Evaluation of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) reared on a genetic sexing strain of *Ceratitis capitata* (Wied.) (Diptera: Tephritidae)

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Received 20 April 2005; accepted 23 August 2005

Available online 14 October 2005

Abstract

If a genetic sexing strain of *Ceratitis capitata* could be used to produce sterile males and to rear parasitoids at the same time, significant amount of resources could be saved in comparison with the production of these two biological agents separately. We studied here the major biological parameters comparing two strains of the parasitoid *Diachasmimorpha longicaudata*, one of them reared on a wild type strain of *C. capitata*: DL(+), and the other on a genetic sexing strain of *C. capitata*: DL(sw). The mean longevity, fecundity, and sexual proportion of their respective offspring showed no significant difference. Moreover, no difference was observed in population parameters such as mean generation time, net reproductive rate, finite rate of increase, doubling time, and intrinsic rate of increase. The biological parameters of other artificially reared parasitoids in the Tephritidae family are reviewed, and the conclusion is reached that, rearing the parasitoid on this particular genetic sexing strain of *C. capitata* does not produce any negative effect on the biological parameters studied. © 2005 Elsevier Inc. All rights reserved.

Keywords: *Diachasmimorpha longicaudata*; *Ceratitis capitata*; Life table analysis; Genetic sexing strain; Integrated pest management; Biological control; Sterile insect technique

1. Introduction

There are two economically important fruit flies (Diptera, Tephritidae) pests in Argentina: the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and the South American fruit fly, *Anastrepha fraterculus* (Wiedemann) (Maddison and Bartlett, 1989). Annual losses by their direct damage have been estimated between 15 and 20% of the national fruit yield (Aruani et al., 1996). In addition, the presence of any of these two species cause quarantine restrictions for fruit exportation (SENASA, 1998).

Different methods have been used worldwide to control fruit flies species, but the sterile insect technique (SIT) and the augmentative biological control (ABC) through the use of fruit fly parasitoids are the two most environmentally friendly strategies available. Integration of these two techniques would be highly desirable. Theoretical studies (Barclay, 1998; Knipling, 1992), have shown that augmentative parasitoids releases used in conjunction with the SIT have a synergistic effect to suppress tephritid population. Besides, the integration of the mass production of sterile males and parasitoids may result in a considerable reduction of costs compared to producing these agents separately.

Diachasmimorpha longicaudata (Ashmead) is a larval–pupal parasitoid of fruit flies. It has been found in numerous countries in Southeastern Asia, where it parasitizes at

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least 14 species of the genus *Bactrocera* (Bess et al., 1961; Clausen et al., 1965; Wharton and Gilstrap, 1983). Following its introduction to several other countries, *D. longicaudata* has been reported parasitizing *Bactrocera dorsalis* (Hendel), *C. capitata* (Wiedemann), and some species of the genus *Anastrepha* (Montoya et al., 2000; Ovruski et al., 1999). Likewise, this parasitoid has been used in ABC strategies in several countries (Clausen et al., 1965; Sivinski et al., 1996; Vargas et al., 1993).

In Argentina, SIT has been successfully applied to control *C. capitata* (Aruani et al., 1996; De Longo et al., 2000). However, less attention has been paid to parasitoid wasps as biological control agents (Ovruski et al., 1999). The natural parasitism of *C. capitata* and *A. fraterculus* in wild and cultivated fruits is very low, due fundamentally to the inability of the native braconid parasitoids to attack these tephritids (Ovruski et al., 2004). During the years 60s and 80s, several small scale releases of *D. longicaudata* were conducted, without subsequent evaluations (Ovruski et al., 2004). Recently, *D. longicaudata* has been reported in Argentina's northeastern province of Misiones (Schliserman et al., 2003).

The objective of the present study is to use life table analysis to evaluate a genetic sexing strain of *C. capitata* as potential host for a mass rearing program of *D. longicaudata*. We worked with a genetic sexing strain of *C. capitata* based on a mutation of the gene *sw* affecting the rate of development (Manso and Lifschitz, 1992). In this strain, females have a longer developmental time than males (Delprat et al., 2002) so they can be separated from males early in their life cycle (Viscarret et al., 2004). Female larvae could be used for rearing parasitoids to release in ABC programs, while the male larvae (previous irradiation at pupal stage) could be used for the SIT after their emergence (Sivinski and Calkins, 1990).

