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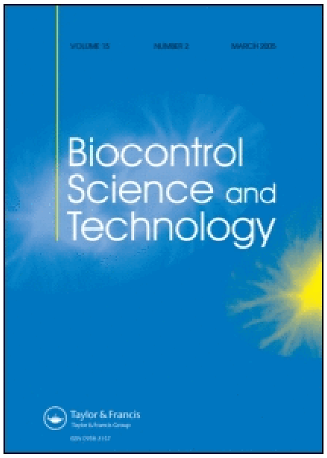

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Ecology and biological control application of multicoloured Asian ladybird, **Harmonia axyridi**s: A review

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REVIEW

Ecology and biological control application of multicoloured Asian ladybird, *Harmonia axyridis*: A review

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Abstract
The ecology of and biological control by multicoloured Asian ladybird beetle, *Harmonia axyridis* (Pallas) are reviewed. Our emphasis is on assembling and interpreting information on general characteristics, invasion and establishment, sexual activity, foraging and predation, development, survival and reproduction, predator–predator interactions, natural enemies, biocontrol, non-target effects and status of *H. axyridis* as a pest of fruits. Colonization of *H. axyridis* for aphid biocontrol in the USA have been successful in terms of its establishment, but its abundance is turning out to be a nuisance to humans. Its harmful non-target impact on beneficial organisms, humans and native species is becoming a debatable issue. The question on its present position, whether it is a biocontrol agent or pest, is a critical issue and discussed. Inferences from the empirical data are made and new avenues for future research are suggested.

Keywords: Harmonia axyridis*, Coccinellidae, biological control, ecology, aphids, scale insects*

Introduction

Generalist ladybirds (Coleoptera: Coccinellidae) can be important biocontrol agents of aphids, scales and other phytophagous pests. Recent reviews on the ecology and biocontrol potential of generalist ladybirds (Symondson et al. 2002), particularly *Cheilomenes sexmaculata* (Fabr.) (Agarwala & Yasuda 2000), *Coccinella septempunctata* L. (Omkar & Pervez 2002), and *Chilocorus nigritus* (Fabricius) (Omkar & Pervez 2003) supported the idea of generalists being potential biocontrol agents, as they can easily establish themselves in new habitats by switching to alternative prey in absence of target prey species. Multicoloured Asian ladybird beetle, *Harmonia axyridis* (Pallas), is one of the popular generalist ladybirds, gaining much scientific attention due to its ubiquitous properties, biocontrol potential, easy establishment and controversy about its negative impacts. Often referred to as Halloween beetle (as its

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massive migrations occur around Halloween, i.e., late October in North America), this Japanese beetle is now a successful invader and has been well-established in the United States and Europe.

Koch (2003) emphasised the taxonomy, natural history, biocontrol potential and negative impacts of *H. axyridis*, and raised questions about its introduction into agro-ecosystems. Increasing evidence suggests that *H. axyridis* is turning out to be a disaster rather than a success in terms of biological control (Kidd et al. 1995; Huelsman et al. 2002; Huelsman & Kovach 2004). Harris (1990) stated, "most biocontrol agents that become extremely abundant are a nuisance." *Harmonia axyridis* could be considered as one such example of a biocontrol agent turning into a nuisance to humans. In the United States, it sometimes overwinters in buildings and houses and some people have developed allergic rhino-conjunctivitis to *H. axyridis* (Huelsman et al. 2002; Magnan et al. 2002; Yarbrough et al. 1999), while others have been bitten (Huelsman et al. 2002).

Koch (2003) comprehensively reviewed the ecology of *H. axyridis*. We focus on issues he did not address along with more recent research. This includes general characteristics, invasion and establishment, sexual activity, foraging, development and survival, predator–predator interactions, defense and natural enemies, non-target impacts and frugivory. Inferences and interpretation from empirical data have been made and new fields of research have been suggested. We discuss whether *H. axyridis* is beneficial in agro-ecosystems or whether it is becoming a pest due its harmful impact on non-target beneficial organisms and humans.

