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

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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much of the continental United States, except for Montana, Wyoming, and parts of the southwestern United States (RLK, unpublished data).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 (Ipert and Bertand, 2001, Katsoyannos et al., 1997) and was recently recorded in South America (de Almeida and da Silva, 2002).

Taxonomic History

H. axyridis is currently placed in the tribe Coccinellini of



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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 26° C on a diet of *Acyrtosiphon 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 11.2° C in the United States (LaMana and Miller, 1998), and 231.3 degree days above a lower developmental threshold of 10.5° 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 18° 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 flights 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 –19° C and –16° 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-detering 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 Tetranychidae (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 Yeorgan, 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 tricuspidatus*, 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 Doult, 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 tsugae* 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 Nijima (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, Nijima 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 Ipert (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 *Beauveria 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)
Beauveria bassiana, strain GHA	7.5 ml/l	L:DR(s)	—	Low	(Smith and Krischik, 2000)
Bifentate	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)
Phosпамidon	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. Adults 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 Douth, 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 of 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 Katsuhiko, 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	<i>Adalia bipunctata</i>	PP, P	(Sakuratani et al., 2000)
			L	(Kajita et al., 2000)
			E	(Lynch et al., 2001)
			E	(Burgio et al., 2002)
		<i>Adonia variegata</i>	E	(Lynch et al., 2001)
		<i>Coleomegilla maculata</i>	E, L	(Cottrell and Yeargan, 1998)
		<i>Coccinella septempunctata</i>	L	(Hironori and Katsuhiko, 1997)
			L	(Yasuda and Ohnuma, 1999)
			L	(Yasuda et al., 2001)
		<i>C. septempunctata brucki</i>	P	(Takahashi, 1989)
			L	(Dixon, 2000)
		<i>Cycloneda sanguinea</i>	E, L	(Michaud, 2002b)
		<i>Propylea japonica</i>	L	(Dixon, 2000)
Lepidoptera	Nymphalidae	<i>P. quatuordecimpunctata</i>	E	(Lynch et al., 2001)
		<i>Danaus plexippus</i>	E, L	(Koch et al., 2003)
Neuroptera	Chrysopidae	<i>Chrysoperla carnea</i>	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 (Teddars 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 where *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.

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