It is well known that the quality of artificially reared parasitoids, measured by biological parameters such as flight ability, longevity, fecundity, etc., largely depends on the host used for that purpose (Cancino et al., 2003). Compared to the regular wild type strain of *C. capitata*, the larvae of the genetic sexing strain presented here as rearing substrate for *D. longicaudata*, are on average bigger (for being mostly larvae of female) and metabolically slower (homozygous for the gene *sw*), than the wild type. The probable effect of these two novelties introduced in the rearing substrate, i.e., the population of larvae that we offer, deserve investigation.

2. Materials and methods

All parasitoids and fruit flies used in this study were reared at Instituto de Genética (INTA, Castelar). *C. capitata* wild type strain was MI94 (originated from the colony reared in the Mendoza Insectary, Argentina and introduced into the lab at INTA Castelar Argentina, on September 1994). The genetic sexing strain was Cast 191 (Delprat et al., 2002). The colony of *D. longicaudata* was initiated with individuals from CIRPON, San Miguel de Tucumán (Ovruski et al., 2003).

We established two strains of *D. longicaudata* rearing wasps during 8–10 generations on these two different strains of *C. capitata*. The one on the wild-type strain MI94 was named *DL*(+), whereas the one reared on the genetic sexing strain Cast 191 was named *DL*(*sw*), because the females flies are homozygous for the gene *sw*.

3. Experimental procedure

Fifteen pairs (<24 h old) were sampled from both strains of parasitoids. Each female represented a replicate. When the male of any couple died, it was replaced by another male of similar age until the female died. All pairs were provided water and honey throughout the assay.

An oviposition unit (a Petri dish, 3 cm diameter, covered with a mesh) containing seven-days-old larvae of *C. capitata* was offered (ad libitum) to each couple every other day. Samples of larvae set aside until emergence showed that *DL*(*sw*) was rearing on 70% female larvae, while *DL*(+) on the usual 50%. The exposure period lasted for 5 h. Afterwards, larvae were kept in a vial with medfly fresh artificial diet (Terán, 1977). Vermiculite was used as pupation substrate. The pupae obtained from each exposition and for each pair were separated and kept in flasks until the parasitoids and fruit flies emerged.

For each replicate, the number of pupae obtained, the number and sex of parasitoid offspring and the number of fruit flies emerged, were recorded every other day. Female survival was also noted.

Larvae and pupae were maintained at *T* (mean $\pm$ standard error): $24.61 \pm 0.33^\circ\text{C}$; HR (mean $\pm$ standard error): $65.00 \pm 2.75\%$, and continuous light. Adults were kept at *T*: $22.90 \pm 2.90^\circ\text{C}$; RH: $47.73 \pm 1.66\%$, and 12L:12D photoperiod.

4. Preoviposition and oviposition periods, longevity, survival, fecundity, and sex proportion

After all data were registered we calculated the following variables:

- (1) Mean preoviposition period (Σ number of days until the *i* female begun to lay eggs/initial number of females).
- (2) Mean ovipositional period (Σ number of days during which the female *i* laid eggs/number of initial females).
- (3) Mean longevity of the adult female (Σ lifespan of the *i* female/initial number of females).
- (4) Mean survival by age (l_x), (number of female at age *x*/initial number of females).
- (5) Specific fecundity by age (m_x), (mean number of female offspring by female at age *x*).
- (6) Mean fecundity (Σ number of female offspring of the *i* female/total number of females).
- (7) Mean daily sexual proportion ($(\Sigma$ number of female offspring of the *i* female in the *j* day/ Σ total number of offspring of the *i* female in the *j* day)/number of remaining females in the *j* day).

One-Way ANOVA ($P < 0.05$) was used to compare between parasitoid strains for preoviposition period, oviposition period, mean fecundity, mean longevity, and mean daily sex proportion, as all this variables satisfied the assumptions required by that test.