General characteristics

Harmonia axyridis shows a high level of genetic polymorphism, *i.e.* multiple genotypes occur in a population, resulting in differences not only in shape and size (Soares et al. 2001, 2003) but also in strikingly different colour forms. Phenotypes are classified into two groups: the *succinea* group characterised by a light reddish or brownish ground colour, and the melanic group, which includes the *conspicua*, *spectabili*s, and *aulica* subgroups, characterised by melanic elytral patterns (Komai 1956). Rare phenotypes, such as pure black *nigra* occur in natural habitats (Tan 1946). Almost fifty phenotypes were identified in a Chinese population (Wu et al. 1987). However, these varieties could be grouped into two morphs, i.e., light-coloured *aulica* and dark coloured *nigra* (Soares et al. 2003). The *aulica* morph is bigger in size than *nigra* and has a higher prey consumption rate. This could be due to higher thermal optima of *aulica* adults (3.7°C higher than that of *nigra*; Soares et al. 2003). Predation by *nigra* was more affected at the upper tolerance limit (30°C) indicating it is more stenothermic than *aulica*. Due to its bigger size, *aulica* consumes greater number of prey (Soares et al. 2003). Existence of a seasonal-dependent size variation is more prominent in *nigra*, with males obtained in spring being significantly larger than those in summer (Osawa 2001), while the reverse is true for *nigra* females. The micro-geographical variation in *H. axyridis* (that is, differences in the relative frequency of elytral pattern phenotypes between host plants in the same habitat) may possibly be correlated with differences in the composition of aphid populations (Komai & Hosino 1951). Both *aulica* and *nigra* morphs of *H. axyridis* seem to have different nutritive requirements due to their different responses towards *Aphis fabae* Scopoli and *Myzus persicae* (Sulzer) (Soares et al. 2005). The reproductive capacity of *nigra* females (but not *aulica* females) is significantly superior when fed *A. fabae* rather than *M. persicae*, which suggests that differences occur in the degree of prey suitability. Thus, it is likely that dissimilar phenotypes fed the same prey species could perform differently and that different prey species could have distinct effects on the biological performance of a given predator phenotype.

Adult diet has a very strong effect on the development of colour over time. Diets with high-quality aphid, *viz. Myzus nicotianae* Blackman, produce vibrantly coloured red adults, whereas a lower-quality pollen diet produces pale orange adults (Grill et al. 1997; Grill 1999). It appears that besides a genetic influence, melanism in ladybirds might also be dependent on factors, such as nutritional intake at the larval stage.

Ladybirds that cannot survive freezing temperatures use one or more mechanisms to avoid them, e.g., by moving to physically protected areas, or by supercooling. Supercooling is the depression of the freezing point of body fluids to levels where crystallisation is avoided (Lee 1991) and the temperature at which spontaneous freezing of the body fluids occurs is referred to as the supercooling point (SCP). The potential geographic range of *H. axyridis* may depend on its overwintering behaviour and cold hardiness. Adults overwinter close to prominent objects on the horizon (e.g., buildings or mountains) which may confer a degree of protection from low temperatures (Koch 2003). In addition, they acquire cold hardiness by cold acclimation and protect themselves against low temperatures by supercooling (Watanabe 2002; Carrillo et al. 2004; Koch et al. 2004a). Due to chill tolerance the adults of a Japanese strain can survive up to 200 days at −5°C (Watanabe 2002). The Chinese strain can also overwinter safely and its mean supercooling temperature ranges from −7.8 to −2.8°C, with an average of −5.1°C (Sun XingQuan et al. 2002).

Harmonia axyridis shows both facultative aestivation and overwintering (Coderre et al. 1995) and is very resistant to winter conditions, surviving temperatures as low as −30°C for short periods (Iablokoff-Khnzorian 1982). Cold tolerance in adults of *H. axyridis* changes seasonally. The adults accumulate a relatively large amount of myo-inositol during winter. The myo-inositol content is synchronized seasonally with supercooling capacity, lower lethal temperature and chilling tolerance, suggesting the importance of myo-inositol in cold tolerance (Watanabe 2002).

Invasion and establishment

Harmonia axyridis is a successful invader in North America and Europe. Much about its invasion and establishment in North America has been previously reviewed (Koch 2003). Though a commonly encountered ladybird in eastern North Carolina, its impact on the native coccinellid fauna has yet to be determined (Nault & Kennedy 2003). Its rapid establishment has led to a decline in the population of native ladybird species and has negatively impacted the populations of aphid midge, *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (Brown 2003). It has also spread rapidly in Quebec, Canada since 1994, and become a problem because of its aggregation in a large number in buildings during autumn and winter (Lucas et al. 2002). The reason most often invoked to explain this behaviour is the weak resistance of the species to low temperatures (Berthiaume et al. 2003).

