

Comparative demography of the exotic *Harmonia axyridis* with other aphidophagous coccinellids reared on artificial diet

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Abstract – The objective of this work was to compare biological aspects and life table parameters of the coccinellids *Harmonia axyridis*, *Cycloneda sanguinea* and *Hippodamia convergens*. Insects were fed eggs of *Anagasta kuehniella*, and reared at $24.5 \pm 1^\circ\text{C}$, $70 \pm 10\%$ relative humidity, with a 12-hour photophase. *Hippodamia convergens* took about 1.6-day to complete development, longer than *H. axyridis*, and 2.4-day longer than *C. sanguinea*. At immature stages, *H. axyridis* exhibited the highest survival percentage (49.2%), in comparison to the other coccinellids. For mean adult longevity, *H. convergens* was deficient, in comparison with the other species. Mean period of pre-oviposition was the longest in *C. sanguinea*; the longest oviposition time occurred for *H. axyridis*; and the post-oviposition period was similar between the coccinellids. Considering the reproductive parameters, *H. axyridis* showed the best performance in all aspects. For life table, the values of *H. convergens* were higher than, although close, to those of *H. axyridis*. Nevertheless, the high net reproductive rate of *H. axyridis* showed this species potential to increase population size. The biological characteristics of the exotic *H. axyridis* favors its invasion and establishment in Brazil, corroborating results noticed in other countries.

Index terms: *Cycloneda sanguinea*, *Hippodamia convergens*, biological control, developmental stages, invasive species, life table.

Demografia comparativa da exótica *Harmonia axyridis* com outros coccinelídeos afidófagos criados com dieta artificial

Resumo – O objetivo deste trabalho foi comparar aspectos biológicos e parâmetros da tabela de vida dos coccinelídeos *Harmonia axyridis*, *Cycloneda sanguinea* e *Hippodamia convergens*. Os insetos foram alimentados com ovos de *Anagasta kuehniella* e criados a $24,5 \pm 1^\circ\text{C}$, à umidade relativa de $70 \pm 10\%$, com fotofase de 12 horas. Para completar o desenvolvimento, *H. convergens* levou aproximadamente 1,6 dia a mais do que *H. axyridis*, e 2,4 dias a mais do que *C. sanguinea*. Nos estágios iniciais, *H. axyridis* apresentou a maior percentagem de sobrevivência (49,2%), em comparação aos outros coccinelídeos. Quanto à longevidade média de adultos, *H. convergens* foi deficiente, em comparação às outras espécies. A média do período de pré-oviposição foi mais longo em *C. sanguinea*; o tempo de oviposição mais longo ocorreu em *H. axyridis*; e o período de pós-oviposição foi similar entre os coccinelídeos. Considerando-se os parâmetros reprodutivos, *H. axyridis* apresentou a melhor performance em todos os aspectos. Quanto à tabela de vida, os valores de *H. convergens* foram mais altos, embora aproximados dos de *H. axyridis*. No entanto, a alta taxa líquida de reprodução de *H. axyridis* mostrou o potencial desta espécie para aumentar o tamanho populacional. As características biológicas de *H. axyridis* favorecem a invasão e o estabelecimento dessa espécie exótica no Brasil, o que corrobora os resultados observados em outros países.

Termos para indexação: *Cycloneda sanguinea*, *Hippodamia convergens*, controle biológico, fases de desenvolvimento, espécie invasora, tabela de vida.

Introduction

The Coccinellidae family (Coleoptera) is of great economic and ecological importance, due principally to the predatory habit exhibited by the majority of them. There is a substantial variety of consumed prey,

but coccinellids feed on mostly aphids and coccids (Hemiptera) (Almeida & Ribeiro-Costa, 2009). Many coccinellids prey on pests of agricultural concern and are well-known biological control agents with various successful cases described in the literature (Roy & Migeon, 2010).

Harmonia axyridis (Pallas 1773) (Coleoptera: Coccinellidae), originally from Central Asia, has been introduced in many countries for the control of aphids and other insect pests, but recent reports indicate that the species has caused serious problems for the native insect community (Vilcinskis et al., 2013). Despite the benefits it offers as a biological control agent, *H. axyridis* is perhaps better known for its adverse impacts. Koch & Galvan (2008) reviewed the North American experience with *H. axyridis*, focusing on these adverse impacts, which have been arranged into three general categories: on non-target arthropods, on fruit production, and impacts as a household invader.

