



Article

Laboratory and Semi-Field Cage Demography Studies of Diachasmimorpha longicaudata Mass-Reared on Two Ceratitis capitata Strains

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Simple Summary

The reproductive capacity of parasitoid wasps during their lifetime plays a crucial role in understanding their potential as biocontrol agents and the host-parasitoid dynamics. An interesting system to study involves the Southeast Asia-native parasitoid Diachasmimorpha longicaudata and its host Ceratitis capitata, commonly known as the Mediterranean fruit fly or medfly, which is a serious invasive fruit fly pest in Argentina. This study compared reproductive parameters of two parasitoid population lines reared at the biofactory San Juan on different medfly strains. One line was mass-reared on medfly larvae of a genetic sexing strain (= $Dl_{(Cc\text{-tsl})}$) and the other on larvae of a wild biparental medfly strain (= $Dl_{(Cc\text{-bip})}$). The goal was to provide information for improving parasitoid mass production and evaluating its performance under natural conditions. For this, laboratory and semi-field cage trials were conducted at the San Juan Biofactory. Firstly, laboratory trials showed that $Dl_{(Cc\text{-bip})}$ females displayed higher reproductive and population rates than those of $Dl_{(Cc-ts)}$ females. Secondly, semi-field cage trials revealed that females of both $Dl_{(Cc-tsl)}$ and $Dl_{(Cc-tsl)}$ had similar and high reproductive potential in late spring and summer, when environmental conditions are temperate—warm. However, unlike $Dl_{(Cc\text{-ts}]}$ females, $Dl_{(Cc\text{-bip})}$ females were reproductively active in early autumn, albeit at very low rates due to colder environmental conditions. The current study provides novel data to improve the productivity of D. longicaudata mass rearing and to achieve the most effective medfly control through parasitoid releases in the semi-arid, fruit-growing areas of Argentina.

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Abstract

Ceratitis capitata (Wiedemann) or medfly is a polyphagous pest of fruit crops worldwide. The Asian-native larval parasitoid *Diachasmimorpha longicaudata* (Ashmead) is mass-reared at the San Juan Biofactory and is currently released for medfly control in Argentina. Information on parasitoid survival, reproduction, and population growth parameters is critical

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for optimizing the mass-rearing process and successfully achieving large-scale release. This study provides a first-time insight into the demography of two population lines of D. longicaudata: one mass-reared on medfly larvae of the Vienna-8 temperature-sensitive lethal genetic sexing strain and the other on larvae of the wild biparental medfly strain. The aim was to compare both parasitoid populations to improve mass-rearing quality and to assess performance on medfly in a semi-arid environment, typical of Argentina's central-western fruit-growing region. Tests were performed under laboratory and non-controlled environmental conditions in semi-field cages during three seasons. $Dl_{(Cc\text{-bip})}$ females exhibited higher reproductive potential than did $Dl_{(Cc\text{-tsl})}$ females under lab conditions. However, both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$ were found to be similar high-quality females with high population growth rates in warm–temperate seasons, i.e., late spring and summer. $Dl_{(Cc\text{-bip})}$ females were only able to sustain low reproductive rates in early autumn, a colder season. These results are useful for improving the parasitoid mass production at the San Juan Biofactory and redesigning parasitoid release schedules in Argentina's irrigated, semi-arid, fruit-growing regions.

Keywords: Mediterranean fruit fly; parasitoid mass rearing; demographic parameters; rearing quality control parameters; fruit fly biological control

1. Introduction

In several Latin American countries where fruit production, marketing, and export are affected by tephritid fruit fly species of economic and quarantine importance, such as *Ceratitis capitata* (Wiedemann), *Anastrepha fraterculus* (Wiedemann), *A. suspensa* (Loew), *A. obliqua* (Macquart), *A. striata* Schiner, and *A. ludens* (Loew) (Diptera: Tephritidae), among other fruit fly species, a renewed use of biological control against those pests is currently underway [1–4]. Among the different natural enemies evaluated are entomopathogenic fungi, nematodes, bacteria, viruses [5], predators, and parasitoid wasps [3], but the last of these comprise the most widely used method as a valid alternative in fruit fly biological control programs [3,6–9]. This is related to two major linked trends: (1) the development and improvement of successful mass-rearing techniques of exotic and native parasitoids for augmentative releases [10–15] and (2) the use of different eco-friendly tactics that preserve biodiversity and reduce agrochemical use [16,17].

The use of a parasitoid species to implement an augmentative biological control program, which involves the large-scale release of mass-reared parasitoids [18], requires the release of high-quality individuals, i.e., adults with higher reproductive potential, longer lifespans, and higher host-searching and parasitism abilities, among other key attributes [19-22]. Therefore, understanding the demography of fruit fly parasitoids provides useful information about their reproductive and population biology, an essential tool for assessing the performance of different species as biocontrol agents [23,24]. In this regard, demographic parameters can be used to compare the effect of different hosts on the production of parasitoids and thus optimize their rearing on a particular host under artificial conditions [15,25–27]. Population growth parameters are also helpful in testing the performance of parasitoid species in controlling target pest populations under different environmental conditions and/or on diverse hosts [28–34]. Furthermore, an in-depth study on the parasitoid demography enables an interdisciplinary approach involving genetic, evolutionary, and ecological aspects, and environmental factors [35]. In this regard, demographic parameters should be evaluated in relation to the weather variables of the region where the parasitoid species will be released, in order to ensure the viability of the

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individuals in the new area [36]. Air temperature is an environmental variable predictor of insect development dynamics [37] and is therefore a determining climatic factor for parasitoid establishment and performance in the environment where it is released [38]. Air temperature directly affects the survival and fecundity of parasitoids and also influences the parasitism rate [39–45].

Such knowledge about parasitoids may help with the successful biological control of the globally invasive *C. capitata* or medfly in Argentina. The medfly is one of the main fruit pests severely constraining exports for Argentinian fruit and vegetable producers, which has a negative socioeconomic cost on the country [46]. This exotic fruit fly pest has spread throughout almost all fruit-growing regions of Argentina. The medfly currently covers a large area of the country from 22° S to 36° S as a result of both its biological plasticity for adapting to different climatic conditions and its broad host range, involving commercial and wild fruit species [47,48]. In this context, medfly control actions have been based on the integrated use of the Sterile Insect Technique (SIT); chemical, cultural, and trapping methods; and quarantine protection systems during the last 30 years [49]. A biological control method was added in 2008 to the integrated management strategies of the San Juan Fruit Fly Control and Eradication Program (ProCEM-San Juan, Spanish acronym) [50]. Such a control tactic was implemented to achieve mass rearing of the Indo-Pacific parasitoid Diachasmimorpha longicaudata (Ashmead) (Hymenoptera: Braconidae) at the San Juan Biofactory to release it in fruit-producing semi-arid valleys of the San Juan province, central-western Argentina. The lack of resident parasitoid species attacking medflies in the region [50] supported the introduction and release of D. longicaudata, which was released under different environmental conditions [51–54]. This exotic braconid wasp was originally introduced and released in several Latin American countries, including Argentina, as a classical biological control agent for fruit fly pests between the 1960s and 1980s [3,4,6]. Specimens of *D. longicaudata* were recovered in citrus-growing areas of northern Argentina approximately 40 years after its first release in that region [3]. Diachasmimorpha longicaudata is currently one of the most widely used parasitoid species for augmentative biological control of fruit fly pests [3,6,11]. It is a generalist, larval, koinobiont, and solitary endoparasitoid of several tephritid fruit fly species [3,55]. Females of D. longicaudata forage on fallen infested fruits and also on fruit still in the tree canopy, and they always oviposit into a host larva by drilling with their ovipositor into the fruit pericarp from outside [56]. There were no records of this exotic parasitoid attacking non-target hosts or beneficial insect species in those American countries where it was released [3].

