Demographic analysis of the immature stages of the parasitoid *Diachasmimorpha longicaudata* under mass rearing conditions

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ABSTRACT

Objective: To analyze the mortality of the immature stages of the parasitoid *D. longicaudata* using demographic parameters from a life table.

Design/methodology/approach: Evaluations were carried out with three cohorts, each with a different level of superparasitism: puparia from 1 to 5, 6 to 10, and 11 to 15 scars (oviposition or attempted oviposition). The analysis of data was performed by life table parameters.

Results: Mortality was very noticeable in the egg stage and the first larval stage. Mortality was higher in hosts with high levels of superparasitism. After the second stage, mortality was reduced. The parameters of mortality in one day in proportion to the number of the cohort (dx) and mortality per day (qx), had their highest values between the 3rd and 4th of parasitoid development. Life expectancy at baseline was 7, 5.3 and 4.9 days at the three corresponding levels of superparasitism. After the second instar, life expectancy increased, with a steady drop until the 15th day of development. The highest emergence of adults was obtained at the average level of superparasitism (58.33%) and the lowest when the levels of superparasitism were higher (44.66%).

Findings/conclusions: Intraspecific competition, host mortality due to trauma and possibly infections can be considered as the main causes of mortality in immature stages in proportions that may explain the emergence percentages obtained in mass rearing.

Keywords: Life table, immature stages, insect mortality, immature stage mortality, intraspecific competence.

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INTRODUCTION

Evaluation of mortality in immature stages of parasitoids is usually a problem, because, mainly to a few indications are presented, also normally they are protected by the the host (Xu *et al.*, 2007; Weinersmith, 2019). This situation is more complicated in endoparasitoids, in which develop is inside the host, so mortality evaluations of immature stages are scarce.

However, during this phase, parasitoids carry out one of the most important parts of their development, which manifests itself in a basic and fundamental feeding activity based on intrinsic physiological interactions (Uçkan & Ergin, 2002; Saini *et al.*, 2019). In most cases, adult parasitoids are considered to emerge with a basic food supplement for their reproduction and even for their survival

(Harvey & Malcicka, 2016; Farahani *et al.*, 2016). This leads to the assumption that during the development of immature stages, the parasitoids receive complete or adequate nutrition for its subsequent adult performance. In the adult state, it has been reported that adult parasitoids, unlike other insects, do not have the capacity for lipogenesis or proteogenesis (Visser & Ellers, 2008; Visser *et al.*, 2023). They can be considered to emerge with a very complete and special load of food. In this regard, in adults, the requirements focus on carbohydrates as a basic resource to extend survival, although with very little contribution to increase or extend fecundity (Kishinevsky & Keasar, 2021; Cavallini *et al.*, 2023).

Considering the influence of immature parasitoid stages, is important to know more about their development in order to make inferences or analysis in the biological potential of adults. In this work we report the results of an analysis with life table parameters in immature stages of the parasitoid of fruit flies (Diptera: Tephritidae), *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). This parasitoid has been used by augmentative releases for the suppression and control of populations of different pest species of fruit flies (Montoya *et al.*, 2000; Harbi *et al.*, 2019; Suárez *et al.*, 2024). According to Mensah Agboka *et al.* (2023), the releases of this insect promotes its establishment and can provide a benefit in a 9:1 ratio. Due the importance of this parasitoid in the biological control, mass rearing has been established in which the adult emergence is a crucial indicator to meet the quality. Adult emergence varied and depend mainly on the quality of the host, this ranges from 30 to 80% (Cai *et al.*, 2018; Cruz *et al.*, 2018; Carta Gadea *et al.*, 2020; Cancino *et al.*, 2023). This raises an initial question: What are the levels of mortality that occur during the development of *D. longicaudata*? In this regard, few references are known, from the classic evaluations that were carried out with immature stages of Opiinae: Braconidae parasitoids reported by Pemeberton and Willard (1918) and in recent years a very complete work of the immature stages description of *D. longicaudata* was introduced by Carabajal-Paladino *et al.* (2010).

The usefulness of knowing the levels of mortality in *D. longicaudata* in immature stages may be important for mass rearing where is a basic need to reinforce the establishment of quality parameters, where emergence is a central indicator (Van Nieuwenhove *et al.*, 2012; Harbi *et al.*, 2016; Suárez *et al.*, 2019). However, it can also be useful to be able to infer the mortality results of hosts in the field where percentages of parasitism are usually obtained based on emergence (Montoya *et al.*, 2000; Cancino *et al.*, 2019).

