



# Comparative demography of three neotropical larval-prepupal parasitoid species associated with *Anastrepha fraterculus* (Diptera: Tephritidae)



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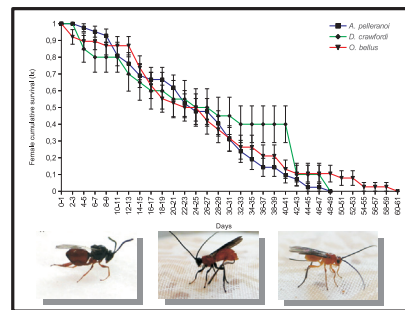
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## HIGHLIGHTS

- Comparative demography and survival of three neotropical parasitoids of fruit fly.
- First detailed studies of parasitoids reared on the native *A. fraterculus* fruit fly.
- We found a possible biological control agent candidate to be reared in mass.

## GRAPHICAL ABSTRACT



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## ABSTRACT

The South American fruit fly, *Anastrepha fraterculus* (Wiedemann), is one of two fruit fly species of economic importance in Argentina, which along with the exotic Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) produce annual losses of nearly US\$ 90 million for fruit production in this country.

Biological control may contribute to integrated approaches to manage both pestiferous species.

Information on survival, reproduction and population growth parameters, critical for successful augmentation of natural enemies, is provided for three fruit fly neotropical parasitoids, *Aganaspis pelleranoi* (Hymenoptera: Figitidae), *Opius bellus* and *Doryctobracon crawfordi* (Hymenoptera: Braconidae). *A. pelleranoi* had the highest intrinsic reproductive rate ( $r$ ), survival time and reproductive time, followed by *O. bellus*. Meanwhile *D. crawfordi* showed the lowest values for reproductive and population growth parameters.

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## 1. Introduction

The South American Fruit Fly *Anastrepha fraterculus* (Wiedemann), is a polyphagous Tephritid that belong to a cryptic species complex (Steck, 1991, 1999; Hernández-Ortiz et al., 2012). Native

of the neotropical region, the complex is distributed throughout continental America from Mexico to Argentina (Norrbon, 2004). Its status as a pest of commercially grown fruit varies depends on region. For example, the Mexican form of *A. fraterculus* is not considered a commercially important pest (Aluja et al., 2003), whereas some of the South American morphotypes cause economic damage to several cultivated, exotic fruit species in Argentina (Ovruski et al., 2003), Brazil (Zucchi et al., 1999), Colombia (Nuñez-Bueno, 1999), and Venezuela (Briceño, 1979).

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Genetic evidence has shown that Argentinean populations of *A. fraterculus* belong to a single biological entity whose range extends to Southern Brazil (Alberti et al., 2002; Rull et al., 2012).

Within Argentina, *A. fraterculus* is mainly restricted to the northern region between 22° and 31°S latitude, where it coexists with the exotic Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann). These two tephritid species breed in a broad range of native and exotic plant species (Ovruski et al., 2003). Commercial fruit infestation levels from both vary between 15% and 20% of overall Argentinian fruit production, which represents an annual loss of nearly US\$ 90 million. This issue is aggravated by the fact that the presence of these two tephritid species limits fresh fruit exports due to quarantine restrictions imposed by importing countries (Guillén and Sánchez, 2007).

There is an increasing interest in development of integrated approaches to management of both *A. fraterculus* and *C. capitata* in the different fruit-growing regions of Argentina, through the use of environmentally friendly practices, sterile flies, natural enemies, biorational bait sprays, and mass trapping (Guillén and Sánchez, 2007). Based on this goal, biocontrol is currently receiving renewed attention in Argentina (Ovruski et al., 2012). Consequently, two lines of investigation are fostered, first, the mass-rearing and augmentative release of the Indo-Pacific species *Diachasmimorpha longicaudata* (Ashmead), and second, studies on colonization and mass rearing of several neotropical parasitoid species (Núñez-Campero et al., 2012). This approach was originally proposed by Aluja et al. (2009a) for the biological control of *A. ludens* (Loew) in Mexico. For this purpose, numerous surveys of the native parasitoids of frugivorous tephritids were performed over the past 12 years in the subtropical rain forests of Northwestern and Northeastern Argentina, locally known as “Yungas” and “Paranaense” forests, respectively. Sixteen parasitoid species have been recorded from those surveys, of which 13 species are indigenous to the Neotropics (Ovruski and Schliserman, 2012). Among these neotropical species, koinobiont solitary larval-prepupal endoparasitoids belonging to the Opiinae (Braconidae) and Eucilinae (Figitidae) are the most commonly found in association with *A. fraterculus* on wild native and exotic host plants (Ovruski et al., 2005, 2008; Schliserman et al., 2010). These parasitoid species include the opiines *Doryctobracon brasiliensis* (Szépligeti), *D. areolatus* (Szépligeti), *D. crawfordi* (Viereck), *Opius bellus* Gahan, and *Utetes anastrephae* (Viereck), the alysine *Asobara anastrephae* (Muessebeck), and the eucilines *Aganaspis pelleranoi* (Brèthes), *Lopheucoila anastrephae* (Rohwer), *Odontosema anastrephae* Borgmeier, and *Dicerataspis grenadensis* Ashmead. From these, *A. pelleranoi*, *O. bellus*, and *D. crawfordi*, which are widespread species that occur from Mexico to Argentina (Ovruski et al., 2000), have been recently colonized on *A. fraterculus* larvae at the PROIMI's Biological Control Laboratory in Tucumán (Northwestern Argentina).

Certain biological features of three of these native parasitoid species were considered promising as potential biological control agents. *A. pelleranoi* is capable of successful development on larvae of either *A. fraterculus* or *C. capitata* (Ovruski et al., 2005) and has the ability to locate the host larvae by entering holes in fruit on the ground (Aluja et al., 2009b). This figitid is able to attack host larvae in a wide variety of fruit species because it is able to attack their hosts from inside the fruit (Wharton et al., 1998) and pest populations can be targeted during periods of extreme susceptibility as overwintering hosts. *O. bellus* has been recorded attacking several *Anastrepha* species and *C. capitata* on diverse host plant species (Ovruski et al., 2000). However, this opiine is more specialized on *Anastrepha* and it mainly forages for hosts on small- and medium-sized native fruits (Ovruski et al., 2004). *Doryctobracon crawfordi* has one of the longest ovipositors of any native *Anastrepha* opiine parasitoid (Sivinski et al., 2001), and was recovered from *Anastrepha* infesting ‘large cultivated fruits’, such as citrus,