Among European countries, it has successfully established itself in Germany (Klausnitzer 2002; Tolasch 2002; Bathon 2003) and has heavily suppressed the indigenous coccinellid fauna in Belgium, where it is being regarded as a threat to the native aphid predators (Adriaens et al. 2003). It was introduced into France for the biological control of damson hop aphid, *Phorodon humuli* (Schrank), where it performed best in managing early aphid infestations (Trouve 1995). Importations from France to Greece in 1994 for the biocontrol of aphids, *Toxoptera aurantii* (Boyer de Fonscolombe), *Aphis spiraecola* Pagenstecher and *Aphis gossypii* Glover in citrus orchards were successful (Katsoyannos et al. 1997). It has thrived in the European landscape and appears highly tolerant to climate of the region. This predator appears to have a very wide host range allowing it to feed on a wide array of new prey aphids.

Sexual activity

The adult *H. axyridis* needs 7–10 days to mature sexually (Obata & Johki 1991). Both chemical and visual cues seem to be involved in mate recognition by males. Prior to mating, the male performs five pre-mating steps, *viz*. approach, watch, examine, mount and copulatory attempt, (Obata 1987). Gonadal immaturity affects the receptivity in females, as they show prominent rejection displays, such as, running away, lifting their abdomen upwards, dropping down from a height and subsequently displacing males (Obata 1988). The probability of mating acceptance by the females increases with their age due to progress in ovarian development. Poor quality food negatively affects mating (Obata 1988). Prominent abdominal shakings occur during mating that may last up to two hours. Virgins mate longer than non-virgins. Minutes after termination of mating (14.8 min), females eject a spermatophore, which is eventually consumed. The frequency of spermatophore ingestion is almost 95% (Obata & Hidaka 1987; Obata & Johki 1991).

There is a high frequency of multiple insemination in natural populations of *H. axyridis* (Osawa 1994). In addition, evidence from field studies reveals that very few males contribute to progeny production, suggesting intensive selection pressure among sperm for fertilisation. This might be attributed to the fact that mating in fields is not as frequent as it appears in the laboratory. Ueno (1996) reported that only 13.8% of adults mated more than twice in one field study. The sperm from the last mating seemingly has precedence over stored sperm from the other males due to limited sperm retaining capacity of spermathecae (Ueno 1994). Larger males had higher fertilisation success than smaller ones with seemingly larger ejaculate size and longer duration of sperm transfer (Ueno 1994). The adult males involved in mating were usually larger than the solitary ones suggesting that increased body size is positively correlated with male mating success. In addition, melanism also plays a role in male mating success in *H. axyridis* due to possible involvement of thermal absorption pattern (Ueno et al. 1998). A recent review on sexual activity in ladybirds discussed preferential mating and sperm transfer in *H. axyridis* (Hodek & Ceryngier 2000), which have not been taken into account in the present review.

Foraging and predation

Searching

Searching behaviour of ladybirds has been previously reviewed with little information on *H. axyridis* (Hodek & Honek 1996). Both adults and larvae of *H. axyridis* search randomly for prey-location. After locating and contacting a prey, they switch to intensive or area-restricted search (Ettifouri & Ferran 1993; YunDing et al. 1997). Their searching behaviour is dependent on light intensity and degree of starvation (YunDing et al. 1997). A sub-optimal food when substituted with an optimal one helps the larvae of *H. axyridis* in searching for prey (Ettifouri & Ferran 1993). The attraction of adults during flight towards black objects that are vertically positioned on contrasting backgrounds (Nalepa et al. 2005) suggests the importance of visual cues in searching for prey sites. Still, not much is known on the searching efficiency and behaviour of *H. axyridis*. Its invasive nature suggests that it can locate the prey-habitat faster than other ladybird species, which could explain its establishment and dominance in the guild (below). More attention is needed to further explore this aspect.

Predation and diets

Being a generalist, *H. axyridis* has a broad host range, earlier reviewed by Koch (2003). There exists a relationship between prey nutritional content and costs associated with feeding, i.e. searching, prey capture, and consumption. For instance, adults fed on more individuals of *M. persicae* than *A. fabae*, and consumed less biomass from the former (Soares et al. 2004). While feeding on *A. fabae*, which has a higher energy rich contents, adults of *H. axyridis* decrease feeding bouts and increase energetic intake; feeding on *M. persicae* increases feeding bouts and decreases energetic intake. Both adult male and female *H. axyridis* differ in feeding response at different levels of prey abundance. While males show a constant feeding preference for *M. persicae*, females did not show any preference (Soares et al. 2004). The prey consumption rate increases with increase in larval stage and temperature (Cho & Kim 1984). However, high temperatures, i.e., 30°C and above, reduce the voracity of larvae and adults (Cho & Kim 1984).

