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THE IMPACT OF TEMPERATURE ON BIOLOGICAL ASPECTS AND LIFE TABLE OF *HARMONIA AXYRIDIS* (PALLAS) (COLEOPTERA: COCCINELLIDAE)C. F. CASTRO¹, L. M. ALMEIDA¹ AND S. R. C. PENTEADO²¹Laboratório de Sistemática e Bioecologia de Coleoptera (Insecta), Departamento de Zoologia, Universidade Federal do Paraná, Caixa Postal 19030, Curitiba, Brazil²Laboratório de Entomologia, Embrapa Florestas, Estrada da Ribeira, km 111, Caixa Postal 319, Colombo, Brazil

ABSTRACT

The impacts of temperature on *Harmonia axyridis* and its potential as a control agent of *Cinara atlantica*, the Carolina conifer aphid, were evaluated. The experiments were conducted with eggs from field-collected adults. Each egg batch was kept at 15 °C, 20 °C and 25 °C, 70% RH and 12:12 h. L:D. After hatching, the larvae were reared individually until adult emergence and all insects were kept under the same conditions. The mean period of egg incubation, total developmental time and egg viability were longer at 15 °C than at the other 2 temperatures. Survival was 100% for all the larval, pre-pupal and pupal stages. The longevity was longer at 15 °C and 20 °C than 25 °C. The mean number of eggs produced was significantly higher at 15 °C than at the other 2 temperatures. The post-oviposition period increased with increasing temperature. The highest specific fertility was recorded at 15 °C, followed by 25 °C and 20 °C, respectively. The net reproductive rate was higher at 15 °C than at the 2 higher temperatures. The time interval between each generation (T) decreased with increasing temperature and the population doubling time (DT) was higher at 15 °C than at 20 °C and 25 °C. The intrinsic rates of increase (r_m) were very similar at the 3 temperatures, but the finite rate of population increase (λ) was higher at 25 °C than at the 2 lower temperatures. The results indicate that *H. axyridis* shows great potential as a biological control agent of *C. atlantica*.

Key Words: aphid, developmental time, invasive species, life table, temperature

RESUMO

O impacto da temperatura foi avaliado em *Harmonia axyridis*, assim como seu potencial como agente de controle de *Cinara atlantica*. Os testes foram realizados a partir de posturas obtidas de adultos coletados em campo. Cada uma das posturas foi mantida nas temperaturas de 15 °C, 20 °C e 25 °C, UR de 70% e fotofase de 12 horas. Após a eclosão dos ovos, as larvas foram individualizadas até a emergência do adulto e os insetos foram mantidos sob as mesmas condições. O tempo médio de incubação dos ovos foi maior a 15 °C. O tempo total de desenvolvimento e a viabilidade dos ovos foram maiores a 15 °C. Para todos os estágios larvais, para a pré-pupa e pupa a sobrevivência foi de 100%. As maiores longevidades ocorreram a 15 °C e a 20 °C. A média de ovos produzidos foi significativamente maior a 15 °C. O período pós-reprodutivo aumentou com o acréscimo da temperatura. A maior fertilidade específica ocorreu a 15 °C, seguida de 25 °C e 20 °C. A taxa líquida de reprodução foi maior a 15 °C. O intervalo de tempo entre cada geração (T) decresceu com o aumento da temperatura e o intervalo de tempo para duplicação da população (DT) foi maior a 15 °C. A taxa extrínseca de aumento da população (r_m) foi próxima em todas as temperaturas e a razão finita de aumento (λ) foi maior a 25 °C. Os resultados indicam que *Harmonia axyridis* apresenta grande potencialidade como agente de controle biológico de *Cinara atlantica*.

Palavras-Chaves: afídeos, tempo de desenvolvimento, espécie invasora, tabela de vida de fertilidade, temperatura

Translation provided by the authors.

Harmonia axyridis (Pallas 1773) is a species of Coccinellidae (Coleoptera) originating from northeast Asia (Yasumatsu & Watanabe 1964; Hukusima & Kamei 1970; Hukusima & Ohwaki 1972; Kuznetsov 1997), and is used in the biological control of aphids which are considered as pests of many economically important crops. Tan (1946) has described its original distribution,

which extends from southern Siberia (Altai mountains) to Manchuria, Korea, Japan and China.

