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Survival analysis and demographic parameters of the pupal parasitoid *Coptera haywardi* (Hymenoptera: Diapriidae), reared on *Anastrepha fraterculus* (Diptera: Tephritidae)

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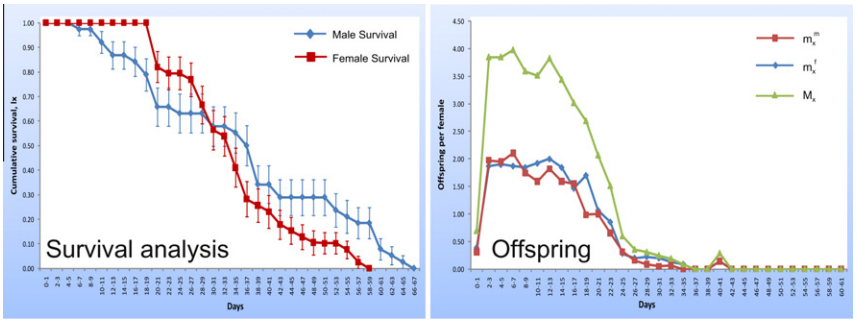
HIGHLIGHTS

- Demographic, reproductive and survival parameters of *Coptera haywardi* reared on *Anastrepha fraterculus* are shown.
- Data showed that *C. haywardi* is suitable for use as a biocontrol agent against *A. fraterculus.*
- The parametric survival analysis is essential for modeling host–parasitoid interaction.

GRAPHICAL ABSTRACT



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ABSTRACT

Coptera haywardi is an idiobiont pupal parasitoid of Tephritidae, and native to the Neotropical region. A survival analysis using a parametric survival fit approach was performed to generate survival curves and information relevant to mass rearing for augmentative biological control. Survival data for both male and female individuals were fitted to several distributions (Weibull, exponential, loglogistic, and lognormal), and the survival functions were described by means of distribution parameters selected *a priori*. Parasitism rates, adult parasitoid emergence rates, pre-oviposition and oviposition periods, sex ratio, longevity, and standard life table parameters were also determined.

This study is an initial attempt to document the demography of *C. haywardi* reared on the damaging and economically important South American fruit fly *Anastrepha fraterculus*.

The results of the study showed that *C. haywardi* reached ~7% of daily parasitism, with a female mean lifetime survivorship of 32.52 days and a high net reproduction rate of 17.10. The demographic parameters found for *C. haywardi* were similar to those recorded for other fruit fly parasitoid species already used with positive results against Tephritidae in augmentative biocontrol programmes.

We conclude that *C. haywardi* is potentially suitable for mass-rearing to be use in augmentative biological control programmes of *A. fraterculus.*

1. Introduction

Most studies on animal survival are based on standard life tables, which show the number of individuals that have survived to different stages of their life cycle along with reproductive output (Bellows, 1999). A life table is a convenient starting point for

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understanding some demographic features, but it should only be viewed as a tool for beginning a more general exploratory analysis of survival (Fox, 2001).

In this context, failure-time methods, a statistical approach to the analysis, summarize and presentation of survival data, have several important advantages over classic life tables. They allow data to be compared at different time scales, they do not assume that the failure times of a group are normally distributed, and they can hold censored data. Moreover, they permit standardization of information about survival curves, thus allowing comparison with other work that has been carried out using similar methods (Fox, 2001).

The present study focuses on the fruit fly parasitoid *Coptera haywardi* (Ogloblin), an idiobiont pupal parasitoid that attacks its host after pupation in the soil (López et al. 1999; Guillén et al. 2002, Baeza Larios 2002, Ovruski et al., 2000). This diapriid is a native hymenopter of the Neotropical region. It was originally described in Argentina, where it was found to attack both *Anastrepha fraterculus* (Wiedemann) and *Anastrepha schultzi* Blanchard (Loiácono, 1981). *C. haywardi* has also been recovered from *A. obliqua* (Loew) pupae in central México (López et al., 1999), from *Anastrepha serpentina* and *Anastrepha striata* Schiner in Venezuela (García and Montilla, 2001), and from *A. fraterculus* and *Anastrepha sororcula* Zucchi in Brazil (Aguiar-Menezes et al., 2003). These hosts are all major agricultural pests. Nevertheless, there is little biological information on *C. haywardi* in association with *A. fraterculus*. Previous studies have provided data on the development of *C. haywardi* reared in irradiated and unirradiated pupae of the Caribbean fruit fly (*Anstrepha suspensa*) and the Mediterranean fruit fly (*Ceratitis capitata*) (Menezes et al., 1998), bionomics using *Anastrepha suspensa* as host (Sivinski et al., 1998), the ability to locate and attack pupae of *C. capitata* under seminatural conditions (Baeza-Larios, 2002), and performance under different soil conditions using *Anastrepha ludens* pupae (Guillén et al., 2002). Recent studies have described colonization and domestication methods under laboratory conditions (Aluja et al., 2009), and rearing on irradiated *A. ludens* pupae (Cancino et al., 2009). Such studies indirectly refer to survival, development, parasitism rate and demographic parameters, but they have not addressed the topic systematically.

