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ORIGINAL ARTICLE

Life table parameters of the parasitoid *Cephalonomia tarsalis* (Hymenoptera : Bethylidae) and its host the saw-toothed grain beetle *Oryzaephilus surinamensis* (Coleoptera : Silvanidae)

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Abstract

Biological parameters of the larval parasitoid *Cephalonomia tarsalis* (Ashmead) (Hymenoptera : Bethylidae) and its host the saw-toothed beetle *Oryzapehilus surinamensis* (L.) (Coleoptera : Silvanidae) were studied in the laboratory. The duration of the immature period, survival during development, as well as adult longevity and the number of progeny of both insects were recorded. Our data were used for the estimation of several demographic parameters and life table construction of both the host and the parasitoid. The wasp managed to complete its development (egg – adult) in 19.8 days at 25°C, whereas the adult female lived for 24.3 days. The host *O. surinamensis* demonstrated a longer developmental period (30.5 days) and adult female longevity (103.0 days). Female wasps laid an average of 66.4 eggs throughout their lifetime whereas their beetle hosts laid five times more eggs (313.9). Life table parameters of *C. tarsalis* were estimated for the first time. The intrinsic rate of natural increase (r_m) was 0.124 which was almost double that of its host (0.056). Our results are discussed on the basis of evaluating and improving the performance of *C. tarsalis* as a biocontrol agent against *O. surinamensis* in storage facilities.

Keywords: biological control, demography, intrinsic rate of increase, stored products

Introduction

Serious quantitative and qualitative losses are recorded every year during the storage period of many agricultural products, as a consequence of infestation by more than 600 species of beetle pests, 70 species of moths and about 355 species of mites (Rajendran 2002). In grain commodities, the most important stored products, insect infestation and contamination are important quality control problems. The control of pests in stored grain today is mainly chemical, based on applications of fumigant and residual insecticides (Zettler and Arthur 2000; Heaps 2006). However, several biological, environmental, economic and sociological factors are causing a gradual shift from chemical-based pest management to integrated pest management by utilizing other methods such as biological control (Arbogast 1984; Brower *et al.* 1996; Schöller *et al.* 1997, 2006; Flinn and Schöller 2012).

Insect pests of stored products are attacked by many groups of natural enemies, such as predatory insects and mites, parasitoids, vertebrates, and pathogenic microorganisms. Parasitic wasps are natural components of storage ecosystems and the most promising biocontrol agents against stored product pests. Research during the last 30 years has developed mass rearing as well as release methods for many hymenopteran parasitoids and their efficacy in controlling storage pests has been demonstrated (Flinn and Hagstrum 2001; Phillips and Throne 2010; Flinn and Schöller 2012; Adarkwah *et al.* 2014).

However, their practical application for the control of stored product pests remains very limited, mainly because of the very low (zero tolerance) economic injury level of many stored products. Furthermore, wasps are slow-acting, which may limit their use in

products intended for export. They also may give insufficient control where high pest infestations have already occurred (Schöller *et al.* 2006). Therefore, optimization of biological control methods is essential for their practical implementation. In order to achieve that goal more detailed studies on the biology and ecology of parasitoids of stored product pests should be carried out.

The bethylid *Cephalonomia tarsalis* (Hymenoptera Bethylidae) is a larval ectoparasitoid of beetle pests of stored products, mainly of the genus *Oryzaephilus* spp. (Amante *et al.* 2017). It has been the subject of a few morphological (Howard 1998), ecological (Johnson *et al.* 2000; Lord 2001, 2006; Žďárková *et al.* 2003; Zimmermann *et al.* 2008; Latifian *et al.* 2011), biological (Lukáš and Stejskal 2005; Lukáš 2007, 2008; Eliopoulos *et al.* 2016; Eliopoulos and Kontodimas 2016) and behavioral studies (Howard *et al.* 1998; Cheng *et al.* 2003, 2004; Collatz and Steidle 2008; Collatz *et al.* 2009; Schmid *et al.* 2012). Until very recently, it has not been thoroughly evaluated as a biocontrol agent, although it is the major natural enemy of the saw-toothed grain beetle *O. surinamensis*, a very common pest of many agricultural stored products. Despite its common presence in storage facilities this wasp is regarded as a "poor" biocontrol agent, given that significant beetle infestation occurs even in cases where the wasp population is very high (Powell 1938; Eliopoulos *et al.* 2002).

