

Biological and Microbial Control

Functional response and parasitism of *Doryctobracon brasiliensis* (Hymenoptera: Braconidae) on *Anastrepha fraterculus* (Diptera: Tephritidae)

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Subject Editor: Christie Bahlai

The biological control for fruit flies in Brazil has been extended with the introduction of the parasitoid *Diachasmimorpha longicaudata* (Ashmead, 1905) (Hymenoptera: Braconidae) and native parasitoids, such as *Doryctobracon brasiliensis* (Szepligeti, 1911) (Hymenoptera: Braconidae), which show great potential for control. Among the main pest species of fruit flies, *Anastrepha fraterculus* (Wiedemann, 1830) (Diptera: Tephritidae) and *Ceratitis capitata* (Wiedemann, 1830) (Diptera: Tephritidae) have a wide geographic distribution in the South American continent. The objectives of this study were to evaluate the functional response of *D. brasiliensis* to the density of *A. fraterculus* larvae and to model the parasitism rates of *D. longicaudata* and *D. brasiliensis* on *A. fraterculus* and that of *D. longicaudata* when exposed to *C. capitata*. The experiments were conducted to evaluate the parasitism rate, and the data were subjected to statistical analysis, verifying the probability distribution. The parasitism rate of *D. brasiliensis* ranged from 82.2% to 35% when 5 and 30 larvae were offered to each female, respectively. The results revealed a type II functional response, indicating that the parasitism rate reached a saturation point as the larval density increased. In *A. fraterculus*, the average number of larvae parasitized by *D. longicaudata* females was higher than that of *C. capitata* at nearly all host densities. The highest percentage of parasitism (55%) was observed at the density of 3 larvae per parasitoid, similar to what was recorded for *C. capitata*. The results obtained support the biological control program for fruit flies in Brazil, optimizing laboratory rearing and field release.

Keywords: biological control, parasitoid-host interaction, density-dependent, fruit flies, bioecology, probability distributions

Introduction

Fruit flies (Diptera: Tephritidae) are considered one of the main fruit pests worldwide because of the large number of pest and host species and the high economic impact on crops (Dias et al. 2018). In Brazil, the South American fruit fly *Anastrepha fraterculus* (Wiedemann, 1830) and the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann, 1824) are considered the main fruit pests, requiring the adoption of control measures to avoid economic losses (Nava and Botton 2010, Botton et al. 2023). Population control of *A. fraterculus* is achieved by application of organophosphate and pyrethroid insecticides over the total area in accordance with a predefined schedule (Arioli et al. 2004). Applications are based on coverage (total area) and/or the use of toxic baits (Nava and Botton 2010). However, systemic organophosphate insecticides have been gradually

withdrawn from the worldwide market, and the use of chemical insecticides with contact and ingestion actions alone is insufficient. This scenario highlights the need to identify new alternatives for controlling fruit flies that can be used in different management strategies by fruit growers while minimizing the impact on the environment and humans.

Biological control using both exotic and native parasitoids is an option for managing fruit flies. The rearing and release of exotic parasitoids to control fruit flies has been shown to be successful in several countries (Wong et al. 1991, Duan and Messing 1997, Montoya et al. 2013, Sivinski et al. 2000, Garcia et al. 2020, Dias et al. 2022). In Brazil, the introduction of exotic species has been unsuccessful; therefore, the focus of research has been on native species of braconid parasitoids, which are considered the most important biological control

Received: 08 May 2025. Revised: 16 September 2025. Accepted: 17 September 2025

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agents for fruit flies. Currently, 13 species are registered in Brazil and are distributed across different regions (Paranhos et al. 2023). Among these, the larva-pupa endoparasitoid *Doryctobracon brasiliensis* (Szepilgeti, 1911) (Hymenoptera: Braconidae) is geographically distributed in countries on the South American continent and parasitizes larvae in different fruit fly hosts (Aguiar-Menezes and Menezes 1997, Raga et al. 2004, Marinho et al. 2009, Nunes et al. 2012). Recently, *D. brasiliensis* has been studied in order to assess its potential as a biological control agent. To this end, bioecological experiments and trials for the development of rearing techniques have been conducted (Poncio et al. 2016, Poncio et al. 2018, Gonçalves et al. 2023), yielding encouraging results. However, further advancements will require perfecting the production of *D. brasiliensis* in the laboratory and conducting evaluations under field conditions.

Unlike *D. brasiliensis*, *Diachasmimorpha longicaudata* (Ashmead, 1905) (Hymenoptera: Braconidae) is the most widely used parasitoid in fruit fly biological control programs worldwide. In Brazil, this parasitoid was introduced for classical biological control in 1994, but its populations could not be established, probably because of the climatic conditions in Brazil (Paranhos et al. 2023). However, its use in biological control with inundative releases has contributed to the control of fruit flies when releases are associated with other control methods (Garcia et al. 2020, Suárez et al. 2023). Studies based on the parasitoid/host relationship were carried out by Ovruski et al. (2011), focusing on the preference of *D. longicaudata* for larvae of *A. fraterculus* and *C. capitata*, and by Camargo et al. (2018), who determined its dispersal in guava orchards. However, there is a lack of studies that analyze this relationship based on mathematical modeling.