In the Americas, *H. axyridis* was introduced in 1916 in California. However, in the 1970s and 1980s, introductions of this species were carried out more often in other parts of the United States and Canada, and later in Mexico (Koch et al., 2006). In South America, it was introduced intentionally in Mendoza, Argentina, at the end of the 1990s, for aphid control; and in 2001, its presence was recorded in Buenos Aires (Saini, 2004). In Brazil, this coccinellid was detected for the first time in Curitiba, PR, in April 2002, feeding on the aphid *Tinocallis kahawaluokalani* (Kirkaldy, 1907) (Hemiptera: Aphididae) (Almeida & Silva, 2002). Since then, *H. axyridis* has been found in various municipalities, in the states of the Central-West, Southeast and South regions of the country (Milléo et al., 2008; Martins et al., 2009; Bernardi et al., 2010; Koch et al., 2011). More recently, it was recorded in other South American countries including Chile (Grez et al., 2010), Uruguay (Nedved & Krejčík, 2010), Colombia (Amat-García et al., 2011), Peru (Iannacone & Perla, 2011) and Ecuador (González & Kondo, 2012).

The interest on studying this insect has been due to many reasons, such as its efficiency in the control of aphids, its high capacity of dissemination in different habitats, and its effect on intraguild interactions. Its relatively large size, aggressive behavior, extreme polyphagy, and effective strategies of physical and chemical defense make *H. axyridis* an exceptional predator and competitor (Pell et al., 2008).

Hippodamia axyridis impacts other species indirectly through competition, and directly through intraguild predation. Performed surveys in different areas around the world indicate increases of *H. axyridis* and decreases of native species (Milléo et al., 2008;

Martins et al., 2009; Almeida & Ribeiro-Costa, 2009; Bernardi et al., 2010).

Cycloneda sanguinea (Linnaeus, 1763) and *Hippodamia convergens* Guerin-Meneville, 1842 (Coleoptera: Coccinellidae), are native to the Nearctic and Neotropical regions and play an important role as generalist predators of hemipterans. Before the recording of *H. axyridis* in Brazil, these species were abundant in surveys of insects associated with aphids in the country (Mendes et al., 2000; Michelotto et al., 2003; Guerreiro et al., 2005).

A better understanding of the coexistence mechanisms between *H. axyridis* and native coccinellids is essential to reduce possible negative effects on native species (Pell et al., 2008; Meisner et al., 2011). Proposals by Pell et al. (2008) suggest that pest management strategies, aimed at maintaining predator diversity through habitat manipulation, and the diversification of our agricultural landscapes could help decline predator diversity associated with the arrival of *H. axyridis*.

Accordingly, comparative analysis of the performance of an exotic species in relation to local species provides information on species potential population growth and mechanisms of intraguild competition. For this reason, *H. axyridis* has been the subject of extensive research in Europe and North America (Koch, 2003; Lanzoni et al., 2004; Koch et al., 2006; Koch & Galvan, 2008). However, Brazil lacks studies on the interaction of *H. axyridis* with local fauna, including the guild of predatory insects. Studies involving demographic parameters, such as those obtained by designing life tables are thus of utmost importance for the knowledge of introduced species potential, mainly with respect to their ability to compete, to prey and even to exclude other species.

The objective of this work was to compare biological aspects and life table parameters of the coccinellids *Harmonia axyridis*, *Cycloneda sanguinea* and *Hippodamia convergens*.

Materials and Methods

Adults of the three species of Coccinellini (*C. sanguinea*, *H. axyridis*, and *H. convergens*) were collected in March 2012 on sorghum [*Sorghum bicolor* (L.) Moench.], at Fazenda Areão, (22° 42'30"S, 47° 30'00"W), an area close to the Campus of the

Escola Superior de Agricultura Luiz de Queiroz (Esalq), Piracicaba, SP, Brazil.

After collection, the insects were transported to the Laboratório de Ecologia de Insetos (Esalq), where the species were separated into couples. Each couple was stored in 9 cm Petri dishes, in moistened cotton with a honey-water solution (50%), and daily fed ad libitum with frozen eggs of *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae). The alternative diet was chosen, due to the positive results obtained by Kato et al. (1999) for *H. convergens* and by Santos et al. (2009) for *H. axyridis*, as well as the ease of obtaining and their neutrality in preference for the three coccinellids, since in the field these species are not fed with this diet.

Breeding stock was maintained in an acclimatized room at $24.5 \pm 1^\circ\text{C}$, $70 \pm 10\%$ relative humidity, and 12-hour photophase. Petri dishes were changed every 48 hours, and the observations were made daily. The trials were conducted according to availability of species. From the second generation, 10 couples of each species were formed (10 replicates per species), with adults selected from different maternal lines to avoid consanguinity. Each couple was kept in a 9 cm Petri dish and daily fed ad libitum with eggs of *A. kuehniella*. The number of eggs laid per female was recorded daily until death. Egg clusters were separated daily from the adults to prevent cannibalism on the eggs. Male deaths during the experimental period were recorded, and replaced until the death of females to continue with the registry of postures.