Predators respond to increasing prey density by consuming more prey. There are three types of functional responses, *viz*. Type I, II and III, yielding linear, curvilinear and sigmoidal curves, respectively (Holling 1959, 1965). Type I and II responses have been reported in *H. axyridis*. The type I response was observed using aphid, *Rhopalosiphum prunifoliae* (Noda) as prey (Lou 1987). The type II response was obtained on aphids, *A. gossypii* (Lei & Chen 1987), *Chaitophorus populialbae* (Boy.) (Li et al. 1993), *Hyalopterus arundinis* (Fabr.) (DongChang et al. 2001) and *M. nicotianae* (JianHua et al. 2002). Usually, aphidophagous ladybirds represent a Type II functional response revealing a negative density dependence to the increasing prey density (Omkar & Srivastava 2003a; Pervez & Omkar 2003, 2005; Omkar & Pervez 2004). The predators that exhibit a Type III response indicate a positive density dependent response to prey density in terms of increased rate of prey consumption. The differential functional responses by *H. axyridis* to different prey species might be attributed to the difference in palatability, efficiency of prey capturing and nutritional value of the prey attacked.

Adults of *H. axyridis* can be reared successfully on a large scale for many generations on non-insect diets (Freier & Triltsch 1995). Japanese workers have intensively worked to develop suitable artificial diets, largely composed of pulverised drone honey bee powder, which can support the immature development and reproduction of *H. axyridis* (Niijima et al. 1997). Recently, four diets were tested: the egg yolk diet containing 33.0 g of fresh egg yolk and 150.0 g of distilled water; the whole egg diet, containing 100.0 g of whole egg and 155.0 g of water; the gelatin diet, containing 0.5 ml formaldehyde (37% solution), 170.0 g of water, and 5.0 g of gelatin; and the starch diet, which contained 150.0 g of water and 1.5 g of maize starch (Dong et al. 2001). Though development was delayed, survival was high on all the tested diets. It is thus easy to rear this ladybird on artificial diets; however, there are some negative effects on foraging efficiency, as larvae lose the ability to switch from extensive to intensive search (Ferran et al. 1997).

Development, survival and reproduction

The developmental period of *H. axyridis* is largely dependent on temperature and food quality. It was shorter when the larvae were fed on optimal diets and longer on sub-optimal ones (Table I). The ratio of time spent by four larval stages was 1.12, 1.00, 1.36 and 2.00, respectively (Table I), revealing that second instars moult faster than others. The total development period of *H. axyridis* varies with prey quality, e.g., 19.92 days on *A. gossypii* (Kim & Choi 1985), and 18.0 days on *Anagasta kuehniella* Zell. (Brun 1993). The larvae reared on *A. pisum* showed a shorter developmental period and a heavier pupal mass than those raised on *Aphis craccivora* Koch or on artificial diet (Ueno 2003). This emphasizes the influence of diets on immature development in *H. axyridis*.

Survival of immature stages of *H. axyridis* is also diet dependent, as percent survival was 85.9% on *A. gossypii* (Kim & Choi 1985) and 88.3% on *A. kuehniella* eggs (Abdel-Salam et al. 1997). This also suggests that immature survival is also largely dependent on prey quality. A similar effect of prey diet on the development and immature survival is also reported in other ladybird species (Omkar & Srivastava 2003b; Pervez & Omkar 2004; Omkar & James 2004; Omkar & Bind 2004). Prey quality largely affects reproduction in *H. axyridis* (Table II). The adults reared on better quality prey were more fecund and have high reproductive rates. Published fecundity values varied from 257 to 3,819 eggs, with a reproductive rate of 25.1 eggs/day in one study (Hukusima & Kamei 1970) (Table II). The inter-oviposition period of *H. axyridis* obtained in a single study on *M. persicae* was 3.6 ± 0.8 days, which was longer than those of other ladybird species (Lanzoni et al. 2004). Crowding of females has a trade-off with fecundity of ovipositing female *H. axyridis,* as fecundity decreases with an increase in density of females (Abdel-Salam & Abdel-Baky 2001). Age-specific fecundity in *H. axyridis* is triangular in function (oviposition increases with reproductive age, peaks and thereafter decreases on further aging) (Lanzoni et al. 2004), as also observed in other ladybirds (Dixon & Agarwala 2002; Omkar & Pervez 2002; Pervez & Omkar 2004). The highest reported oviposition rate (30 eggs/day) in *H. axyridis* was obtained at 16 days (Lanzoni et al. 2004).