mango (Sivinski et al., 2000) and guava (Ovruski et al., 2005). *D. crawfordi*, *O. bellus* and other fruit fly opiine parasitoids remain on the fruit surface searching for host larvae (Sivinski and Aluja, 2003). *D. crawfordi* and *A. pelleranoi* were successfully mass-reared on *A. ludens* in Mexico (Aluja et al., 2009a; Cancino et al., 2009), and *O. bellus* has displayed a relatively rapid adaptation to artificial laboratory conditions in Argentina (Schliserman et al. Unpublished data). The use of native parasitoids as tephritid biocontrol agents has important advantages over the use of exotics, because it prevents negative impacts on non-target hosts (Simberloff and Stiling, 1996; Cory and Meyers, 2000; Pearson and Callaway, 2003), avoids competitive exclusion (Sivinski et al., 1997; Human and Gordon, 1996), and by-passes importation and quarantine protocols (Gates et al., 2002). In addition, native parasitoids are more resistant to local environmental conditions in their natural occurring areas, than exotics ones. (Aluja et al., 1998; Sivinski et al., 2000; Van Driesche et al., 2007). The present paper provides information on the survival, reproductive and population growth parameters of *A. pelleranoi*, *O. bellus*, and *D. crawfordi* in light of their potential for mass-rearing on *A. fraterculus* larvae, and ultimately establishing low *A. fraterculus* prevalence areas in northern citrus-producing regions (Ovruski and Schliserman, 2012).

## 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 (LIE-MEN) of the Planta Piloto de Procesos Microbiológicos Industriales y Biotecnología (PROIMI), San Miguel de Tucumán, Argentina. The three parasitoid species used in the study were successfully reared under artificial conditions using larvae of a laboratory strain of *A. fraterculus* at 25 ± 1 °C, 75 ± 5% RH, and a 12:12 (L:D) h photoperiod. Adult parasitoids were provided with honey and water *ad libitum*, held in Plexiglass cages (30 × 30 × 30 cm), and offered third instar larvae of *A. fraterculus* every other day. After exposure, larvae were placed in plastic containers (8 cm in diameter, 5 cm in depth) with vermiculite (100 cm<sup>3</sup>) as a pupation substrate and kept until the adults emerged. The general *A. fraterculus* rearing procedure was carried out following methods outlined in Vera et al. (2007). The *A. pelleranoi*, *O. bellus* and *D. crawfordi* cohorts used in the experiment were at their 11, 38 and 46 generation under artificial rearing, respectively.

### 2.2. Experimental procedure

Thirty-eight, forty-two and twenty female-male pairs of *O. bellus*, *A. pelleranoi* and *D. crawfordi*, respectively, were individually placed into transparent plastic cages (7 × 14 × 10 cm). Parasitoids were provided with water and honey every other day. Thirty laboratory-reared third-instar *A. fraterculus* larvae (9–10 day-old) were placed inside artificial units and exposed to each parasitoid pair of the three species for 4 h period. The oviposition units consisted of a plastic dish (6 cm diameter, 2 cm high) filled with naked host larvae (without rearing diet) and covered with a piece of organdie cloth. Larval exposure was conducted every other day until all female parasitoids died. After each exposure, the host larvae were placed in plastic containers (8 cm in diameter, 5 cm in depth) with vermiculite (100 cm<sup>3</sup>) as pupation substrate. Puparia were kept inside containers until adult emergence. Once adults emerged, the number and sex of parasitoid offspring, flies, and non-emerged puparia were recorded. Two weeks after the last parasitoid emergence, non-emerged puparia were dissected with the aim of determining the presence of parasitoid adult cadavers or parasitoid

pre-imaginal stages. The experiment was performed under the same environmental conditions to those described for laboratory parasitoid rearing.

### 2.3. Life-table parameters, population increase parameters, fecundity and parasitism

Standard life tables were constructed to obtain the following parameters: the proportion of individuals surviving to start of the age interval ( $l_x$ ), the proportion of individuals surviving through the period ( $p_x$ ), proportion of individuals dying through the period ( $q_x$ ), the fraction of the original cohort dying at age  $x$  ( $d_x$ ), life expectancy ( $e_x$ ), female offspring produced per female at age  $x$  ( $m_x$ ), and the gross reproductive rate (GRR) or number of daughters produced by a female to the next generation (Carey, 1993).

Daily mean parasitism were calculated as the number of emerged and non-emerged parasitoids divided by the total number of pupae offered to females and multiplied by 100.

The mean pre-oviposition period was estimated as the mean number of days between female emergence and the day of the first oviposition. The oviposition period was estimated as the mean number of days between the first and last oviposition. The daily sex ratio was estimated by dividing the number of female offspring by the total number of progeny (males + females) emerged per day and multiplied by 100.

The following population increase parameters were calculated: net reproductive rate ( $R_0$ ) or per generation contribution of new born females to the next generation, intrinsic rate of natural increase ( $r$ ) or rate of natural increase in a closed population, finite rate of increase ( $\lambda$ ) or factor by which a population increases in size from time  $t$  to time  $t + 1$ , mean generation time ( $T$ ) or time required for a new born female to replace herself  $R_0$ -fold (Carey, 1993). For the estimation of these parameters the 'Two-Sex Life Table' software was used; this software allows use of the 'bootstrap technique' (Chi and Liu, 1985; Chi, 1988, 2012; Huang and Chi, 2012) 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 (egg + larvae + pre-pupae + pupae) for each parasitoid species. This pre-imaginal stage period was loaded in the software to estimate the population increase parameters representing the overall life cycle.

### 2.4. Survival analysis

A univariate survival analysis (SAS Institute Inc, 2007) was also conducted. For the selection of the density function, survival frequency data was fitted to different distributions (weibull, threshold weibull, exponential, loglogistic, and lognormal) (Fox, 2001). The distributions above mentioned were compared in order to choose the best data fit by selecting the lowest value of the Akaike information criterion corrected (AICc). As an alternative, we used the BIC index to support the AICc criterion (Akaike, 1974; Burnham and Anderson, 1992; Burnham and Anderson, 2004). Survival data were modelled following methods outlined in Fox (2001) using the selected distribution to obtain the parameter estimates of the corresponding function. The Crámer-von Mises test ( $W^2$ ) was used as boundary of fit test.

The mean lifetime probability ( $lx_{50}$ ) was estimated from the probability density function (PDF) (Lee and Wang, 2003). The survival curves with the corresponding standard errors for male and female of each species studied are also presented.

### 2.5. Statistical analysis of data

Data on parasitism, pre-oviposition and oviposition periods were compared statistically among the three parasitoid species

using nonparametric Kruskal–Wallis tests ( $p = 0.05$ ). The nonparametric Log-Rank and Wilcoxon tests were conducted in order to find differences between survival curves.