The number of hatched larvae from these eggs was determined by analysing the viability (number of eggs hatched \times 100 / number of eggs laid) for each species. Starting with the second oviposition, larvae were randomly selected, and on alternate days, 10 recently hatched larvae of each couple (totaling 100 larvae of the 1st instar of each species = 100 replicates per species) were individualized in Petri dishes; larvae also fed ad libitum on eggs of *A. kuehniella*, and were examined daily to determine ecdyses. Deaths were recorded, and the individuals were replaced with new larvae of the 1st instar because only the larvae that reached adult age were considered for determining the development time of each stage.

The following biological variables were evaluated: period of incubation and viability of eggs; duration and viability of each instar; sex ratio (number of females in

100); longevity of adults; periods of pre-oviposition; oviposition and post-oviposition; fecundity (mean number of laid eggs per female); and fertility (mean number of viable eggs). These data were used to construct life tables.

After verification of data normality and homogeneity by the tests of Shapiro-Wilk (W) and Bartlett, respectively; means were subjected to analysis of variance and compared by Tukey's test, at 5% probability. Results showing no normal tending distribution, even after data transformation, were subjected to the nonparametric Kruskal-Wallis test, with the means of the ranked data compared at 1 or 5% probability. Analysis employed the R 2.13.1 statistical program (R Development Core Team, 2011).

The fertility in the life table was calculated using the TabVida computational system (Penteado et al., 2010) as follows: specific fertility (m_x = number of descendent produced per female at age x and that result in females); survival rate (l_x = life expectancy to age x , expressed as fraction of an initial population of one female); net reproductive rate [$R_o = \sum (m_x l_x)$]; time interval between each generation [$T = (\sum m_x l_x x) / \sum (m_x l_x)$]; innate capacity for increase in numbers ($r_m = \log R_o / T$); finite ratio of population increase ($\lambda = e^{r_m}$); and population doubling time [$TD = \log(2) / r_m$].

Results and Discussion

The development periods (egg–adult) differed between the three species (Table 1). To complete its development, *H. convergens* took about 1.6-day longer than *H. axyridis* and 2.4-day longer than *C. sanguinea*. In general, *H. convergens* had the longest larval stage compared to the other species. Significant differences were found for the incubation period, 1st instar, 2nd instar, 3rd instar and 4th instar. However, there was a longer pre-pupal period in *C. sanguinea* and longer pupal period in *H. axyridis*.

The highest percentage of females was shown by *H. axyridis* (54%), followed by *H. convergens* (50%) and *C. sanguinea* (48%). This result is advantageous for *H. axyridis* because it causes indirectly increase in the prole.

Cardoso & Lázari (2003) researched *C. sanguinea* feeding of *Cinara* spp. at 25°C , and found a longer incubation period of 4 days, in comparison with 3.20

days in this study. In the current study, the larval stage duration (9.26 days) was longer than those reported by Cardoso & Lázari (2003) (8.6 days) and Santa-Cecilia et al. (2001) (males 8.2 days, and females 8.5 days) for *C. sanguinea* feeding on *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) at 25°C. In this species, a longer pupal period was observed by Cardoso & Lázari (2003) (4.7 days), but the authors did not make reference to the pre-pupal period, which was probably included in this count. Santa-Cecilia et al. (2001) obtained a shorter time for pupal stage, 3.0 days for both sexes, in comparison to 3.77 days in the present study. Despite the small differences between the duration of each stage, the egg–adult time (17.40 days) was close to the 17.5 days found by Cardoso & Lázari (2003) for *C. sanguinea* kept at 25°C.

Embryonic development of 2.97 days for *H. axyridis* was similar to that obtained by Abdel-Salam & Abdel-Baky (2001) with species feeding on *Sitotroga cerealella* fresh and frozen grain moth eggs at 27±1°C, 75±5% relative humidity, and 16:8-hour photophase (2.8 to 3.1 days). Also, embryonic development obtained in the present work was similar to that observed by Lanzoni et al. (2004) (2.8 days) for *H. axyridis* feeding on *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) at 25±1°C, 60-80% relative humidity, and 16:8-hour photophase, but less than the 3.4 days reported by Castro et al. (2011), for *H. axyridis* feeding on *Cinara atlantica* (Wilson) (Hemiptera: Aphididae) at 25±1°C, 70±10% relative humidity, and 12-hour photophase. The duration of the larval period of this species (9.38 days) was lesser than that reported by other authors:

10.1 days, Santos et al. (2009), 10.5 days, Lanzoni et al. (2004); between 11.2 and 13.4 days, Abdel-Salam & Abdel-Baky (2001); and 13.1 days, Castro et al. (2011). *Harmonia axyridis* remained pupated for 4.75 days, close to the period found by Santos et al. (2009) for this species feeding on *A. kuehniella* eggs at 27°C (4.1 days), Castro et al. (2011) (4.7 days), and Abdel-Salam & Abdel-Baky (2001) (4.9 to 6.0 days), but lesser than the 6.6 days reported by Lanzoni et al. (2004), who added the pre-pupal period. The value of 18.19 days, obtained for the egg–adult cycle, is close to the results by Abdel-Salam & Abdel-Baky (2001) (18.9 to 22.5 days), and by Lanzoni et al. (2004) (19.8 days), and lesser than the value obtained by Castro et al. (2011) (22.3 days). The sex ratio (54%) of *H. axyridis* was higher than that observed by Lanzoni et al. (2004) which was 39%.

Embryonic period of 3.21 days of *H. convergens* coincided with that found by Kato et al. (1999) in *A. kuehniella* at 25°C (3.1 days). Larval stage duration of *H. convergens* (11.02 days) was approximately the same as the results by Cardoso & Lázari (2003) at 25°C (10.9 days), and shorter than that reported by Kato et al. (1999) (13.7 days). The duration of 4.48 days for the pupal period was similar to the 4.5 days obtained by Kato et al. (1999), and shorter compared to the 6.3 days determined by Cardoso & Lázari (2003), who added to this time the pre-pupal stage. *Hippodamia convergens* sex ratio (50%) was lower than the 60% proportion found by Kato et al. (1999).

First and second instar larvae, which were more prone to intraguild predation attack and cannibalism, showed a slow development which was injurious for *H. convergens*, in comparison to the other species. With respect to biological control, Lanzoni et al. (2004) considered the advantage of the longer duration of the 4th instar because, in this phase, the Coccinellini show high predatory activity. The authors obtained a higher value for *H. axyridis* than for *H. variegata* and *A. bipunctata*, unlike in the present study, which included *H. convergens*. However, the most rapid development of 1st and 2nd instar larvae of *H. axyridis* was found in both studies, which can be a positive factor for the species, since in the early stages larvae are more subject to predation.

Harmonia axyridis (49.2%) exhibited the highest percentage for mortality rate, followed by *H. convergens* (49.0%), and *C. sanguinea* (42.0%).

Table 1. Development periods (days) of *Cycloneda sanguinea*, *Harmonia axyridis*, and *Hippodamia convergens* feeding on eggs of *Anagasta kuehniella*, at 24.5±1°C, 70±10% relative humidity, and 12-hour photophase (mean±standard deviation)⁽¹⁾.

Stage	<i>C. sanguinea</i>	<i>H. axyridis</i>	<i>H. convergens</i>	Chi-squared	p-value
Egg	3.20±0.20b	2.97±0.08c	3.21±0.15a	22.26	0.01
1 st instar	2.88±0.31b	2.64±0.19c	3.26±0.16a	39.10	0.01
2 nd instar	1.80±0.20c	1.83±0.11b	2.11±0.08a	20.91	0.01
3 rd instar	1.98±0.06b	1.97±0.07c	2.35±0.11a	40.52	0.01
4 th instar	2.60±0.08c	2.94±0.29b	3.30±0.14a	55.84	0.01
Pre-pupal	1.17±0.08a	1.09±0.09b	1.07±0.03c	7.04	0.05
Pupal	3.77±0.03c	4.75±0.12a	4.48±0.11b	123.05	0.01
Egg–dult	17.40±0.24c	18.19±0.44b	19.78±0.25a	142.70	0.01

⁽¹⁾Means followed by equal letters in the lines do not differ by the t test, at 1 or 5% probability.

This highest rate in the three species corresponded to a high number of nonviable eggs (Figure 1). Regarding the survival of immature stages, two factors contributed to the high embryonic mortality rate in the present study, which are: cannibalism by larvae that hatched earlier; and the high percentage of infertile eggs laid by longer-living females, mainly among *H. axyridis*. The low percentage of survival, due to low viability of eggs, was also observed by Lanzoni et al. (2004) in evaluating *H. axyridis*, *H. variegata* and *A. bipunctata*.

Cardoso & Lázari (2003) followed the development of 20 eggs of *C. sanguinea*, at 25°C, and found a high viability of 93.3%, in comparison with 55.2% in the present study. For *H. axyridis*, a viability of 52.4% was similar to 53.0% as reported by Lanzoni et al. (2004) in 42 eggs, and less than the 90.7% found by Castro et al. (2011) at 25°C. Among the three evaluated species, *H. convergens* exhibited the best performance for viability, at 65.4%, which was lower than the value (86.3%) found by Kato et al. (1999) in *A. kuehniella*.