Unlike other fruit fly pupal parasitoids from Argentina, such as *Pachycrepoideus vindemmiae* (Rondani), *Trichopria anastrephae* (Costa Lima), *Pachyneuron* sp., and *Spalangia* sp., (Ovruski et al., 2000), *C. haywardi* is only known to parasitize the pupae of Tephritidae (Sivinski et al., 1998). This biological feature turns *C. haywardi* into a potential fruit fly control agent, owing to the reduced risk of negative effects on non-target hosts (Baeza-Larios et al., 2002, Guillén, 2002, Aluja et al., 2009).

In Argentina, two economically important fruit fly species are the chief causes of fruit damage. These species are the exotic *C. capitata* (Wiedemann) (Mediterranean fruit fly or Medfly), and the native *A. fraterculus* (Wiedemann) (South American fruit fly) (Aruani et al., 1996). These two tephritid species are responsible for approximately 15 to 20% of the losses caused by direct damage in Argentinean fruit production (Guillén and Sanchez, 2007). The gross value of these direct losses for citrus alone has been estimated to reach 75 million USD annually. Further indirect losses result from export restrictions imposed by countries free of these pests, and costs related to control programmes (Guillén and Sanchez, 2007).

Biological control by means of parasitoid releases integrated into a fruit fly pest management programme (Aluja and Rull, 2009) is a valid alternative for use against both *A. fraterculus* and *C. capitata* in Argentinean fruit-growing areas. *C. haywardi* is currently being studied under laboratory and field conditions as a possible biological control agent against both damaging tephritid species in Argentina. To provide new biological information on *C. haywardi*, we determined population increasing and reproductive parameters under rearing conditions using *A. fraterculus* pupae as host, by performing a standard life tables. In addition, a detailed survival analysis by failure time approaches was developed. Such information is useful to establish ideal mass-rearing conditions, to define efficient release times, and to predict survival in the field for the proper timing of release intervals to maximize the impact of the parasitoid on the target pest populations.

2. Materials and methods

2.1. Insect rearing

The study was performed at the Laboratorio de Investigaciones Ecoetológicas de Moscas de la Fruta y sus Enemigos Naturales (LIEMEN) of the Planta Piloto de Procesos Microbiológicos Industriales y Biotecnología (PROIMI), located in San Miguel de Tucumán, Argentina. *Coptera haywardi* was successfully reared under artificial conditions using laboratory-reared *A. fraterculus* pupae at 25 ± 1 °C, 75 ± 5% RH, and a 12:12 (L:D) h photoperiod. *C. haywardi* adults were held and exposed to pupae inside Plexiglass cages (30x30x30 cm) and were provided with honey and water *ad libitum*. Naked pupae were exposed to parasitism every other day in plastic Petri dishes 12 cm in diameter for a 48 h period. After exposure, pupae were placed in plastic containers (8 cm in diameter, 5 cm deep) with a 1 cm-vermiculite layer as pupation substrate and kept inside cages until the adults emerged. *Anastrepha fraterculus* were reared following methods described by Vera et al. (2007). The *C. haywardi* cohort used in the experiment was in its 22nd generation of artificial rearing.

2.2. Experimental procedure

Thirty-nine *C. haywardi* pairs (female-male) less than 24 h old were individually placed into transparent plastic cages (7 × 14 × 10 cm) with 30 laboratory-reared *A. fraterculus* 1–2-d old pupae. Pupae were placed inside a plastic Petri dish (6 cm in diameter, 0.8 cm in depth) and exposed to parasitoids for a 24 h period. Pupal exposure was conducted every other day until all female parasitoids died. The parasitoids were given honey and water every day. After each exposure, the host pupae were placed in plastic containers (8 cm in diameter, 5 cm in depth) with a 1 cm-vermiculite layer as pupation substrate and were kept inside the dishes until the adults emerged. At the time of adult emergence, the number and sex of parasitoids, flies, and non-emerged pupae were recorded. Two weeks after the last parasitoid emerged, unemerged fly pupae were dissected to determine the presence of adult and preimaginal stages of *C. haywardi*. The experiment was performed under environmental conditions similar to those described for laboratory parasitoid rearing.