Mortality data from the immature stages of development of *D. longicaudata* were processed using different demographic parameters (Vargas *et al.*, 2002; Carabajal-Paladino *et al.*, 2010; Estrada-Marroquín *et al.*, 2022). Within these evaluations, superparasitism was considered as an influential factor in egg mortality and the first stage. Based on the above, the objective was to analyze the mortality of the immature stages of the parasitoid *D. longicaudata* using demographic parameters from a life table.

MATERIALS AND METHODS

Biological material. Eggs-larvae-pupae of *D. longicaudata* hosted into puparia of *Anastrepha ludens* (Loew), were sampled from larvae previously exposed to parasitization in the mass rearing of *D. longicaudata* parasitoids of the Moscafrut Plant. Cohorts were formed with samples of larvae recently exposed to parasitization (24 h after exposure) to *D. longicaudata*.

Host sampling

A total of 4500 larvae recent exposed to parasitization were randomly sampled. The total was the cumulative of five samples, each one considered as the same cohort. When the formation of the puparium began (sclerotization covering the host), 24 h after parasitization, three groups were formed in each sample. In each one, observations of the number of oviposition scars were carried out. These groups were formed under the assumption that superparasitism is very frequent in the oviposition of *D. longicaudata* under rearing conditions. The three groups, with different ranges of scars were: puparia of 1 to 5, 6 to 10 and 11 to 15 scars (result of oviposition or attempted oviposition of the parasitoid female) on the sclerotized cuticle. On the first four days, 15 puparia/day of each scar range were taken for dissection, and from the fifth day until day 15, 30 puparia/day were taken for dissection. Of the total sample, the groups were formed by 900 puparia, a total of 2970 puparia were analyzed with dissection.

Mortality assessment

Immediately after the groups were formed, one day after exposure to parasitization, dissection of the puparia began. Daily, from 1st to 15th day (time of immature develop of *D. longicuadata*), randomly was taken the sample of puparia. With the use of forceps and dissection needles, the central part of the puparium was opened, observing the immature stages of the parasitoid with a microscope (CarlZeiss® Stemi 305, Jena, Germany). In the first four days, the microscope was calibrated to 4.0 X to observe eggs on the first two days and to 2.5 X to observe first-instar larvae, in the third and fourth days. From the fifth day, observations were carried out at 1.5 X. Due to the constant presence of supernumeraries as a result of the superparasitic activity of *D. longicaudata* under mass rearing conditions, the number of eggs and larvae of the first instar present per puparium was counted in the first four days. From the fifth day onwards, larvae of the second to fourth instar or pupae of individual parasitoids per puparium were usually present. In each dissection, the number of live and dead immature parasitoids was counted.

Photos were taken using a digital camera (Nikon® D550, Minato, Tokyo, Japan), coupled to a stereo microscope (Nikon® SMZ-U Zoom 1:10, Tokyo, Japan) and digitized. The images were stacked in Helicon Focus and edited in Adobe Photoshop, to morphologically characterize each of the states and stages in the development of *D. longicaudata*. During the 15 days of development of the immature stages of the parasitoid, the samples of puparia were in cylindrical plastic containers (5 cm in diameter by 7 cm high, 150 ml capacity) with moist vermiculite maintained into a bioclimatic laboratory (Memmert® ICH110L GmbH, Co. KG, Germany), at a temperature of 26±1 °C and 60-70% RH.

Emergence and sexual proportion

An additional sample of 100 puparia from each group was kept separately in a plastic container (5 cm in diameter by 7 cm high, 150 ml capacity) with a thin layer of vermiculite.

They were kept into the bioclimatic previously mentioned. After 15 days the adults began emerged and the number and sex of adult parasitoids were counted.

Data analysis

Due to the presence of supernumerary individuals per pupary, mortality in the first four days of each group was analyzed using the average per puparia. From the fifth day onwards, mortality was counted individually per puparium. Based on living and dead individual data, the following parameters were obtained: the average number of living individuals per day, lx (No. of living individuals/No. of individuals from the initial cohort); dx, fraction of the original cohort dead in one day $lx-lx+1$; qx, fraction of living individuals who died in a day $(1-(lx+1/lx)$; px, fraction of living individuals in a day $(lx+1/lx)$ and Ex, individual average of days to live $(1/2+(lx+1+lx+2\ldots 1\infty/lx))$ (Carey, 2001). The survival curves from day 1 to day 15 (egg-pupal development) and from day 5 to day 15 (development of individual larva from second instar to pupa) were compared using a log-rank analysis (JMP® Version 16. SAS Institute Inc., Cary, NC, 1989-2023). We obtained the averages of total emergence and sex proportion.