Few studies emphasize egg–adult survival. In the present study, egg–adult survival for *C. sanguinea* (42.0%) was lower than that described by Cardoso & Lázari (2003) of 78.3% at 25°C; and in *H. Axyridis*, the rate of 49.2% was similar to the 49.4% rate found by Lanzoni et al. (2004), but lower than the results by Abdel-Salam & Abdel-Baky (2001), which were

between 84 to 80%, and by Castro et al. (2011) which was 90.7%.

Regarding the mean longevity of adults, *H. convergens* appeared deficient in comparison with the other species, and no significant difference was observed between lifespan of females of *C. sanguinea* and *H. axyridis* (Table 2). However, for males, lifespan was longer in *H. axyridis*, followed by *C. sanguinea* and *H. convergens*.

The mean period of pre-oviposition was the longest in *C. sanguinea*, and similar for *H. axyridis* and *H. convergens*. *H. axyridis* had the longest oviposition time, and the result for *C. sanguinea* was statistically similar as that of the two other species. The post-oviposition period was similar between the coccinellids.

Considering the reproductive parameters, *H. axyridis* showed the best performance in all aspects. For fecundity, the number of eggs laid by *H. convergens* was statistically similar to that of *C. sanguinea*. Taking into account the number of viable eggs, *H. convergens* and *C. sanguinea* had similar results; and for the number of eggs per oviposition, *H. convergens* superseded *C. sanguinea* (Table 2).

Cardoso & Lázari (2003) observed that adults of *C. sanguinea* had longevity of 167.1 days when kept at 20°C and, despite the difference in temperature, these results are close to the values of 147.0 (females) and 162.8 days (males) found in the present study.

Adults of *H. axyridis* lived a mean of 148.9 (females) and 220.3 days (males); these values were much higher than those reported by the following authors: Lanzoni et al. (2004), who observed that the lowest longevity was 44 days; by Abdel-Salam & Abdel-Baky (2001), who found 43.9 (fresh eggs) and 62.2 days (frozen eggs); by Castro et al. (2011) with 89.1 days; and by Santos et al. (2009), who observed variations between 74.1 and 76.2 days (females), and 67.3 and 70.3 days (males), at 27°C. This long life time made the oviposition period (129.9 days) longer than that found by Lanzoni et al. (2004) (13.7 days), Abdel-Salam & Abdel-Baky (2001) (45.3 to 49.0 days), Santos et al. (2009) (47.3 days), and Castro et al. (2011) (76.87 days).

The pre-oviposition period (9.4 days) was similar to the results observed by Abdel-Salam & Abdel-Baky (2001) (between 8.1 and 9.5 days), and Santos et al. (2009) (9.8 days), but longer than the 7.4 days observed by Lanzoni et al. (2004), and 5.8 days by Castro et al.

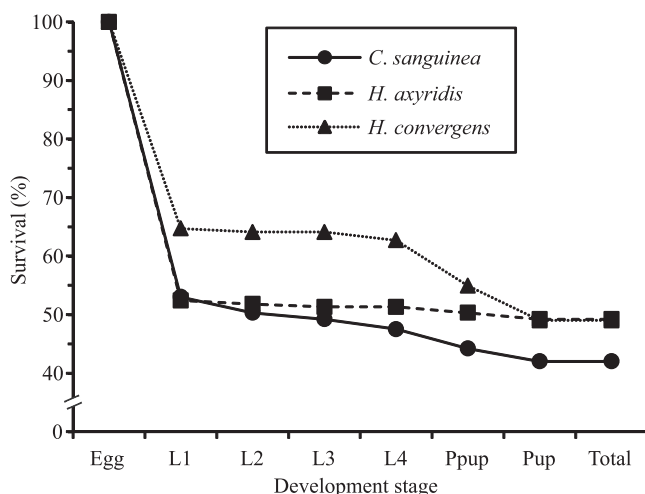


Figure 1. Survival rate of immature stages of *Cycloneda sanguinea*, *Harmonia axyridis*, and *Hippodamia convergens* fed eggs of *Anagasta kuehniella*, at 24.5±1°C, 70±10% relative humidity, and 12-hour photophase.

(2011). The post-oviposition period of 9.8 days was about the same as that of 10.8 days found by Castro et al. (2011), shorter compared to the results of Santos et al. (2009) (17.0 days), and longer than that of 5.1 to 6.8 days reported by Abdel-Salam & Abdel-Baky (2001). This long oviposition period directly influenced fecundity of females that oviposited a mean of 4,453.5 eggs, a much higher number than that reported by Lanzoni et al. (2004) (560.5), Castro et al. (2011) (614.0), Abdel-Salam & Abdel-Baky (2001) (606.6 to 715.3), and Santos et al. (2009) (887.6). A mean of 48.79 eggs per oviposition was determined, which is higher than the value observed by 18.5 of Castro et al. (2011).