2.3. Parasitism, emergence rate, pre-oviposition and oviposition periods, sex ratio, longevity and life table parameter determination

The overall percentage of pupal parasitism was calculated as the number of emerged and unemerged parasitoids divided by the total number of pupae offered to females, multiplied by 100. The daily mean parasitism was also calculated in this way. The proportion of emerged parasitoids was calculated by dividing the number of adult parasitoids by the total number of parasitized pupae. The mean pre-oviposition period was estimated as the mean number of days between female emergence and the first oviposition day, and the oviposition period was estimated as the mean number of days between the first and last oviposition. The

post-oviposition time was calculated as the mean of days from the last oviposition and the female death.

The overall sex ratio of the parasitoid progeny was estimated as the total number of females divided by the total number of males emerged throughout the entire parental female's lifetime. The daily sex ratio was estimated by dividing the number of females emerging daily by the number of males emerging daily. For each couple, the female and male lifespans were also recorded. A standard life table was constructed to obtain the following basic biological parameters: the survival fraction (l_x), survival period (p_x), mortality period (q_x), fraction of the original cohort dying at age x (d_x), life expectancy (e_x), female and male offspring per female at age x (m_x^f and m_x^m, respectively), and gross maternity or number of daughters produced by a female to the next generation (M_x) (Carey, 1993).

2.4. Population increase parameters

The following population increase parameters were calculated from the life-table data: net reproductive rate (Ro), intrinsic rate of natural increase (r), finite rate of increase (λ), mean generation time (T) and doubling time (DT) (Carey, 1993). TABLAVI software (La Rossa and Kan, 2003) was used to estimate these parameters, and the jackknife technique (Tukey, 1958) was applied to obtain the standard error of the mean value for each population parameter. Developmental duration of each immature stage was not estimated, so it was calculated by means of a previous assay as an overall pre-imaginal stage, from 16 individual pupae emergency recorded in order to obtain the mean and de standard error. This pre-imaginal stage period was used into the TAVLAVI software for estimating the population increase parameters.

2.5. Survival analysis

A univariate survival analysis (SAS Institute Inc., 2007) was conducted. To select the density function, we fitted frequency data to four different distributions (Weibull, exponential, loglogistic, and lognormal) (Fox, 2001). Then we compared the four distributions above mentioned selecting the lowest value of the Akaike information criterion (corrected) for choosing the best data fit. As an alternative, we used the index BIC to support the AICc criterion (Akaike, 1974; Burnham and Anderson, 1992, 2004). For the Weibull distribution, we used the alpha–beta parameterization found widely in relevant literature (Nelson, 1990), and for the lognormal distribution we used two parameters, location and scale, corresponding to the mean and standard deviation of the normal distribution of the natural logarithm of the variable time (SAS Institute Inc., 2007). Survival data were modeled following methods outlined in Fox (2001) by using the selected distribution to obtain the parameter estimates of the corresponding function. The mean lifetime probability ($l_{(50)}$) was estimated from the probability density function (PDF) (Lee and Wang, 2003). Standard survival curves with the corresponding male and female standard errors are presented for comparison.

3. Results

The daily mean percentage of parasitism recorded for *C. haywardi* was 6.8% ± 1.21 (mean ± SE) per female, whereas the mean parasitoid emergence percentage was 86.07% ± 6.68. The pre-oviposition period was estimated as 2.5 ± 0.28 days, and the length of the oviposition period was 20.3 ± 1 days over the entire female lifespan, while the post-oviposition time was 9.23 ± 0.99 days. The mean sex ratio was estimated at 0.71 ± 0.08 (female/male). Fig. 1 shows the daily sex ratio. The parasitoid female/male ratios of offspring produced by females between 1–27 d in age were, despite some fluctuations, similar to the overall mean values and progressively decreased until the last oviposition (32–33 days). The immature development time registered for *C. haywardi* was 33.81 ± 0.21 days.