Harmonia axyridis was introduced into the U.S.A. as a biological control agent at different times as follows: in California in 1916, 1964 and 1965; in Washington in 1978 and 1982; in Connecticut, Georgia, Louisiana, Maryland, Wash-

ington D.C., Delaware, Maine, Mississippi, Ohio, Pennsylvania and North Carolina in 1978 and 1981 (Gordon 1985), but it only became established in 1988 (Chapin & Brou 1991). It has also been liberated in Chihuahua (Quiñones et al. 2001), Colima and Yucatán (Koch et al. 2006) in Mexico. It is already established in Canada (Koch 2003) and also in various European countries, including Greece (Katsoyannos et al. 1997), south-east France (Iperti & Bertand 2001), Germany (Klausnitzer 2002), Belgium (Adriaens et al. 2003) and the United Kingdom (Majerus et al. 2006).

In the latter part of 1990, *H. axyridis* was introduced as a biological control agent to South America in Mendoza, Argentina. It was detected in Buenos Aires in 2001, associated with *Monellia caryella* (Fitch) (Hemiptera: Aphididae), on pecan, *Carya illinoensis* (Fagales: Juglandaceae) (Saini 2004). It has also been reported in Chile (Grez et al. 2010) and Peru (González & Vandenberg 2007).

Harmonia axyridis was observed for the first time in Brazil in 2002 at Curitiba (PR), probably due to accidental introduction. Larvae and adults of *H. axyridis* were collected while predating on *Tinocallis kahawaluokalani* (Kirkaldy 1907) (Hemiptera: Aphididae). *Tinocallis kahawaluokalani* is a pest of *Lagerstroemia indica* Linnaeus (Lythraceae), a common ornamental plant species in urban areas of south Brazil and also on pine trees (Pinaceae), predating the Carolina conifer aphid, *Cinara atlantica* (Wilson 1919), and *Cinara pinivora* (Wilson, 1919) (Lachninae) (Almeida & Silva 2002).

Many species have been introduced at new sites for biological control (De Bach & Rosen 1991). However, some authors have commented on the potential adverse effects of introducing exotic species, including the competitive suppression or displacement of native natural enemies or even the extinction of potentially beneficial predator species, which have still not been exploited for this purpose (Elliott et al. 1996). Also, Kenis et al. (2008) commented that *H. axyridis* has become a human nuisance, a grape and grapevine pest and a threat to native biodiversity. The competition of *H. axyridis* with *Coleomegilla maculata* (DeGeer 1775), a native Coccinellidae species and important predator, has been observed in the USA. This native predator feeds on many aphid species and also on the eggs of other insects and arthropods (Hodek & Honek 1996).

There have been few studies in Brazil on the biology and behavior of *H. axyridis* since its discovery in 2002. Martins et al. (2009) studied population fluctuations, tritrophic relationships and occurrence and abundance of *H. axyridis* in comparison with native species. The authors observed that this species competes mainly with *Cycloneda*

sanguinea (L. 1763) (Coleoptera: Coccinellidae), the species most commonly recorded. A large reduction in coccinellid abundance and diversity occurred after the introduction of *H. axyridis* in 2002 (Martins et al. 2009). This suggests a possible displacement of native or established coccinellid species.

Considering the recent introduction of *H. axyridis* into Brazil, the objective of this study was to study its biology and population growth parameters at 3 different temperatures.

MATERIALS AND METHODS

Adult *H. axyridis* were collected from pine trees in September 2008 at Curitiba, PR, Brazil and reared in 500 mL plastic dishes in rearing chambers (BOD) (Eletrólabs, São Paulo, SP) at $25\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$, $70\% \pm 10\%$ R.H. and 12:12 h L:D. The food, *C. atlantica*, was supplied daily to maintain the population stock. The adults were later sexed based on McCornack et al. (2007) methodology, and the eggs were transferred to Petri dishes with moistened filter paper for biological studies. The plastic dishes were changed and cleaned every 48 h and observations made daily.

The egg masses, with approximately 20 eggs, were kept at $15\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$, $20\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$ and $25\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$ with $70\% \pm 10\%$ RH and 12:12 h L:D with a total of 45 replications and 15 larvae for each of the 3 temperatures.

After egg eclosion, the larvae were placed individually in Petri dishes lined with filter paper and a ball of cotton moistened with a drop of honey. The aphids were separated by size into groups to feed the coccinellids: small aphids (1st and 2nd instar nymphs), medium (3rd and 4th instar nymphs and adults). Five to 6 small aphids were offered as food to each 1st instar larva, 12 to 13 to the 2nd instar, 22 to 23 to the 3rd instar, 46 to 47 to the 4th instar and 22 to 23 aphids to each of the adults.