Larval mortality was a key factor in regulating populations of *H. axyridis*. Fourth instars suffered maximum mortality as compared to other life stages (Osawa 1992a). Evidence from the demographic parameters of *H. axyridis* (Table III) revealed that this ladybird can easily be reared in the laboratory. However, low demographic values for this predator (i.e., $R_o = 26.27$ and $r_m = 0.089$) in Italy, using *M. persicae* as prey in the laboratory ($25 \pm 1°C$; RH 60–80% and 16:8 LD photoperiod) was far lower than when reared on diet, suggesting biological traits do not contribute to the invasiveness of *H. axyridis* (Lanzoni et al. 2004). This laboratory study was made by rearing the eggs of *H. axyridis* individually in plastic cylindrical containers until adult emergence

Table I. Developmental period ($\bar{x}$±SEM, in days) of *H. axyridis* on its various prey species.

Prey Species	L_1	L_2	L_3	L_4	Pupal period	Total development period	References
Fresh eggs of *Sitotroga cerealella*	2.34±0.18	2.00±0.10	2.95±0.11	3.90±0.08	4.90±0.10	18.89±0.32	Abdel-Salam and Abdel-Baky (2001)
Frozen eggs of *Sitotroga cerealella*	3.04±0.12	2.47±0.09	3.09±0.10	4.80±0.19	6.00±0.21	22.50±0.21	Abdel-Salam and Abdel-Baky (2001)
A. pisum	1.79±0.03	1.87±0.03	2.28±0.05	3.62±0.09	4.90±0.10	14.46±0.13	Specty et al. (2003)
Ephestia kuchniella	1.70±0.07	1.58±0.05	2.48±0.06	3.50±0.01	4.85±0.08	14.12±0.11	Specty et al. (2003)
M. persicae	2.30±0.10	1.50±0.10	2.00±0.10	4.70±0.10	6.60±0.10	19.80±0.20	Lanzoni et al. (2004)

L_1–L_4 = first to fourth larval durations.

Table II. Reproductive attributes of *H. axyridis* on its different prey species.

Prey species	Pre-OP	OP	POP	Fec	Lon	RR	References
Fresh eggs of *S. cerealella*	8.1	49.0	5.1	715.3	62.2	14.59	Abdel-Salam and Abdel-Baky (2001)
Frozen eggs of *S. cerealella*	9.5	45.3	6.8	606.6	61.6	13.39	Abdel-Salam and Abdel-Baky (2001)
A. gossypii	*	*	*	*	31.4	15.90	Kim and Cho (1985)
A. pisum	7.3	45.2	*	718.7	*	*	McClure (1987)
Diuraphis noxia (Kurdj.)	*	*	*	1536	*	*	Anonymous 1997
A. fabae	*	*	*	834	*	*	Anonymous 1997
M. persicae	*	*	*	3819	*	25.1	Hukusima and Kamei 1970
Pink bollworm eggs	14.8	49.0	37.0	257	100.8	5.24	Abdel Salam et al. 1997
M. persicae	7.4	13.7	*	560.5	*	18.3	Lanzoni et al. 2004
A. fabae	10.8	60.7	5.3	1641.6	76.8	27.04	Stathas et al. (2001)

Pre-OP, pre-oviposition period; OP, oviposition period; POP, post-oviposition period; Fec, fecundity (in eggs); Lon, longevity; RR, reproductive rate (eggs/day). *Data not available; periods and longevity in days.

on the above prey species. Results could not be generalized as *M. persicae* used in this study might not be as suitable as to other ladybird species.