We used a life-table approach in order to explain this phenomenon. Life tables are an indispensable tool for biological control workers, especially in evaluating a biocontrol agent against a pest under various conditions (Birch 1948; Bellows *et al.* 1992; Jervis and Copland 1996; Pilkington and Hoddle 2007; Kakde *et al.* 2014; Tuan *et al.* 2015), but also in enhancing mass rearing methods (Portilla *et al.* 2014). Such demographic data can be very useful for choosing the most effective biocontrol agents, designing mass rearing programs as well as deciding the timing of introduction in inoculative releases.

The aim of this study was to estimate and evaluate specific demographic and life table parameters of the wasp as a basis for improving mass rearing and release programs. This may allow us to manipulate this beneficial wasp in a more efficient way in order to enhance its ability to control *O. surinamensis* in storage facilities.

Materials and Methods

Insect cultures

Oryzaephilus surinamensis was kept in cultures in the laboratory using a mixture of broken wheat : rolled oats : dried yeast (5 : 5 : 1). The wasp was kept in culture using the rearing medium of the beetle, with a large number of full-grown host larvae. Small pieces of corrugated paper were put in the wasp culture in order to be used as "shelters" by female wasps (Powell 1938; Eliopoulos *et al.* 2016; Eliopoulos and Kontodimas 2016). All insect cultures were kept under controlled environmental conditions [25 ± 1°C, 60–65% relative humidity (RH), total darkness].

Experimental procedure

Duration and survival of pre-imaginal development as well as adult longevity and the number of progeny of the wasp and its host were recorded for the estimation of several demographic parameters and life table construction.

Oryzaephilus surinamensis: Eggs were collected from ~50 female beetles confined with a small quantity of food (~10 gr) for 24 h. One egg and one rolled oat were placed in a small plastic vial (1.2 × 2.3 cm). A hole in the cap covered with fine mesh provided ventilation. Vials were held under the same conditions as the stock culture and were checked daily (twice a day for the egg stage). Any changes of the developmental stage or death of experimental individuals were recorded until adult eclosion. Fifty eggs (replications) were used to record the development.

To collect females of *O. surinamensis*, we collected pupae from stock cultures and checked them daily for adult emergence. Each newly emerged female was transferred to a small plastic Petri dish (6 cm diameter) with three males from the culture (1–3 weeks old), and a few rolled oats. Sex separation of collected adults was achieved by morphological characters of the hind leg. Males, but not females, have the posterior margin of the hind trochanter and the upper margin of the hind femur medially with a spine-like projection (Olsen 1977; Bousquet 1990; Mason 2003).

Once a week, living males and the female were transferred to an identical Petri dish with new food. Old dishes were examined for eggs or newly hatched larvae. Progeny production was recorded until the death of the parental female. Dead males were replaced until the death of the female. Twenty-seven replications (females) were used for estimation of demographic parameters.

Cephalonomia tarsalis: Data on the duration of developmental stages at 25°C were adopted from a recent study of the first author on the same stock culture of *C. tarsalis* (Eliopoulos *et al.* 2016).

To collect females of *C. tarsalis*, we collected pupae (cocoons) from stock cultures and checked them daily for adult emergence. Newly emerged females were transferred to small plastic Petri dishes (6 cm diameter)

with one male from the culture (2–5 days old), small pieces of corrugated paper to be used as shelters, and an excess number of hosts (10–15). The female was transferred daily to an identical Petri dish with new hosts and shelters. Dead males were replaced until the death of the female. Progeny production (male and female offspring) was recorded until the death of the parental female. Ten replications (females) were used.

Life table construction

Data regarding the number of progeny, duration and survival of pre-imaginal development of tested insects were combined for the estimation of several demographic parameters and life table construction. The estimated parameters were: the intrinsic rate of natural increase (r_m), the net reproductive rate (R_o), the mean generation time (G), the finite capacity of increase (λ), the gross reproductive rate (GRR), the doubling time (DT), the reproductive value (V_x) and the life expectancy (e_x). Their calculation was conducted according to the equations presented in Table 1. Equations and the life table construction method were adopted from Birch (1948) and Jervis and Copland (1996). For all estimated parameters raw data were used.

Statistical analysis

Development data were subjected to analysis of variance with $\alpha = 0.05$. Our data had been previously tested for assumptions of normality of distribution and homogeneity with SPSS v.24.0 (IBM 2016). Means were separated using the Tukey-Kramer HSD Test (Sokal and Rohlf 2012). Statistical analysis was performed using the statistical package JMP (SAS 2007).