The number of aphids provided as food was based on Santos (2009). After pre-pupal formation and until adult emergence, the insects were kept under the same conditions without any aphids. In order to maintain enough aphids for the biological studies, they were first collected in the field on pine branches infested with *C. atlantica* at Curitiba, PR and taken to the insect rearing laboratory of the Zoology Department of the Universidade Federal do Paraná, where they were kept at $21\text{ }^{\circ}\text{C} \pm 1^{\circ}\text{C}$, $70\% \pm 10\%$ RH and a photoperiod of 24 h. The aphids were removed from the field-collected pine branches with the help of a small paintbrush and transferred to new plants acquired from a commercial nursery. Additional aphids were added to maintain the stock population and later used to feed *H. axyridis*, using the same transfer technique.

Statistical Analysis

Arithmetic means and standard deviations were calculated for the statistical analyses. The means were submitted to an analysis of variance (ANOVA) and the means were compared with the Tukey test at 5% probability using the Statistica 7.0 program. The population growth parameters were calculated using the *Tabvida* computational system (Penteado et al. 2010). The life parameters evaluated were: specific fertility (m_x : number of females produced/female); net reproductive rate (R_x : $\sum (m_x l_x)$); time interval between generations (T : $\sum (m_x l_x x) / \sum (m_x l_x)$); intrinsic rate of increase (r_m : $\ln R_x / T$); the finite rate of population increase (λ : e^{r_m}) and population doubling time (DT: $\ln(2)/r_m$).

RESULTS AND DISCUSSION

Development

The mean period for egg incubation in *H. axyridis* at 15 °C was 6 d and decreased with increasing temperature: 4 and 3.4 d at 20 °C and 25 °C, respectively (Table 1). Lamana & Miller (1998) feeding *H. axyridis* with *Acyrtosiphon pisum* (Harris, 1776) (Hemiptera: Aphididae), also observed a longer incubation time at lower temperature with a reduction occurring when the temperature increased. The mean egg incubation period observed by Lanzoni et al. (2004) using *Myzus persicae* (Sulzer 1776) (Hemiptera: Aphididae) as food at 25 °C, RH 60-80% and a photoperiod of 16:8 h L:D was 2.8 d, hence, shorter than in the present study at the same temperature. In a study with *H. axyridis* by Abdel-Salam & Abdel-Baky (2001) using fresh and frozen *Sitotroga cerealella* (Olivier, 1789) (Lepidoptera: Gelechiidae) eggs as food at 27 °C, 75% RH and a pho-

toperiod of 16:8 h L:D, the mean incubation time was 2.8 and 3.1 d respectively. At 15 °C, developmental time was longer for all immature stages. The developmental times of the 4th instar and the pupa were longer for the 3 temperatures evaluated. In the egg, 1st and 3rd instars and the pupal stages, the developmental time differed significantly for the 3 temperatures studied. The developmental times of the 2nd instar at 15 °C and 25 °C were significantly different. At 25 °C, the 4th instar developmental time differed significantly from the other temperature while the pre-pupal development at 15 °C was significantly different from the development at other temperature.

Lamana & Miller (1998) also recorded longer developmental times for *H. axyridis* at lower temperature. With insects fed on *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs and *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) adults at 27 °C, a photophase of 12 h and 50 ± 10% RH, Santos et al. (2009) observed that the larval stages were shorter. At 25 °C, the results obtained by Lanzoni et al. (2004) were very similar to those found in the present study. Abdel-Salam & Abdel-Baky (2001) also observed lower values for the development stages of *H. axyridis*. In rearing *H. axyridis* fed with *Aphis gossypii* Glover (Hemiptera: Aphididae) at 26 °C, 50% RH and a photoperiod of 16:8 h L:D, Tsaganou et al. (2004) observed lower values for the development stages than recorded in the present study. Specky et al. (2003) observed a mean developmental time of 14.5 d for 1st to 4th instar larvae and 4.90 d for the pupa for *H. axyridis* fed with *A. pisum* eggs at 23.5 °C, RH 75 ± 5% and a photoperiod of 16:8 h L:D. For individuals fed on *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), the mean developmental time was shorter, 14.1 d

TABLE 1. DEVELOPMENT PERIOD IN DAYS (MEAN ± STANDARD DEVIATION) OF HARMONIA ARYXIDIS FED WITH CINARA ATLANTICA AT 3 DIFFERENT TEMPERATURES.