RESULTS AND DISCUSSION

Mortality assessment

In the comparison of survival curves, two important things stand out: firstly, the mortality was more accentuated in eggs and larvae of the first instar; and secondly, that mortality in this initial period of development was higher in puparia with a greater number of scars and superparasitism ($\chi^2=52.16$, d.f.$=2$, $P<0.0001$) (Figure 1a).

A direct relationship was obtained between the number of scars and the number of supernumeraries per puparium, with a correlation of 75% ($r^2=0.75$). When parasitoids reached the second stage of development (usually from the fifth day onwards) mortality decreased, keeping survival more constant. However, the mortality continued higher in parasitoids developed from superparasitism range from 11 to 15 scars/puparium. The comparison of partial survival curves, from the second larval stage to the end of pupal development, it was obtained that individuals in the range of 6 to 10 scars were the longest-lived, followed by individuals in the range of 1 to 5 scars, and those that developed in puparia with a range of 11 to 15 scars remained the least long-lived ($\chi^2=16.54$, d.f.$=2$, $P<0.0003$) (Figure into Figure 1a).

The number of deaths per day considering the original cohort size (dx) was more prominent between day 3 and day 4. The puparia with the highest range of scars experienced the highest mortality rates within the original cohort on day 4 (Figure 1b). The mortality of individuals observed per day (qx) shown that only in puparia containing 1 to 5 scars is where the highest mortality occurred on day 3, while for puparia with the highest number of scars, the mortality was higher on day 4 (Figure 1c). Puparia with the highest scar range experienced the lowest survival fraction per day (px) on the day 4, while puparia within the lower scar range (1 to 5 scars) experienced the lowest survival fraction on day 3 (Figure 1d). Life expectancy (Ex) was about 7 days for individuals with 1 to 5 scars, but it was reduced

