

Stathas GJ, Eliopoulos PA, Kontodimas DC, Giannopapas J. 2001. Parameters of reproductive activity in females of *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology 98: 547-549.

Stuart RJ, Michaud JP, Olsen L, McCoy CW. 2002. Lady beetles as potential predators of the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida citrus. Florida Entomologist 85: 409-416.

Sun B, Liang S, Zhao W. 2000. Outbreak of soybean aphid in suihua District in 1998 and its control strategies. Soybean Bulletin 1: 5.

Sun R, Yin C, Li A, Sun J, Gu H. 1999. The effect of dichlorbenzuron on *Lithocolletis ringoniella* and its two natural enemies. Natural Enemies of Insects 21: 1-5.

Sun XQ, Chen WL, Chen ZB, He JL, Ye WJ. 1996. A preliminary study on the artificial diet of an aphidophagous coccinellid, *Harmonia axyridis* (Pallas), and its use to control strawberry aphids under plastic covering. Journal of Shanghai Agricultural College 14: 133-137.

Svihla A. 1952. Two-spotted lady beetles biting man. Journal of Economic Entomology 45: 134.

Takahashi K. 1987. Differences in oviposition initiation and sites of lady beetle, *Coccinella septempunctata bruckii* Mulsant and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the field. Japanese Journal of Applied Entomology and Zoology 31: 253-254.

Takahashi K. 1989. Intra- and interspecific predations of lady beetles in spring alfalfa fields. Japanese Journal of Entomology 57: 199-203.

Takizawa T, Yasuda H, Agarwala BK. 2000a. Effect of three species of predatory ladybirds on oviposition of aphid parasitoids. Entomological Science 3: 465-469.

Takizawa T, Yasuda H, Agarwala BK. 2000b. Effects of parasitized aphids (Homoptera: Aphididae) as food on larval performance of three predatory ladybirds (Coleoptera: Coccinellidae). Applied Entomology and Zoology 35: 2000.

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

Tedders WL, Schaefer PW. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. Entomological News 105: 228-243.

Tourniaire R, Ferran A, Gambier J, Giuge L, Bouffault F. 1999. Locomotor behavior of flightless *Harmonia axyridis* Pallas (Col., Coccinellidae). Journal of Insect Behavior 12: 545-558.

Tourniaire R, Ferran A, Gambier J, Giuge L, Bouffault F. 2000. Locomotory behavior of flightless *Harmonia axyridis* Pallas (Col., Coccinellidae). Journal of Insect Physiology 46: 721-726.

Trouve C, Ledee S, Ferran A, Brun J. 1997. Biological control of the damson-hop aphid, *Phorodon humuli* (Hom.:Aphididae), using the ladybeetle *Harmonia axyridis* (Col.: Coccinellidae). Entomophaga 42: 57-62.

Vincent C, Ferran A, Guige L, Gambier J, Brun J. 2000. Effects of imidacloprid on *Harmonia axyridis* (Coleoptera: Coccinellidae) larval biology and locomotory behavior. European Journal of Entomology 97: 501-506.

Wagner JD, Glover MD, Moseley JB, Moore AJ. 1999. Heritability and fitness consequences of cannibalism in *Harmonia axyridis*. Evolutionary Ecology Research 1: 375-388.

Wallace MS, Hain FP. 2000. Field surveys and evaluation of native and established predators of the hemlock wooly adelgid (Homoptera: Adelgidae) in the Southeastern United States. Environmental Entomology 29: 638-644.

Wang LY. 1986. Mass rearing and utilization in biological control of the lady beetle *Leis axyridis* (Pallas). Acta Entomologica Sinica 29: 104.

Wang C, Chen J, Guo Y, Gong X, Xu Z, Lin C. 1998. Development and control of soybean aphid *Aphis glycines* in Heillonjiang Province. Soybean Bulletin 6: 15.

Wang Z, Ba F. 1998. Study of the optimum control of soybean aphid. Acta Phytophylacica Sinica 25: 151-155.

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

Weissenberger A, Brun J, Herold D. 1997. Essais de toxicite d'un aphicide (Confidor) sur la Coccinelle *Harmonia axyridis* Pallas. Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent. 62: 589-593.

Weissenberger A, Brun J, Piotte C, Ferran A. 1999. Comparison between the wild type and flightless type of the coccinellid *Harmonia axyridis* (Pallas) in control of the damson hop aphid. Fifth International Conference on Pests in Agriculture. Association Natioale pour la Protection des Plantes (ANPP), 727-734. Paris and Montpellier, France.

Wells ML, McPherson RM. 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). Environmental Entomology 28: 768-773.

Wells ML, McPherson RM, Ruberson JR, Herzog GA. 2001. Coccinelids in cotton: population response to pesticide application and feeding response to cotton aphids (Homoptera: Aphididae). Environmental Entomology 30: 785-793.

With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL. 2002. Threshold effects of landscape structure on biological control in agroecosystems. Ecological Applications 12: 52-65.

Wold SJ, Burkness EC, Hutchison WD, Venette RC. 2001. In-field monitoring of beneficial insect populations in transgenic sweet corn expressing a *Bacillus thuringiensis* toxin. Journal of Entomological Science 36: 177-187.

Yarbrough JA, Armstrong JL, Blumberg MZ, Phillips AE, McGahee E, Dolen WK. 1999. Allergic rhinoconjunctivitis caused by *Harmonia axyridis* (Asian lady beetle, Japanese lady beetle, or lady bug). Journal of Allergy and Clinical Immunology 104: 705.

Yasuda H, Ishikawa H. 1999. Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. Journal of Applied Entomology 123: 585-589.

Yasuda H, Kikuchi T, Kindlmann P, Sato S. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. Journal of Insect Behavior 14: 373-384.

Yasuda H, Kimura T. 2001. Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. Entomologia Experimentalis et Applicata 98: 17-25.

Yasuda H, Ohnuma N. 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. Entomologia Experimentalis et Applicata 93: 63-67.

Yasuda H, Takagi T, Kogi K. 2000. Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). European Journal of Entomology 97: 551-553.

Yasumatsu K, Watanabe C. 1964. A Tentative Catalogue of Insect Natural Enemies of Injurious Insects in Japan — Part 1. Parasite-Predator Host Catalogue. Fukuoka, Japan: Entomological Laboratory, Faculty of Agriculture Kyushu University.

Ying SH. 1982. The ovicidal activity of new insecticides. Acta Entomologica Sinica 25: 289-293.