	Mean ± (SD)		
	15 °C	20 °C	25 °C
Egg	6.00 ± 0.00 Ca	4.00 ± 0.00 Bb	3.40 ± 0.83 Bc
1º instar	7.00 ± 0.00 Ba	4.00 ± 0.00 Bb	3.47 ± 0.64 Bc
2º instar	3.43 ± 0.52 Da	3.00 ± 0.00 Cab	2.73 ± 0.96 BCb
3º instar	6.33 ± 1.63 BCa	3.47 ± 0.52 BCb	2.33 ± 0.90 Cc
4º instar	7.80 ± 0.86 Ba	7.47 ± 1.81 Aa	4.60 ± 0.74 Ab
Pre-Pupa	1.53 ± 0.74 Ea	1.00 ± 0.00 Db	1.00 ± 0.00 Db
Pupa	11.00 ± 0.85 Aa	7.87 ± 0.74 Ab	4.73 ± 0.46 Ac
Total	43.1	30.8	22.3

Mean values within a column followed by the same capital letter are not significantly different, means values within a line followed by the same small letter are not significantly different, P < 0,05, Tukey's test

(with the exception of the 3rd instar) for 1st to 4th instar larvae and 4.85 d for the pupa.

The total developmental time from egg to adult emergence decreased with increasing temperature (Table 1). Lamana & Miller (1998) also observed a reduction in developmental time with increasing temperatures for the complete development of *H. axyridis*. The total developmental time of *H. axyridis* fed with fresh *S. cerealella* eggs was 18.89 d and 22.5 d for those individuals fed with frozen eggs at 27 °C (Abdel-Salam & Abdel-Baky 2001). At 25 °C, Lanzoni et al. (2004) found a shorter developmental time for *H. axyridis* than in the present study.

The viability of *H. axyridis* eggs in the present study was 80.1% at 15 °C, 79.6% at 20 °C and 90.7% at 25 °C. Survival was 100% for the larval, pre-pupal and pupal stages in all the repetitions.

Abdel-Salam & Abdel-Baky (2001) recorded lower mean survival levels for *H. axyridis* fed on fresh (84%) and frozen (87%) *S. cerealella* eggs. Mean survival was also much lower in the Lanzoni et al. (2004) study, being 49.4% at 25 °C. In both studies, the mean survivals were calculated from the egg to adult emergence.

Temperature has an important influence on developmental time, with higher temperature resulting in more rapid development and vice versa (Hodek & Honek 1996). Besides the temperature, the type of food and nutritional quality should also be considered.

Longevity and Reproductive Capacity

Although longevity was greater at 15 °C, there were no statistical differences among the 3 temperatures studied (Table 2). Longevity was much shorter at 25 °C (27.5 d) for *H. axyridis* (Lanzoni et al. 2004). Abdel-Salam & Abdel-Baky (2001) observed a shorter longevity for *H. axyridis* adults. Santos et al. (2009) also noticed a shorter longevity for *H. axyridis* adults fed on *A. kuehniella* eggs and *S. graminum* adults at 27 °C: 74.1d and 76.2 d for the females and 67.3 d and 70.3 d for the males, respectively. *H. axyridis* adults kept at 22 °C, RH 75% and a photoperiod of 16:8 h, fed on a diet of *Aphis fabae* Scopoli, *M. persicae* and *E. kuehniella* eggs had a longevity of

86.8 d (melanic) and 59.5 d (non-melanic) (Soares et al. 2001).

The pre-oviposition and oviposition periods of *H. axyridis* were very similar at the 3 temperatures with no significant differences (Table 2). Lanzoni et al. (2004) observed a longer pre-oviposition period for the same species than seen in the present study (7.4 d) and an even longer period was recorded by Mignault et al. (2006) for this species fed on *Aphis glycines* Matsumura at 24 °C.

At a higher temperature of 27 °C, higher values were observed by Abdel-Salam & Abdel-Baky (2001), i.e., 8.1d and 9.5 d, when the species was fed on fresh and frozen *S. cerealella* eggs respectively. At the same temperature, Santos et al. (2009) observed a period of 9.8 d for *H. axyridis* fed on *A. kuehniella* eggs, and 10.6 d when fed on *Schizaphis graminum* adults.

The oviposition period of *H. axyridis* was 82.4 d at 15 °C, 74.9 d at 20 °C and 76.9 d at 25 °C with no significant differences (Table 2). Lanzoni et al. (2004) observed a much shorter period (13.7 d) than that observed in the present study. For Santos et al. (2009) at 27 °C, the oviposition period was 47.3 d and 51.7 d for adults fed on *A. kuehniella* eggs and *S. graminum* adults, respectively. Similar results were observed by Abdel-Salam & Abdel-Baky (2001): 49 d and 45.3 d for individuals fed on fresh and frozen *S. cerealella* eggs respectively at the same temperature.

