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LIFE TABLE ANALYSIS AND CONSUMPTION CAPACITY FOR HARMONIA AXYRIDIS (COLEOPTERA: COCCINELLIDAE), FEEDING ON CINARA ATLANTICA (HEMIPTERA: APHIDIDAE)

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Abstract

The objective of this study was to analyze the development, reproductive parameters and consumption capacity of *Harmonia axyridis*, using *Cinara atlantica* as food. The average time of egg incubation was 3 d, duration of larval instars was 3.5, 2, 2.2 and 4.1 d, respectively, and duration of the pupal stage was 5.8 d. Longevity was 85.6 d and the life cycle lasted 107.2 d. Egg viability was 92.7% and all stages had 100% survival. Adults consumed, on average, 1.892 aphids. Pre-oviposition, oviposition and post-oviposition periods lasted 6.8, 44.3, and 32.9 d, respectively. Fertility was 633.2 eggs per female. Each instar consumed, on average, 19.4, 24.8, 49.7 and 188.9 aphids, respectively. The life table results, together with biological data, indicated that *Harmonia axyridis* is an efficient predator of *C. atlantica*, having high fertility, egg viability, rapid development and high levels of predation.

Key Words: biological control, cannibalism, Cinara atlantica, development, life table

RESUMO

O objetivo deste estudo foi analisar o desenvolvimento, os parâmetros reprodutivos e a capacidade de consumo de *Harmonia axyridis*, utilizando *Cinara atlantica* como alimento. O tempo médio de incubação dos ovos foi de 3 dias, duração dos estágios larvais foi de 3,5, 2, 2,2 e 4,1 dias, respectivamente, e a duração da fase de pupa foi de 5,8 dias. A longevidade foi de 85,6 dias e o ciclo de vida durou 107,2 dias. A viabilidade dos ovos foi de 92,7% e em todas as fases a sobrevivência foi de 100%. Os adultos consumiram, em média 1892 pulgões. Os períodos de pré-oviposição, oviposição e pós-oviposição duraram 6,8, 44,3, e 32,9 dias, respectivamente. A fertilidade foi 633,2 ovos por fêmea. Cada instar consumiu, em média, 19,4, 24,8, 49,7 e 188,9 pulgões, respectivamente. Os resultados da tabela de vida, juntamente com os dados biológicos, indicaram que *Harmonia axyridis* é um predador eficiente de *Cinara atlantica*, com alta fertilidade, viabilidade dos ovos, desenvolvimento rápido e altos níveis de predação.

Palavras Chave: controle biológico, canibalismo, Cinara atlantica, desenvolvimento, tabela de vida

Harmonia axyridis (Pallas, 1773) (Coleoptera: Coccinellidae) is an Asian species that is used in the biological control of aphid pests of pecan, alfalfa, cotton, tobacco and wheat (Burgio et al. 2002), and currently is spread around the world (Castro et al. 2011).

In South America, *H. axyridis* was introduced as biological control agent against aphids in Mendoza, Argentina at the end of the 1990's. By the end of 2001 it was detected in Buenos Aires, in association with *Monellia caryella* (Fitch) (He-

miptera: Aphididae) on pecan, *Carya illinoinensis* (Fagales: Juglandaceae) (Saini 2004).

In Brazil, *H. axyridis* was detected for the first time in 2002, in Curitiba, Parana feeding on *Tinocallis kahawaluokalani* (Kirkaldy 1907) (Hemiptera: Aphididae) adults and nymphs, which were on *Lagerstroemia indica* Linnaeus, an ornamental plant cultivated in southern Brazil (Almeida & Silva 2002). The introduction of the coccinellid in this country probably was accidental.

Harmonia axyridis is very efficient in locating aphids. Individuals of this voracious species are larger than the average aphidophagous coccinellid (Osawa 1993). As an exotic species, H. axyridis may have negative impacts on the local biodiversity, causing competitive suppression, displacement of natural enemies of aphids, and the extinction of non-target species, some of which are beneficial (Elliott et al. 1996). Despite its advantages as a biological control agent, particularly aphids, this coccinellid has the capacity to rapidly colonize large areas. After dispersing through flight or in commercial cargos, it is able to colonize large areas and to displace native coccinellids, becoming dominant in the aphidophagous guild (Adriaens et al. 2003; Koch et al. 2006).