5. Population parameters

The following population parameters were estimated using the program “TABLAVI” (La Rossa and Kahn, 2003):

- (1) Net reproductive rate (R_0): average number of individuals (females in this case) produced by one female along its life (Begon et al., 1988).
- (2) Finite rate of increase (λ): factor by which a population increases in size from time t to time $t+1$ (Ravinovich, 1980).
- (3) Intrinsic rate of increase (r_m): rate at which the population increases in size. It is the change in the population size per individual per unit of time (Begon et al., 1988).
- (4) Mean generation time (T): mean time between the birth of an individual and the birth of its offspring (Begon et al., 1988).
- (5) Doubling time (t): time required for the population to reach a twofold increase in size (Messenger, 1964).

All estimated parameters were compared with a T test ($P < 0.05$) (Steel and Torrie, 1980).

6. Results

6.1. Preoviposition and oviposition periods, longevity, survival, fecundity, and sex proportion

Both *D. longicaudata* strains, *DL*(sw) and *DL*(+) presented a preoviposition period and there was no significant difference between them (Table 1). Besides, the difference between strains in oviposition period did not reach the level of significance (Table 1).

Table 1

Preoviposition and oviposition periods, longevity, mean fecundity, and sexual proportion (Mean $\pm$ standard error, (n)), for *DL*(sw) and *DL*(+) parasitoid strains of *D. longicaudata*

Parameter ^a	<i>D. longicaudata</i> (sw)	<i>D. longicaudata</i> (+)	<i>P</i>	<i>DF</i>
Preoviposition period (days)	3.23 $\pm$ 0.62 (13)	3.57 $\pm$ 0.81 (15)	0.75	1,25
Oviposition period (days)	28 $\pm$ 2.56 (13)	22.57 $\pm$ 1.87 (15)	0.10	1,25
Longevity (days)	34.08 $\pm$ 3.13 (13)	28.33 $\pm$ 2.07 (15)	0.13	1,26
Mean fecundity (F/F)	32.92 $\pm$ 5.05 (13)	32.53 $\pm$ 5.65 (15)	0.96	1,26
Sexual proportion (F/(F+M))	0.55 $\pm$ 0.04 (13)	0.56 $\pm$ 0.05 (15)	0.70	1,26

Variables were compared using a one-way ANOVA.

^a F: female; M: male.

The mean longevity of female was not significantly different between parasitoid strains (Table 1), *DL*(sw) showing an $l_{50} = 39$ days and *DL*(+) $l_{50} = 33$ days (Fig. 1).

The two strains were not different for mean fecundity (Table 1). Both strains showed similar curves (Fig. 2). These curves show a daily fluctuation but there is a general trend to a gradual increase during the first week, reaching a maximum on the second week, and then gradually falling down on the third week. The strain *DL*(sw) reached its highest fecundity between 11th and 27th day of its lifespan (Fig. 2), with three peaks on the days 15 (4.75 ± 1.06 females/female), 19 (4.82 ± 0.99 females/female), and 25 (4.92 ± 1.50 females/female). The strain *DL*(+) reached the highest fecundity between the days 11 and 27 with two peaks on 15 (6.67 ± 1.18 females/female) and 19 (6.69 ± 1.30 females/female) days.

Fig. 1. Survival of adult females (number of female to start the age interval x /initial number of females) for strains *DL*(+) and *DL*(sw) of *D. longicaudata*.

Fig. 2. Mean daily fecundity (number of females/female/day) for strains *DL*(+) and *DL*(sw) of *D. longicaudata* ($\pm$ standard error).

Fig. 3. Mean daily sexual proportion (F/(F+M)) for strains *DL*(+) and *DL*(sw) of *D. longicaudata* ($\pm$ standard error).

The mean daily sexual proportion of offspring was high for both parasitoid strains between 3rd and 30th day of female life span, approximately. The means ($\pm$ standard errors) for this period were 0.62 ($\pm$ 0.03) for *DL*(+) and 0.67 ($\pm$ 0.05) for *DL*(sw) (Fig. 3). Values observed from day 31 onward are irrelevant due to low number of parental females still alive. The overall proportion of female offspring was similar in both parasitoid strains (Table 1).