In this context, knowledge of the functional response of a parasitoid to its host can help optimize laboratory breeding and define the quantity of parasitoids to be released in the field, although the application of this information in the field shows little reproducibility (Munyanze and Obrycki 1997). Functional responses, according to Holling (1959), Royama (1971), and Rogers (1972), can be categorized into 3 types, namely Type I, Type II and Type III.

In 2012, Southern Brazil initiated a project to establish a management program for *A. fraterculus* (called Moscasul) using alternative control techniques to the use of chemical insecticides. One of the strategic approaches was the use of biological control with native parasitoids, which are better adapted to local conditions than the exotic parasitoid *D. longicaudata*. To better understand the parasitoid-host relationship, this study aimed to evaluate the functional response of *D. brasiliensis* in relation to the density of *A. fraterculus* larvae and to model the parasitism rate of *D. longicaudata* and *D. brasiliensis* on *A. fraterculus* and that of *D. longicaudata* exposed to *C. capitata*. This knowledge is crucial for optimizing biological control practices, enhancing the effectiveness of interventions, and minimizing the use of chemical insecticides, thereby promoting sustainable agriculture.

Materials and Methods

Insect Rearing

The colonies of *A. fraterculus* and *D. brasiliensis* were maintained in the Entomology Laboratory of Embrapa Clima Temperado

for approximately 50 and 10 generations, respectively, under controlled conditions of temperature ($25 \pm 1^\circ\text{C}$), relative humidity ($70 \pm 20\%$), and a 12:12 h photoperiod (light:dark).

Anastrepha fraterculus colonies were maintained as described by Gonçalves et al. (2023). The larvae were fed an artificial diet based on wheat germ and yeast in jars (20 long $\times$ 15 cm wide $\times$ 5 cm high), while the adults were kept in plastic cages (30 cm long $\times$ 50 cm wide $\times$ 30 cm high) (Tupperware, Itapevi, SP, Brazil) and fed a diet based on sugar, yeast, and wheat germ. *D. brasiliensis* was kept in plastic cages (30 cm long $\times$ 50 cm wide $\times$ 30 cm high) (Tupperware, Itapevi, SP, Brazil) covered with nylon fabric (0.5 $\times$ 0.5 mm). The adults were fed a 30% (w/w) honey solution, kept in glass containers (5 mL), and offered to the parasitoids using a dental roll, which was made available by capillarity. Three guava fruits (*Psidium guajava* L., Myrtaceae) were cut at the top to remove part of the pulp, and around 200 third-instar *A. fraterculus* larvae were placed inside and reared on an artificial diet according to the protocol described by Nunes et al. (2013). Guavas containing the larvae were placed at the base of *D. brasiliensis* adult rearing cages so that the females could parasitize the larvae inside the fruit. The fruit remained inside the cage for 24 h, after which the larvae were removed from the fruit and placed in a Gerbox container (11 cm long $\times$ 11 cm wide $\times$ 3.5 cm high) (Prolab—São Paulo, SP, Brazil) on a layer of moistened vermiculite, where they remained until the parasitoids emerged.

Obtenção de Dados de Parasitismo de *D. longicaudata* em *A. fraterculus*

To model *D. longicaudata* in *A. fraterculus* and *C. capitata*, data were obtained from the study by Altafini et al. (2021), who used fruit fly larval densities of 1, 3, 5, 10, 25, 35, and 55 larvae per unit parasitism. The number of replicates per density varied according to host availability, being 46, 20, 35, 34, 35, 28, and 20 replicates, respectively, for *C. capitata* and 20 for *A. fraterculus*.

Parasitism Rate of *D. brasiliensis* as a Function of the Number of *A. fraterculus* Larvae

To obtain data for the parasitism of *D. brasiliensis* on *A. fraterculus*, laboratory experiments were carried out under controlled conditions of temperature ($25 \pm 1^\circ\text{C}$), relative humidity ($70 \pm 20\%$), and a 12:12 h photoperiod (light: dark).

Five-day-old pairs of *D. brasiliensis* were individually placed in cages made of plastic cups (500 mL) (Prolab—São Paulo, SP, Brazil), with the upper part containing nylon fabric (0.5 $\times$ 0.5 mm) to allow aeration and to enable the females to parasitize the larvae inside the parasitism units placed on top of the cage. Five, 10, 15, 20, 25, and 30 third-instar larvae were exposed to *D. brasiliensis* females for 24 h in parasitism units composed of acrylic plates (1.7 cm in diameter $\times$ 0.5 cm in height) (Prolab—São Paulo, SP, Brazil) containing guava pulp wrapped in voile-type fabric. After the parasitization period, the larvae were transferred to acrylic vials (5 cm in diameter $\times$ 6 cm in height), where they pupated, and either flies or parasitoids emerged.