Since the detection of *H. axyridis* in Brazil in 2002, there have been few efforts to study the biology of the species in the country. Martins et al. (2009) studied population fluctuations, tritrophic interactions, and the occurrence and abundance of this exotic coccinellid, which they compared with other, well established species. According to their results, the invasive coccinellid competes strongly with *Cycloneda sanguinea* (L., 1763) (Coccinellidae), a common species in Southern Brazil. Martins et al. (2009) also found that the introduction of *H. axyridis* was associated with a reduction in the abundance and diversity of native and established coccinellids, suggesting that the latter species are displaced by *H. axyridis*.

The aphids of the genus *Cinara* Curtis are important pests of conifers in several countries. In Brazil, the giant conifer aphid, *Cinara atlantica* (Wilson, 1919) has damaged commercial plantations of *Pinus* spp. and biological control with predators can be a better option than chemical control (Zaleski et al. 2005).

Castro et al. (2011) evaluated the impact of temperature on the biological and life table parameters of *H. axyridis*. They observed that, on a diet of *Cinara atlantica* (Wilson, 1919) (Hemiptera: Aphididae), *H. axyridis* is able to survive, develop and reproduce at 15 °C, 20 °C and 25 °C. They observed even faster development and better results on the fertility and life tables at 25 °C. The fertility and life table results, together with biological data, indicated that *H. axyridis* is a potential biological agent against *C. atlantica*.

In view of the recent introduction of *H. axyridis* in Brazil, as well as the occurrence of the *C. atlantica* in areas reforested with *Pinus* spp., we aimed to study the biology, behavior, reproductive parameters and consumption capacity of *H. axyridis*, in order to verify its potential as a biological control agent.

MATERIALS AND METHODS

In order to maintain a stock population of aphids to study coccinellid biology, C. atlantica

aphids were collected from *Pinus* sp. in Curitiba, Paraná, Brazil, and were taken to the laboratory of the Entomology Department, Embrapa Florestas, where they were maintained at 21° C \pm 1° C, 70% \pm 10% RH and 24 h photoperiod. Aphids were removed from the pine needles with the help of a brush and were transferred to young pines obtained from a commercial nursery. Additional aphids were further introduced to maintain the stock population. Aphids offered to the predators were counted every 24 h in order to estimate food intake, and were replaced so that there was always plenty of food available for the experimental coccinellids.

Adult *H. axvridis* were collected in Curitiba. Paraná, Brazil from Pinus sp., in Sep 2007. They were taken to the laboratory and reared in 500 ml plastic containers in brood chambers (BOD) at 24° C \pm 1° C, 70% \pm 10% RH and 12:12 h L:D. In order to maintain the coccinellid stock population, aphids (*C. atlantica*) were offered daily. Adults were sexed based on the methodology of McCornack et al. (2007), and their eggs were transferred to Petri dishes with moistened filter paper for biological studies. The containers used for rearing were changed every 48 h and observed daily. The egg masses were maintained under the same conditions. After hatching, larvae were placed in Petri dishes lined with filter paper and a drop of honey. Aphids were separated into size groups before they were offered to the coccinellids, i.e., small nymphs (1st and 2nd instars), and medium nymphs (3rd and 4th instars) and adults.

During pupation, the coccinellids were kept under the same temperature and humidity conditions. In order to determine the duration of the pupal period, and to assess adult longevity and aphid consumption, observations were made daily. Furthermore, egg viability, mortality rates for each larval instar and for the pupal stage, and adult survival were also calculated.

In experiments on reproduction, 10 females of *H. axyridis* were used in each replicate. In consumption experiment, 10 individuals of *H. axyridis* were used, randomly, and in predation and cannibalism experiments, 10 *H. axyridis* individuals were used for each diet, randomly. All experiments were conducted with a total of 10 replicates.