7. Population parameters

The mean generation time (T), the net reproductive rate (R_0), the finite rate of increase (λ), the doubling time (t), and the intrinsic rate of increase (r_m) did not differ between parasitoid strains (Table 2).

8. Discussion

The two strains of parasitoids compared here show similar biological characteristics. All the variables estimated indicate that rearing the parasitoid on the metabolically slower (homozygous for the gene *sw*) larvae of female of the fruit fly genetic sexing strain Cast191 does not affect its biological quality.

The oviposition period registered in the present work is longer than cited in the literature for *D. longicaudata* and other fruit fly parasitoids (Table 3). Also the longevity registered in the present study was, in general, higher than that registered for other parasitoids, except for *Psytalia cosyrae* (Wilkinson) using *C. capitata* and *C. cosyra* (Walker) as hosts (Mohamed et al., 2003) (Table 3). For all the variables registered, the different environmental conditions and host species used can satisfactorily explain the differences between our results and the ones obtained by other authors.

In relation to female survival, Ramadan et al. (1995) gave a curve for *Fopius vandenboschi* similar to ours but with a more pronounced slope. Mohamed et al. (2003) reported, for *P. cosyrae*, curves similar to those found in this work. In the case of *D. longicaudata* (host: *B. dorsalis*) Vargas et al. (2002) observed a higher mortality rate at the beginning of their life

Table 2
Population parameters estimated for strains *DL*(sw) and *DL*(+) of *D. longicaudata* (Mean $\pm$ standard error, (n))

Population parameter	<i>D. longicaudata</i> (sw)	<i>D. longicaudata</i> (+)	<i>P</i>	<i>DF</i>
T (Mean generation time, days)	39.37 $\pm$ 0.55 (13)	37.93 $\pm$ 0.68 (15)	0.12	26
R_0 (Net reproductive rate, F/F) ^a	33.84 $\pm$ 5.14 (13)	32.54 $\pm$ 5.65 (15)	0.87	26
λ (Finite rate of increase, per day)	1.0990 $\pm$ 0.004 (13)	1.102 $\pm$ 0.006 (15)	0.69	26
t (Doubling time, days)	7.36 $\pm$ 0.28 (13)	7.11 $\pm$ 0.38 (15)	0.61	26
r_m (Intrinsic rate of increase, day ⁻¹)	0.094 $\pm$ 0.004 (13)	0.098 $\pm$ 0.005 (15)	0.55	26

Variables were compared using a T test.

^a F, female.

Table 3
Biological parameters of fruit flies parasitoids

Species	Oviposition period (days)	Fecundity	Longevity (days)	Sexual rate	Experimental conditions	Authors
<i>Fopius arisanus</i> ^(a)	11.0 $\pm$ 1.78	119.40 $\pm$ 24.71 (eggs/F)	17.30 $\pm$ 3.89	—	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>F. vandenboschi</i> ^(a)	11.0 $\pm$ 1.50	33.38 $\pm$ 5.92 (eggs/F)	22.0 $\pm$ 4.35	0.57 $\pm$ 0.08 (Female proportion)	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>F. vandenboschi</i> ^(a)	6.1 $\pm$ 1.1	33.3 $\pm$ 6.0 (eggs/F)	22.0 $\pm$ 1.3	57 $\pm$ 4.6 (Female percentage)	$26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Ramadan et al. (1995)
<i>D. longicaudata</i> ^(a)	9.33 $\pm$ 1.64	93.00 $\pm$ 3.88 (eggs/F)	15.67 $\pm$ 4.10	0.59 $\pm$ 0.05 (Female proportion)	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>Psytalia incisif</i> ^(a)	16.50 $\pm$ 2.08	90.90 $\pm$ 12.98 (eggs/F)	36.60 $\pm$ 3.89	0.49 $\pm$ 0.10 (Female proportion)	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>P. fletcheri</i> ^(b)	8.80 $\pm$ 0.81	69.30 $\pm$ 11.21 (eggs/F)	13.40 $\pm$ 3.89	0.64 $\pm$ 0.05 (Female proportion)	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>P. cosyrae</i> ^(c)	—	—	55.0 $\pm$ 4.2	—	$T: 25^\circ\text{C}; \text{RH}: 60\text{--}70\%$	Mohamed et al. (2003)
<i>P. cosyrae</i> ^(d)	—	—	77.5 $\pm$ 3.9	—	$T: 25^\circ\text{C}; \text{RH}: 60\text{--}70\%$	Mohamed et al. (2003)
<i>D. tryoni</i> ^(e)	6.60 $\pm$ 0.78	50.40 $\pm$ 6.67 (eggs/F)	13.40 $\pm$ 3.89	0.55 $\pm$ 0.6 (Female proportion)	$T: 26 \pm 2^\circ\text{C}; \text{RH}: 60 \pm 10\%$	Vargas et al. (2002)
<i>D. krausii</i> ^(e)	—	111.7 $\pm$ 11.29 (F+M/F)	27.6 $\pm$ 4.55	0.28 $\pm$ 0.03 (Male proportion)	$T: 25 \pm 1^\circ\text{C}; \text{RH}: 60 \pm 5\%$	Rungrojwanich and Walter (2000)