The mass rearing of D. longicaudata was successfully established on irradiated larvae of the medfly Vienna-8 temperature-sensitive lethal genetic sexing strain without inversion (= Cc_{tsl} strain) at the San Juan Biofactory between 2011 and 2012, although this strain has high production costs [48]. This medfly strain is currently used for producing sterile males of the pest to apply the SIT in irrigated fruit crops throughout San Juan province [57]. From 2012 to 2016, augmentative releases of D. longicaudata were carried out in fruit crops of different fruit-growing areas of the San Juan province to evaluate its performance as a medfly biocontrol agent under semi-arid climatic conditions [51,58]. The use of augmentative biological control in San Juan achieved a medfly population control between 40 and 70% [58]. These promising outcomes encouraged research to improve both the mass production of D. longicaudata and the quality of its individuals yielded at the San Juan Biofactory.

Given this, it was first hypothesized that the use of larvae of a biparental medfly strain native to San Juan (= Cc_{bip} strain) as a host to rear *D. longicaudata* instead of the Cc_{tsl} strain enhances and optimizes the parasitoid production, providing individuals with higher reproductive capacity. Therefore, the first aim of this study was to compare relevant population and reproductive parameters under laboratory rearing conditions between

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two D. longicaudata population lines, one reared on the Ccbip strain and the other on the Cc_{tsl} strain. Secondly, it was hypothesized that population lines of D. longicaudata reared on either of the two medfly strains perform better, based on their reproductive success, when released during the spring-summer period. Thus, the second aim of this study was to compare the parasitoids' performance of the two *D. longicaudata* population lines among three seasons, namely spring, summer, and autumn, under natural weather conditions in the area of interest using semi-field cages. During such seasons, the medfly is particularly active in irrigated fruit-growing valleys of San Juan due to the abundance of different host fruit species [59]. Among host plants, peaches and figs, which occur between late spring and mid-summer, are multiplying fruits for C. capitata populations in the study region [50,58,59]. In addition, large fruits, such as citrus fruits, particularly oranges and grapefruits, can support C. capitata populations during less favorable environmental periods, such as autumn and winter [48,58]. In this regard, it is a significant challenge for the exotic D. longicaudata to adapt to the fruit-growing region due to its temperate and semi-arid climatic characteristics, and its broad thermal variations between seasons, and also throughout the day. The significance of this study is discussed regarding the use of D. longicaudata in augmentative biological control against fruit fly pests in Argentina.

2. Materials and Methods

2.1. Insect-Rearing Procedures

Parasitoids and flies came from colonies kept in the San Juan Insect Mass Rearing Biofactory, which belongs to the Plant, Animal, and Food Health Bureau (=PAFHB) of the government of the San Juan province, located in the central-western fruit-growing region of Argentina. Two D. longicaudata population lines (from now on, DlPLs) were used in the trials. One of them was reared on C. capitata third-instar larvae of the Cc_{tsl} strain (from now on, $Dl_{(Cc-tsl)}$) and the other one on C. capitata third-instar larvae of the Cc_{bip} strain (from now on, $Dl_{(Cc\text{-bip})}$). The Cc_{tsl} strain was established at the San Juan Biofactory in the early 2000s, which is currently reared. This medfly strain was brought from the Km-8 Pilot Biofactory located in the neighboring province of Mendoza, but originally the strain was sent by the International Atomic Energy Agency. Such a strain is currently reared through different colonies at the Medfly Rearing Laboratory (=MRL) from the San Juan Biofactory. Egg incubation begins at moderate temperatures, i.e., 24 °C, which allows for hatching and larval development on a suitable diet (described below). The first colony is the "Filter" colony, where the most suitable adults are manually selected for reproduction. The eggs from this colony give rise to the second colony of females, the "Injection" colony, whose eggs originate the third colony, the "Renewal" colony, which in turn produces the fourth colony, the "Release" colony. This then gives rise to the last colony, the "Thermal" colony, where the eggs undergo heat treatment at restrictive high temperatures, i.e., between 34 and 35 °C, for 48 h to selectively eliminate heterozygous females. As a result, a male-only population emerges from brown pupae, which are irradiated for use in SIT programs. The Cc_{bip} strain originated from wild medfly larvae recovered from figs, peaches, and plums collected from orchards in the fruit-growing valley of Tulum, San Juan, between December 2018 and January-February 2019. Larvae of both medfly strains were reared at the MRL on an artificial diet based on wheat bran (17%), yeast (8%), sugar (10%), hydrochloric acid (0.8%), poplar wood chips (8.8%), water (54.9%), and food preservative, such as sodium benzoate (0.3%) and methylparaben (0.2%). The medfly strains were reared in separate rooms, as the Cctsl strain involves a higher degree of complexity for its production. The colonies of the two DIPLs were kept in rectangular iron-framed, voile-covered cages ($60 \times 60 \times 30$ cm) at 24 ± 1 °C, $65 \pm 5\%$ RH, and at 12:12 (L:D) h, but in different rooms from the Parasitoid Rearing Laboratory at the San Juan Biofactory. Adult parasitoids were provided with pure

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bee honey and, individually, water through troughs with a yellow absorbent cloth wick every other day. Medfly larvae aged 6 d old and irradiated at 90 Gy were daily exposed to parasitoid females. The irradiation of larvae from both medfly strains was performed using an IMO-1 mobile irradiator with a Co-60 source of γ irradiation, which belongs to the National Atomic Energy Commission from Argentina but is located at the San Juan Biofactory. The larval quality of both medfly strains was evaluated using the average weight of 300 6 d old larvae samples per batch. Batches with 12.2 \pm 0.5 mg (Mean \pm SE) mean weight larvae were used in the trials as suggested by Suárez et al. [60]. Cohorts from $Dl_{(Cc\text{-tsl})}$ and $Dl_{(Cc\text{-bip})}$) colonies at their 60th and 10th generations under artificial rearing conditions were used in the assays.