Hippodamia convergens females had longevity of 89.4 days, and the males had 63.2 days; these values were coincident with those observed by Kato et al. (1999), who found a mean longevity of 88.9 days for adults fed *A. kuehniella*. Pre-oviposition and oviposition periods, 12.2 and 72.1 days were close to those obtained by Kato et al. (1999), which were 12.8 and 68.8 days; but a post-oviposition of 5.1 days was shorter than that of 11.1 days found by the same authors. The number of eggs per oviposition (27.62) of *H. convergens* was higher than the value of 11.0 eggs reported by Kato et al. (1999) for feeding with *A. kuehniella*.

The rate survival (l_x) of *C. sanguinea* stayed the same up to the 96th day, when other deaths gradually occurred after a prolonged oviposition period, and the last individual died on the 201th day (Figure 2 A). The oviposition period occurred between the 17th and the

173th day with a peak on the 42th day (22.1 eggs). The highest values of specific fertility (m_x) were observed from the 29th to the 81st day, when a gradual decrease occurred up to the last oviposition, except for the 114th day with m_x of 5.88.

Harmonia axyridis had a survival rate constant (l_x) up to the 85th day, with a gradual decrease up to the 214th day, followed by a sudden decline, showing again a decrease up to the 242nd day. The oviposition period occurred between the 10th and the 197th day, with a peak on the 35th day (81.7 eggs). Specific fertility (m_x) was the highest on the 15th to the 98th day, which afterwards markedly declined (Figure 2 B). For Castro et al. (2011), *H. axyridis* (feeding *C. atlantica* at 25°C) found l_x constant up to the 59th day, and the last individual died at the 124th day. These insects laid eggs from the 4th to the 118th days with high m_x from the 7th to the 34th days. Abdel-Salam & Abdel-Baky (2001) evaluated the life table parameters of *H. axyridis*, comparing results among insects when feeding on fresh and frozen eggs of grain moth (*S. cerealella*). These authors obtained l_x constant until the 34th and 30th days, the last individuals died after the 52th and 49th days in fresh and frozen eggs, respectively. Pre-oviposition period observed by Abdel-Salam & Abdel-Baky (2001) was of 8.1 to 9.5 days; thereafter *H. axyridis* remained laying eggs until almost to the death of individuals, and the higher m_x found was 18.44 (2nd day of oviposition) and 17.44 (8th day of oviposition) for fresh and frozen eggs, respectively.

The survival rate (l_x) recorded for *H. convergens* remained constant up to the 44th day and, then,

Table 2. Biological periods, longevity (days), and reproductive parameters in adults of *Cycloneda sanguinea*, *Harmonia axyridis*, and *Hippodamia convergens* feeding on eggs of *Anagasta kuehniella*, at 24.5±1°C, 70±10% relative humidity, and 12-hour photophase (mean±standard deviation)⁽¹⁾.

Parameter	<i>C. sanguinea</i>	<i>H. axyridis</i>	<i>H. convergens</i>	Test F	Test χ^2	p-value
Longevity						
Female	147.00±12.41a	148.90±6.22a	89.40±18.99b	5.79	-	0.01
Male	162.80±18.97b	220.30±3.56a	63.20±11.93c	-	25.18	0.01
Period						
Pre-oviposition	24.30±1.36a	9.50±0.42b	12.20±8.89b	-	12.73	0.01
Oviposition	108.70±14.95ab	129.90±6.95a	72.10±16.70b	5.54	-	0.01
Post-oviposition	14.00±6.85a	9.50±2.08a	5.10±3.54a	ns	ns	-
Reproductive						
Fecundity	998.00±99.40b	4453.50±301.90a	1189.40±191.74b	36.67	-	0.001
Fertility	549.90±90.70b	2340.50±114.32a	778.40±81.85b	35.11	-	0.001
Eggs/oviposition	17.94±0.34c	48.79±3.90a	27.62±2.03b	43.12	-	0.01

⁽¹⁾Means followed by equal letters in the lines do not differ by Tukey test, at 5% probability, or by the t test, at 1 or 5% probability. χ^2 , chi-squared.

decreased markedly and stabilized between the 85th and the 128th day until the death of the last individual on the 187th day. The oviposition period occurred between the 5th and the 101st day with a peak on the 30th day (33.6 eggs). The highest values of specific fertility (m_x) occurred from the 28th to the 92nd day and, in a few days females stopped ovipositing (Figure 2 C). Golizadeh & Jafari-Behi (2012) compared the performance of *Hippodamia variegata* (Goeze, 1777) feeding on three species of aphids [*Aphis gossypii* Glover, *Aphis fabae* Scopoli e *Macrosiphum rosae* (L.) (Hemiptera: Aphididae)] at 25±1°C, 65±5% relative humidity, and 16:8-hour photophase. These authors observed that aphid species significantly affect the parameters of the life table, but in all three treatments, the insects showed a decrease of l_x before they begin

to lay eggs, remaining constant for about 20 to 70 days, and then they went into gradual decline until the latter's coccinellid death (between 90 to 100 days). *H. variegata* showed oviposition period between the 20th and the 90th days with m_x higher when fed *A. fabae*. In the present study, the three coccinellids species showed a greater longevity and a larger oviposition period than the results found by other authors.