The hosts were: ^(a) *Bactrocera dorsalis*, ^(b) *Bactrocera cucurbitae*, ^(c) *Ceratitis capitata*, ^(d) *Ceratitis cosyra*, ^(e) *Bactrocera tryoni*.

Table 4
Population parameters of fruit flies parasitoids

Species	<i>T</i>	<i>R</i> ₀	λ	<i>t</i>	<i>r</i> _m	Authors
<i>Fopius arisanus</i> ^(a)	27.3	27.4	1.13	—	0.12	Vargas et al. (2002)
<i>F. arisanus</i> ^(b)	26.69	16.21	1.11	6.3	0.10	Bautista et al. (1998)
<i>F. arisanus</i> ^(b)	—	117.4 ± 0.8	—	—	—	Zenil et al. (2004)
<i>F. arisanus</i> ^(c)	—	14.5 ± 0.4	—	—	—	Zenil et al. (2004)
<i>F. arisanus</i> ^(d)	—	58.0 ± 0.7	—	—	—	Zenil et al. (2004)
<i>F. vandenboschi</i> ^(a)	30.3	10.1	1.08	—	0.08	Vargas et al. (2002)
<i>Diachasmimorpha longicaudata</i> ^(a)	27.2	28.2	1.13	—	0.12	Vargas et al. (2002)
<i>D. tryoni</i> ^(b)	27.8	16.4	1.11	—	0.10	Vargas et al. (2002)
<i>Psytalia incisi</i> ^(a)	33.4	29.4	1.12	—	0.10	Vargas et al. (2002)
<i>P. fletcheri</i> ^(c)	28.3	21.5	1.11	—	0.11	Vargas et al. (2002)

T (mean generation time, days); *R*₀ (net reproductive rate, female/female); λ (finite rate of increase, per day); *t* (doubling time, days); *r*_m (intrinsic rate of increase/day). The hosts were: (a) *Bactrocera dorsalis*; (b) *Ceratitidis capitata*; (c) *Anastrepha ludens*; (d) *Anastrepha serpentina*; (e) *Bactrocera cucurbitae*.

span, but a similar pattern after the initial period. Graphical estimation of *l*₅₀ for all the mentioned species, produced lower values than the ones observed in the present assay, but note that Cancino Díaz and Yoc (1993) also registered low values of *l*₅₀ for *D. longicaudata*.

The highest fecundity of different species of fruit flies parasitoids, including *D. longicaudata*, on different host occurs between 7th and 15th day of the adult female life span (Ashley and Chambers, 1980; Bautista et al., 1998; Cancino Díaz and Yoc, 1993; Greany et al., 1976; Rungrojwanich and Walter, 2000). However, Zenil et al. (2004), reported for *Fopius arisanus* a high daily number of offspring extending to the 25th day of the female life. In the present article, the fecundity curve (Fig. 2) was similar to those reported in other fruit fly parasitoid species (Ashley and Chambers, 1980; Bautista et al., 1998; Greany et al., 1976; Rungrojwanich and Walter, 2000; Vargas et al., 2002; Zenil et al., 2004).