Results

The duration and survival of immature stages of the wasp and its host are presented in Table 2. It can be clearly seen that the development of the wasp and its host lasted almost 20 and 30 days, respectively. For this reason, during life table construction we assumed that all wasps emerged on the 20th day after oviposition, and beetles on the 30th. The duration of developmental stages differed significantly between the wasp and its host in all cases (egg: $F_{1,91} = 518.2951$, $p < 0.001$, larva: $F_{1,80} = 1019.3940$, $p < 0.001$, pupa: $F_{1,74} = 275.9739$, $p < 0.001$, total: $F_{1,73} = 527.7761$, $p < 0.001$).

Table 1. Demographic parameters of *Cephalonomia tarsalis* and *Oryzaephilus surinamensis* estimated during the present study

Parameters	Explanations and formulas
x (days)	Age class of females from egg stage
n_x	Number of surviving females entering age class x
ℓ_x	Probability to survive from birth to the beginning of age class x
m_x (females/female/day)	Mean number of female progeny per female of age class x
R_0 (females/female/generation)	R_0 (net reproductive rate) $= \sum \ell_x m_x$
G (days)	G (mean generation time) $= \frac{\ln R_0}{r_m}$
λ (females/female/day)	λ (finite capacity of increase) $= e^{r_m}$
DT (days)	DT (doubling time) $= \frac{\ln 2}{r_m}$
r_m (females/female/day)	$\sum \ell_x m_x e^{-r_m x} = 1$
V_x	V_x (reproductive value) $= \frac{\ell_t}{\ell_x} m_t$ where $m_t = \sum_x^w m_x$ and $\ell_t = \sum_x^w \ell_x$
e_x (days)	e_x (life expectancy) $= \frac{T_x}{L_x}$ where $T_x = \sum L_x$ and $L_x = \frac{\ell_x + \ell_{x+1}}{2}$
GRR (females/female/generation)	GRR (gross reproductive rate) $= \sum m_x$

Table 2. Duration of development in days (mean ± S.E.) of *Cephalonomia tarsalis* and its host *Oryzaephilus surinamensis* (25 ± 1°C, 60–65% RH, total darkness, *n* = 50 eggs)

Insect species	Egg	Larva	Pupa	Total
C. tarsalis[1]	1.6 ± 0.3 a (94.0%) [1–2]	8.0 ± 1.4 a (87.2%) [6–12]	10.2 ± 1.3 a (95.1%) [9–14]	19.8 ± 2.2 a (78.0%) [16–28]
O. surinamensis	4.3 ± 0.8 b (92.0%) [3–5]	20.7 ± 2.2 b (89.1%) [17–23]	6.1 ± 0.9 b (90.2%) [5–8]	30.5 ± 1.8 b (72.0%) [26–34]

Means of the same column followed by different letters were significantly different (Tukey – Kramer HSD, α = 0.05)
[1]data from Eliopoulos and Kontodimas (2016)
() – % survival during the developmental stage
[ ] – maximum and minimum value

Reproductive performance of experimental adults during the present study is presented in Table 3. Female wasps laid 40–92 eggs during their lifetime and more than half of them resulted in female progeny (sex ratio 53–60%). On the other hand, the beetle host demonstrated almost quintuple mean fecundity ($F_{1,35}$= 120.4836, $p < 0.001$) and female production ($F_{1,35}$ = 113.1871, $p < 0.001$), compared to its natural enemy, laying 313.9 eggs/female resulting in 161.4 female offspring during its lifetime. Females of *O. surinamensis* lived significantly longer (103.0 days) than their hosts ($F_{1,35}$ = 36.6373, $p < 0.001$).

Life table parameters of the two species are presented in Table 4. The intrinsic rate of increase of *C. tarsalis* and *O. surinamensis* reached 0.124 and 0.056 females/female/day, respectively, under our experimental conditions. Survival rate (l_x) and age-specific fecundity (m_x) of experimental adults are depicted in Figure 1. Adult wasps initiated ovipostion from the first day of their adult life, lived up to 42 days and produced eggs throughout almost their entire lifetime. On the other hand, *O. surinamensis* females needed a pre-oviposition period of 6–10 days, lived up to 175 days (from egg to death) with long living beetles (>130 days) ceasing oviposition 36–49 days before their death.

Wasp life expectancy (e_x) and reproductive value (V_x) presented maximum values (22.9 and 1346.9, respectively) in the stage of newly-emerged adults and decreased with wasp age thereafter (Fig. 2). Maximum values of respective parameters for the host were estimated to be 11.75 (life expectancy of 14 day old adults) and 369.17 (reproductive value of 7 day old adults).