## 3. Results

### 3.1. Life-table parameters

The life table parameters recorded for *D. crawfordi*, *A. pelleranoi*, and *O. bellus* are presented in Appendix A. Female life expectancy of the three native parasitoid species ranged between 19.2 and 24.2 days at the time of adult emergence. However, *O. bellus* females showed a higher increase in the life expectancy values at 24–25 age intervals than those recorded from females of both, *D. crawfordi* and *A. pelleranoi* (Fig. 1a). The males' life expectancy for both, *O. bellus* and *A. pelleranoi* had similar initial values to those showed by females (Fig. 1b). In contrast, males of *D. crawfordi* showed the most extreme values for initial life expectancy, although from 38–39 age interval the life expectancy fell below values obtained for *O. bellus* males (Fig. 1b).

### 3.2. Fecundity, oviposition period, parasitism percentage and sex ratio

The highest GRR was obtained for *A. pelleranoi*, which achieved  $35.81 \pm 4.18$  offspring/female, followed by *O. bellus* and *D. crawfordi* with values of  $28.89 \pm 2.27$  and  $5.41 \pm 1.35$  offspring/female respectively. *A. pelleranoi* females began to produce daughters immediately from the 0–1 age interval, while females of both *O. bellus* and *D. crawfordi* did so after the 2–3 age interval (Fig. 2).

The mean daily parasitism percentage recorded for *A. pelleranoi* ( $15.5 \pm 2.6\%$  larvae parasitized/day) was around 3- and 5-times higher than those recorded for *O. bellus* and *D. crawfordi*, respectively ( $K-W$ ,  $df = 2$ ,  $H = 15.28$ ;  $p = 0.0005$ ). Fluctuation of daily

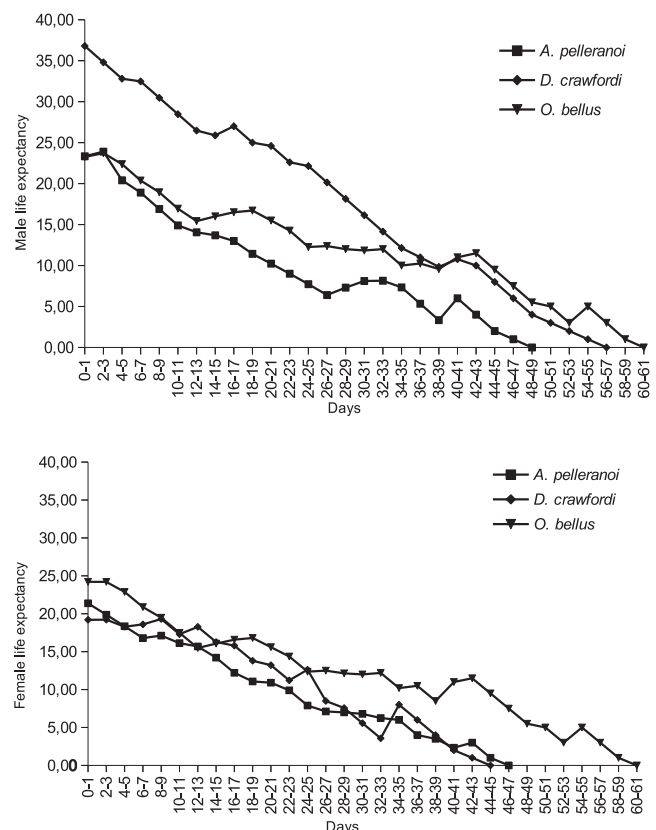


Fig. 1. Comparative life expectancy ( $e_x$ ) for *A. pelleranoi*, *D. crawfordi* and *O. bellus* males and females.

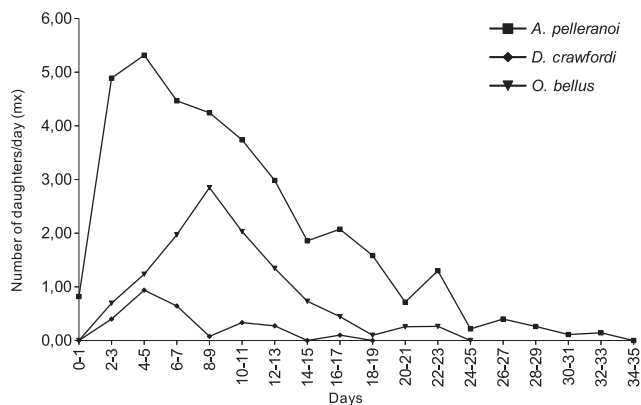


Fig. 2. Daily mean number of daughter produce per adult female of *A. pelleranoi*, *D. crawfordi* and *O. bellus* (mean daily fecundity).

parasitism percentage as a function of the parental female age intervals showed that both *A. pelleranoi* and *D. crawfordi* reached the maximum peak at the 4–5 day age interval, whereas *O. bellus* achieved a maximum peak at the 8–9 day age interval (Fig. 3).

The pre-oviposition period recorded from *A. pelleranoi* was significantly shorter than those obtained from the other two parasitoid species ( $K-W$ ;  $df=2$ ,  $H=26.82$ ,  $p=0.0001$ ) (Fig. 4). The oviposition time recorded from *D. crawfordi* was significantly shorter than that obtained from the other two parasitoid species ( $K-W$ ;  $df=2$ ,  $H=19.64$ ,  $p=0.0001$ ) (Fig. 4).

The daily percentage of daughters produced by a female varied in function of the parental female age interval (Fig. 5). *O. bellus* exhibited female-biased sex ratios from parasitoid female age interval 8–9 to 16–17, whereas *A. pelleranoi* and *D. crawfordi* only showed a female-biased sex ratio for female age classes 2–3 and 10–11, respectively. However, offspring sex ratio produced by the cohort under study of the three parasitoid species throughout their entire life did not reach an equitable proportion, showing an overall male-biased sex ratio, especially in the case of *D. crawfordi* (*A. pelleranoi* 0.74:1, *O. bellus* 0.96:1 and *D. crawfordi* 0.38:1, female:male for the cohort).

### 3.3. Population increase parameters

Population increase parameters recorded from the three parasitoid species are shown in Table 1. *A. pelleranoi* reached the highest  $R_0$  and  $r$  values. The three native parasitoid species showed growing populations, with  $r$  and  $\lambda$  values greater than 0 and 1, respectively.

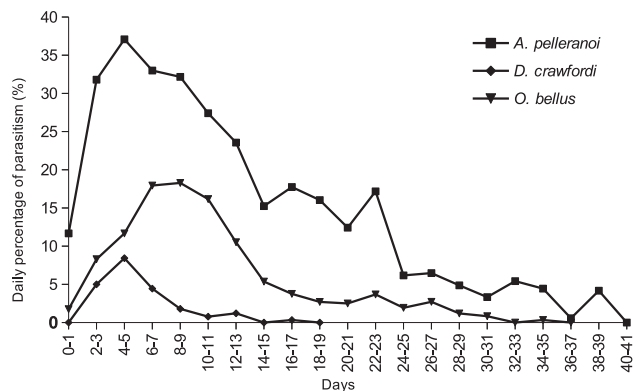


Fig. 3. Mean daily percentage of parasitism recorded for *A. pelleranoi*, *D. crawfordi* and *O. bellus* (mean  $\pm$  SE) after daily exposure of 9–10 day-old *A. fraterculus* larvae during 4 h periods through the females' lifespan.