The life table parameters obtained for both male and female parasitoids are shown in the Appendix A. The daily life table expectancy (e_x) for both males and females is shown in Fig. 2. The number of female and male offspring produced per female at age x (m_x^f and m_x^m, respectively) and gross maternity (Mx) are shown in Fig. 3. The greatest production of parasitoid offspring was recorded for 6–7-d-old females.

The results of the increasing population parameter values are shown in Table 1.

Fig. 4 shows the survivorship curve for both sexes and the standard deviation for each survival event. This approach allowed us to

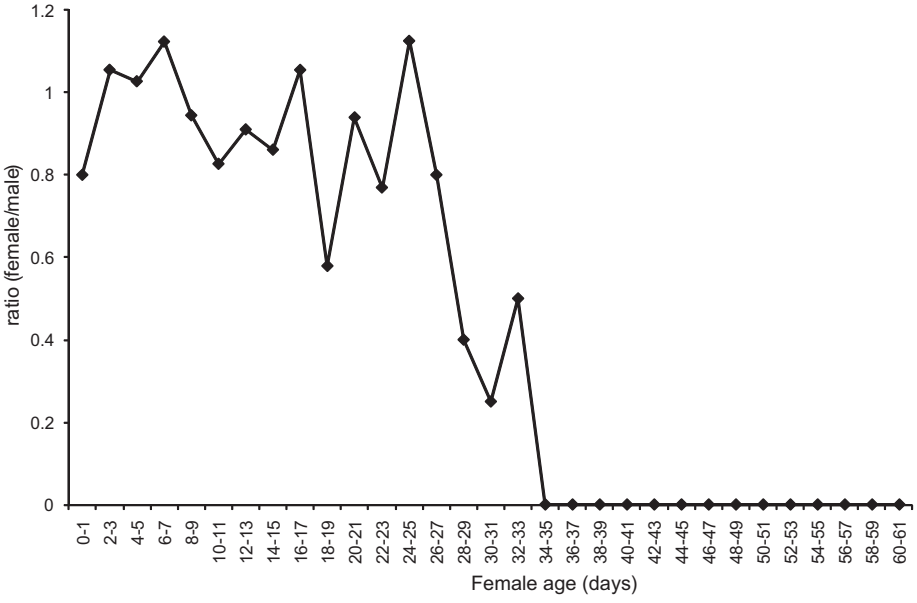

Fig. 1. Daily proportion of the sexes of the offspring (*female*/*male*) across the parental female's lifespan.

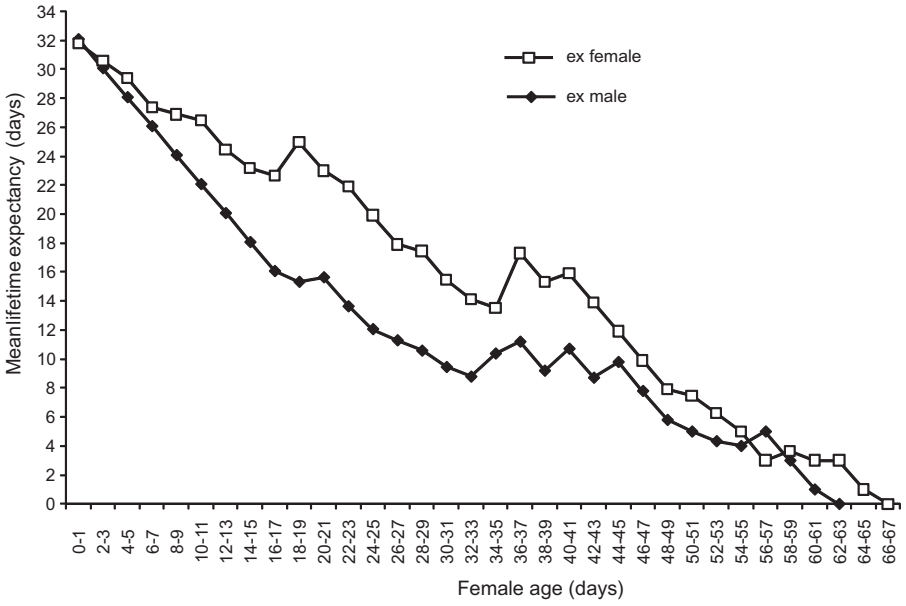

Fig. 2. Daily life expectancy of *C. haywardi* for both sexes.