The experiment was conducted in a completely randomized design in a unifactorial scheme using 100 replicates, with each replicate consisting of a pair of *D. brasiliensis*. The treatment factors tested were different numbers of *A. fraterculus* larvae. The parameters evaluated were the number of offspring and

percentage of parasitism, taking into account the number of flies and parasitoids that emerged and dissecting the host to assess the possible presence of the parasitoid.

Exposure Time of *A. fraterculus* Larvae to *D. brasiliensis* Parasitism

Five-day-old 25 pairs of *D. brasiliensis* were individually housed in cages made of plastic cups (500 mL) with the top part containing nylon fabric (0.5 × 0.5 mm) to allow aeration and allow females to parasitize the larvae inside the parasitism units placed on top of the cage. Third-instar *A. fraterculus* larvae were offered in a parasitism unit consisting of an acrylic plate (1.7 cm in diameter × 0.5 cm in height) (Prolab—São Paulo, SP, Brazil) containing guava pulp wrapped in voile fabric. The larvae were exposed to parasitism for periods of 3, 6, 9, 12, 15, 18, 21, and 24 h, and then transferred to acrylic jars (5 cm in diameter × 6 cm in height) containing moistened fine vermiculite for pupation.

Mathematical Model and Statistical Analysis

To define the mathematical model, 3 equations proposed by Holling (1959), Royama (1971), and Rogers (1972) were analyzed, which provided a solution assuming saturation of parasitism, as shown in Equation 1:

$$N_e = N_0 \left(1 - \exp \left(a N_0^q (h N_e - T) \right) \right) \quad (1)$$

where N_e is the host density; N_0 is the initial prey density; T is the experimental time (hours or days); a is the consumer's

resource capture rate; h represents the time spent ingesting and digesting each prey item; and q is a scaling exponent that defines the extent to which the functional response changes from hyperbolic to sigmoidal deceleration (Pritchard et al. 2017). When $q=0$, the capture rates are constant with the density of resources (hyperbola), yielding a type II functional response. In this study, the behavior of *D. brasiliensis* was similar to that of a predator, except that it did not consume the host.

For an effective choice between type I, type II, and type III functional responses, logistic regression of the proportion of parasitized hosts in relation to host density was performed. The workflow followed the steps described by Pritchard et al. (2017): model selection, model fitting, and comparison of fits and coefficients. The functional responses of types I, II, and III were compared using the Akaike information criterion (AIC) (Akaike 1974) and the Bayesian information criterion (BIC) (Schwarz 1978). Functional response analysis and adjustment were performed using the FRAIR package (Pritchard et al. 2017) available in R software version 4.1.0 (R Core Team 2024).

Probability Distributions

The distribution of the parasitized larvae was analyzed using log-normal and gamma-probability distributions. At low host densities, the number of parasitized larvae increases rapidly with increasing host density. However, as host density continues to rise, the parasitism rate tends to decline. This pattern reflects the saturation effect inherent in the probabilistic models used, which capture this asymmetric behavior. Brief descriptions of these two distributions are presented in the following section.