Statistical Analysis

The arithmetic means and standard deviations were calculated for statistical analysis. The population growth parameters were calculated using the Tabvida computational system (Penteado et al. 2010). The life parameters evaluated were: net reproductive rate (Ro: Σ (m,l,)); time interval between generations (T: Σ (m,l,)); intrinsic rate of increase (r,: In Ro/T); the finite rate of population increase (λ : e'm) and popula-

tion doubling time (DT: In $(2)/r_m$), where x = age interval in which the sample was taken, $m_x = spe$ cific fertility, and $l_x = survival$ rate.

RESULTS AND DISCUSSION

Development

Egg incubation lasted on average 3 d (Table 1) and egg viability was 92.7%. Soon after eclosion, larvae remained from 4 to 6 h over the remaining eggs, eating those that were not viable or which had not yet hatched. This behavior can be advantageous for larvae that emerge first, since 1st instar larvae are inefficient in capturing food (Agarwala & Dixon 1992); it can also be beneficial in the case of low prey densities (Hagen 1962).

The results of Castro et al. (2011) on H. axyridis were similar to ours with respect to egg incubation lasting 3.4 d. They also offered C. atlantica to their coccinellids, and maintained the eggs at 25 °C. Lamana & Miller (1998) obtained 2.8 d for egg incubation period of *H. axyridis* fed with Acyrthosiphon pisum (Harris, 1776) aphids. Their results are consistent with those of Lanzoni et al. (2004), who fed their coccinellids with Mizus persicae (Sulzer, 1776), at 25 °C, obtaining a viability of 49.4%. Abdel-Salam & Abdel-Baky (2001) reared H. axyridis at 27 °C and fed the adults fresh and frozen eggs of Sitotroga cerealella (Olivier, 1789) (Lepidoptera, Gelechiidae), obtaining a period of incubation of 2.8 and 3.1 d, respectively, and a mean viability of 84 and 87%, respectively.

The mean duration of the development period from first larval phase to adult emergence was 18.6 d, and 1st, 2nd, 3rd, and 4th instars lasted 3.5; 2; 2.2; and 4.1 d, respectively. The pre-pupal period lasted on average one day, whereas the pupal period lasted 5.8 d (Table 1). In all replicates and larval stages, including pre-pupal and pupal, coccinellid survival was 100%.

Table 1. Developmental period of Harmonia aryxi-DIS in days (mean \pm SD) when fed Cinara ATLANTICA APHIDS AT 24 °C, 12:12 H L:D and $70\% \pm 10\%$ RH.

Number of days (Mean \pm SD)		
Egg	3.0 ± 0	
1st instar	3.5 ± 0.27	
2nd instar	2.0 ± 0.44	
3rd instar	2.2 ± 0.17	
4th instar	4.1 ± 0.31	
Pre-pupa	1.0 ± 0	
Pupae	5.8 ± 0.17	
Adult	85.6 ± 17.78	
Larva-Adult	18.6 ± 2.6	
Total	107.2 ± 18.62	

Similar results were observed by Lamana & Miller (1998) for the 4 instars and pupa (2.5, 1.5, 1.8, 4.4 and 4.5 d) and by Lanzoni et al. (2004) (2.3; 1.5; 2; 4.7 and 6.6 d). Tsaganou et al. (2004) obtained 1.8; 3.0; 3.0; 4.0 d for the 4 larval instars and 1.0 and 3.1 d for the pre-pupa and pupa of H. axyridis fed with A. gossypii at 26 °C, 50% RH and photoperiod of 16:8 h L:D. Castro et al. (2011) observed a period of 3.4; 2.7, 2.3, and 4.6 for the 4 instars and 1.0 and 4.7 for the pre-pupa and pupa.

The average development times observed by Abdel-Salam & Abdel-Baky (2001) was 2.3; 2.0; 2.9 and 3.9 d for the larva and 4.9 d for the pupa, using fresh eggs, and 3.0; 2.4; 3.0 and 4.8 for the larva and 6.0 d for the pupa, using frozen eggs of *S. cerealella*.