2.2. Experimental Setup

2.2.1. Laboratory Trials

Survival and lifetime reproductive parameters of both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-bip})}$ were assessed and compared under the same lab-controlled conditions described above. Twenty-five female/male pairs of $Dl_{(Cc\text{-tsl})}$ and $Dl_{(Cc\text{-bip})}$ were individually placed into transparent cubical Plexiglas cages (10 cm). All 25 pairs of each parasitoid population line remained isolated during their lifetime. Parasitoids were provided with water and honey every other day. Ninety lab-reared 6 d old larvae of the C. capitata strain belonging to the respective parasitoid population line, i.e., Cc_{tsl} and Cc_{bip} , were placed inside artificial units and exposed to each parasitoid pair for 2 h under a lighting condition of 1200 lux provided by six 36W-fluorescent light tubes distributed throughout the room. The oviposition devices were 5×0.7 cm (diameter \times height) voile screen-covered plastic dishes holding naked irradiated host larvae, i.e., no larval-rearing diet. Larval exposure was performed every other day until all female parasitoids died. After exposure to parasitoids, host larvae were removed from each oviposition device and placed in 8×7 cm (height \times diameter) voile-covered plastic cups with poplar shaving (Populus alba L., Salicaceae) at the bottom as a pupation substrate. Puparia were kept inside cups until adult parasitoid emergence. Standard life tables were developed in order to calculate demographic parameters such as lx, the proportion of individuals surviving to start of the age interval; px, the proportion of individuals surviving through the period; qx, proportion of individuals dying through the period; dx, the fraction of the original cohort dying at age x; ex, life expectancy of individuals surviving at age x; and mx, female offspring produced per female at age x [61]. In this study, lx and ex were calculated based on surviving females (= lx_f and ex_f , respectively). Based on basic life table parameters, key population increase parameters were calculated such as R₀, net reproductive rate or contribution of newborn females by progeny to the next generation; r, intrinsic rate of natural increase or rate of natural increase in a closed population; λ , finite rate of increase or rate at which a population increases from time t to time t + 1; and T, mean generation time or average time needed for a newborn female to replace herself R_0 -times [61].

2.2.2. Semi-Field Cage Trials

Survival and lifetime reproductive rates of both $Dl_{(Cc\text{-}tsl)}$ and $Dl_{(Cc\text{-}bip)}$ were assessed and compared inside a 3.5 \times 3.0 m (diameter \times height) nylon semi-field cage under natural weather conditions at an experimental plot of the PAFHB, located at 31°31′ S, 68°36′ W, and 710 m.a.s.l. in the Tulum Valley, San Juan province. Such San Juan lowlands have a semi-desert climate with a mean annual temperature of ~18 °C, and rainfall is restricted to the early and mid-summer (January–February) [62]. Mean air temperature was calculated by averaging daily maximum and minimum temperatures, mean maximum air temperature, mean minimum air temperature, and mean relative humidity for each season in the months

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during which the tests were performed (Table 1). A digital weather station (LUFT[®], model WS80, Shenzhen, China) located in the experimental plot was used for this purpose.

Table 1. Mean (\pm SE) air temperature (T_{mean}), mean (\pm SE) maximum air temperature (T_{max}), mean (\pm SE) minimum air temperature (T_{min}), mean (\pm SE) range air temperature (T_{range}), mean (\pm SE) relative humidity (RH_{mean}), mean (\pm SE) maximum relative humidity (RH_{max}), mean (\pm SE) minimum relative humidity (RH_{min}), and mean (\pm SE) range relative humidity (RH_{range}) recorded during semifield cage trials between October and November/2019 (spring), February and March/2020 (summer), and May/2020 (autumn) in the experimental plot of the Plant, Animal, and Food Health Bureau, Rivadavia District, Tulum Valley, San Juan province, central-western Argentina.

| | Temperature (°C) | | | | Relative Humidity (%) | | | |
|---------|------------------|----------------|----------------|----------------|-----------------------|----------------|----------------|---------------------|
| Seasons | T_{mean} | T_{max} | T_{min} | T_{range} | RH_{mean} | RH_{max} | RH_{min} | RH _{range} |
| Spring | 19.6 ± 0.6 | 26.2 ± 0.8 | 13.7 ± 0.6 | 17.3 ± 0.9 | 48.3 ± 2.2 | 69.4 ± 2.8 | 27.4 ± 2.4 | 42.4 ± 3.0 |
| Summer | 22.0 ± 0.5 | 30.3 ± 0.7 | 13.9 ± 0.6 | 22.7 ± 0.8 | 51.2 ± 1.0 | 78.1 ± 1.5 | 23.6 ± 1.1 | 54.6 ± 1.5 |
| Autumn | 12.7 ± 0.3 | 20.0 ± 0.6 | 5.3 ± 0.5 | 13.6 ± 0.9 | 62.8 ± 1.1 | 83.5 ± 2.1 | 42.0 ± 0.9 | 41.6 ± 2.4 |

The semi-field cage was placed under poplar trees, providing a windbreak and a constant natural shade. In spring, the study was carried out from October to November 2019, in summer between February and March 2020, and in autumn during May 2020. This design provided a comparison of population and reproductive parameters of both DlPLs under meteorological variations in the same season and between seasons. Forty 15×20 cm (diameter ×height) experimental cylindrical iron-framed, voile-covered cages (=ECs) were placed into the semi-field cage. A total of 20 ECs held one female–male pair of the $Dl_{(Cc-tsl)}$ population line each, whereas the other 20 ECs held one female–male pair of the $Dl_{(Cc-bip)}$ each. All ECs were placed on a table in the center of the field cage and 1 m above the ground. Every 24 h, the position of each EC was changed in a clockwise rotation. Parasitoids were provided with water and bee honey daily. The oviposition units are described above. Ninety lab-reared 6 d old larvae of Cc_{tsl} or Cc_{bip} were exposed to $Dl_{(Cc-tsl)}$ or $Dl_{(Cc-bip)}$ females, respectively, in previously described oviposition units for 2 h. Larval exposure was held from 10 to 12 a.m. every other day for 19 days only. In each EC, the survival of individuals was recorded daily. Dead parasitoids were removed to avoid fungal and/or bacterial contamination. Once the exposure period was over, host larvae were handled and kept as previously reported. Standard life tables were developed in order to calculate key population parameters as previously explained.

2.3. Data Analysis

Life tables, population parameters, survival, fecundity, and relationships between weather predictors and both lx_f and mx parameters were analyzed using the R-4.4.2 software [63]. Life tables were constructed for both $Dl_{(Cc\text{-}bip)}$ and $Dl_{(Cc\text{-}bip)}$ using experimental data on mean fecundity per maternal female age interval and female survivorship proportion with the tidyverse [64] and boot [65,66] packages. Data preprocessing included transformations via mutate() and grouping with group_by() to calculate relative age (x) from dates, mx, and lx_f . Key population parameters, such as R_0 , r, λ , and T, were computed via custom-defined functions. Standard errors (SE) and 95% confidence intervals (CIs) for each population parameter were estimated through stratified bootstrap resampling (R = 1000), significant differences in the population parameters of both strains were established through confidence interval analysis, thereby avoiding inferences derived from bootstrap-generated datasets according to Pritchard et al. [67]. The ex_f was derived from the cumulative sum of lx_f (Tx), and lx_f , ex_f , and mx curves were plotted using ggplot2 [68]. Log-Rank tests were performed using the survival package [69,70] to compare lx curves for $Dl_{(Cc\text{-}bip)}$ and $Dl_{(Cc\text{-}tsl)}$.