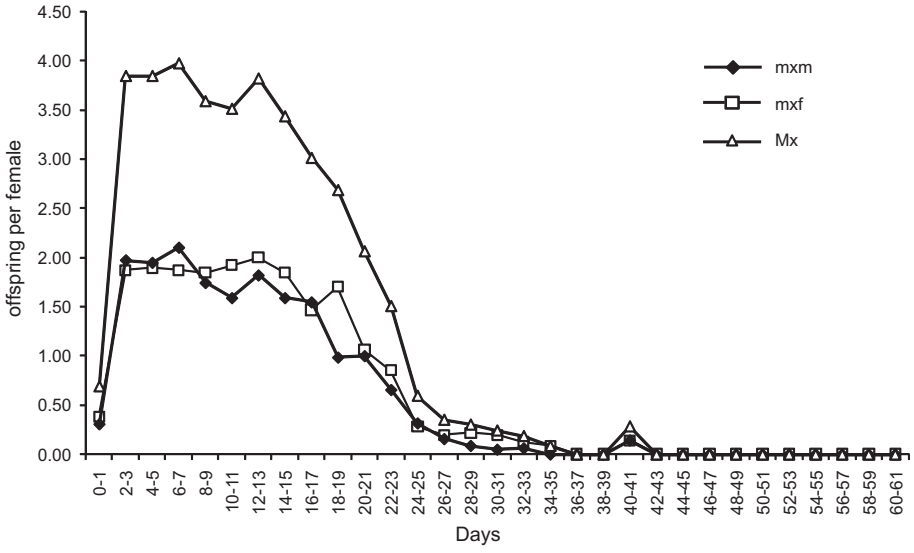

Fig. 3. Daily female (m_x^f) and male (m_x^m) offspring emergence per female and gross maternity (M_x).

visualize a survival range or survival area, rather than a unique survival point for each age.

The values of the AICc and BIC resulting from the comparison of different survival models to select the curve with the best fit for males and females are shown in Table 2.

From Table 2 may by determine that the Weibull distribution gave the best fit to the male survival curve. The parameter estimates obtained were $\alpha = 40.2047 \pm 3.2266$ and $\beta = 2.1264 \pm 0.2813$ (Cramer–von Mises W test of goodness of fit; W–$S = 0.1109$, $p = 0.25$). While, the female survival curve best fitted a lognormal distribution with location = 3.4819 ± 0.0508 and scale = 0.3176 ± 0.0359 (Kolmogorovs D goodness of fit: $D = 0.1165$, $p = 0.15$).

The mean lifetime ($l_{(50)}$) was 33.84 days for males (95% confidence bounds: [28.37, 40.36]) and 32.52 days for females (95% confidence bounds: [29.43, 35.93]).

Table 1
Demographic parameters for *Coptera haywardi*.

Parameters	Estimation (mean ± SE)
Net reproduction rate (*Ro*)	17.1010 ± 1.5013
Finite rate of increase (λ)	1.0744 ± 0.0026
Mean generation time (T)	39.6324 ± 0.4311
Intrinsic rate of increase (r)	0.0719 ± 0.0023
Doubling time (DT)	9.6601 ± 0.3347

4. Discussion

This study is the first to determine the population, reproductive and survival parameters of *C. haywardi* reared on *A. fraterculus* as a host. Cancino et al. (2009) have estimated some population and reproductive parameters of *C. haywardi* reared on irradiated pupae

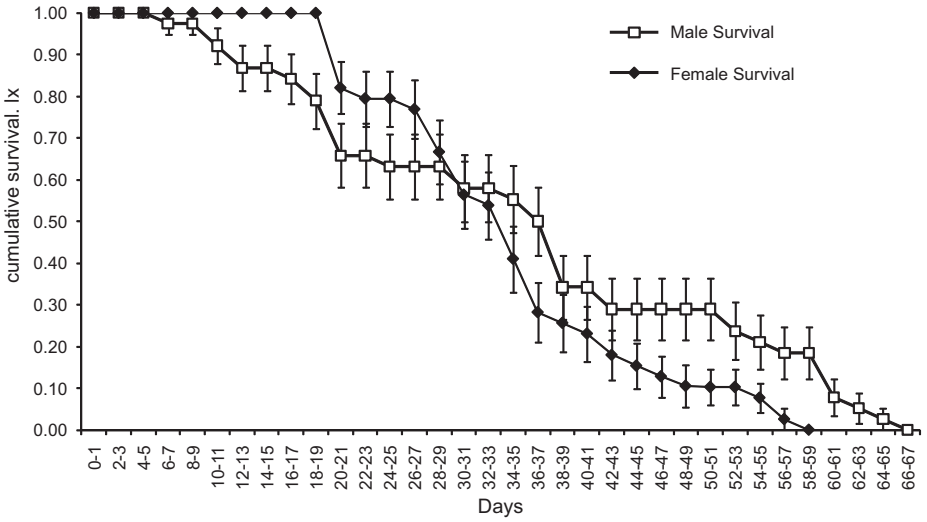

Fig. 4. Survivorship curves for male and female of *C. haywardi*.