The temperature influences the development time: higher temperatures result in faster development and vice versa. Besides this parameter, the type of food and the nutritional quality of it should also be considered (Castro et al. 2011; Hodek et al. 2012).

Longevity

The mean observed longevity of *H. axyridis* was 85.6 d (Table 2) and the total development period from larva to adult emergence was on average 18.6 d. Similar results were reported by Soares et al. (2001) (86.8 d), in which specimens were maintained at 22 °C, 75% RH and 16:8 h L:D photoperiod and were fed Mysus percicae, Aphis phabae and eggs of Ephestia kuehniella (Zeller, 1879) (Lepidoptera, Pyralidade); and by Castro et al. (2011) (longevity = 89.1 d and total development = 22.3 d). Abdel-Salam & Abdel-Baky (2001) observed a mean longevity of 62.2 and 61.6 d, respectively, using fresh and frozen eggs of S. cerealella. Abdel-Salam & Abdel-Baky (2001) observed a mean longevity of 62.2 and 61.6 d, respectively, using fresh and frozen eggs of S. cerealella.

Reproductive Capacity and Life Expectancy Table

The pre-oviposition period of *H. axyridis* lasted 6.8 d (Table 2), a little longer than in the results of Castro et al. (2011) (5.8 d), and shorter than in

Table 2. Reproductive period and longevity (days) (mean \pm SD) of *Harmonia Axyridis* Adult females fed *Cinara Atlantica* aphids at 24 °C, 12:12 H L:D and 70% \pm 10% RH.

Parameters	Days
Pre-oviposition	6.8 ± 2
Oviposition	44.3 ± 9
Pos-oviposition	32.9 ± 9.2
Longevity	85.6 ± 17.7

those of Abdel-Salam & Abdel-Baky (2001), i.e., 8.1 d for fresh eggs and 9.5 d for frozen eggs, as well as the results of Lanzoni et al. (2004) (7.4 d) and Mignault et al. (2006) (9.6 d).

The oviposition period lasted 44.3 d (Table 2), similar to the results of Abdel-Salam & Abdel-Baky (2001) (49 and 45.3 d) for fresh and frozen eggs, respectively. In the results of Lanzoni et al. (2004), the oviposition period lasted 13.7 d, much shorter than in this work, whereas in Castro et al. (2011) it was even longer (76.8 d).

The mean fecundity of *H. axyridis* was 682.1 eggs (15.69 eggs/day/female) (Table 3). In the results of Abdel-Salam & Abdel-Baky (2001), mean fecundity was 715.3 and 606.6 eggs, respectively, for females fed fresh and frozen eggs. The daily fecundity rate obtained by them was similar to ours (14.59 eggs/day) when females in their experiment were fed fresh eggs of S. cerealella. However, when their females were fed frozen eggs, a lower daily fecundity resulted (13.39 eggs/ day). Castro et al. (2011) obtained a mean fecundity of 614 eggs and 8.2 eggs/day/female. Lanzoni et al. (2004) obtained a mean number of 550.5 eggs/female, whereas Mignault et al. (2006) obtained 2008.4 eggs/female, a significantly greater number. Soares et al. (2001) obtained 23.5 eggs/ female/day, for the non-melanic form.

The greatest rates of oviposition were observed between the 11th and the 45th day of the reproductive period, and the rate fell drastically after the 49th day (Fig. 1). The average number of egg masses by *H. axyridis* females was 36.6 during the reproductive period, with 18.7 eggs/egg mass (Table 3). According to Takahashy (1987), the mean number of egg/egg mass may be up to 30, depending on the substrate and the quality of the food offered to the adults. According to Castro et al. (2011) the highest oviposition rates occurred between the 7th and the 34th day of the reproductive period, whereas the mean number of postures was 35.9/female, with 18.5 egg/egg mass.