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Additionally, a linear model with interaction was fitted, and the effect of both Cc_{tsl} and Ccbip strains on curve shape was assessed via ANOVA. Both mx and ex parameters for $Dl_{(Cc-bip)}$ and $Dl_{(Cc-tsl)}$ were compared using a Generalized Additive Model (GAM) fitted with the mgcv package [71]. The model included both Cc_{tsl} and Cc_{bip} strains as a categorical predictor and female age as a smoothed continuous term, estimated via restricted maximum likelihood (REML). This approach enabled flexible modeling of age-dependent fecundity and life expectancy patterns while accounting for differences due to parasitoids reared on Cc_{tsl} or Cc_{bip} strains. Model diagnostics and visualization of the smooth term were performed using built-in functions from mgcv. The influence of weather predictors, derived from temperature and relative humidity, was evaluated on lx and mx of both $Dl_{(Cc-bip)}$ and Dl_(Cc-tsl). Data were analyzed employing the ggplot2, dplyr [72], tidyr [73], relaimpo [74], betareg [75], car, and mgcv [76] packages. Initial models included all weather variables (T_{max}, T_{min}, T_{mean}, T_{range}, RH_{max}, RH_{min}, RH_{mean}, and RH_{range}) and were individually fitted for $Dl_{(Cc-bip)}$ and $Dl_{(Cc-tsl)}$ using linear regression. Model selection was performed via stepwise procedures based on Akaike's Information Criterion (AIC) to identify the most informative predictors. The relative importance of variables was assessed using the LMG method. A beta-regression approach was applied for lx_f , due to the continuous and bounded nature (0–1) of the variable [77]. Collinearity diagnostics were conducted using variance inflation factors, and non-identifiable terms were excluded. Final models incorporated female age and selected weather variables, which provide a sound basis for making inferences about survival effects.

3. Results

3.1. Life Table and Population Increase Parameters Under Laboratory Conditions

The life table parameters recorded for both DlPLs are presented in File S1. The survival of females from both DlPLs was not significantly different (Log-rank $\chi^2 = 3.4$, df = 1, p = 0.07) (Figure 1). The 50% of $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-bip})}$ females were alive (l_{50}) at 39 and 29 days, respectively (Figure 1).

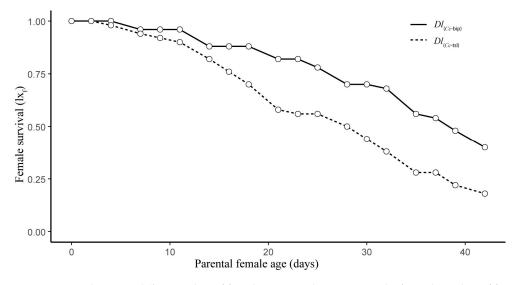


Figure 1. Female survival (lx_f , number of females to start the age interval x/initial number of females) for two population lines of *D. longicaudata* ($Dl_{(Cc\text{-tsl})}$ and $Dl_{(Cc\text{-bip})}$).

The life expectancy of $Dl_{(Cc\text{-bip})}$ females was significantly higher than that of $Dl_{(Cc\text{-tsl})}$ females ($F_{(3,34)} = 1701$, $p < 2.2 \times 10^{-16}$, adjusted $R^2 = 0.993$) (Figure 2). This variation between both DlPLs was influenced by the statistical significance of the parasitoid female's age (F = 4777.64, df = 1, p = 0.000), the DlPL (F = 217.93, df = 1, p = 0.000), and the interaction

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between both fixed factors (F = 106.32, df = 1, p = 0.000). Female life expectancy was 15 and 12 days for $Dl_{(Cc\text{-}\text{bip})}$ and $Dl_{(Cc\text{-}\text{tsl})}$, respectively, at the time of adult emergence.

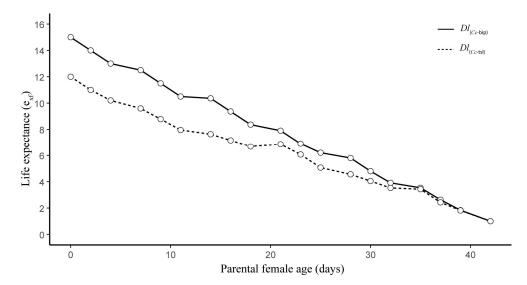


Figure 2. Female life expectancy (ex_f) life expectancy of females surviving at age x for two population lines of *D. longicaudata* ($Dl_{(Cc\text{-bip})}$) and $Dl_{(Cc\text{-bip})}$).

Both DlPLs showed fecundity curves (mx) with relatively similar trends, albeit with significantly different mean values of female offspring per mother per day (Figure 3). Over her lifetime, $Dl_{(Cc\text{-tsl})}$ produced 1.88 (± 0.42) fewer daughters than $Dl_{(Cc\text{-bip})}$ (t = 4.34, df = 1, p = 0.0001). The age of the parental female was a significant factor influencing the difference between female offspring productions in both DlPLs (F = 5.76, e.df = 5.84, Ref.df = 6.99, p = 0.0001, $R^2_{(adj)}$ = 0.61). The mx curves showed three peaks of daughter production, which were at 9, 16, and 25 d old for $Dl_{(Cc\text{-bip})}$ parental females and at 4, 11, and 25 d old for $Dl_{(Cc\text{-tsl})}$ parental females (Figure 3). A slightly female-biased offspring sex ratio, 1.3:1 and 1.1:1 females/male, was recorded for $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$, respectively.

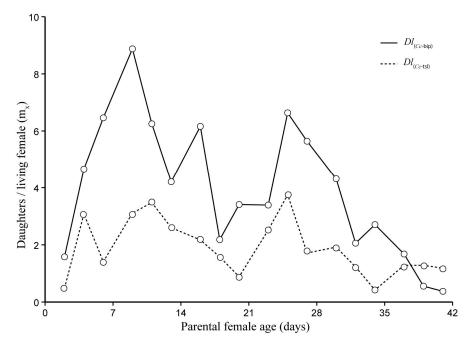


Figure 3. Daily fecundity (mx, number of daughters/parental female/day) for two population lines of *D. longicaudata* ($Dl_{(Cc\text{-bip})}$).

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Based on confidence intervals, the population increase parameters R_0 , r, and λ recorded for $Dl_{(Cc\text{-bip})}$ were higher than those for $Dl_{(Cc\text{-tsl})}$, whereas T was similar in both DlPLs (Table 2).

Table 2. Population parameters [Net reproductive rate (R_0), intrinsic rate of increment (r), mean generation time (T) and finite rate of increase (λ)] for two population lines of D. longicaudata ($Dl_{(Cc\text{-tsl})}$) and $Dl_{(Cc\text{-bip})}$) under constant laboratory conditions [Mean \pm standard error (SE), and confidence intervals (CI) with lower and upper bounds (lo–hi)]. Different letters indicate significant differences between values by CI comparison.

| | Population Increase Parameters | | | | |
|--------------------------------|---|--|---|--|--|
| Parasitoid Population Lines | R_0 (Females/Female Per Generation) | r (Per Day) | T (Days) | λ (Per Day) | |
| $Dl_{(Cc	ext{-bip})}$ | $109.80 \pm 3.46 \\ [108.8 – 122.4] ^{a}$ | 0.32 ± 0.00 [0.29–0.32] ^a | 14.63 ± 0.30 [14.53–15.82] ^a | 1.37 ± 0.00 [1.34–1.38] ^a | |
| $Dl_{(Cc	ext{-tsl})}$ | 63.94 ± 3.35 [68.3–81.4] ^b | $0.29 \pm 0.00 \ [0.24 – 0.28]^{b}$ | 14.22 ± 0.58 [15.12–17.50] ^a | 1.33 ± 0.01 [1.28–1.32] ^b | |