Table 2
Comparison of survival models fitted to four different distributions, for male and female *Coptera haywardi* using AICc and BIC indexes.

Distribution	Male survival model fitting		Distribution	Female survival model fitting	
	AICc	BIC		AICc	BIC
Weibull	327,88256	330,81488	Lognormal	297,14942	300,14321
Lognormal	333,87972	336,81204	Loglogistic	298,86213	301,85592
Loglogistic	335,25967	338,19198	Weibull	302,26433	305,25812
Exponential	349,50819	351,03466	Exponential	355,6334	357,18886

of *A. ludens*. Although their study is a very important biological contribution, its specific objective was to determine the fitness of the parasitoids reared on irradiated flies. The scope of their study is narrower than the present. Using the same host, Aluja et al. (2009) have described colonization techniques for seven parasitoid species, including *C. haywardi*. They also recorded some population parameters and survival curves. However, the main focus of their study was to describe colonization techniques.

This study found a higher level of parasitism (6.8%) than the 3.8% and 4.5% obtained by Aluja et al. (2009) for vermiculite-covered and vermiculite-uncovered pupae, respectively. Data on preovipositional and ovipositional periods has never been recorded previously for this species, and this information is thus highly relevant to parasitoid rearing because it allows the efficient determination of the date of exposure of host pupae and of the discard age for adult parasitoids.

The daily sex ratio was estimated at 0.71 female/male, less than one female per male. These values remained nearly constant until the females reached 22–24 days of age. Aluja et al. (2009) and Cancino et al. (2009) have recorded higher values, up to 2–3 females/male.

Differences like those cited above could accompany superparasitism. In other parasitoids, such as *Diachasmimorpha longicaudata*, superparasitism produces a female-biased sex ratio (Gonzalez et al. 2007). Kazimírová and Vallo (1999) have described superparasitism in *Coptera occidentalis*, but superparasitism has not yet been reported in *C. haywardi*, and its possible effects on sex ratio would need to be measured. However, an effect similar to those previously reported could explain differences in the sex ratios found in our study.

The mean life expectancy (33.84 and 32.52 days for males and females, respectively) is essential information for determining the average lifetime of insects in a mass-rearing colony. This information is also needed for determining the release intervals to be used in the field.

The population increase parameters measured in this study, such as net reproductive rate (Ro), the finite rate of increase (λ) and the intrinsic rate of increase (r), had lower values than those found by Aluja et al. (2009).

Three factors could explain the differences between the population parameters of Aluja et al. (2009) and the present work. First, the host/parasitoid proportion was different. The value of parasitoid ratio differed, 0.66:1 (less than one pupa per female) in Aluja et al. (2009) and 30:1 in this work. The relative scarcity of pupae in the former might have resulted in more superparasitism, whereas the lack of host limitation in our study may have allowed the female parasitoids to choose to produce male or female offspring without bias. Second, the two studies used different fly species as hosts. *A. ludens* was used in Aluja et al. (2009), but *A. fraterculus* was used in our study. Finally, quality of the host pupae (i.e., age, size, and diets used for host larva rearing) (Cancino and Montoya, 2008) may have differed between the two studies.

We also obtained population parameters for *C. haywardi* that were similar to those obtained by Cancino et al. (2004) for the pupal parasitoid *P. vindemmiae*, a species that has been used as a biological control agent against *C. capitata* in El Salvador and Costa Rica with satisfactory results (Jimenez, 1967; Camacho, 1994). In addition, Guillen et al. (2002) found that *C. haywardi* is a better forager than *P. vendimmiae*, so this suggest that *C. haywardi* might also be a good candidate for fruit flies biological control. Additionally, *C. haywardi* has the added advantage of being specific to Tephritidae and therefore poses no risk to non-target Diptera. However, studies under field-cage conditions would be needed to achieve deeper insight into the performance of *C. haywardi* as a fruit flies biological control agent.