Predator–predator interactions

Cannibalism

Harmonia axyridis is a cannibalistic species. Eating conspecifics is advantageous, as larvae can develop and become adults and migrate to other prey habitats without starving, thus protecting their genotypes (Kindlmann & Dixon 1993). Sibling cannibalism of eggs by neonates is frequent in egg batches throughout the oviposition period, regardless of the site of oviposition (Osawa 1992a). It mainly occurs due to asynchrony in hatching, and existence of infertile or unhatched eggs (Kawai 1978). Such eggs have no reproductive value and are usually laid purposefully by the females to serve as nurse or trophic eggs (Perry & Roitberg 2005). However, the mechanism involved in the production of unhatched eggs is not yet fully understood, except that it may be due to infertility or bacteria that kill male embryos (Hurst & Majerus 1993). It appears that sibling cannibalism in *H. axyridis* is one of the maternal investments directly under the control of adult females (Osawa 2003). They attain almost equal reproductive fitness at low aphid densities, regardless of the intensity of sibling cannibalism, suggesting that eating siblings is not maladaptive. At high aphid densities, however, the fitness of the mother decreased with intensity of sibling cannibalism, indicating that it was maladaptive for the mother when larval food

Table III. Demographic parameters of *H. axyridis* on its different prey species.

Prey species	R_o	r_m	λ	GT	DT	References
Fresh eggs of *S. cerealella*	289.11	0.153	1.166	37.87	4.53	Abdel-Salam and Abdel-Baky (2001)
Frozen eggs of *S. cerealella*	234.96	0.121	1.128	45.04	5.72	Abdel-Salam and Abdel-Baky (2001)
M. persicae	26.27	0.089	*	38.81	*	Lanzoni et al. (2004)

R_o, net reproductive rate; r_m, intrinsic rate of increase (in day^{-1}); λ, finite rate of increase (in day^{-1}); G.T., generation time (in days); DT, doubling time (in days). *Data not available availability was high (Osawa 1992b). The effects of sibling cannibalism on life history traits are seemingly sex-differentiated and males benefit more than females (Osawa 2002, 2003). Considering the cost and benefits of sibling cannibalism, this trait was clearly beneficial to the cannibal at low prey (aphid) density (Osawa 1992b). Sibling cannibalism promotes faster development and larger sized adults (Osawa 2002). Faster development may be adaptive for resource tracking, and large adult size may increase fecundity in females and mating success in males through female mate choice, both resulting in an increase in the fitness of cannibals.

Intraguild predation

Harmonia axyridis is a dominant intraguild species and has out-competed nearly all the coccinellid species in its guild (a common prey patch shared by many predators). It is, thus, an extraordinary species in this regard possessing many intrinsic advantages that render it a formidable competitor amongst coccinellids. It appears to be strongly chemically protected against predation by other ladybirds, including *C. septempunctata* (Yasuda & Shinya 1997) and *Coccinella septempunctata brucki* Mulsant (Sato & Dixon 2003). It could be successfully reared on an exclusive diet of *Chrysoperla carnea* (Stephens) eggs (Phoofolo & Obrycki 1998) and *C. septempunctata* larvae (Yasuda 1999). The reverse, however, was not true as other species could not complete their development on the exclusive eggs or larvae of *H. axyridis*. The larvae of *H. axyridis* have higher attack, escape and predation rates than *C. septempunctata*; the latter is considered an intraguild prey for *H. axyridis* (Yasuda et al. 2001). The native species in the USA, *viz. Coccinella transversoguttata* Brown and *Hippodamia convergens* Guerin were victimised more often when kept with *H. axyridis* (Snyder et al. 2004a).

Intraguild predation is not only dependent on size disparity between predator and prey but is also determined by behavioural and defensive differences influencing: (1) ability to capture intraguild prey, and (2) ability to avoid attack by an intraguild predator. *Harmonia axyridis* is evidently using both types of mechanisms to gain advantage over the native species. As an intraguild predator, *H. axyridis* captured and killed larvae of two native species over 70% of the time, while as a prey, it was captured and killed by the superior predator only 25% of the time (Snyder et al. 2004a).

Survival of *H. axyridis* larvae decreased after eating eggs of *A. bipunctata* and *C. septempunctata brucki*, indicating their reluctance to feed on heterospecific eggs (Santi et al. 2003; Sato & Dixon 2003). Seemingly low susceptibility to fungus, *Beauveria bassiana* (Balsamo) (found to infect other native species, especially *Olla v-nigrum* Casey) may provide an intraguild advantage to *H. axyridis* (Cottrell & Shapiro-Ian 2003). The aggressive behaviour and voracity of *H. axyridis* (Soares et al. 2005) along with its chemical defense could be the probable reasons for its dominance in the guild and its establishment. It is evident that *H. axyridis* is altering insect communities by out-competing native coccinellids.