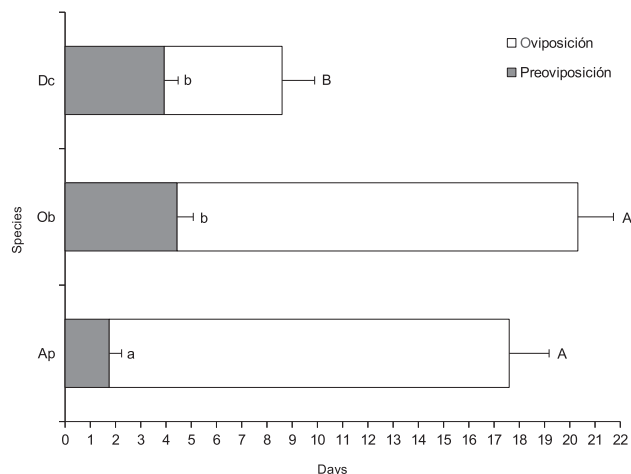


Fig. 4. Length of the pre-oviposition and oviposition period (days) of *A. pelleranoi* (Ap), *D. crawfordi* (Dc) and *O. bellus* (Ob). Significant differences are shown in lowercase and in uppercase for pre-oviposition and oviposition periods, respectively ( $K-W$  test,  $p=0.05$  level).

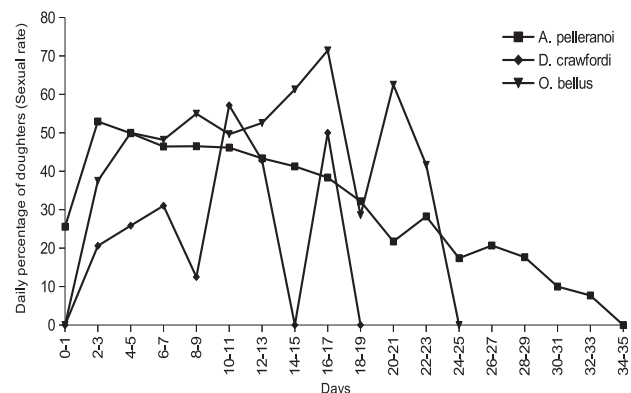


Fig. 5. Daily sex ratio (female offspring proportion) for *A. pelleranoi*, *D. crawfordi* and *O. bellus*, registered through the females' lifespan.

Table 1

Population increase parameters (mean  $\pm$  SE) of the parasitoids *A. pelleranoi*, *D. crawfordi* and *O. bellus*.

Parameters	<i>A. pelleranoi</i>	<i>O. bellus</i>	<i>D. crawfordi</i>
$R_0$ (Net reproductive rate)	30.33 $\pm$ 3.49	16.85 $\pm$ 2.27	5.00 $\pm$ 1.28
$r$ (Intrinsic rate of increment)	0.08 $\pm$ 0.2 <sup>-2</sup>	0.06 $\pm$ 0.01	0.05 $\pm$ 0.8 <sup>-2</sup>
$\lambda$ (Finite rate of increment)	1.08 $\pm$ 0.2 <sup>-2</sup>	1.06 $\pm$ 0.01	1.05 $\pm$ 0.9 <sup>-2</sup>
$T$ (Mean gen. time)	39.69 $\pm$ 0.54	44.34 $\pm$ 6.18	29.33 $\pm$ 1.23

### 3.4. Survival analysis

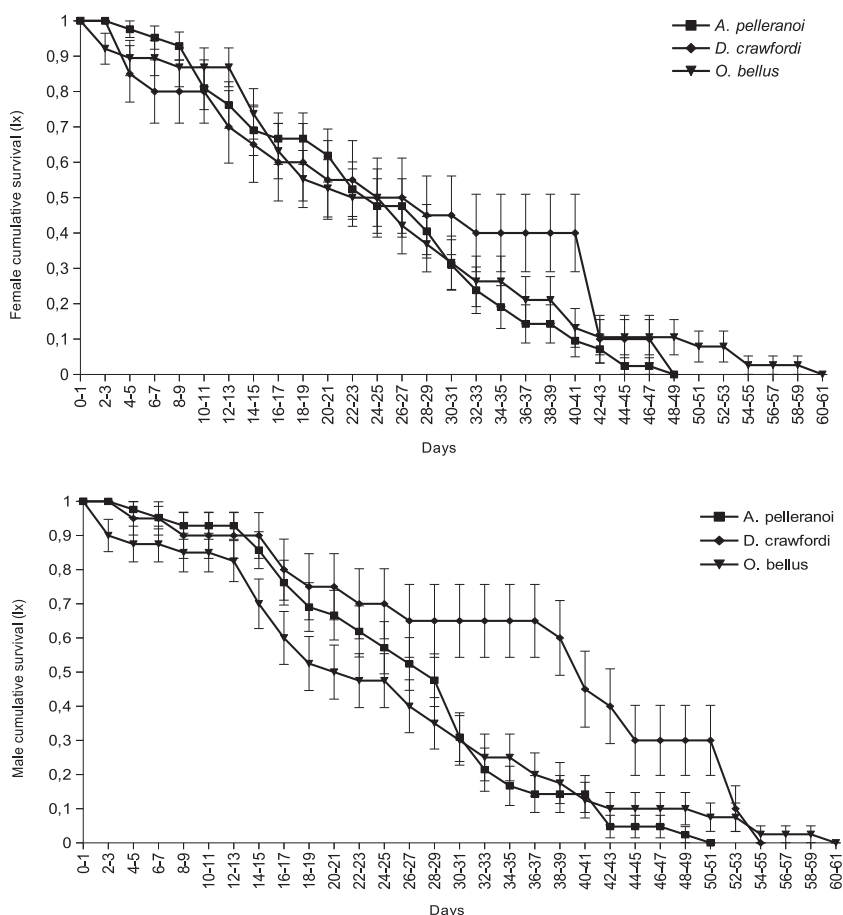
From the univariate survival analysis it was possible to determine the best fitted distribution for each survival data set, both male and female have a better fit to a Weibull distribution, with the only difference shown by males of *D. crawfordi* who showed a better fit to a Weibull with threshold distribution, Table 2 shows the parameters calculated for each distribution for males and females of different parasitoid species.