The post-reproductive period of *H. axyridis* was 32.9 d (Table 2), a number greater than that obtained by Abdel-Salam & Abdel-Baky (2001) (5.1 and 6.8 d) for females fed fresh and frozen eggs

Table 3. Reproduction of Harmonia Axyridis adult females fed giant pine aphids, Cinara atlantica, at 24 °C, 12:12 H L:D and 70% \pm 10% RH. Each parameter value is given as the mean \pm SD.

Parameters	Number of eggs
Fecundity (eggs/female)	682.1 ± 114
Fertility (viable eggs/female)	633.2 ± 112
Eggs/female/day	15.69 ± 2.4
Number of egg masses/female	36.6 ± 6.5
Eggs/egg mass	18.7 ± 6.2

of *S. cerealella*, respectively; and by Mignault et al. (2006) (5.7 d) and Castro et al. (2011) (10.8 d).

Fertility Life Table for *H. axyridis*

The net reproductive rate was 632.7 ($R_{_{\circ}})$ (Table 4) and the Time Interval between Consecutive Generations (T) was 26.7 d. Castro et al. (2011) observed a much lower value of $R_{_{\circ}}$ (278.03) and a higher T value (39.48) for the same species and under same laboratory conditions.

If compared with Cinara atlantica, in 2 weeks, the aphid is able to increase 17 times its population (Penteado 2007), indicating the efficiency of H. axyridis. According to Horm (1988), if $R_{\rm o}$ is greater than 1, then the population will increase, which was verified in the present study. These parameters could vary in the field under the influence of factors, such as food availability, humidity, temperature, intraguild competition and presence of natural enemies.

Natality was higher than mortality for H. axyridis, resulting in positive Intrinsic Rate of Increase (r_m) value (0.24), and indicating population growth (Table 4). At the same temperature, Castro et al. (2011) obtained a lower value (0.14).

Penteado (2007) obtained $r_{_{\rm m}}$ values of 0.006; 0.11; 0.136; 0.138; 0.142; 0.188 and 0.226 for C.atlantica reared on pine seedlings from 7 different origins. Van Lenteren (1986) considers a biological control agent as effective if its r_m values are similar or greater than those of its prey, which will favor the establishment of the natural enemy and, in this case, the introductions of the predator should be regular. Therefore, *H. axyridis* shows a good innate capacity to increase its numbers since the r_ values were greater than most of the values observed for *C. atlantica*; and this will favor its establishment at certain sites (Penteado 2007). The r_ value observed is similar to the parasitoid Xenostigmus bifasciatus Ashmed, 1891 (Hymenoptera: Braconidae), which is specific to *C. atlantica*, showing the efficiency of *H. axyridis* to control this aphid in the absence of this parasitoid.

The value of λ was 1.27, confirming the high value of Ro (net reproductive rate), which shows that the *H. axyridis* population increased strongly from one generation to the next (Table 4).

The time necessary for the *H. axyridis* population to double in size was 2.87 d (Table 4), faster than observed by Castro et al. 2011 (4.95 d) in the same temperature, although, as the authors observed, DT can decrease with increasing temperatures.

Food Consumption

Coccinellid larvae were fed from the 2nd day of their development; their mean food consumption was 19.4; 24.8; 49.7 and 188.9 aphids for each of the 4 instars, respectively. First instar larvae were fed small aphids and the other stages were

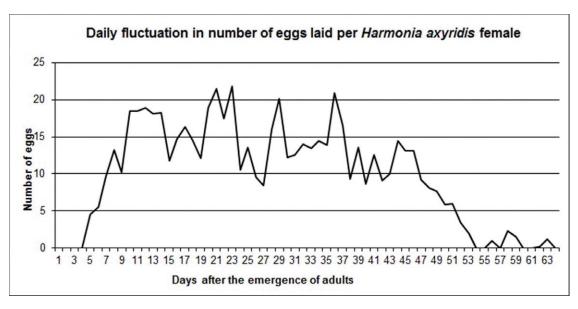


Fig. 1. Mean daily fluctuation of eggs/Harmonia axyridis female fed Cinara atlantica aphids at 24 °C, 12:12 h L:D and $70\% \pm 10\%$ RH.