3.2. Life Table and Population Increase Parameters Under Semi-Field Cage Conditions

The life table parameters recorded for both DlPLs during semi-field cage trials in spring, summer, and autumn are presented in Files S2–S4. Survival curves of females from both DlPLs were significantly different in spring (Log-rank $\chi^2 = 4.17$, df = 1, p = 0.041) (Figure 4A), but significantly similar in both summer (Log-rank $\chi^2 = 1.27$, df = 1, p = 0.259) (Figure 4B) and autumn (Log-rank $\chi^2 = 0.01$, df = 1, p = 0.929) (Figure 4C). The survival rate for $Dl_{(Cc\text{-bip})}$ was slightly higher than that for $Dl_{(Cc\text{-tsl})}$ in spring (Figure 4A). Fifty percent of $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-bip})}$ females were alive (l_{50}) at 18, 17, and 2 d old, and at 17, 16, and 2 d old in spring, summer, and autumn, respectively. According to the beta regression model, both T_{\min} and RH_{\min} were weather factors that accurately fitted the model when survival of both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$ was analyzed ($Dl_{(Cc\text{-bip})}$, Log-likelihood = 19.53, df = 5, Pseudo- $R^2 = 0.6083$; $Dl_{(Cc\text{-tsl})}$ Log-likelihood = 20.96, df = 5, Pseudo- $R^2 = 0.6584$). However, the T_{\min} significantly influenced both DlLPs ($Dl_{(Cc\text{-bip})}$, z = 3.029, p = 0.00245; $Dl_{(Cc\text{-tsl})}$, z = 3.505, p = 0.00046), whereas the RH_{min} did not significantly affect both DlLPs ($Dl_{(Cc\text{-bip})}$, z = 1.779, z = 0.07527; $Dl_{(Cc\text{-tsl})}$, z = 1.884, z = 0.05962).

The life expectancy of females between both LPPs was significantly different during semi-field cage trials at three tested stations (spring, t=5.004, df=1, p<0.0001; summer, t=2.892, df=1, p=0.0139; autumn, t=3.156, df=1, p=0.0125). Over $Dl_{(Cc\text{-tsl})}$ females' lifespan, the ex_f was 0.61 (\pm 0.12), 0.18 (\pm 0.06), and 0.34 (\pm 0.11) days significantly lower than that of $Dl_{(Cc\text{-bip})}$ females during spring (Figure 5A), summer (Figure 5B), and autumn (Figure 5C). The parental female age significantly influenced the life expectancy of both DlPLs females (spring, F=184.9, e.df=8.186, Ref.df=8.817, $p=2.0\times10^{-16}$, adjusted- $R^2=0.979$; summer, F=436.5, e.df=8.395, Ref.df=8.90, $p=2.0\times10^{-16}$, adjusted- $R^2=0.995$, autumn, F=89.87, e.df=7.311, Ref.df=7.93, $p=2.0\times10^{-16}$, adjusted- $R^2=0.977$).

Both DlPLs showed fecundity curves (mx) that were significantly similar in spring (t = 0.266, df = 1, p = 0.792) (Figure 6A) and summer (t = 0.806, df = 1, p = 0.436) (Figure 6B). In contrast, a significant difference was found in autumn (t = 2.551, df = 1, p = 0.032) (Figure 6C). Over $Dl_{(Cc\text{-tsl})}$ females' lifespan, 0.49 (± 0.19) significantly fewer daughters than $Dl_{(Cc\text{-bip})}$ were produced in autumn. In spring, the $Dl_{(Cc\text{-bip})}$ females showed five peaks of daughter production between 2 and 28 d old, whereas $Dl_{(Cc\text{-tsl})}$ females showed four peaks of daughter production between 2 and 24 d old (Figure 6A). In summer, the $Dl_{(Cc\text{-bip})}$ females showed three peaks of daughter production between 3 and 19 d old, whereas $Dl_{(Cc\text{-tsl})}$ females showed two pronounced peaks of daughter production be-

tween 6 and 16 d old (Figure 6B). In autumn, the $Dl_{(Cc ext{-bip})}$ females developed two very pronounced peaks of daughter production between 3 and 7 d old, and one slight peak of daughter production at 17 d old, whereas $Dl_{(Cc\text{-tsl})}$ females developed one pronounced peak of daughter production at 3 d old, followed by a couple of slight increases in the female offspring at 7 and 17 d old (Figure 6C). The parental female age significantly influenced the female offspring yields in both DIPLs during the three tested seasons (spring, F = 8.688, e.df = 2.942, Ref. df = 3.688, p = 0.0001, adjusted $R^2 = 0.461$; summer, F = 4.624, e.df = 7.782, $Ref. df = 8.625, p = 0.0084, adjusted-R^2 = 0.626; autumn, F = 3.844, e.df = 7.216, Ref. df = 7.817,$ p = 0.0378, adjusted- $R^2 = 0.635$). According to the linear model, both T_{min} and RH_{max} were weather factors that fitted to the model when the fecundity of both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$ was analyzed ($Dl_{(Cc\text{-bip})}$, F = 16.78 on 2 and 35 df, $p = 7.320 \times 10^{-7}$, adjusted- $R^2 = 0.5614$; $Dl_{(Cc\text{-tsl})}$, F = 21.95 on 2 and 35 df, $p = 6.636 \times 10^{-7}$, adjusted- $R^2 = 0.5311$). Both T_{min} and RH_{max} significantly influenced both DlLPs ($Dl_{(Cc\text{-bip})}$: T_{\min} , t = 2.657, p = 0.0119, and RH_{max} , t = 2.193, p = 0.0353; $Dl_{(Cc-tsl)}$: T_{min} , t = 6.607, $p = 1.240 \times 10^{-7}$, and RH_{max} , t = 3.601, p = 0.0009). Female-biased offspring sex ratios were recorded for both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$ in spring and summer (1.4:1 and 1.7:1 $Dl_{(Cc\text{-bip})}$ females/male, respectively; 1.1:1 $Dl_{(Cc\text{-tsl})}$ females/male in both seasons). A male-biased offspring sex ratio was recorded for both DlLPs in autumn (0.7:1 $Dl_{(Cc\text{-bip})}$ females/male and 0.5:1 $Dl_{(Cc\text{-tsl})}$ females/male).

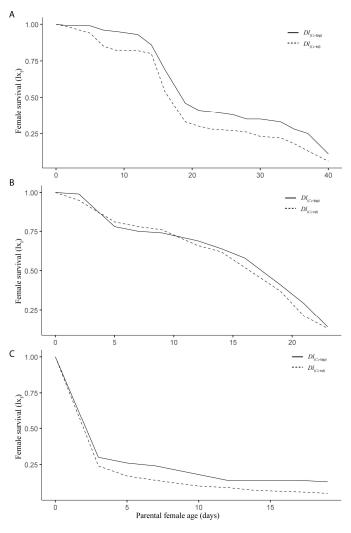


Figure 4. Female survival (lx_f), number of female to start the age interval x/initial number of females) for two population lines of D. longicaudata ($Dl_{(Cc-tsl)}$ and $Dl_{(Cc-tsl)}$) recorded from semi-field cage trials in spring (**A**), summer (**B**), and autumn (**C**) in the Tulum Valley, San Juan Province, central-western Argentina.