The fecundity and the mean daily number of eggs produced per female at 15 °C, were significantly greater than at the other temperatures (Table 3). At 25 °C, Lanzoni et al. (2004) recorded a mean egg number per female of 550.5, a much lower value than in the present study. However, the daily number of eggs per female was higher: 18.3. These authors also observed a similar value for *Adalia bipunctata* (L.), 537.0 (16.0 eggs/female/d) and a higher value for *Hippodamia variegata* (Goeze), 841.7 (21.2 eggs/female/d). For females fed with *A. glycines*, Mignault et al. (2006) observed a much higher fecundity of 2,008.4 eggs per female.

The mean number of egg masses laid was significantly different at 15 °C and 25 °C, but at 20 °C there was no difference with the other temperature. The number of eggs per batch was significantly higher at 15 °C (Table 3).

TABLE 2. PRE-OVIPOSITION, OVIPOSITION, POST-OVIPOSITION PERIODS AND LONGEVITY (DAYS) (MEAN ± SD) OF ADULTS OF *HARMONIA AXYRIDIS* FED WITH *CINARA ATLANTICA* AT 3 DIFFERENT TEMPERATURES.

Parameters	15 °C	20 °C	25 °C
Pre-oviposition	6.10 ± 1.03 a	6.20 ± 1.01 a	5.80 ± 1.70 a
Oviposition	82.40 ± 9.23 a	74.93 ± 12.99 a	76.87 ± 22.59 a
Post-oviposition	6.87 ± 0.83 a	8.40 ± 0.91 a	10.80 ± 4.26 b
Longevity	95.33 ± 9.36 a	89.93 ± 12.87 a	89.13 ± 18.61 a

Mean values within a line followed by the same letter are not significantly different, p < 0.05, Tukey's test.

TABLE 3. REPRODUCTION PARAMETERS (MEAN ± SD) OF ADULT *H. axyridis* FED WITH *CINARA ATLANTICA* AT 3 DIFFERENT TEMPERATURES.

Parameter	15 °C	20 °C	25 °C
Fecundity	805.7 ± 127.3 a	608.5 ± 113.7 b	614 ± 129.2 b
Fertility	647.1 ± 115.5 a	484.8 ± 94.9 b	556.1 ± 111.9 ab
Eggs/day	9.77 ± 1.0 a	8.15 ± 0.9 b	8.24 ± 1.3 b
No. of egg masses	39.3 ± 5.2 a	35.2 ± 6.4 ab	35.9 ± 8.2 b
Eggs/posture	20.6 ± 2.0 a	17.3 ± 1.30 b	18.5 ± 1.6 b

Mean values within a line followed by the same letter are not significantly different, $p < 0.05$, Tukey's test.
Note: Fecundity is the total number of eggs laid by a female, and fertility is the number (or percent) of eggs that hatch into larvae.

The post-reproductive period for female *H. axyridis* increased with higher temperatures, being the longest at 25 °C, which was significantly different (Table 2). Mignault et al. (2006) observed a shorter period.

Fertility Life Table for *H. axyridis*

Specific Fertility (mx)

The greatest specific fertility was observed at 15 °C, followed by 25 °C and 20 °C. At 15 °C, from the 5th to the 109th d, the females continued to oviposit, with the highest specific fertility observed between 8 and 66 d of age. Later, there was a decrease in fertility until the 104th d and after this interval the mx value increased until the 109th d, followed by another gradual fall. The survival rate ($lx = 1.00$) stayed constant until the 82nd d, when 2 deaths were

registered and a steep decrease occurred from the 91st d ($lx = 0.73$) (Fig. 1). The same oviposition period was observed for 20 °C (from the 5th to the 109th d), with a higher mx value between 9 and 71 d, after which it began to fall. The survival rate ($lx = 1.00$) stayed constant up to the 70th d, when the first death was recorded and by the 87th d more than half the females had already died with only 1 remaining alive until the 117th d (Fig. 2). The oviposition period at 25 °C was long but between the 4th and the 118th d, the highest specific fertility was only observed for a reduced time period (7th to 34th d), probably because both the life cycle and the developmental periods are faster at this temperature. The first death occurred on the 59th d ($lx = 1.00$ had stayed constant up to then), and after the 82nd d there was a significant reduction in females although one individual stayed alive until the 124th d, which