The shortest time interval between each generation (T) was found for *H. convergens* (38.34 days), followed by *C. sanguinea* (51.43 days) and *H. axyridis* (55.39 days) (Table 3). The interval between generations of *H. axyridis* was higher than those obtained by: Lanzoni et al. (2004), which was 38.81 days, when this species fed *M. persicae* at 25°C; Castro et al. (2011), which was 39.48 days; and by Abdel-Salam & Abdel-Baky (2001), between 37.87 at 45.04 days, for fresh and frozen eggs of *S. cerealella*, respectively. An intermediate value was obtained, when comparing the "T" of *H. convergens* (38.34 days) with certain results of *H. variegata* when fed aphids. Lanzoni et al. (2004) registered 41.88 days, and Golizadeh & Jafari-Behi (2012) reported values between 30.23 and 33.37 days, according to the consumed aphid.

Castro et al. (2011) noted that *H. axyridis* in Brazil is a multivoltine species, which means that it shows several generations per year, depending on the region where it is located. Thus, temperature and type of food are factors that are influencing the interval between each generation in this insect.

The longer life cycle was compensated in the species *H. axyridis* by the high net reproductive rate (R_0) of 2,226.89, which is about five times greater than that of *H. convergens* and *C. sanguinea* (Table 3). For *H. convergens*, the value was higher than that

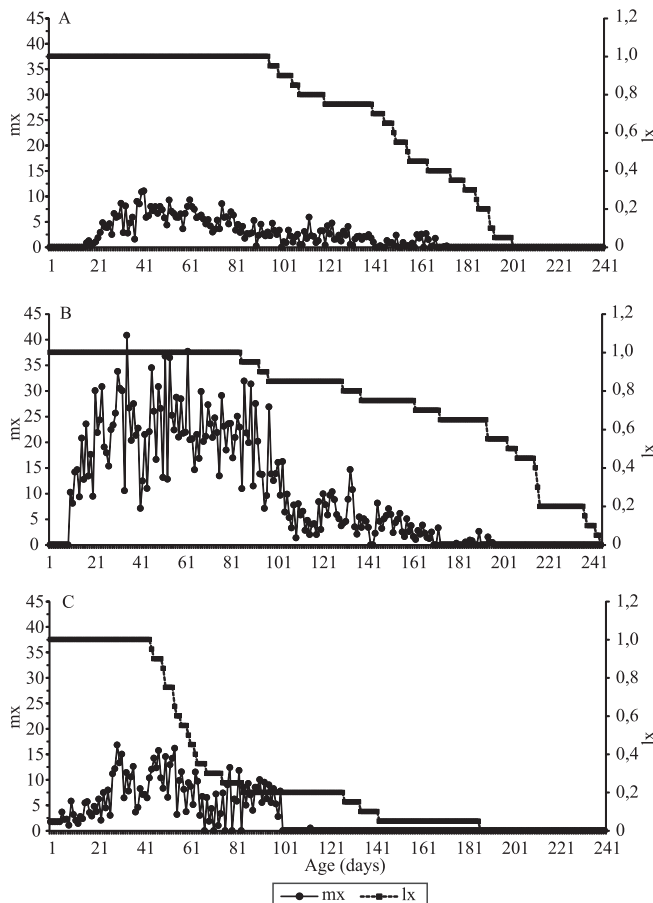


Figure 2. A, *Cycloneda sanguinea*; B, *Harmonia axyridis*; C, *Hippodamia convergens*. Specific fertility (m_x) and survival rate (l_x) of coccinellids feeding on eggs of *Anagasta kuehniella*, at 24.5±1°C, 70±10% relative humidity, and 12-hour photophase.

Table 3. Estimated life Table parameters of *Cycloneda sanguinea*, *Harmonia axyridis*, and *Hippodamia convergens* feeding on eggs of *Anagasta kuehniella*, at 24.5±1°C, 70±10% relative humidity, and 12-hour photophase.