Table 4. Estimated life-table parameters for Har-MONIA axyridis fed with CINARA atlantica at 24 °C, 12:12 H L:D and $70\% \pm 10\%$ RH. Each parameter value is given as the mean \pm SD.

Reproductive Parameters	
$\overline{R_{_{o}}}$	632.7 ± 3.9
T	26.74719456 ± 0.1
$\mathbf{r}_{_{\mathrm{m}}}$	0.24114665 ± 0
λ	1.272707665 ± 0
TD	2.874380297 ± 0

 $R_{,:}$: Net reproductive rate (the number of female descendants from an average female in one generation); T: time interval between each generation; r_{m} : rate of population increase; λ : finite rate of population increase; and TD: population doubling time.

given aphids of medium size. The average daily consumption for each of the 4 larval instars was 5.9; 12.7; 22.9 and 46 aphids (Table 5; Fig. 2). It is possible that the latter was greater because the predator needs an increased amount of food reserves for the pupal period, when the insect needs

a greater amount of energy reserves to complete its development (Hodek et al. 2012). Tsaganou et al. (2004) obtained higher consumption daily averages: 58.1, 64.5, 101.0 and 232.7 aphids, respectively, from the 1st to the 4th instar. However, Lee & Kang (2004) obtained greater values, a mean consumption of 4.5; 7.3; 26.7 and 86.4, respectively, from the 1st to the 4th larvae fed *Aphis gossypii*, at $25\,^{\circ}\mathrm{C}$, 60-70% RH and 16: $8~\mathrm{h}$ L: D.

The greatest average total food consumption was achieved by individuals in the adult phase, totaling 1,892 aphids (Fig. 2), with an average daily consumption of 22.3 aphids (Table 5). The great food consumption of H. axyridis adults is likely associated with the longer duration of this phase, the abundance of aphids offered, as well as the confined environment.

Lucas et al. (1997) obtained an average daily consumption of 35.8 *Aphis citricola* under the same temperature and humidity and 16:8 h L: D. Lee & Kang (2004) observed that an average of 74.8 aphids was eaten per day, under the same temperature. Soares et al. (2001) observed that an average daily consumption of 45.8 and 35.4 aphids by *H. axyridis*, when they were fed *M. persiacae* and *A. phabae*, respectively.

Table 5. Daily Consumption (mean \pm SD) Of Cinara atlantica by Harmonia axyridis at 24 °C, 12:12 H L:D and 70% \pm 10% RH.

		Mean ± (SD)			
n	1st instar	2nd instar	3rd instar	4th instar	Adult
10	5.9 ± 1.2	12.7 ± 3.4	22.9 ± 5.6	46 ± 6.8	22.3 ± 1.4

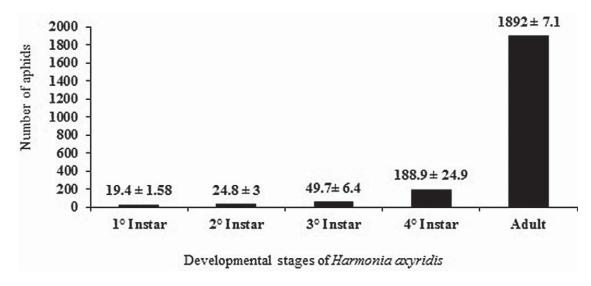


Fig. 2. Average total consumption of *Cinara atlantica* aphids (mean \pm SD) by *Harmonia axyridis* per individual of each of its instars and the adult at 24 °C, 12:12 h L:D and 70% \pm 10% RH.

Yasuda & Ishikawa (1999) noted that predation on *H. axyridis* adults was more intense when *A. gossypii* individuals were in high densities and were clustered on the central portion of the plant, and less intense when aphids were more evenly distributed on the plant and were in smaller numbers.

This variation in the consumption data is likely to be associated with the size of *Cinara atlantica*, also known as the giant pine aphid, a species that has elevated biomass and is one of the largest aphids known.