The values of the population parameters found in this study were also similar to those obtained by Vargas et al. (2002) for the braconid *Fopius vanderboschi* (Fullaway). This larval parasitoid of tephritids has been used successfully against *Bactrocera dorsalis* (Hendel) (Bess et al., 1961; Clausen et al., 1965; Haramoto and Bess, 1970; Nishida, 1953; Stark et al., 1991; Vargas et al., 1993).

The survival data revealed a mean survival time of 32.52 days and an oviposition period of 22.80 days and the last ovipositions occurred at 34–35 days for *C. haywardi*. The fact that all females were able to survive for at least 19 days, and that the oviposition

period ranged between 2.5 and 22.8 days, the maximal pest population suppression in the field would therefore be expected to occur during this period. These data have important implications for mass rearing facilities and parasitoid field releases.

This detailed survival study is the first to be conducted for fruit fly parasitoids using an approach based on the fitting of parametric models. The mathematical description of the survival curve reported here is essential in comparative studies of survival and for the construction of insect interaction models. The parameters resulting from the adjustment of the survival function summarize all the information contained in a life table because survival, density and the hazard function are the three most important functions that characterize a survival distribution.

5. Conclusions

The use of *C. haywardi* is a valid option in augmentative biological control programmes against *A. fraterculus* in Argentina, considering the high parasitism percentage (~7%), the high female survivorship ($L_{(50)}$ = 32.52 days), a long oviposition period (~20 days), and a net reproduction rate of 17.10, together with the specific tendency to attack tephritids (Sivinski et al., 1998) and the ability to avoid hyperparasitism by detecting previously parasitized pupae (Cancino and Montoya, 2008).

The data presented herein are important for optimising the mass rearing of *C. haywardi* using *A. fraterculus* pupae as host. The suitability of this parasitoid has been demonstrated in Mexico, where the parasitoid is already being reared in mass and released in the field against other fruit fly species (Cancino and Montoya, 2008).

The parameter estimates obtained from the survival function will allow the development of interaction models with stochastic values. These models could be used to evaluate the parasitoid as a biological control agent or to draw comparisons with the survival functions obtained for other species or for the same species under different experimental conditions. We hope that statistical techniques like failure-time became wider in scientist literature to describe insect's survival.

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Appendix A

Life table parameters of the parasitoid *C. haywardi*.