Parameter ⁽¹⁾	<i>C. sanguinea</i>	<i>H. axyridis</i>	<i>H. convergens</i>
T	51.43	55.49	38.34
R_0	499.00	2226.89	450.15
r_m	0.12	0.13	0.16
λ	1.1283	1.1490	1.1727
TD	5.73	4.99	4.35

⁽¹⁾T, time interval between each generation; R_0 , net reproductive rate; r_m , innate capacity to increase in numbers; λ , finite ratio of population increase; TD, population doubling time.

obtained for *H. variegata* by Lanzoni et al. (2004) of 52.75, and by Golizadeh & Jafari-Behi (2012), which was varying between 183.23 and 236.54. *H. axyridis*, in this present study, showed a very high value in relation to those by: Lanzoni et al. (2004), 26.27; Castro et al. (2011), of 278.03; and Abdel-Salam & Abdel-Baky (2001), between 234.96 at 289.11. Although only one generation of laboratory has been monitored, the high value of R_0 obtained by exotic species shows that this insect had a rapid adaptation to diet of *A. kuehniella* eggs, and that its potential for population increase is much higher than those of the other coccinellids.

Cycloneda sanguinea and *H. axyridis* displayed close values of intrinsic growth rate (r_m), 0.12 and 0.13, respectively; while a higher value (0.16) was shown by *H. convergens* (Table 3). This indicates that although the predator survives, grows, and reproduces with an alternative diet of *A. kuehniella* eggs, it has a limited population growth when receives a natural diet. The intrinsic rate increase of *H. axyridis* was higher than that found by Lanzoni et al. (2004) which was 0.09, and it approximates the results by Abdel-Salam & Abdel-Baky (2001), which were between 0.12 at 0.15 for fresh and frozen eggs of *S. cerealella*, respectively, and by Castro et al. (2011), which was 0.14 at 25°C. The r_m of 0.16 for *H. convergens* was superior to the results obtained by Lanzoni et al. (2004) for *H. variegata* (0.114), and approximates the values recorded for Golizadeh & Jafari-Behi (2012) (0.156 a 0.183).

According Southwood & Henderson (2000), from the life table parameters, the intrinsic rate of increase is the most useful one to compare the potential population growth, under specific conditions of temperature and food, and reflects the overall effects of predation on the development, reproduction characteristics, and survival of a population. According to Andrewartha & Birch (1954), the higher the value of r_m , more effective will be the species in a certain environment. In this study, *H. convergens* showed to be more successful when fed *A. kuehniella* eggs under the conditions of temperature, relative humidity and constant photophase.

The higher finite ratio of population increase (λ) indicates the number of females that are added to the population by each female. *Hippodamia convergens* had the highest values of increase, followed by *H. axyridis* and *C. sanguinea* (Table 3). To this rate, *H. axyridis* had similar value to that obtained by

Castro et al. (2011) 1.1502 at 25°C, and intermediate to the results of Abdel-Salam & Abdel-Baky (2001), from 1.166 to 1.128, for fresh and frozen eggs of *S. cerealella*, respectively. According to Golizadeh & Jafari-Behi (2012), in *H. variegata* these values varied between 1.201 and 1.198 depending on the consumed aphid; these values are close to those obtained for *H. convergens* in the present study. The λ values confirm the results of R_0 , indicating that the population of the three species increased from one generation to another and, thus, found ideal conditions for their development.

The least time needed for the population to double in number (TD) was observed for *H. convergens*, followed by *H. axyridis* and *C. sanguinea* (Table 3). Other authors found similar values to those found here for TD. Castro et al. (2011) found 4.95, and Abdel-Salam & Abdel-Baky (2001) found between 4.53 and 5.72 for *H. axyridis*; Golizadeh & Jafari-Behi (2012) found between 3.79 and 4.44 for *H. variegata*.

In general, the biological characteristics of *H. axyridis* favor the invasion and establishment of this species in Brazil, corroborating the results obtained by researchers in other countries. *Harmonia axyridis* in comparison to *H. convergens* and *C. sanguinea* showed a shorter duration of early larval stages, greater longevity of adults and, consequently, a longer oviposition period, high rates of fecundity and fertility, and a greater number of eggs per oviposition. Meanwhile, other results such as duration of 4th instar, survival percentage of immatures, and shorter pre-oviposition period were similar to those shown for *H. convergens*.

Life table of fertility showed that *H. convergens* had higher values, although close, to those of *H. axyridis*, except for the high value for the net reproductive rate (R_0) of *H. axyridis*, showing that the potential for population increase of the invasive species was very high in comparison with the other two evaluated species. *Cycloneda sanguinea* has fragility when compared to *H. axyridis* and *H. convergens*. The nutritional quality of the alternative diet might have affected the performance of *C. sanguinea*.

Conclusion

The greatest longevity, the longest oviposition period, and the greatest number of eggs and viability of instars of the exotic *Harmonia axyridis* are very

important characteristics which increased the net reproduction rate, which brings benefits for this species population, in comparison to *Hippodamia convergens* and *Cycloneda sanguinea*.

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