Cannibalism

In the tests evaluating egg predation by *H. axyridis* larvae and adults, it was possible to observe intense cannibalism in 3 out of the 4 bioassays (Table 6).

During tests that evaluated egg predation, when the coccinellids were in the presence of aphids, we found that the predation rate by 4th instar larvae was 53%, whereas adults were not found eating eggs in any of the repetitions. However, in the absence of aphids, which were substituted with water and honey, the rate of egg

predation jumped to 100%, by both larvae and adults. Eggs can be considered a good source of food, because 4th instars reared on this diet reach the adult stage.

Osawa (1993) reared *H. axyridis* larvae with 8 different species of aphids as food and observed egg predation rates of 54.5%, similar to what we found in this research. However, Osawa (1989) recorded different egg predation rates when *H. axyridis* larvae consumed siblings (24.7%) or non-siblings (36.1%). According to this author, not only the availability of aphids, but also the parental lineage influences the rate of egg cannibalism in *H. axyridis*.

Cannibalism among Harmonia axyridis Larvae

Cannibalism may be an important survival strategy among insects, particularly predators. In this study, cannibalism was observed in the presence of the 2 diets tested, being most intense when larvae were offered only water + honey as food. Cannibalism was present in the 10 repetitions evaluated (Table 7). Of the 10 repetitions, 4 had 2 instances of cannibalism, and 6 had 3. A lower incidence of cannibalism was observed

Table 6. Harmonia axyridis % predation (mean \pm SD) eggs/adults and 4th instar larvae fed with two diets at 24 °C, 12:12 H L:D and 70% \pm 10% RH.

\overline{n}	Diet	Stages	Eggs	Percent Predation
10	Cinara atlantica	4th Instars	20	53 ± 3.6
10	$Cinara\ atlantica$	Adults	20	0 ± 0
10	Water + honey	4th Instars	20	100 ± 0
10	Water + honey	Adults	20	100 ± 0

Table 7. Harmonia axyridis cannibalism among four 4th instar larvae fed with two diets at 24 °C, 12:12 H L:D and $70\% \pm 10\%$ RH.

\overline{n}	Diet	Stages	Eggs	Predation (%)
10	$Cinara\ atlantica$	Larvae Adults	20 20	53 ± 3.6 0 ± 0
10	Whater + Honey	Larvae Adults	20 20	100 ± 0 100 ± 0

when *C. atlantica* was offered as food, and cannibalism was observed only in 3 repetitions with a single event in each one.

Michaud (2003), studying cannibalism in *H. axyridis* larvae confined 3 individuals and offered them eggs of *Ephestia kuehniella* Zeller, 1879 (Lepidoptera: Pyralidae) and pollen as food. Out of 80 repetitions, 29 had one instance of cannibalism, and 5 repetitions had 2.

The intensity of cannibalism among *H. axyridis* larvae is related with prey availability (Yasuda & Shinya 1997; Burgio et al. 2002), low levels of nutrients or food toxicity (Wagner et al. 1999).

Even though we did not evaluate the cannibalism of pupae by larvae and larvae by adults of *H. axyridis*, we observed these behaviors in the field when we were collecting individuals to imitate the experiments.

CONCLUSIONS

The life table results, together with biological data indicated that *Harmonia axyridis* is an efficient predator of *C. atlantica*, consuming them in high rates. It also presents high fertility, egg viability, fast development and high levels of predation. Egg viability, fecundity, fertility and reproductive capacity were high, and immature development was fast when compared with other coccinellid predators.

Harmonia axyridis is a voracious, aggressive predatory species, with high mobility and great consumption capability, which means that it has great potential as biological control agent of *Cinara atlantica*, an aphid that has caused irreparable damage to *Pinus* spp. plantations.

Given the problems reported in countries where *H. axyridis* was introduced, other aspects of the life history of this species should be observed in the environment. In studies of basic biology, both native and introduced species need to be taken into account to understand their tritrophic relationships and to apply the knowledge to biological control and management.

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