Discussion

Data regarding the biology of *C. tarsalis* are rare in the literature. Czech researchers reported that the wasp completed its development (from egg to adult) in 16.7 days at 24°C and that the mean longevity of females varied from 43 days at 30°C to 82 days at 21°C. They

Table 3. Longevity and progeny of adults of tested insects (25 ± 1°C, 60–65% relative humidity, total darkness, *n* = 10)

Insect species	Initial number of females	Female longevity (days)	Progeny (eggs/female)	Female offspring (females/female)	Sex ratio (females/total)
Cephalonomia tarsalis	10	24.3 ± 9.8 a [10–42]	66.4 ± 18.0 a [40–92]	38.1 ± 10.7 a [21–52]	0.57 ± 0.02 [0.53–0.60]
Oryzaephilus surinamensis	27	103.0 ± 36.7 b [27–175]	313.9 ± 68.4 b [130–399]	161.4 ± 34.0 b [71–206]	0.52 ± 0.02 [0.48–0.55]

Means of the same column followed by different letters were significantly different (Tukey – Kramer HSD, α = 0.05)
C. tarsalis was daily supplied with 10–15 host larvae and paper oviposition shelters
[ ] – maximum and minimum value

Table 4. Life table parameters of *Cephalonomia tarsalis* and *Oryzaephilus surinamensis*

Insect species	*n*	r_m	R_o	*G*	λ	*GRR*	*DT*
C. tarsalis	10	0.124	29.42	27.27	1.13	55.20	5.59
O. surinamensis	27	0.056	20.15	53.05	1.06	26.30	12.24

n – number of tested females; r_m – intrinsic rate of natural increase (females/female/day); R_o – net reproductive rate (females/female/generation); *G* – mean generation time (days); λ – finite capacity of increase (females/female/day); *GRR* – gross reproductive rate (females/female/generation); *DT* – doubling time (days); *C. tarsalis* was daily supplied with 10–15 host larvae and paper oviposition shelters

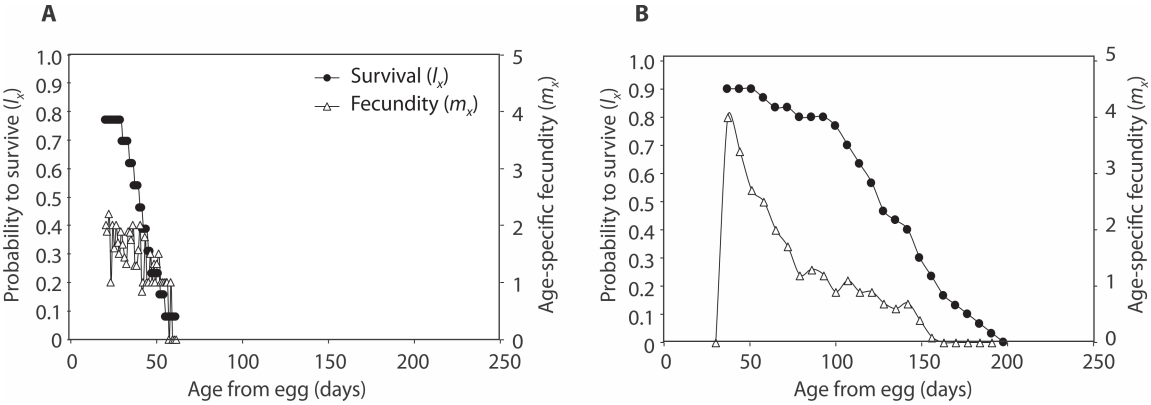

Fig. 1. Survival rate (l_x) and female fecundity (m_x) of *Cephalonomia tarsalis* (A) and *Oryzaephilus surinamensis* (B) adults