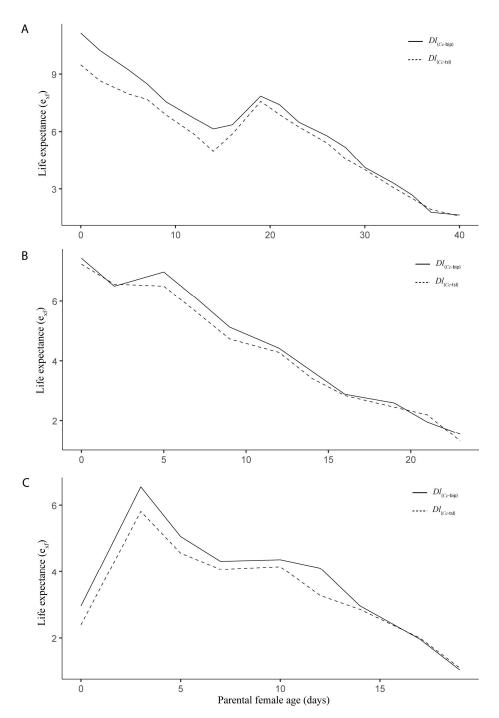


Figure 5. Female life expectancy (ex_f) (life expectancy of females surviving at age x) for two population lines of *D. longicaudata* ($Dl_{(Cc\text{-}tsl)}$) and $Dl_{(Cc\text{-}bip)}$) recorded from semi-field cage trials in spring (**A**), summer (**B**), and autumn (**C**) in the Tulum Valley, San Juan Province, central-western Argentina.

The population increase parameters (R_0 , r, T, and λ) of each DlPL varied substantially between different seasons during which the semi-field cage trials were performed (Table 3). Only the R_0 parameter recorded in spring and summer was similar for each DlPL, and between both DlPLs (Table 3). The highest r parameter was recorded in summer in both DlPL, and their mean values were substantially similar. The lowest r was recorded in autumn for both DlPL, with a substantially higher mean value for $Dl_{(Cc\text{-bip})}$. (Table 3).

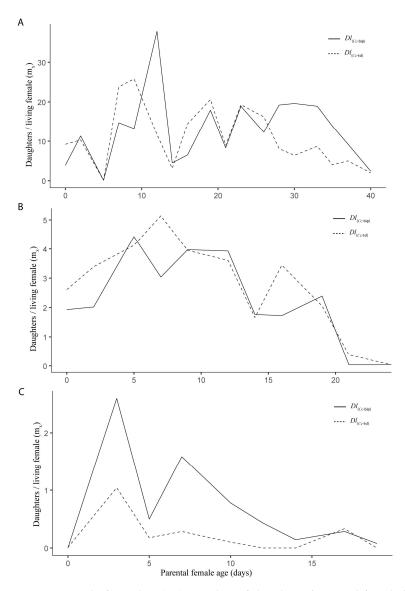


Figure 6. Daily fecundity (mx), number of daughters/parental female/day) for two population lines of D. longicaudata ($Dl_{(Cc-tsl)}$ and $Dl_{(Cc-bip)}$) recorded from semi-field cage trials in spring (\mathbf{A}), summer (\mathbf{B}), and autumn (\mathbf{C}) in the Tulum Valley, San Juan Province, central-western Argentina.

Table 3. Population parameters [Net reproductive rate (R_0), intrinsic rate of increment (r), mean generation time (T) and finite rate of increase (λ)] for two population lines of D. longicaudata ($Dl_{(Cc\text{-tsl})}$) and $Dl_{(Cc\text{-bip})}$) under semi-field cage conditions at three different seasons (spring, summer and autumn) [Mean \pm standard error (SE), and confidence intervals (CIs) with lower and upper bounds (lo–hi)]. Different letters indicate significant differences between values by CI comparison.

| | | Population Increase Parameters | | | | |
|--------------------------------|---------|---|--|---|---|--|
| Parasitoid Population Lines | Seasons | R ₀ (Females/Female Per Generation) | r (Per Day) | T (Days) | λ (Per Day) | |
| $Dl_{(Cc	ext{-bip})}$ | Spring | $23.26 \pm 3.45 \ [16.93-30.17]^{a}$ | $0.15 \pm 0.02 \ [0.12-0.20]^{\mathrm{b}}$ | $20.67 \pm 2.75 \ [15.74-26.16]^{a}$ | 1.16 ± 0.03 $[1.12-1.23]^{b}$ | |
| | Summer | 19.80 ± 3.37 [11.29–25.50] ^a | 0.35 ± 0.09 [0.21–0.56] ^a | 8.42 ± 1.73 [5.45–12.21] ^b | $1.42 \pm 0.14 \ [1.24-1.75]^{a}$ | |
| | Autumn | $rac{1.56 \pm 0.72}{[0.40 - 3.09]^{\mathrm{b}}}$ | $0.08 \pm 0.10 \ [-0.09$ –0.27] $^{ m c}$ | $5.72 \pm 1.94 \ [3.78-10.82]^{\mathrm{b}}$ | 1.08 ± 0.11 [0.92–1.31] $^{\rm c}$ | |
| $Dl_{(Cc	ext{-tsl})}$ | Spring | 19.76 ± 3.17 [13.61–26.05] ^a | 0.17 ± 0.03 [0.12-0.25] ^b | 17.15 ± 2.52 [12.65–22.15] ^a | 1.19 ± 0.04 $[1.13-1.28]^{b}$ | |
| | Summer | 22.48 ± 4.21 [14.41–30.05] ^a | 0.41 ± 0.11 [0.03–0.12] ^a | 7.65 ± 1.69 [4.82–11.77] ^b | 1.50 ± 0.18 [1.27–1.97] $^{ m a}$ | |
| | Autumn | 0.36 ± 0.23 [0.06–0.85] ^c | $-0.23 \pm 0.10 \ [-0.440.04]^{d}$ | 4.50 ± 2.28 [3.19–11.07] ^b | 0.80 ± 0.08 [0.64-0.96] ^d | |

4. Discussion

One of the strategic goals of demographic studies on parasitoids is to provide valuable input on their use as potential biological pest control agents and the stability of hostparasitoid systems. The reproductive capacity of females during their lifetime plays a crucial role in understanding the parasitoid population dynamics [28,30]. Such information, as other parasitoid life history traits, is essential to the success of biological control programs, mainly in the context of reducing environmental impact and supporting sustainability [78]. Within this framework, the current study reports a comparative demographic analysis of the exotic parasitoid D. longicaudata reared on two different strains of the invasive pest C. capitata, one wild-type and one genetically modified. Tests were carried out in the laboratory and, for the first time, under semi-field cage conditions. The latter enables the performance of both DlPLs to be assessed when released at different seasons in the fruitgrowing semi-arid region of central-western Argentina. The results underscore important findings as follows: (1) the $Dl_{(Cc\text{-tsl})}$ was slightly outperformed by the $Dl_{(Cc\text{-tsl})}$ in terms of the female ex, lx and population growth rates, when both DlPLs were assessed under laboratory conditions; (2) $Dl_{(Cc ext{-}bip)}$ females displayed lx- and ex-values higher than those recorded for $Dl_{(Cc-tsl)}$ females in spring, whereas the mx-parameter was similar in both DIPLs during spring and summer trials, but it was strongly different between DIPLs in the autumn; (3) both DILPs recorded high and similar R_0 - and r-values in spring and summer, but these parameters were low and different between the two DIPLs in autumn; and (4) the T_{min} had a significant influence on the temporal variation in lx- and mx-parameters in both DlPLs, and the RH_{max} only on the mx-parameter in the two DlPLs during semi-field cage studies.