Age (d)	Male								Female							
	N	l_x	d_x	p_x	q_x	Lx	T_x	e_x	N	l_x	dx	px	qx	Lx	T_x	e_x
0–1	39	1.0000	0.0256	0.9744	0.0256	1.9744	31.7692	31.7692	39	1.0000	0.0000	1.0000	0.0000	2.0000	32.0769	32.0769
2–3	38	0.9744	0.0256	0.9737	0.0263	1.9231	29.7949	30.5789	39	1.0000	0.0000	1.0000	0.0000	2.0000	30.0769	30.0769
4–5	37	0.9487	0.0000	1.0000	0.0000	1.8974	27.8718	29.3784	39	1.0000	0.0000	1.0000	0.0000	2.0000	28.0769	28.0769
6–7	37	0.9487	0.0513	0.9459	0.0541	1.8462	25.9744	27.3784	39	1.0000	0.0000	1.0000	0.0000	2.0000	26.0769	26.0769
8–9	35	0.8974	0.0513	0.9429	0.0571	1.7436	24.1282	26.8857	39	1.0000	0.0000	1.0000	0.0000	2.0000	24.0769	24.0769
10–11	33	0.8462	0.0000	1.0000	0.0000	1.6923	22.3846	26.4545	39	1.0000	0.0000	1.0000	0.0000	2.0000	22.0769	22.0769
12–13	33	0.8462	0.0256	0.9697	0.0303	1.6667	20.6923	24.4545	39	1.0000	0.0000	1.0000	0.0000	2.0000	20.0769	20.0769
14–15	32	0.8205	0.0513	0.9375	0.0625	1.5897	19.0256	23.1875	39	1.0000	0.0000	1.0000	0.0000	2.0000	18.0769	18.0769
16–17	30	0.7692	0.1282	0.8333	0.1667	1.4103	17.4359	22.6667	39	1.0000	0.0000	0.9231	0.0769	1.9231	16.0769	16.0769
18–19	25	0.6410	0.0000	1.0000	0.0000	1.2821	16.0256	25.0000	36	0.9231	0.0769	0.8611	0.1389	1.7179	14.1538	15.3333
20–21	25	0.6410	0.0256	0.9600	0.0400	1.2564	14.7436	23.0000	31	0.7949	0.1282	1.0000	0.0000	1.5897	12.4359	15.6452
22–23	24	0.6154	0.0000	1.0000	0.0000	1.2308	13.4872	21.9167	31	0.7949	0.0000	0.9677	0.0323	1.5641	10.8462	13.6452
24–25	24	0.6154	0.0000	1.0000	0.0000	1.2308	12.2564	19.9167	30	0.7692	0.0256	0.9000	0.1000	1.4615	9.2821	12.0667
26–27	24	0.6154	0.0513	0.9167	0.0833	1.1795	11.0256	17.9167	27	0.6923	0.0769	0.8889	0.1111	1.3077	7.8205	11.2963
28–29	22	0.5641	0.0000	1.0000	0.0000	1.1282	9.8462	17.4545	24	0.6154	0.0769	0.9167	0.0833	1.1795	6.5128	10.5833
30–31	22	0.5641	0.0256	0.9545	0.0455	1.1026	8.7179	15.4545	22	0.5641	0.0513	0.8636	0.1364	1.0513	5.3333	9.4545
32–33	21	0.5385	0.0513	0.9048	0.0952	1.0256	7.6154	14.1429	19	0.4872	0.0769	0.6842	0.3158	0.8205	4.2821	8.7895
34–35	19	0.4872	0.1538	0.6842	0.3158	0.8205	6.5897	13.5263	13	0.3333	0.1538	0.7692	0.2308	0.5897	3.4615	10.3846
36–37	13	0.3333	0.0000	1.0000	0.0000	0.6667	5.7692	17.3077	10	0.2564	0.0769	1.0000	0.0000	0.5128	2.8718	11.2000
38–39	13	0.3333	0.0513	0.8462	0.1538	0.6154	5.1026	15.3077	10	0.2564	0.0000	0.7000	0.3000	0.4359	2.3590	9.2000
40–41	11	0.2821	0.0000	1.0000	0.0000	0.5641	4.4872	15.9091	7	0.1795	0.0769	1.0000	0.0000	0.3590	1.9231	10.7143
42–43	11	0.2821	0.0000	1.0000	0.0000	0.5641	3.9231	13.9091	7	0.1795	0.0000	0.7143	0.2857	0.3077	1.5641	8.7143
44–45	11	0.2821	0.0000	1.0000	0.0000	0.5641	3.3590	11.9091	5	0.1282	0.0513	1.0000	0.0000	0.2564	1.2564	9.8000
46–47	11	0.2821	0.0000	1.0000	0.0000	0.5641	2.7949	9.9091	5	0.1282	0.0000	1.0000	0.0000	0.2564	1.0000	7.8000
48–49	11	0.2821	0.0513	0.8182	0.1818	0.5128	2.2308	7.9091	5	0.1282	0.0000	0.8000	0.2000	0.2308	0.7436	5.8000
50–51	9	0.2308	0.0256	0.8889	0.1111	0.4359	1.7179	7.4444	4	0.1026	0.0256	0.7500	0.2500	0.1795	0.5128	5.0000
52–53	8	0.2051	0.0256	0.8750	0.1250	0.3846	1.2821	6.2500	3	0.0769	0.0256	0.6667	0.3333	0.1282	0.3333	4.3333
54–55	7	0.1795	0.0000	1.0000	0.0000	0.3590	0.8974	5.0000	2	0.0513	0.0256	0.5000	0.5000	0.0769	0.2051	4.0000
56–57	7	0.1795	0.1026	0.4286	0.5714	0.2564	0.5385	3.0000	1	0.0256	0.0256	1.0000	0.0000	0.0513	0.1282	5.0000

Appendix A (*continued*)

Age (d)	Male								Female							
	N	l_x	d_x	p_x	q_x	*Lx*	T_x	e_x	*N*	l_x	*dx*	*px*	*qx*	*Lx*	T_x	e_x
58–59	3	0.0769	0.0256	0.6667	0.3333	0.1282	0.2821	3.6667	1	0.0256	0.0000	1.0000	0.0000	0.0513	0.0769	3.0000
60–61	2	0.0513	0.0256	0.5000	0.5000	0.0769	0.1538	3.0000	1	0.0256	0.0000	0.0000	1.0000	0.0256	0.0256	1.0000
62–63	1	0.0256	0.0000	1.0000	0.0000	0.0513	0.0769	3.0000	0	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
64–65	1	0.0256	0.0256	0.0000	1.0000	0.0256	0.0256	1.0000								
66–67	0	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000								

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