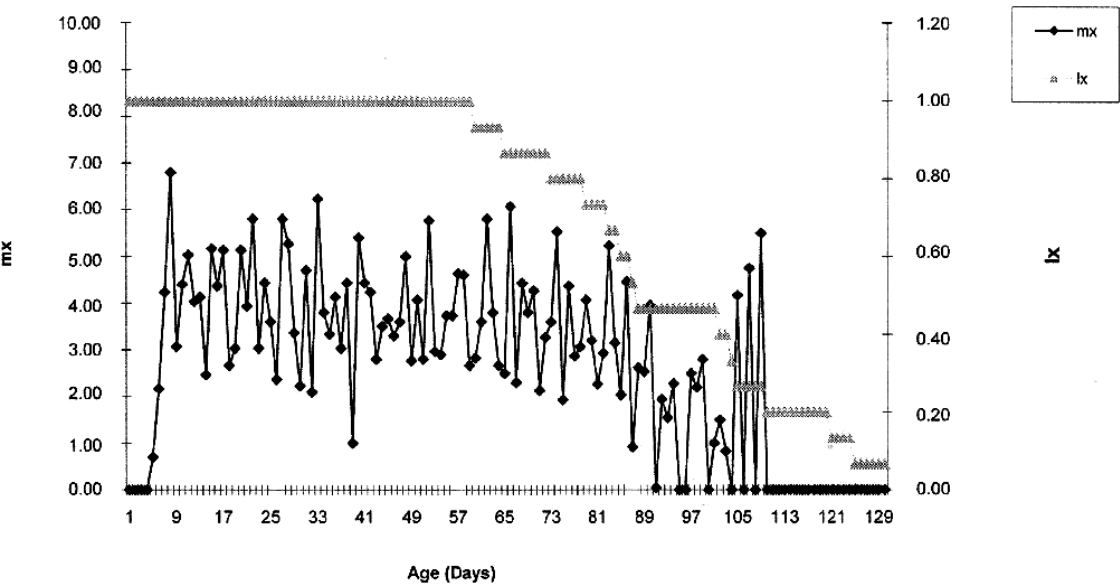


Fig. 1. Survival probability (lx), expressed in percentage, and specific fertility (mx) expressed as average number of eggs per day of *Harmonia axyridis* fed on *Cinara atlantica* at 15 °C.

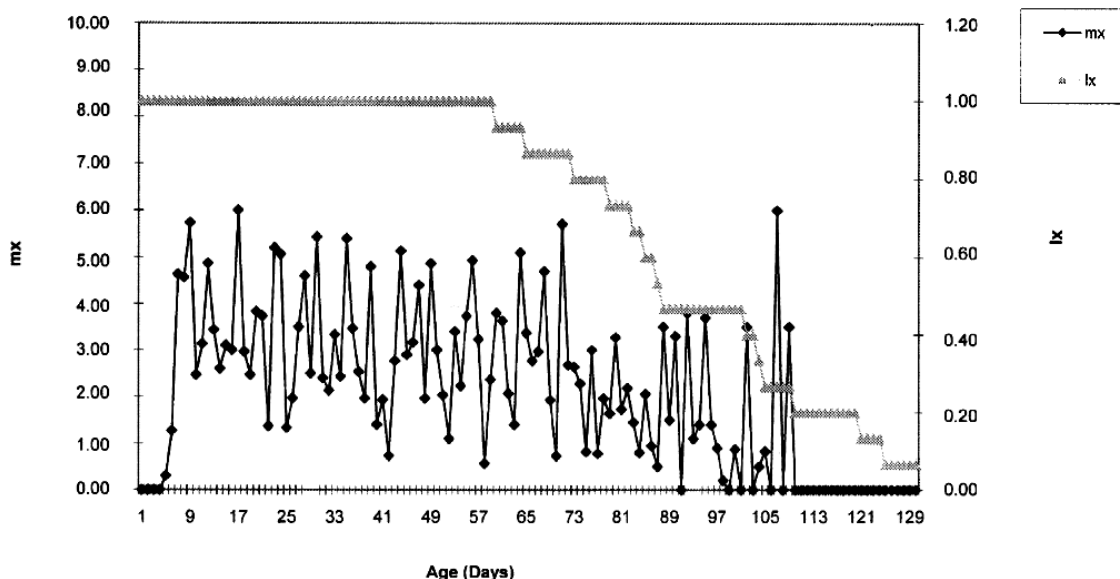


Fig. 2. Survival probability (l_x), expressed in percentage, and specific fertility (m_x) expressed as average number of eggs per day of *Harmonia axyridis* fed on *Cinara atlantica* at 20 °C.

was the highest value recorded for the three temperatures studied. The highest m_x value for the 3 temperatures was recorded at 25 °C (9.30) on the 21st d (Fig. 3).