The first finding revealed higher ex- and mx-values for $Dl_{(Cc\text{-bip})}$ females than those recorded for $Dl_{(Cc\text{-tsl})}$ females. In addition, R_0 , r, and λ estimated for $Dl_{(Cc\text{-bip})}$ were also higher than those for $Dl_{(Cc-tsl)}$. Among those parameters, the r is the most outstanding concerning their importance in assessing parasitoid population dynamics [28,29,31]. Such parameters involve both survival and reproductive data of a parasitoid population, and it is therefore an important indicator for describing the potential population growth over time, under rearing conditions, or when released [23,24,28,79]. More suitable hosts may ensure a high production and better quality of offspring while maintaining acceptable parasitoid rearing costs [80]. Although $Dl_{(Cc\text{-bip})}$ females displayed a better reproductive capacity under laboratory conditions, it is important to take into account that the results of the current study may be related to the age of the DIPL cohorts used in trials. In this regard, $Dl_{(Cc-tsl)}$ females were kept under rearing conditions using the Cc_{tsl} strain for 50 generations longer than $Dl_{(Cc\text{-bip})}$. The D. longicaudata colony established on the Cc_{bis} strain was only 10 generations old when the study was performed. Thus, it appears reasonable to assume that the demographic parameters and population increase values may differ, as shown in this study. Consistent with that thought, some studies on the *D. longicaudata* demography performed in the laboratory point to the effect of time elapsed under rearing conditions using different host species [24,81,82], host stage age [44], or host strains [83]. Older parasitoid cohorts may have lower survival rates, which influences the reproductive rate and overall population growth of that parasitoid species [84,85]. Nevertheless, the potential influence of the *C. capitata* strain cannot be ruled out in the current study, which requires further in-depth research on this topic. Interestingly, the crucial *r*-parameter, which stands for the instantaneous or per capita population growth rate, recorded for both DIPLs, was appreciably higher than that recorded in other laboratory studies on D. longicaudata reared on other tephritid host species or on different *C. capitata* strains (see Table 4). The *r*-value recorded for both DlPLs outperformed the highest values of r published for C. capitata, A. fraterculus, and Bactrocera dorsalis Hendel (Diptera: Tephritidae) by 2.1- and 2.3-fold,

1.9- and 2.1-fold, and 1.7- and 1.9-fold, respectively (Table 4). Laboratory conditions, larval diets, host larval age, the host species, and/or the medfly strains could probably explain the difference between those values.

Table 4. Intrinsic rate of natural increment (*r*) recorded in the literature for *Diachasmimorpha longicaudata* under laboratory conditions at different temperature ranges.

| Host Species | Intrinsic Rate of Natural Increment (<i>r</i>) | Laboratory-Tested Temperatures (°C) | References |
|--|---|---|----------------------|
| Anastrepha fraterculus (Wiedemann) | 0.17 ± 0.03 | 25.0 ± 2.0 | [81] |
| Ceratitis capitata (Wiedemann) | 0.14 ± 0.02 | 25.0 ± 2.0 | [81] |
| C. capitata (wild strain) | 0.098 ± 0.005 | 22.9 ± 2.9 | [82] |
| C. capitata (genetic sexing strain Cast-191) | 0.094 ± 0.004 | 22.9 ± 2.9 | [82] |
| Bactrocera dorsalis Hendel B. dorsalis B. dorsalis | $0.003 \pm 0.001 - 0.145 \pm 0.001 \ -0.0240 - 0.1318 \ 0.12$ | $ \begin{array}{c} 15-30 \\ 15-30 \\ 26.0 \pm 2.0 \end{array} $ | [44] [39] [24] |

The second finding showed interesting data on *lx-*, *ex-* and *mx-*parameters of both DIPLs recorded during field-cage trials. Although in spring the lx- and ex-parameters recorded for $Dl_{(Cc\text{-bip})}$ females were higher than those of $Dl_{(Cc\text{-tsl})}$ females, the mx in both DlPLs was statistically similar. Each $Dl_{(Cc\text{-bip})}$ female and each $Dl_{(Cc\text{-tsl})}$ female produced 57.6 ± 6.4 and 52.9 ± 3.8 daughters over their lifetime in the spring, respectively. During summer semi-field cage trials, $Dl_{(Cc\text{-bip})}$ females recorded a slightly higher ex than $Dl_{(Cc\text{-bip})}$ females, but both lx- and mx-parameters were similar between the two DlPLs. The production of daughters per living maternal female of both $Dl_{(Cc-tsl)}$ and $Dl_{(Cc-tsl)}$ during the summer trial was 31.5 ± 1.2 and 34.1 ± 1.8 daughters over their lifetime, respectively. Surprisingly, in the autumn semi-field cage trials, both ex- and mx-parameters recorded for $Dl_{(Cc\text{-bip})}$ increased substantially compared to that reported for $Dl_{(Cc\text{-tsl})}$. However, the lxwas similar, and females of both DIPLs did not reach 20 d old. Such information is relevant as it highlights two outstanding issues. Firstly, the performance of females from the two DIPLs in terms of their female offspring production was similar under temperate-to-warm natural environmental conditions, with mean daily temperatures between 20 and 22 °C, as recorded during trials in late spring and midsummer. Secondly, $Dl_{(Cc-bip)}$ females could be more successfully productive than $Dl_{(Cc-tsl)}$ females under natural conditions with colder temperatures (mean daily temperature around 13 °C), as recorded during early autumn trials. This finding may indicate a higher biological plasticity in $Dl_{(Cc\text{-bip})}$ females; that is, these females may tolerate a broader temperature range than $Dl_{(Cc-ts]}$ females. Data recorded in the autumn showed that the production of daughters per $Dl_{(Cc ext{-}bip)}$ maternal female doubled that of $Dl_{(Cc\text{-tsl})}$ females up to the first 10 days of the females' lives. Thus, the mean number of female offspring per living maternal female of both $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$ during the autumn trial was 4.5 ± 1.0 and 2.1 ± 0.8 daughters over their lifetime, respectively. However, such an assumption must be further tested with new trials under natural conditions throughout autumn for at least two consecutive years. *Diachamimorpha* longicaudata evidently can adapt and establish itself in environments that exhibit significant seasonal variation in temperature, humidity, and precipitation, such as subtropical [44] or semi-desert [50,51] regions, or in Mediterranean climate [42,43], and in tropical environments with a more stable climate [1].