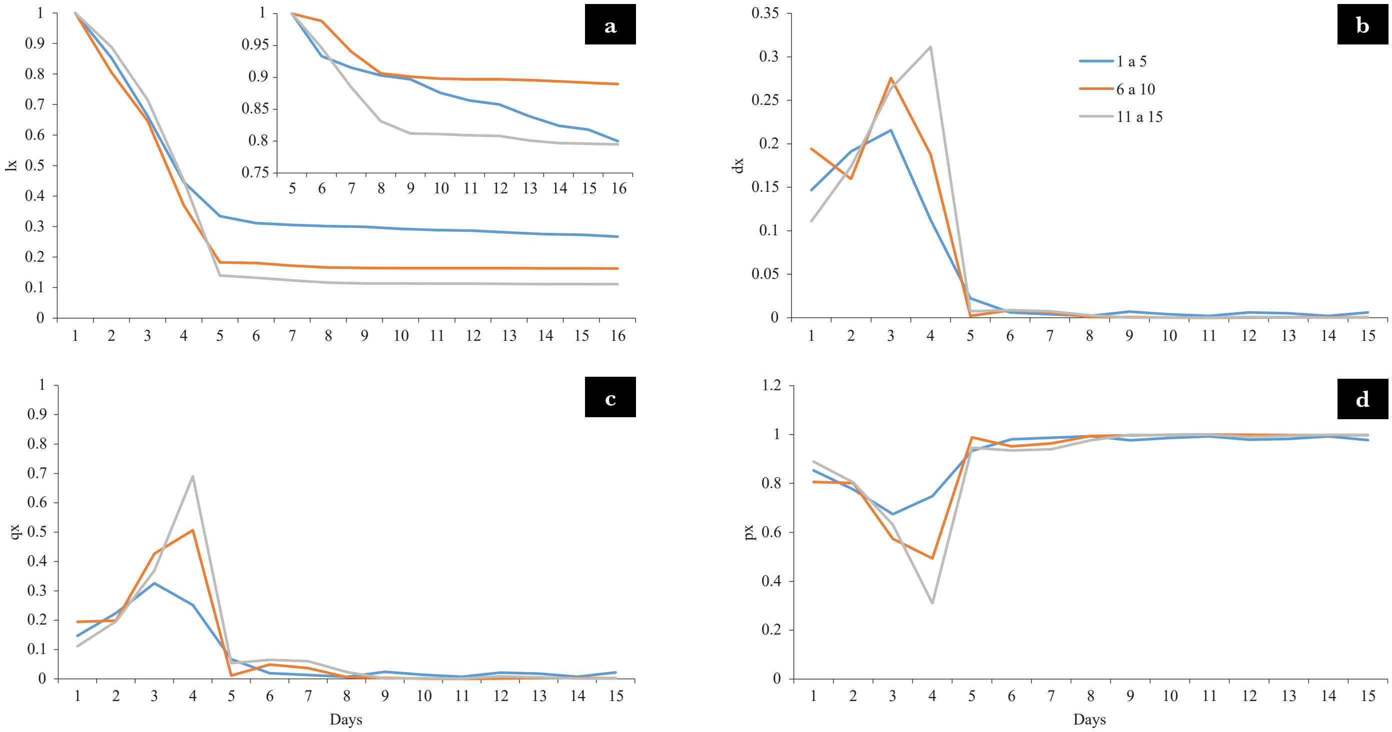

Figure 1. Curves of: a) survivorship (lx), b) mortality in the original cohort (dx), c) mortality per day (qx) and d) survivors per day (px), during the development of immature stages of the pararasitoid wasp, *D. longicaudata*, 24 hours after oviposition to one day prior to adult emergence, categorized into three levels based on the number of scars per host puparium (superparasitism).

to 5.3 days for individuals with 6 to 10 scars and to 4.9 days for individuals containing from 11 to 15 scars (Figure 2a, Table 1).

However, life expectancy remains very similar when the analysis was partial, it begins with individuals developed from the second stage, 5 days old and finalizing in the 15th day. In this case, the average life expectancy was between 10.59 and 11.49 days, with the

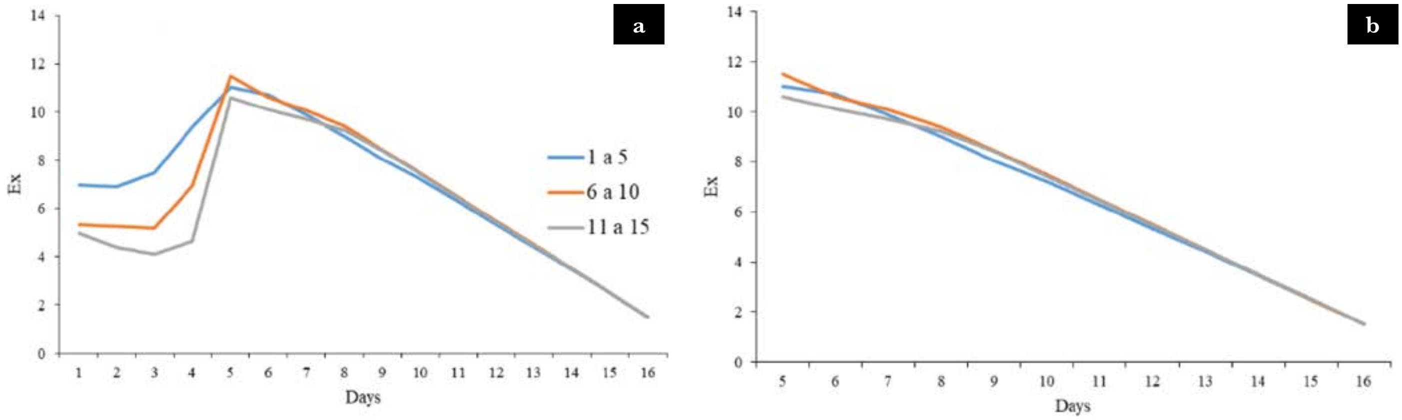

Figure 2. Survivorship curve (Ex) for the different immature stage of development in the *D. longicaudata*, categorized into three levels base on the number of scars on the host pupae (superparasitism), a) complete immature develpment, b) as of the 5th day, beginning of second instar larva to one day before adult emergence.

Table 1. Averages of initial (Eo) and partial (E5) life expectative in immature stages, emergence of adults and sex ratio of adults of the parastioid *D. longicaudata* considering three ranges of scars per puparium from the host.