The respective cumulative survival curves for the three species are shown in Fig. 6a and b. The cumulative survival curves did not differ significantly for females ( $\text{Log-Rank}$ ,  $\chi^2=0.39$ ,  $df=2$ ,  $p=0.82$ ). In contrast, significant differences were observed for male curves of *A. pelleranoi* and *D. crawfordi* ( $\text{Log-Rank}$ ,  $\chi^2=8.43$ ,  $df=1$ ,



**Table 2**  
Parameters of the survival curve fitted to the Weibull and Th. Weibull distribution for male and female of *A. pelleranoi*, *D. crawfordi* and *O. bellus*.

Species	Sex	Distribution	Parameters			$W^2$	$p > W^2$
			$\alpha (\pm EE)$	$\beta (\pm EE)$	$\theta (\pm EE)$		
<i>A. pelleranoi</i>	Male	Weibull	29.59 ± 1.82	2.63 ± 0.32	–	0.079	0.25
<i>A. pelleranoi</i>	Female	Weibull	27.56 ± 2.00	2.23 ± 0.28	–	0.099	0.25
<i>D. crawfordi</i>	Male	Th. Weibull	36.84 ± 1.02	2.47 ± 0.23	4	0.177	0.25
<i>D. crawfordi</i>	Female	Weibull	27.28 ± 4.13	1.55 ± 0.29	–	0.155	0.25
<i>O. bellus</i>	Male	Weibull	26.83 ± 2.82	1.57 ± 0.20	–	0.064	0.25
<i>O. bellus</i>	Female	Weibull	28.05 ± 2.84	1.68 ± 0.22	–	0.07	0.25



**Fig. 6.** Cumulative survival curves ( $lx$ ) for male and female of *A. pelleranoi*, *D. crawfordi* and *O. bellus* (bars represent SE of the proportion surviving).

$p = 0.0037$ ), but not between *A. pelleranoi* and *O. bellus* (Log-Rank,  $\chi^2 = 0.17$ ,  $df = 1$ ,  $p = 0.67$ ), whereas differences between *O. bellus* and *D. crawfordi* were marginally significant (Log-Rank,  $\chi^2 = 3.66$ ,  $df = 1$ ,  $p = 0.056$ ), the Wilcoxon test showed a strong significant difference between *O. bellus* and *D. crawfordi* (Wilcoxon,  $\chi^2 = 5.14$ ,  $df = 1$ ,  $p = 0.023$ ).

The complete data for  $lx_{50}$  are listed in Table 3. The parameter  $lx_{50}$  fluctuated between 21.5 and 25.8 days for both, males and females of the three parasitoids species, except for *D. crawfordi* males which reached 38 days.

**Table 3**  
Days lived by the fifty percent of the population ( $lx_{50}$ ) of *A. pelleranoi*, *D. crawfordi* and *O. bellus* (Confidence interval L95–U95%).

Species	$lx_{50}$ (Male)	L95%	U95%	$lx_{50}$ (Female)	L95%	U95%
<i>D. crawfordi</i>	38.04	31.75	44.32	21.54	15.43	30.07
<i>O. bellus</i>	22.55	18.06	28.15	21.26	16.88	26.77
<i>A. pelleranoi</i>	25.75	22.51	29.46	23.38	19.93	27.43

#### 4. Discussion

The knowledge on fruit fly parasitoid demographic parameters is essential to assess the performance of species to be used as bio-control agent (Carey et al., 1988; Vargas et al., 2002). Although biological data coming from laboratory-reared insects may differ from data from their wild counterparts in some ecological and genetic aspects (Vargas et al., 2002; van Lenteren, 2003), colonization of parasitoid species under laboratory conditions is critical to thoroughly research these natural enemies (Aluja et al., 2009a). On the basis of those assertions, data from the present study on *A. pelleranoi*, *O. bellus* and *D. crawfordi* highlights their potential for mass rearing using *A. fraterculus* as a host. This study is the first examination of the reproductive and population parameters of both, *A. pelleranoi* and *D. crawfordi* reared on *A. fraterculus* larvae. In addition, provide the only known detailed survival analysis of the three indigenous parasitoid species.

As noted by Vargas et al. (2002), fruit fly parasitoids abundance patterns in the field may be influenced by the dominance of species

with elevated reproductive potential, which is mainly depicted by a high  $r$ . This claim is consistent with field abundance data of these three native parasitoid species in Argentina. For instance, several field surveys showed that the figitid *A. pelleranoi* is one of the dominant members of Argentinean *A. fraterculus*-parasitoid guild, whereas the opiines *O. bellus* and *D. crawfordi*, in this order of prevalence, were among the least abundant species (Ovruski et al., 2004, 2005, 2008; Schliserman et al., 2010). Similar abundance patterns of these three parasitoid species were recorded in the Bolivian mountain rainforest (Ovruski et al., 2009), which extends into the northernmost section of Argentinean Yungas rainforest. Based on the highest  $R_0$ ,  $r$ , and  $GRR$  values exhibited by *A. pelleranoi* and *O. bellus*, the results from this study support the pattern observed in subtropical forest environment (Table 1). In addition, *A. pelleranoi* showed the largest parasitism percentage under laboratory conditions, which was around 3- and 7-times higher than those recorded for *O. bellus* and *D. crawfordi*, respectively.

Interestingly, contrary to the data obtained in this study, Aluja et al. (2009a) found a significantly greater reproductive potential for *D. crawfordi* than for *A. pelleranoi* under controlled environmental conditions similar to those described in the present study, but using laboratory-reared *A. ludens* larvae as a host. Furthermore, Aluja et al. (2009a) recorded  $r$  values for the Mexican strains of *D. crawfordi* and *A. pelleranoi* approximately 5- and 2-times as high as those reported for these two neotropical parasitoid species in the present study. This large difference between strains of the same parasitoid species may be explained by, (1) the influence of host species (*A. ludens* in Aluja et al. (2009a) vs. *A. fraterculus* in this study) (Jervis and Copland, 1996; Riquelme-Virgala and Botto, 2010), (2) host larvae age (8–9 vs. 9–10), (3) rearing procedures and handling conditions, such as host exposure period (24–36 h vs. 4 h), (4) exposed host/parasitoid female ratio per hour (0.05–0.35 vs. 7.50 larvae), and (5) type of oviposition unit (fruit filled with host larvae plus artificial diet for *D. crawfordi* and uncovered Petri dishes filled with naked larvae for *A. pelleranoi* vs. organically covered Petri dish filled with naked host larvae for both *D. crawfordi* and *A. pelleranoi*).

Alternatively, given the extremely wide geographical range of *A. pelleranoi* and *D. crawfordi* (Ovruski et al., 2003) it is possible that the biological differences we found between Mexican and Argentinean populations of these hymenopterans can be explained by the fact that these taxa represent cryptic species. In fact, Argentinean and Mexican *A. fraterculus* are distinct morphotypes (Hernández-Ortiz et al., 2004; 2012) and cascading genetic differentiation across trophic levels has been documented for fruit fly parasitoids and their hosts (Forbes et al., 2009).