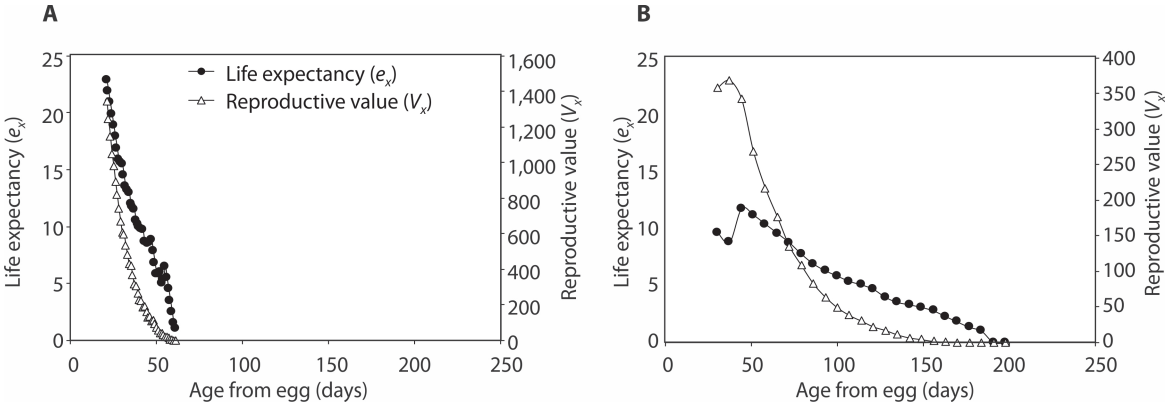

Fig. 2. Life expectancy (e_x) and reproductive value (V_x) of *Cephalonomia tarsalis* (A) and *Oryzaephilus surinamensis* (B) adults

also found a mean fecundity of 110 eggs per female at 27°C to 32 eggs per female at 21°C and a sex ratio of 0.66 at 24°C (Lukáš and Stejskal 2005; Lukáš 2007, 2008). It is evident that these results vary notably with the respective values of the present study. The differences between our results and those of the above-mentioned studies are possibly due to differences in the geographic origin of the wasps and host populations (Czech Republic, Greece). It is well documented that geographic variation can greatly affect parasitoid reproductive performance and that parasitoids from different populations are adapted to region-specific circumstances (Kraaijeveld and Wel 1994; Jervis and Copland 1996).

In contrast, the beetle host *O. surinamensis* has been studied in the past feeding on various commodities. Its total developmental period lasted 20.5 (Arbogast 1976), 23.2 days (Curtis and Clark 1974) or 22.8–29.7 days at 32.5°C on surtees (Komson 1967). Individuals of a pesticide susceptible strain of the beetle completed their development in 34.2 days at 25°C on kibbled wheat (Beckett and Evans 1994), whereas other strains, under the same conditions, had a total immature period of 24.9–30.2 days (Flemming 1988) and 30.9–37.1 days (Jacob and Flemming 1989). Similar results (total developmental period: 30.5 days at 25°C on rolled oats)were obtained in the present study. Any differences may be attributed to different experimental conditions (temperature, food, relative humidity, insect strain) that may affect an insect's immature development.

It is the first time that life table parameters have been estimated for *C. tarsalis*. Thus, this study broadens our knowledge on its biology. The innate capacity for an increase of *C. tarsalis* per week was estimated to be 0.835 during the present study (0.1193 per day) and is notably different (almost double) from its host. Theoretically, this should ensure that *C. tarsalis* would be able to control its host populations in storage facilities, a fact that has not been verified under real conditions (Powell 1938; Eliopoulos *et al.* 2002). However, it should always be kept in mind that values of life table parameters are almost always decreased in natural settings where the wasps are less confined and densities of hosts are lower, thereby reducing host discovery rates.

Collins *et al.* (1989) reported that r_m values of six populations of *O. surinamensis* ranged from 0.679 to 0.848 females/female/week at 30°C and 55% RH, while Arbogast (1976) estimated a weekly r_m 0.733 at 30°C and 74% RH. Our results indicate a notably lower r_m

value of *O. surinamensis* (0.0566 per day or 0.3962 per week). The main reason for this variation may be the different strains of *O. surinemensis* tested in the abovementioned studies. Several strains of the saw-toothed grain beetle have demonstrated different biological characteristics such as developmental period, immature mortality, adult longevity and fertility, etc. (Collins *et al*. 1989; Jacob and Fleming 1989, 1990; Beckett and Evans 1994).

Newly emerged adults of *C. tarsalis* demonstrated maximum values of both e_x and V_x meaning that these individuals will not only live longer but they will also offer more progeny to the next generation than their conspecifics of other age classes. A practical interpretation of this conclusion may be that newly emerged adults are the ideal individuals for inoculative release, taking into account that control is achieved not only by released wasps but mainly by their offspring.

Conclusions

In conclusion, we have theoretically verified that *C. tarsalis* is intrinsically capable of suppressing its hosts as revealed by the rm values. However, we also believe that a more complete evaluation of the potential of this wasp as a biological control agent of *O. surinamensis* requires additional information about behavior and host discovery rates under real conditions. Apart from that, the original findings of the current study provide information that will help to facilitate releasing programs of *C. tarsalis*. In inoculative releases, an effort should be made for the introduction of newly emerged wasps because they not only live longer but also produce more progeny than older conspecifics.

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