Natural enemies

Harmonia axyridis uses its aposematic colouration as a means of defense against predators. The adults reflex-bled on being attacked. Reflex bleeding in *H. axyridis* is a secretion mainly composed of the alkaloid harmonine (Enders & Bartzen 1991). Females of *H. axyridis* are susceptible to bacteria, *Spiroplasma ixodetis* causing mortality of male embryos (Majerus et al. 1999) and parasitism by a tachinid, *Strongygaster triangulifera* (Loew) (Katsoyannos & Aliniazee 1998). Incidence of parasitism by hymenopterans, e.g., *Dinocampus coccinellae* (Shrank) is lower in *H. axyridis* than other ladybird species (Hoogendoorn & Heimpel 2002).

Male-killing bacteria transmitted through egg-cytoplasm (only from mother to daughter) has been observed in ladybird species including *H. axyridis* (Matsuka et al. 1975; Gotoh & Niijima 1986; Hurst & Majerus 1993), affecting its hatching success. This leads to a distorted sex-ratio (usually female biased) of *H. axyridis* in the field. There is more than a 99.0% inheritance rate for male-killing bacteria in female progeny; however, the infected proportion varies in different populations (Majerus et al. 1998). Low proportion of a male-killer, *Spiroplasma* was recorded in females sampled from Muikamachi and Fukuyama, Japan (0.039 and 0.135, respectively) (Nakmura et al. 2005). These bacteria are sensitive to antibiotics that may induce a normal sex-ratio in females (Matsuka et al. 1975; Gotoh 1982; Gotoh & Niijima 1986).

Biological control

Intraguild predation by generalists can disrupt biological control, worsening pest problems (Polis et al. 1989; Rosenheim et al. 1995). However, a recent study using *H. axyridis* suggests that even when rampant intraguild predation does occur in the greenhouse, biocontrol can still be improved by the inclusion of generalists. *Harmonia axyridis* has been used with the parasitoid, *Aphelinus asychis* Walker to work in tandem for the biocontrol of the aphid, *Macrosiphum euphorbiae* Thomas (Snyder et al. 2004b). Together, they complemented rather than disrupted biocontrol of *M. euphorbiae* through intraguild predation (Snyder et al. 2004b).

Successful biocontrol of *A. gossypii* on cucumbers was realized by releasing eggs or flightless adults (below) of *H. axyridis* (Kuroda & Miura 2003). Populations of the aphid, *A. spiraecola*, in apple orchards also declined with the introduction of *H. axyridis* (Brown & Miller 1998). Its inundative release effectively managed the population of the chrysomelid leaf beetle, *Chrysophtharta bimaculata* (Olivier) infesting *Eucalyptus nitens* (Baker et al. 2003). It was successfully used for biocontrol of strawberry aphid, *Chaetosiphon fragaefolii* (Cockerell) in China after raising the adults on artificial diets (XinQuan et al. 1996), and rose aphid, *Macrosiphum rosae* (L.), in France (Ferran et al. 1996). The decline in the population of a recent invasive soyabean aphid pest, *Aphis glycine* in North America was largely due to *H. axyridis* (Landis et al. 2004).

Harmonia axyridis has also been utilised successfully in the biocontrol of scale-insects, like *Matsucoccus massoniana* in China (Wang 1982), *M. matsumurae* (Kuwana) in Japan (McClure 1986a), *Pseudaulacaspis pentagona* (Targioni) in Southern Korea (Park & Kim 1990), and *M. thunbergianae* Miller & Park in Korea (KwangSik et al. 1995). It was amongst the major coccinellid fauna reducing populations of pseudococcid, *Nesticoccus sinensis* Tang and eriococcid, *Rhizococcus transverses*, both important pests of bamboo in Southern Jiangsu, China (Xu & Wu 1989). The success of *H. axyridis* in reducing the size of these pest populations is attributed to its ability to exploit alternative prey in the absence of the target pest (McClure 1986b).