Scars/puparium	Life expectative Initial (Eo)	Partial (E_5)	Percentage of emergence	Sex ratio ♀ : ♂♂
1 a 5	6.97	11.02	53.00	1.52
6 a 10	5.33	11.49	58.33	2.10
11 a 15	4.96	11.59	44.66	4.01

highest value being individuals developed in puparia into a range of 6 to 10 scars (Figure 2b, Table 1). Figure 2a shows that life expectancy in individuals from 1 to 4 days begins with low values, then increases on day 5 to have a constant drop until day 15. When the Ex was graphed from the 5th day of age, a constant steady declining trend is observed (Figure 2b). The images gathered throughout the development of *D. longicaudata* allowed to characterize the morphologies changes that occur during each stage (Figure 3 and Figure 4).

Emergence and sexual proportion

The highest emergence rate occurred in individuals developed in puparia containing 6 to 10 scars, while the lowest emergence was in individuals developed in puparia with the highest number of scars. The sex ratio in all cases was biased to females, with differences between each range, with the proportion of females increasing as the number of scars per puparium increased (Table 1).

In the first four days, the mortality rates for eggs and first instar larvae of *D. longicaudata* were significantly high. Mean mortality rates of 30% were obtained for the original cohort (dx). In a single day, the mortality rate was 70% (qx) when the number of supernumerary puparia ranged from 11 to 15 scars per puparium. Even in the lowest range, from 1 to 5

Figure 3. Immature stages in the development of the parasitoid *D. longicaudata* (a) egg; (b) first larval instar; (c) early second stage; (d) late second stage; (e) third stage; (f) fourth stage-Prepupa.

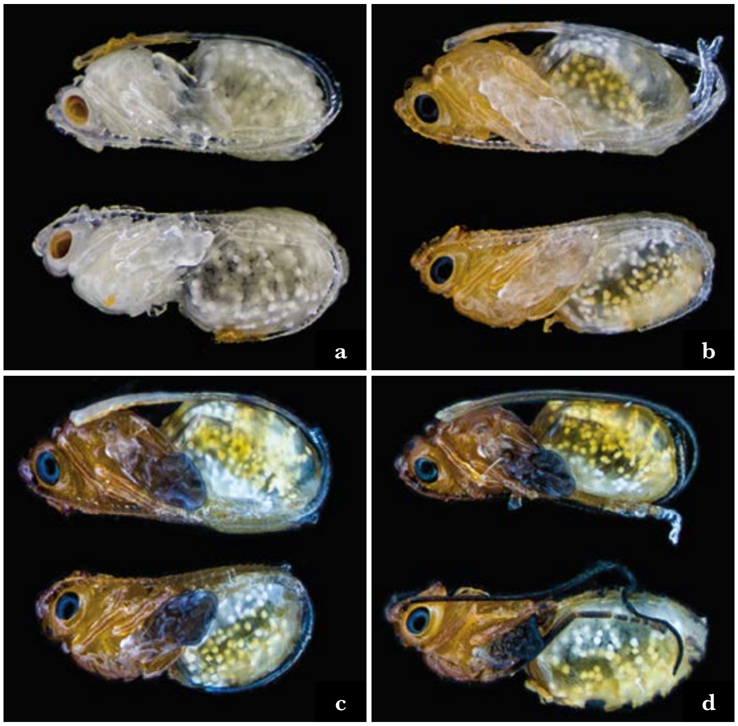

Figure 4. Immature stages of development of the parasitoid *D. longicaudata*, pupa (a, b, c) and pharate (d): female (up) and male (down).

scars per puparium, there was a reduction of up to 20% compared to the original cohort and a 30% mortality rate in a single day.

The increase in egg and first instar larval mortality is likely due to increased competition among the high density of supernumerary parasitoid. Since *D. longicaudata* is a solitary parasitoid (only one adult parasitoid emerges from a single host (Ovruski *et al.*, 2003; Harvey *et al.*, 2012)). The superparasitism in *D. longicaudata* is a very common event (Montoya *et al.*, 2012; Altafini *et al.*, 2013; Devescovi *et al.*, 2017). Therefore, the presence of supernumerary individuals within a host implies intraspecific competition that is expected to intensify when density increases within a single host (Devescovi *et al.*, 2017). The observations focused on quantifying the number of live eggs and first-stage larvae daily, but did not include detailed analysis of mortality causes.