The third finding revealed similar population growth rates in both DlLPs during the spring and summer trials but substantial differences in the autumn trial, when $Dl_{(Cc\text{-bip})}$ females displayed higher reproductive success than $Dl_{(Cc\text{-tsl})}$ females. The above is consistent

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with the *mx*-values recorded in the three seasons and discussed above. The *mx*-parameter is closely linked to the parasitoid population growth, because higher productivity influences the increase in the number of future generations of the parasitoid species [86,87]. Therefore, it was hypothesized that such a population increase improves the parasitoid's ability to control host populations [88]. In this sense, parameters such as R_0 (females produced per generation) and r (maximum potential rate of population growth) are highly influenced by the fecundity [88–90]. However, the complexity of the environmental context, including pest features, food availability, crop management practices, and environmental conditions such as temperature, can hide patterns related to the success of biological control in relation to the parasitoid life history traits and consequently affect its population growth rate [89,91]. Despite this, both R_0 and r, determined particularly under natural environmental conditions, are key parameters for predicting the potential population increase that females of both DIPLs may develop when used in open-field releases. In this regard, results from the current study revealed that R₀-values in both DlPLs recorded in spring and summer trials were 12- to 15-fold and 49- to 58-fold higher than R₀-values recorded in early autumn for $Dl_{(Cc\text{-bip})}$ and $Dl_{(Cc\text{-tsl})}$, respectively. Likewise, the R_0 -value less than 1 recorded in autumn for $Dl_{(Cc-tsl)}$ females indicates a declining population.

In contrast, the R_0 -value slightly greater than 1 recorded for $Dl_{(Cc-bip)}$ females during the autumn trial indicated a population growing on a small scale. The *r*-parameter showed a similar pattern to R_0 about the DlPLs related to the three tested seasons. However, in the summer trial, both *DIPLs* recorded a substantially higher *r*-value compared to spring and autumn. The r-value recorded for $Dl_{(Cc\text{-bip})}$ in summer was 2.3-fold and 10.6-fold higher than that recorded for spring and autumn, respectively. In the same pattern, the *r*-value recorded for $Dl_{(Cc-tsl)}$ in summer was 2.3-fold and more than 41-fold higher than those recorded for spring and autumn, respectively. The negative r-value recorded for $Dl_{(Cc-tsl)}$ females in autumn showed a declining population with more individuals dying than being born. Variations in population growth rates within the same DlPL could be related to changes in weather conditions, mainly temperature. Several laboratory studies have demonstrated the significant effect of temperature on the simulated population growth parameters of D. longicaudata [39,44,82,92], regardless of the host species used in the test. For instance, the simulated r-value for D. longicaudata can substantially increase when the temperature increases between 15 and 30 °C [92]. This is closely associated with a highly temperature-dependent mx-value in D. longicaudata [44], which is described as follows in the fourth finding

Concerning the four findings, the close relationship between air T_{min} and both *lx* and mx recorded for the two DIPLs can be mainly attributed to the decline in the lifespan and reproductive capacity of parasitoid females starting in the early autumn. The coldest environmental conditions in the region under study began during that season. This is consistent with previous authors [39,44,82,92], who have shown through laboratory studies by using life cycle simulation modeling that temperature has a strong effect on the development time, adult survival, and fecundity of D. longicaudata. Different nonlinear models predicted 10.0-10.4 °C and 31.0-33.7 °C as lower and upper thermal thresholds for the survival from egg to adult in D. longicaudata [44,92], and 28.0 °C as the optimum temperature for adult survival [44]. During the semi-field cage trial performed at the study site in the early autumn, the T_{min} ranged between 2.9 and 9.3 $^{\circ}$ C, i.e., values below the lower thermal threshold determined for D. longicaudata. The range of temperatures below 10 °C may clarify the low lx rate of D. longicaudata females in the first week of the trial, with 75% of parasitoid females dying during this period. On the contrary, during spring and summer trials, the T_{min} ranged from 5.3 °C to 22.0 °C, but with a T_{min} mean close to 14 °C in both seasons. Such a mean value exceeds the lower thermal threshold for D.

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longicaudata. Environmental temperature conditions may explain the high survival rate of *D. longicaudata* females, which surpassed 80% in the first week of semi-field cage trials. Similarly to the above, the mx in both DlLPs was influenced by T_{min} . Parasitoid females were considerably more fecund in spring and summer, seasons in which the mean T_{min} was 2.6-fold higher than in autumn. Different authors based on laboratory studies point out that the D. longicaudata fecundity was higher between 24 °C and 30 °C [39,44,92]. This information matches with a previous study in a fig-producing farm located in San Juan province, where it was found that parasitism on *C. capitata*, related to egg-laying by released D. longicaudata females, increased at higher temperatures and relative humidity [50]. Interestingly, a semi-field cage study performed in an area of eastern Spain [42], characterized by a classical Mediterranean climate, pointed out that the parasitism by *D. longicaudata* on C. capitata increased with mean temperature but decreased with mean relative humidity. According to such a study [42], the optimal climatic conditions for the D. longicaudata activity were 16-24 °C and at 45-60% RH, values that match the mean temperatures and RH recorded in spring and summer during the current study. However, the RH_{max} was also an environmental factor influencing the *mx* of both *Dl*PLs, similar to that reported by Sánchez et al. [50], and the mx was mainly conditioned by the T_{min} . This is because the RH_{max} had high values, between 69 and 84%, in the three seasons in which trials were carried out. Thus, the mean RH_{max} was higher in early autumn than that recorded in both summer and spring, but the mean T_{min} was lower than the minimum thermal threshold that D. longicaudata females can tolerate.

5. Conclusions

Results of the comparative laboratory trials may confirm the first hypothesis of this study, whereby $Dl_{(Cc-bip)}$ females exhibited higher reproductive potential than that of $Dl_{(Cc-ts]}$ females. Such findings may optimize the *D. longicaudata* production and quality under mass rearing conditions at the San Juan Biofactory, keeping costs within an acceptable level. Likewise, the results of semi-field cage trials showed high-quality females with high reproductive capacity in both DIPLs. That uncovers a key factor for successful population growth and performance of the parasitoid when used for C. capitata biological control. In this regard, the second hypothesis of this research is also supported. Females of both DIPLs showed high population growth rates during spring and summer, seasons in which the highest population peaks of C. capitata occur in the study region. That suggests the temperature or relative humidity stress probably canceled out any advantage of $Dl_{(Cc ext{-bip})}$ females over $Dl_{(Cc-tsl)}$ females, but during the warmer seasons (spring and summer). This is because this study revealed an engaging, novel, and additional finding. Apparently, $Dl_{(Cc ext{-}bip)}$ females can adapt better to colder environmental conditions than female $Dl_{(Cc ext{-}tsl)}$ females, as they were able to sustain a low population growth rate at least in early autumn. Based on this result, $Dl_{(Cc\text{-bip})}$ females could be released between early and mid-autumn in fruit-growing areas of San Juan, when C. capitata populations are starting to decline. The results reported are important for assessing improvements in D. longicaudata mass production at the San Juan Biofactory and for redesigning the parasitoid release schedule throughout Argentina's irrigated semi-arid fruit-production regions.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/insects16101031/s1. File S1: Life Table-laboratory; File S2: Life Table-spring; File S3: Life Table-summer; File S4 Life Table-autumn; File S5: Life-table-lab.Rmd; File S6: Life-table-Season.Rmd; File S7: model-lx-beta-analysis.Rmd; File S8: model-mx-analysis.Rmd.

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