Recent research in producing a homozygous flightless strain of *H. axyridis* by chemical mutagens has been successful in France (Tournaire et al. 2000). These adults could be used as biocontrol agents as they would not disperse from the release site. When released for the biocontrol of *A. gossypii* in a greenhouse in France, these adults remained on the plant in higher numbers and laid eggs for longer duration than normal adults, but their progeny were less numerous (Ferran et al. 1998). They were also effective against *A. gossypii* in courgettes (*Cucurbita pepo* L., small green marrow eaten as vegetable), aubergines (*Solanum melongena* L.), strawberries (*Fragaria virginiana*) and daisy (*Gerbera jamesonii*) (Bourgeois 2000).

Non-target effects and frugivory

Exotic ladybirds sometimes create adverse ecological effects in habitats they invade and. *H. axyridis* is no exception. A risk assessment of *H. axyridis* to the monarch butterfly (*Danaus plexippus* L.) population revealed that the risk of exposure is low to moderate, meaning that butterfly populations are likely to be reduced somewhat, but not driven to extinction (Koch et al. 2004b). Cage studies indicate that *H. axyridis* will feed on *D. plexippus* larvae in the presence of the aphid, *Aphis nerii* Boy. However, the presence of *A. nerii* lessens the severity of predation on *D. plexippu*s, suggesting a case of 'apparent mutualism' (Koch et al. 2005). A reduction in the per capita predation of a prey species when an alternate prey species is present (Holt 1977).

Harmonia axyridis exhibited potential pest status on autumn-ripening fruit. In autumn, it has been observed feeding on pumpkins, apples, grapes, and raspberries in Minnesota, USA (Koch & Hutchison 2003; Koch et al. 2004c; Kovach 2004). It preferred to eat damaged fruits over undamaged ones and has been reported to damage only raspberries (Koch et al. 2004c). In autumn, it seems that *H. axyridis* is an opportunist, taking advantage of fruit previously damaged by other agents. Its frugivorous habit is largely due to a shortage of aphids. It has also become a significant pest of fall ripening fruit in Minnesota and the Midwestern United States, including infestations in grapes (Anonymous 2004). Live or dead ladybirds, crushed with grapes during the wine-making process, create an unpleasant odour and taste. Economic consequences of this pest include complete losses to growers, or increased costs from additional time and labour needed to wash and process grapes before juicing (Anonymous 2004). Although *H. axyridi*s can cause direct yield loss to grapes, they are primarily a problem at harvest because of their impact on wine quality. They exude a defense compound that can give wine an unpleasant odour. They primarily feed on damaged grapes but may also occasionally feed on damage-free grapes. In fact AzaDirect and Neemix (azadirachtin) have been recommended to kill/repel *H. axyridi*s from fruit orchards (Anonymous 2005).

The fruit-feeding behaviour of *H. axyridis* may be a strategy for attaining simple carbohydrates before overwintering. *Harmonia axyridis* exhibit a strong preference for sugar water compared with water alone (Koch et al. 2004c). This preference for sugar water indicates that *H. axyridis* is not just looking for moisture in autumn but that it is seeking simple carbohydrates.

Conclusion

The information reviewed clearly indicates that *H. axyridis* is highly invasive and now dominates the aphidophaga of North America. Its successful establishment is largely attributed to its polyphagy, wide host range of aphids, and ability to feed on damaged fruits. Its wide prey range has encouraged biocontrol practitioners to use it on a number of phytophagous pests. It has rapidly become established in North America and Europe and its establishment could be considered as beneficial. Thus, its augmentative releases for aphid control is suggested. However, the aggregation of adults and instances of human biting and allergies in the United States is an issue of concern.

The status of *H. axyridis*, whether it is a potential biocontrol agent or a pest, is still debatable (due to the increasing evidence of its negative effects on non-target beneficial fauna, over aggregation, human biting and its negative impact to fruit industries, especially grapes). The unintended adverse ecological effects on native beneficial species might be attributed to its lack of dietary specificity. Its high reproductive capacity and adaptation to a broad range of climates, properties of a good biocontrol agent, may be turning into a curse rather than a blessing. Its population is becoming unmanageable. A cost and benefit analysis of *H. axyridis* is suggested. Risk analysis could be used as a tool to weigh its beneficial impacts against adverse ones.

Comparative studies on foraging, predation and reproduction of *H. axyridis* with other aphidophaga are needed to assess the reasons for its dominance among other aphidophaga. A comparison of reproductive and intrinsic growth rates is suggested. Effects of aging and senescence on reproductive potential and performance need to be assessed. Its field releases in tropical countries like India should be encouraged; however, only after a thorough analysis of the cost and benefit of beneficial and non-target fauna.

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