Net Reproductive Rate (R_0)

The net reproductive rate was higher at 15 °C (Table 4). Lanzoni et al. (2004) observed a much lower value (26.27) for the same species. Comparing the 3 species studied by these authors, *H. variegata* (52.75) showed a net reproductive rate 1.5 and 2.9 times greater than *H. axyridis* and *A. bipunctata* (18.49) respectively.

Abdel-Salam & Abdel-Baky (2001) observed a variation in values for *H. axyridis* fed on fresh and frozen *S. cerealella* eggs: 289.11 and 234.96 respectively. The much lower value recorded by Lanzoni et al. (2004), as well as the variation obtained by Abdel-Salam & Abdel-Baky (2001), may have been due to the nutritional quality of the food used. According to Horm (1988), if R_0 is greater than 1, then the population will increase, which was verified in the present study at the 3 temperatures evaluated.

Time Interval between Consecutive Generations (T)

The value of T decreased with increasing temperatures (Table 4). This period can vary according to environmental conditions in the field. At 25 °C, the value of T was very close to that observed by Lanzoni et al. (2004) (38.81 d) and also for the

other 2 species, *H. variegata* (41.88) and *A. bipunctata* (40.06). The value of T was smaller when females were fed with fresh (37.87) compared to frozen (45.04) *Sitotroga cerealella* eggs (Abdel-Salam & Abdel-Baky 2001), but this was similar to the data recorded in the present study at 20 and 25 °C.

According to Osawa (1993), *H. axyridis* is considered to be bivoltine in Asia. However, in North America and Europe there are records of this species having up to 5 generations per year (Koch et al. 2006; Lamana & Miller 1998; Ongagna et al. 1993; Wang 1986 and Katsoyannos et al. 1997). In Brazil, this species is also multivoltine, depending on the region.

Thus, temperature, together with other factors, such as the type of food or its nutritional quality are important factors, which influence the time interval between generations.

Intrinsic Rate of Increase (r_m)

Natality was higher than mortality for *H. axyridis* at the 3 temperatures studied, resulting in positive r_m values (0.12 to 0.14), and indicating population growth (Table 4).

At 25 °C, Lanzoni et al. (2004) found a much lower r_m value than in the present study. In the same study, the r_m value for *H. axyridis* was lower than for *H. variegata* (0.114) and slightly higher than for *A. bipunctata* (0.081). Under laboratory conditions, with *M. persicae* as the food source, *H. axyridis* did not show a high r_m value compared to

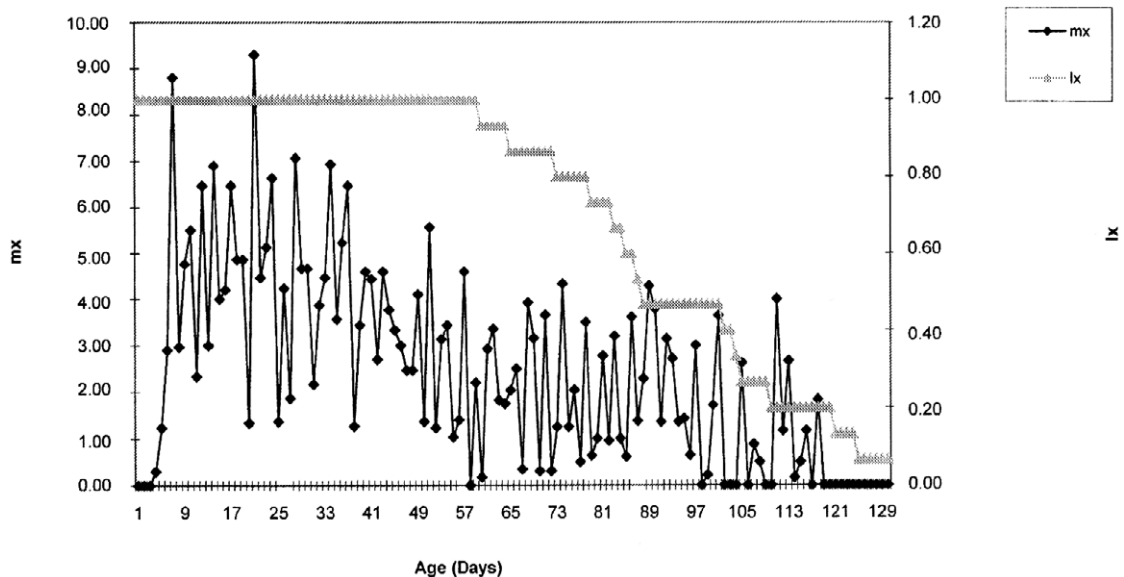


Fig. 3. Survival probability (l_x), expressed in percentage, and specific fertility (m_x) expressed as average number of eggs per day of *Harmonia axyridis* fed on *Cinara atlantica* at 25 °C.