Regarding *O. bellus*,  $R_0$  and  $GRR$  values were 1.7- and 2.4-times higher than that previously recorded by Schliserman (unpublished data) for the same parasitoid strain used in the current study, albeit with a difference in the number of artificial rearing generations (14 vs. 38 generation old). Nevertheless, the  $r$  value was the same, and considering that  $R_0$  values increased, it is possible to observe that the mean generation time was reduced across *O. bellus* generations maintained under laboratory conditions. This finding is consistent with trends produced by artificial selection recorded for some tephritid species (Gilchrist et al., 2012) and reflects a trade-off between reproduction and longevity. In general, selecting individuals that reproduce early in their life results over time in offspring with high reproductive rates and shorter lifespan.

Among the three native parasitoid species studied, *A. pelleranoi* showed an  $r$  value (0.08) similar to that of the exotic larval-preupal parasitoid *D. longicaudata* reared on *C. capitata* (0.09) (Viscarret et al., 2006), and 1.5-times smaller than that recorded from a *D. longicaudata* strain reared on *Bactrocera dorsalis* (Hendel) (0.12) in Vargas et al. (2002). The use of *D. longicaudata* background knowledge as reference is relevant because the exotic opine species is currently

one of the most important biocontrol agents for augmentative releases against pestiferous fruit flies in the world (Montoya et al., 2011; Vargas et al., 2012), including both, *C. capitata* and *A. fraterculus* in Argentina (Ovruski and Schliserman, 2012).

Results of mean survival time ( $lx_{50}$ ), oviposition period, and fecundity, would allow to optimize mass rearing processes, ensuring the time at which at least the 50% of the original colony is reproductively active (Núñez-Campero et al., 2012).

In this sense, *A. pelleranoi* exhibited similar oviposition period and  $lx_{50}$  mean values as those of *O. bellus*, but mean daily female offspring production per parental female ( $m_x$ ) recorded from the figitid species was around 3-times higher than that found for the opine species. Despite the similar  $lx_{50}$  values of *D. crawfordi* of both, *A. pelleranoi* and *O. bellus*, it was the species with the lowest  $m_x$  value and the shortest oviposition period. The pooled analysis of these three biological parameters allowed to indicate the maximum reproductive capacity of each native parasitoid species, among which *A. pelleranoi* stood out. The  $m_x$  values after 23 days (Fig. 2) suggest that for a potential mass rearing of *A. pelleranoi* under controlled environmental conditions previously described here, it would not be advisable to keep parasitoid rearing cages for more than 3 weeks.

The results for the  $lx_{50}$  recorded for *A. pelleranoi* and *D. crawfordi* strains reared from *A. fraterculus* were around 3-times higher than that found by Aluja et al. (2009a) for parasitoid strains reared from *A. ludens*. Moreover, Cancino et al. (2009) reported for both, *A. pelleranoi* and *D. crawfordi* Mexican strains  $lx_{50}$  values closer to those found in this study for the two parasitoid strains from Argentina. Differences in female survival time for the same parasitoid species could be the result of different laboratory conditions and experimental methods. For instance, Miranda (2002) showed that changes in temperature and variations in the host larval age affected *D. crawfordi* survivorship, in the same way, life cycle and body weight may be also influencing the results (Mohamed et al., 2003).

Factors as the absence of fertilization of eggs (Heimpel and Lundgren, 2000), fruit fly host species, quality and age of host larvae, chemical cues derived from host larvae, host exposure time (Messing et al., 1993; Messing and Ramadan, 2000; Cancino and Montoya, 2008; López et al., 1999; Montoya et al., 2011), experimental methods and laboratory conditions (Paranhos et al., 2008), could be the cause of the sex ratio biased toward male of the three native parasitoid species. In contrast, Cancino et al. (2009) and Aluja et al. (2009a) recorded female-biased sex ratios from both laboratory-reared *A. pelleranoi* and *D. crawfordi* Mexican strains.

## 5. Conclusion

Results of the current study involve the first step on the path of the biological knowledge of *A. pelleranoi*, *O. bellus*, and *D. crawfordi* when selecting candidate species for mass rearing using *A. fraterculus* as a host for biological control purposes in Argentina. In this regard, the demographic data obtained from both *A. pelleranoi* and *O. bellus* revealed that these species could be used for starting a mass rearing system. Furthermore, the figitid *A. pelleranoi* has a greater significance because it has been found to attack the exotic *C. capitata* (Ovruski et al., 2004).

It is important understand the factors that influence parasitoid offspring production for successfully artificial rearing of these native parasitoid species, in particular those that affect the sex ratio. Therefore, additional studies in the laboratory focused on the evaluation of the female parasitoid density (Paranhos et al., 2008), ratio of host/female parasitoids, host exposure time to parasitoid (Ramadan et al., 1989; Wong et al., 1992; Montoya et al., 2000), effect of superparasitism on parasitoid emergence (González et al., 2007), and the quality of the host larvae (Messing et al., 1993; Cancino

and Montoya, 2008), should be useful to achieve an efficient adult production of both, *A. pelleranoi* and *O. bellus* on *A. fraterculus* larvae with the highest proportion of female progeny.

Although *D. crawfordi* showed the lowest population increase, fecundity and survivorship parameters of the three native parasitoid species evaluated on *A. fraterculus* larvae in the current study, this opine species should not be discarded as potential biocontrol agent. It is relevant to note that *D. crawfordi* is considered by several authors as an important candidate for mass rearing and augmentative releases in biological control programs against *A. ludens* in Mexico (Miranda, 2002; García-Medel et al., 2007; Aluja et al., 2009a; Cancino et al., 2009). Therefore, as pointed out by Cancino et al. (2009) and Aluja et al. (2009a) for *D. crawfordi* rearing on *A. ludens*, certain qualities of the host larva (size, age, and instar) and experimental conditions (temperature, moisture, light, type of rearing cage) should be carefully and continuously monitored to ensure more efficient rearing of *D. crawfordi* on *A. fraterculus*.

Taking into account that first augmentative releases of *D. longicaudata* in Argentina are currently occurring on commercial fruit crops in semi-arid rural areas of the San Juan province, the availability of other parasitoid species, particularly native ones, for biological control of both, *C. capitata* and *A. fraterculus* would allow release the one best suited to the climatic and ecological conditions of a particular fruit-producing region in Argentina. This approach was previously suggested by Sivinski et al. (2000), García-Medel

et al. (2007) and Aluja et al. (2009a) to reduce populations of *A. ludens* and *A. obliqua* in Mexican fruit-growing areas.