Many variables influence the oviposition behavior of parasitoids. Previous ovipositional experience has been shown to increase oviposition as well as the number of eggs in the ovarioles. The presence of males, a suitable rearing medium and a higher “host : parasitoid” ratio are also positive stimuli (Ashley and Chambers, 1980; Cancino, 1998; Lawrence et al., 1978, 2000; Ramadan et al., 1995; Rungrojwanich and Walter, 2000). In our work females were offered larvae throughout their life span, as well as food, water and males. The “hosts : female” ratio was set to allow females to express their maximum fecundity.

The proportion of female offspring found here for both parasitoid strains was similar to those recorded by other authors (Table 3). Note exception like the low female proportion described for *Psytalia incisi* (Silvestri) and the high female proportion for *P. fletcheri* (Silvestri) (Vargas et al., 2002) and *Diachasmimorpha krausii* (Fullaway) (Rungrojwanich and Walter, 2000). Sex ratios in Opiinae can be affected by different variables, such as larval stage, age, and size of the host, time of exposition to the parasitoids and age of the female. In *F. vandenboschi* (Fullaway) (host: *Bactrocera dorsalis* (Hendel)), Ramadan et al. (1995) found increased female offspring when females were exposed to the second or early third larval stage, but

the proportion of females was lower when using first larval stage, and no female emerged from late third larvae. Likewise, in *D. krausii* (Fullaway) a higher percentage of female offspring developed on intermediate third larval stage of *Bactrocera latifrons* (Hendel) and on early third larval stage of *C. capitata* (Messing and Ramadan, 2000). In *F. arisanus* (Sonan) the production of females increases with the age of the host (Zenil et al., 2004). In regards to host size, *D. krausii* produced a greater proportion of females when reared on *B. latifrons* (bigger larvae) than on *C. capitata* (smaller larvae) (Messing and Ramadan, 2000). A similar situation occurs in *D. longicaudata* (hosts: *Anastrepha ludens* (Loew) and *B. dorsalis*) and other Opiinae fruit flies parasitoids (Cancino Díaz and Yoc, 1993; Messing et al., 1993). In the present work these hypothesis have not been tested, but our results are, in general, similar those cited by the authors for the stages preferred by this parasitoid (Table 3). However, we found no effect of female age on sex ratio as did Bautista et al. (1998) and Ramadan et al. (1994) in other species.

9. Population parameters

The population parameters estimated for *D. longicaudata* in the present work are, for the most part, similar to those described by Vargas et al. (2002) and Bautista et al. (1998) (Table 4). *R*₀ and *T* values were somewhat higher than those observed by the above for *D. longicaudata* and the other parasitoids studied. However, Zenil et al. (2004) for *F. arisanus*, registered lower *R*₀ values when the host was *A. ludens* and higher *R*₀ when it was *C. capitata* and *A. serpentina*. Temperature and the host species could probably explain the values in Table 4.

Our results hold promise since they indicate that the medfly sexing strain, Cast191, could be used to produce sterile males and parasitoids simultaneously. The next step in this research will be to rear and produce at a larger scale both, male-only flies and parasitoids in an integrated way. The joint use of both control measures must also be further investigated. Experiments in Hawaii (Wong et al., 1991) and, more recently in Guatemala (Rendón, 2004) are encouraging.

Acknowledgments

We thank Dr. Silvia López, Lic. Alejandro Pietrek, and two anonymous reviewers for their valuable comments and suggestions on this article, and Leonela Carabajal Paladino, Cynthia Cagnotti, Romina Russo, and María Eugenia Utgés for helping in the laboratory. This work was supported by Grant PICTO 12909 from Agencia Nacional de Promoción Científica y Tecnológica-Instituto Nacional de Tecnología Agropecuaria, Argentina, to J.L.C., and S.M.O.

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