In this regard, two causes of mortality have been proposed, with which the supernumeraries of the host are excluded each other. One is engaging in direct competition in their early stages using physical means like strong mandibles for exclusion or even cannibalism (Lawrence, 1988a; Strand, 2002; Brodeur and Boivin, 2004). Estrada-Marroquin *et al.* (2023) in detailed observations with the braconid parasitoid of fruit flies, *Utetes anastrephae* (Viereck) observed that cannibalism is an exclusive activity among its own species. Another is exclusion due to biochemical changes in the hemolymph of the superparasitized host, where, in addition to a limitation of resources, the environment can negatively impact the survival of individuals who are not well-suited to it which can lead to mortality (Brodeur & Boivin, 2004; Cusumano *et al.*, 2016). It is uncertain whether mortality is a combination of the two causes or a single one, and there is a limited number of studies on this subject (Carbajal-Paladino *et al*., 2010; Devescovi *et al*., 2017).

The initial life expectancy (Ex) of the parasitoid was reduced from around 7 days to around 5 days when parasitoids entered puparia with more than 5 scars (indicator of superparasitism). However, after a period of high competition, where a parasitoid remains a distinct individual within its host, the average life expectancy increased to 11 days across three groups. Mortality decreased by about 80% starting from day 5, coinciding with the onset of the second stage of the parasitoid's development.

In the partial analysis of parasitoid survival, it was found that the mortality rate from the second larval stage to before adult emergence was reduced by only 20%. This likely explains why the surviving parasitoid, after a period of competition with other parasitoids, exhibits a high survival rate (above 80%). However, this high survival rate varied greatly across the different groups of puparia based on the number of scars. Parasitoids with the longest-lifespans were individuals developing into puparia with 6 to 10 scars, with a longevity exceeding those with fewer scars, while in puparia with a high number of scars exhibited the shortest lifespans. One explanation for the higher relative survival rates observed in the mid-stage scar/pupal stage are likely associated with the increased proportion of females emerging with the presence of a moderate range of scars. Adult female *D. longicaudata* wasps typically live longer than adult male. In the range of greater number of scars, the sexual proportion favored females, but increased competition can lead to a reduction in survival (competition for food, reduction of vitality due to competition, etc.) (Montoya *et al*., 2012). In different studies it has been reported that moderate levels of superparasitism (∼<10 immature/puparia) can be beneficial for the mass rearing, because they can lead to a female-biased sex ratio and may not significantly impact offspring survival. This is sometimes considered an adaptive advantage (González *et al*., 2010).

The high mortality rate experienced by *D. longicaudata* during its immature development can be explained in two ways: firstly, it consists of a very high mortality rate experienced by eggs and early larval stages, dominated by intrinsic and intraspecific competition, plus by a possible immune response from the host. Secondly, the mortality can be viewed as relatively stable and is caused by other factors (possibly more related to environmental conditions, nutrition, or disease prevalence, etc.), which presents an apparently constant rate from the second stage onwards.

With respect to the hosts, in mass rearing conditions, for the *A. ludens-D. longicaudata* relationship, between 80-90% were parasitized. This implies that between 10-20% of hosts can emerge as adult flies, however, the emergence of flies is null due to the use of irradiated host larvae in the mass rearing (Cai *et al*., 2018; Suárez *et al*., 2019). Furthermore, an additional 9.4% of parasitized hosts experience initial mortality, without a clear cause (oviposition trauma, microbial infection, etc.). An additional 10-20% mortality occurs during the developmental stage, probably due to the aforementioned causes.

Combining values, about 30-50% non-emergence by mortality could be due to the following causes: parasitization is prevented by radiation (flies not emerged due to radiation), initial mortality (competition as a dominant effect) and mortality caused by different causes present during oviposition or development. The most influential causes of mortality of parasitoids at each age are difficult to determine, they can include, among others, excessive superparasitism, host quality, nutritional deficiency due to excessive competition (Lawrence, 1988 b; Silva-Torres *et al.*, 2009; Couchoux & van Nouhuys, 2014). However, there are also a series of other causes related with the rearing process such as: mass management, environmental conditions or quality of ingredients or the larval diet of the host's development.

This information is key to understanding the behavior of mortality during the development of *D. longicaudata* within the host. The characterization of mortality in the initial period and the period towards adult emergence. Also, this information helps understand the emergence capacity of parasitoids in mass rearing conditions and can prove useful to consider technical measures and reduce mortality during development. Studies on the causes of mortality in the initial phase, during high competition due to superparasitism or during later development could lead to more clearly defined proposals to increase emergence in mass rearing.

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