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## Appendix A

Life table parameters ( $x$ , age range in days;  $lx$ , proportion of individual surviving to start of the age interval;  $dx$ , fraction of the original cohort dying at the age  $x$ ;  $px$ , proportion of the individual surviving through the period;  $qx$ , proportion of the individual dying through the period;  $Lx$ , number of days lived by a mean individual between two time intervals;  $Tx$ , total number of days until the last dying;  $ex$ , life expectancy. (Carey, 1993) for *A. pelleranoi*, *O. bellus* and *D. crawfordi* females and males.

Age range (x)	Female								Male							
	N	lx	dx	px	qx	Lx	Tx	ex	N	lx	dx	px	qx	Lx	Tx	ex
<i>A. pelleranoi</i>																
0–1	42	1.0	0.0	1.0	0.0	2.0	21.4	21.4	42	1.0	0.0	1.0	0.0	2.0	23.3	23.3
2–3	41	1.0	0.0	1.0	0.0	1.9	19.4	19.9	41	1.0	0.0	1.0	0.0	1.9	23.3	23.9
4–5	40	1.0	0.0	1.0	0.0	1.9	17.5	18.4	40	1.0	0.0	1.0	0.0	1.9	19.4	20.4
6–7	39	0.9	0.0	0.9	0.1	1.7	15.6	16.8	39	0.9	0.0	1.0	0.0	1.9	17.5	18.9
8–9	34	0.8	0.1	0.9	0.1	1.6	13.9	17.1	39	0.9	0.0	1.0	0.0	1.9	15.7	16.9
10–11	32	0.8	0.0	0.9	0.1	1.5	12.3	16.1	39	0.9	0.0	0.9	0.1	1.8	13.8	14.9
12–13	29	0.7	0.1	1.0	0.0	1.4	10.8	15.7	36	0.9	0.1	0.9	0.1	1.6	12.0	14.1
14–15	28	0.7	0.0	1.0	0.0	1.3	9.5	14.2	32	0.8	0.1	0.9	0.1	1.5	10.4	13.7
16–17	28	0.7	0.0	0.9	0.1	1.3	8.1	12.2	29	0.7	0.1	1.0	0.0	1.4	9.0	13.0
18–19	26	0.6	0.0	0.8	0.2	1.1	6.9	11.1	28	0.7	0.0	0.9	0.1	1.3	7.6	11.4
20–21	22	0.5	0.1	0.9	0.1	1.0	5.7	10.9	26	0.6	0.0	0.9	0.1	1.2	6.3	10.2
22–23	20	0.5	0.0	1.0	0.0	1.0	4.7	9.9	24	0.6	0.0	0.9	0.1	1.1	5.1	9.0
24–25	20	0.5	0.0	0.9	0.2	0.9	3.8	7.9	22	0.5	0.0	0.9	0.1	1.0	4.0	7.7
26–27	17	0.4	0.1	0.8	0.2	0.7	2.9	7.1	20	0.5	0.0	0.7	0.4	0.8	3.0	6.4
28–29	13	0.3	0.1	0.8	0.2	0.5	2.2	7.0	13	0.3	0.2	0.7	0.3	0.5	2.3	7.3
30–31	10	0.2	0.1	0.8	0.2	0.4	1.6	6.8	9	0.2	0.1	0.8	0.2	0.4	1.7	8.1
32–33	8	0.2	0.0	0.8	0.3	0.3	1.2	6.3	7	0.2	0.0	0.9	0.1	0.3	1.4	8.1
34–35	6	0.1	0.0	1.0	0.0	0.3	0.9	6.0	6	0.1	0.0	1.0	0.0	0.3	1.0	7.3
36–37	6	0.1	0.0	0.7	0.3	0.2	0.6	4.0	6	0.1	0.0	1.0	0.0	0.3	0.8	5.3
38–39	4	0.1	0.0	0.8	0.3	0.2	0.3	3.5	6	0.1	0.0	0.3	0.7	0.2	0.5	3.3
40–41	3	0.1	0.0	0.3	0.7	0.1	0.2	2.3	2	0.0	0.1	1.0	0.0	0.1	0.3	6.0
42–43	1	0.0	0.0	1.0	0.0	0.0	0.1	3.0	2	0.0	0.0	1.0	0.0	0.1	0.2	4.0
44–45	1	0.0	0.0	0.0	1.0	0.0	0.0	1.0	2	0.0	0.0	0.5	0.5	0.1	0.1	2.0
46–47	0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	1	0.0	0.0	0.0	1.0	0.0	0.0	1.0
48–49	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
<i>O. bellus</i>																
0–1	38	1.0	0.0	0.9	0.1	1.9	24.2	24.2	40	1.0	0.0	0.0	1.0	1.9	23.3	23.3
2–3	35	0.9	0.1	1.0	0.0	1.8	22.3	24.2	36	0.9	0.1	0.9	0.1	1.8	21.4	23.7
4–5	34	0.9	0.0	1.0	0.0	1.8	20.5	22.9	35	0.9	0.0	1.0	0.0	1.8	19.6	22.4
6–7	34	0.9	0.0	1.0	0.0	1.8	18.7	20.9	35	0.9	0.0	1.0	0.0	1.7	17.8	20.4
8–9	33	0.9	0.0	1.0	0.0	1.7	16.9	19.5	34	0.9	0.0	1.0	0.0	1.7	16.1	18.9
10–11	33	0.9	0.0	1.0	0.0	1.7	15.2	17.5	34	0.9	0.0	1.0	0.0	1.7	14.4	16.9

(continued)