other native coccinellids, such as *Propylea quatuordecimpunctata* L. ($r_m = 0.15$) (Obrycki et al. 1993) and *C. septempunctata* L. ($r_m = 0.19$) (Phoo-folo & Obrycki 1995). Values close to those in the present study were obtained by Abdel-Salam & Abdel-Baky (2001) for females fed with fresh (0.153) and frozen (0.121) *S. cerealella* eggs.

Penteado (2007) obtained r_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_m values were greater than most of the values observed for *C. atlantica*; and this will favor its establishment at certain sites (Penteado 2007).

For a species to be used in biological control, the predator population should increase (Moreira et al. 1995). According to Kiyindou & Fabres (1987), the rate of population increase is very important for comparing the performance of the same species subjected to different environmental conditions and to being fed on different species under similar conditions.

Finite Rate of Population Increase (λ)

The value of λ increased with increasing temperatures, i.e., 1.1275 females/d at 15 °C, 1.1388 females/d at 20 °C, and 1.1502 females at 25 °C (Table 4). Thus, the population increased daily, and progressively more as the temperature increased.

The value of λ confirms the high value of R_0 (net reproductive rate), which shows that the *H. axyridis* population increased strongly from one generation to the next. The capacity for positive

TABLE 4. ESTIMATED LIFE-TABLE PARAMETERS FOR *HARMONIA AXYRIDIS* FED WITH *CINARA ATLANTICA* AT 3 DIFFERENT TEMPERATURES.

Temperature	R_0	T	r_m	λ	DT
15 °C	322.66	46.36	0.12	1.1275	5.78
20 °C	243.09	42.61	0.13	1.1388	5.33
25 °C	278.03	39.48	0.14	1.1502	4.95

R_0 : 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.

population increase suggests that the conditions to which the insects were submitted correspond to a favorable environment for development (Laroca 1995). Nevertheless, various ecological factors can affect the multiplication of this species in the field and reduce the number of offspring. Ecological life tables can be used to evaluate performance under adverse field conditions. Values of close to those in the present study were recorded by Abdel-Salam & Abdel-Baky (2001) for females fed with fresh (1.166) and frozen (1.128) *S. cerealella* eggs.

Population Doubling Time (DT)

The time necessary for the *H. axyridis* population to double in size decreased with increasing temperatures (Table 4). The values obtained by Abdel-Salam & Abdel-Baky (2001) for females fed on fresh (DT = 4.53 d) and frozen (DT = 5.72 d) *S. cerealella* eggs indicates the influence of food on this parameter.

CONCLUSIONS

Temperature is a very important factor and influences the developmental time: a higher temperature results in faster development compared to a lower temperature. Besides the temperature, the type of food and its nutritional quality should also be considered.

To evaluate the risk of introducing exotic species as biological control agents, especially in the case of polyphagous predators, such as *H. axyridis*, information from fertility life tables should be considered together with other information, such as establishment capacity, dispersal ability, host number and direct and indirect effects on non-target organisms. Information on life history and biology is important for understanding the interspecific relationships between native and exotic species.

Under the experimental conditions, *H. axyridis* was able to survive, develop and reproduce normally when fed on *C. atlantica*, at 15 °C, 20 °C and 25 °C. The development was faster at 25 °C for all stages, as well as the total developmental period, whereas at 15 °C, development was the slowest recorded.

The mean values obtained for fecundity and fertility showed a large reproductive capacity with similar parameters recorded at the 3 temperatures, but for the fecundity, the number of eggs per day and the number of eggs per egg mass were significantly higher at 15 °C.

The results of the fertility life tables, together with the biological data, show that *H. axyridis* is a species with a high potential as a biological control agent of *C. atlantica*. However, other criteria should be considered to use biological control agents due the negative impacts, as discussed

earlier in this paper and by Martins et al. (2010) and Kenis et al. (2008).

The temperature of 25 °C was the most suitable for rearing *H. axyridis*, owing to the shorter developmental time and the best results obtained for the fertility life table.

Considering the recent introduction of *H. axyridis* into Brazil and its capacity to invade and establish in new areas, further studies should be undertaken, including field studies, for better understanding of its biology and ecology, its impact and interaction on other predator species, as well as its role in the biological control of economically important aphid pests.

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