Age range (x)	Female								Male							
	N	lx	dx	px	qx	Lx	Tx	ex	N	lx	dx	px	qx	Lx	Tx	ex
12–13	33	0.9	0.0	0.8	0.2	1.6	13.4	15.5	33	0.8	0.0	1.0	0.0	1.5	12.7	15.4
14–15	28	0.7	0.1	0.9	0.1	1.4	11.8	16.1	28	0.7	0.1	0.8	0.2	1.3	11.2	16.0
16–17	24	0.6	0.1	0.9	0.1	1.2	10.5	16.6	24	0.6	0.1	0.9	0.1	1.1	9.9	16.5
18–19	21	0.6	0.1	1.0	0.0	1.1	9.3	16.8	21	0.5	0.1	0.9	0.1	1.0	8.8	16.7
20–21	20	0.5	0.0	1.0	0.0	1.0	8.2	15.6	20	0.5	0.0	1.0	0.0	1.0	7.8	15.5
22–23	19	0.5	0.0	1.0	0.0	1.0	7.2	14.4	19	0.5	0.0	1.0	0.1	1.0	6.8	14.3
24–25	19	0.5	0.0	0.8	0.2	0.9	6.2	12.4	19	0.5	0.0	1.0	0.0	0.9	5.8	12.3
26–27	16	0.4	0.1	0.9	0.1	0.8	5.3	12.5	16	0.4	0.1	0.8	0.2	0.8	5.0	12.4
28–29	14	0.4	0.1	0.9	0.1	0.7	4.5	12.1	14	0.4	0.1	0.9	0.1	0.7	4.2	12.0
30–31	12	0.3	0.1	0.8	0.2	0.6	3.8	12.0	12	0.3	0.1	0.9	0.1	0.6	3.6	11.8
32–33	10	0.3	0.1	1.0	0.0	0.5	3.2	12.2	10	0.3	0.1	0.8	0.2	0.5	3.0	12.0
34–35	10	0.3	0.0	0.8	0.2	0.5	2.7	10.2	10	0.3	0.0	1.0	0.0	0.5	2.5	10.0
36–37	8	0.2	0.1	1.0	0.0	0.4	2.2	10.5	8	0.2	0.1	0.8	0.2	0.4	2.1	10.3
38–39	8	0.2	0.0	0.6	0.4	0.3	1.8	8.5	7	0.2	0.0	0.9	0.1	0.3	1.7	9.6
40–41	5	0.1	0.1	0.8	0.2	0.2	1.4	11.0	5	0.1	0.1	0.7	0.3	0.2	1.4	11.0
42–43	4	0.1	0.0	1.0	0.0	0.2	1.2	11.5	4	0.1	0.0	0.8	0.2	0.2	1.2	11.5
44–45	4	0.1	0.0	1.0	0.0	0.2	1.0	9.5	4	0.1	0.0	1.0	0.0	0.2	1.0	9.5
46–47	4	0.1	0.0	1.0	0.0	0.2	0.8	7.5	4	0.1	0.0	1.0	0.0	0.2	0.8	7.5
48–49	4	0.1	0.0	0.8	0.3	0.2	0.6	5.5	4	0.1	0.0	1.0	0.0	0.2	0.6	5.5
50–51	3	0.1	0.0	1.0	0.0	0.2	0.4	5.0	3	0.1	0.0	0.8	0.3	0.2	0.4	5.0
52–53	3	0.1	0.0	0.3	0.7	0.1	0.2	3.0	3	0.1	0.0	1.0	0.0	0.1	0.2	3.0
54–55	1	0.0	0.1	1.0	0.0	0.1	0.1	5.0	1	0.0	0.1	0.3	0.7	0.1	0.1	5.0
56–57	1	0.0	0.0	1.0	0.0	0.1	0.1	3.0	1	0.0	0.0	1.0	0.0	0.1	0.1	3.0
58–59	1	0.0	0.0	0.0	1.0	0.0	0.0	1.0	1	0.0	0.0	1.0	0.0	0.0	0.0	1.0
60–61	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
<i>D. crawfordi</i>																
0–1	20	1.0	0.0	1.0	0.0	1.9	19.2	19.2	20	1.0	0.0	0.0	1.0	1.6	21.5	21.5
2–3	18	0.9	0.1	0.9	0.1	1.8	17.3	19.2	20	0.6	0.4	0.6	0.4	1.1	19.9	34.8
4–5	17	0.9	0.1	0.9	0.1	1.6	15.6	18.3	20	0.6	0.0	1.0	0.0	1.1	18.7	32.8
6–7	15	0.8	0.1	0.9	0.1	1.4	14.0	18.6	19	0.5	0.0	1.0	0.1	1.1	17.6	32.5
8–9	13	0.7	0.1	0.9	0.1	1.3	12.6	19.3	19	0.5	0.0	1.0	0.0	1.1	16.5	30.5
10–11	13	0.7	0.0	1.0	0.0	1.2	11.3	17.3	19	0.5	0.0	1.0	0.0	1.1	15.5	28.5
12–13	11	0.6	0.1	0.8	0.2	1.1	10.1	18.3	19	0.5	0.0	1.0	0.0	1.1	14.4	26.5
14–15	11	0.6	0.0	1.0	0.0	1.1	9.0	16.3	18	0.5	0.0	0.9	0.1	1.0	13.3	25.9
16–17	10	0.5	0.1	0.9	0.1	1.0	7.9	15.8	16	0.5	0.1	0.9	0.1	0.9	12.3	27.0
18–19	10	0.5	0.0	1.0	0.0	1.0	6.9	13.8	16	0.5	0.0	1.0	0.0	0.9	11.4	25.0
20–21	9	0.5	0.1	0.9	0.1	0.9	6.0	13.2	15	0.4	0.0	0.9	0.1	0.9	10.5	24.6
22–23	9	0.5	0.0	1.0	0.0	0.9	5.1	11.2	15	0.4	0.0	1.0	0.0	0.8	9.7	22.6
24–25	8	0.4	0.1	0.9	0.1	0.8	5.1	12.6	14	0.4	0.0	0.9	0.1	0.8	8.9	22.1
26–27	8	0.4	0.0	1.0	0.0	0.8	3.4	8.5	14	0.4	0.0	1.0	0.0	0.8	8.1	20.1
28–29	7	0.4	0.1	0.9	0.1	0.7	2.7	7.6	14	0.4	0.0	1.0	0.0	0.8	7.3	18.1
30–31	7	0.4	0.0	1.0	0.0	0.7	2.0	5.6	14	0.4	0.0	1.0	0.0	0.8	6.5	16.1
32–33	7	0.4	0.0	1.0	0.0	0.5	1.3	3.6	14	0.4	0.0	1.0	0.0	0.8	5.7	14.1
34–35	2	0.1	0.3	0.3	0.7	0.2	0.8	8.0	14	0.4	0.0	1.0	0.0	0.8	4.9	12.1
36–37	2	0.1	0.0	1.0	0.0	0.2	0.6	6.0	13	0.4	0.0	0.9	0.1	0.7	4.1	11.0
38–39	2	0.1	0.0	1.0	0.0	0.2	0.4	4.0	12	0.3	0.0	0.9	0.1	0.6	3.4	9.8
40–41	2	0.1	0.0	1.0	0.0	0.2	0.2	2.0	9	0.3	0.1	0.8	0.3	0.5	2.8	10.8
42–43	1	0.1	0.1	0.5	0.5	0.1	0.1	1.0	8	0.2	0.0	0.9	0.1	0.5	2.3	10.0
44–45	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8	0.2	0.0	1.0	0.0	0.5	1.8	8.0
46–47	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8	0.2	0.0	1.0	0.0	0.5	1.4	6.0
48–49	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8	0.2	0.0	1.0	0.0	0.4	0.9	4.0
50–51	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6	0.2	0.1	0.8	0.3	0.3	0.5	3.0
52–53	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4	0.1	0.1	0.7	0.3	0.2	0.2	2.0
54–55	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2	0.1	0.1	0.5	0.5	0.1	0.1	1.0
56–57	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.1	0.0	1.0	0.0	0.0	0.0



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