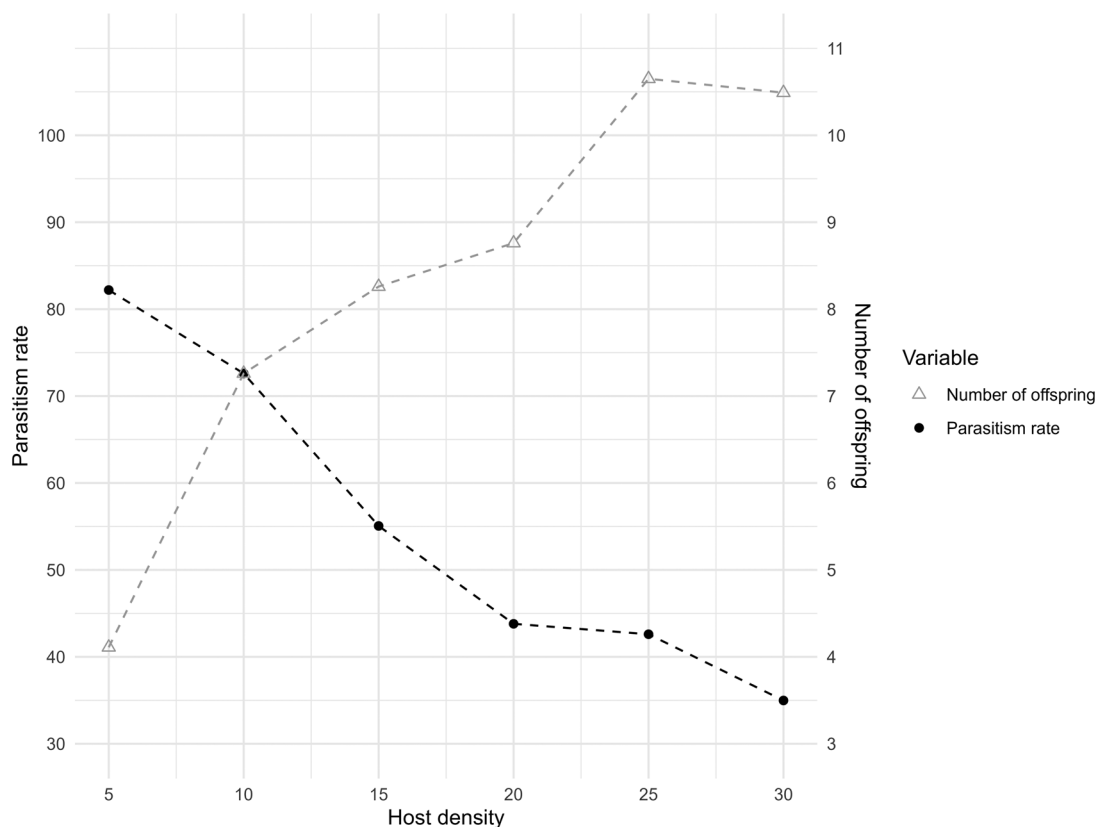


Fig. 1. Parasitism rate (black dashed line) and number of offspring (gray dashed line) of *D. brasiliensis* in relation to different densities of *A. fraterculus* larvae.

Two probability distributions, log-normal (Aitchison and Brown 1957) and gamma (Taveira 2017), were fitted to the parasitism rate data at different host densities: *D. brasiliensis* exposed to *A. fraterculus* larvae, *D. longicaudata* exposed to *A. fraterculus* larvae, and *D. longicaudata* exposed to *C. capitata* larvae.

The methodology utilized was based on fitting a nonlinear model to describe the relationship between host density and the rate of parasitized larvae. First, nonlinear modeling was

conducted using the `nls` function in the `nls2` package (Bates and Watts 1988), and the fitted models were based on log-normal and gamma distributions. The nonlinear least-squares method was used for parameter estimation. This method seeks to minimize the sum of the squares of the residuals, which is the difference between the observed values and the values predicted by the model. Two evaluators compared the quality of the model fits using AIC, BIC, and residual standard deviation (RSD).

Table 1. Parameter estimates for the Log-normal and Gamma models, including AIC, BIC, and residual standard deviation (RSD), for both experiments: *D. brasiliensis* exposed to *A. fraterculus* larvae, *D. longicaudata* exposed to *A. fraterculus* larvae, and *D. longicaudata* exposed to *C. capitata*

	Probability distribution	Parameter estimation	Evaluators		
			AIC	BIC	DPR
<i>D. brasiliensis</i> in <i>A. fraterculus</i>	Log-normal	$\mu = 3.6$ $\sigma = 1.5$	-25.6	-25.8	0.02
	Gamma	$\alpha = 1.5$ $\beta = 0.1$	-13.5	-13.7	0.1
<i>D. longicaudata</i> in <i>A. fraterculus</i>	Log-normal	$\mu = 5.4$ $\sigma = 2.1$	-1.1	-2	0.1
	Gamma	$\alpha = 1.1$ $\beta = 0.04$	1.8	1.01	0.1
<i>D. longicaudata</i> in <i>C. capitata</i>	Log-normal	$\mu = 4.2$ $\sigma = 1.5$	-23.5	-23.7	0.03
	Gamma	$\alpha = 1.4$ $\beta = 0.04$	-19.3	-19.6	0.04

Results and Discussion

The type II functional response determined for *D. brasiliensis* when offered *A. fraterculus* larvae in the laboratory followed the behavior of parasitoid species, where the saturation point in terms of parasitism was reached after a certain host density. Parasitism behavior in the face of different host densities is important to understand the control potential of a parasitoid and define parameters to maximize its rearing in the laboratory, as well as its population dynamics in an agricultural environment.

The number of parasitized hosts increased rapidly up to a density of 25 larvae, with approximately 11 hosts, and then slowed down, stabilizing at 25 larvae per female parasitoid (Fig. 1). However, the parasitism rate decreased as the density of larvae increased, ranging from 82.2% when 5 larvae were offered to 35% when 30 larvae were offered. In a later section, we will present the fitting of two probability distributions that describe the behavior of the parasitism rate. An analysis of the ideal density for offering *D. brasiliensis* females led to the conclusion that 10 larvae per female in 24 h is the value at which

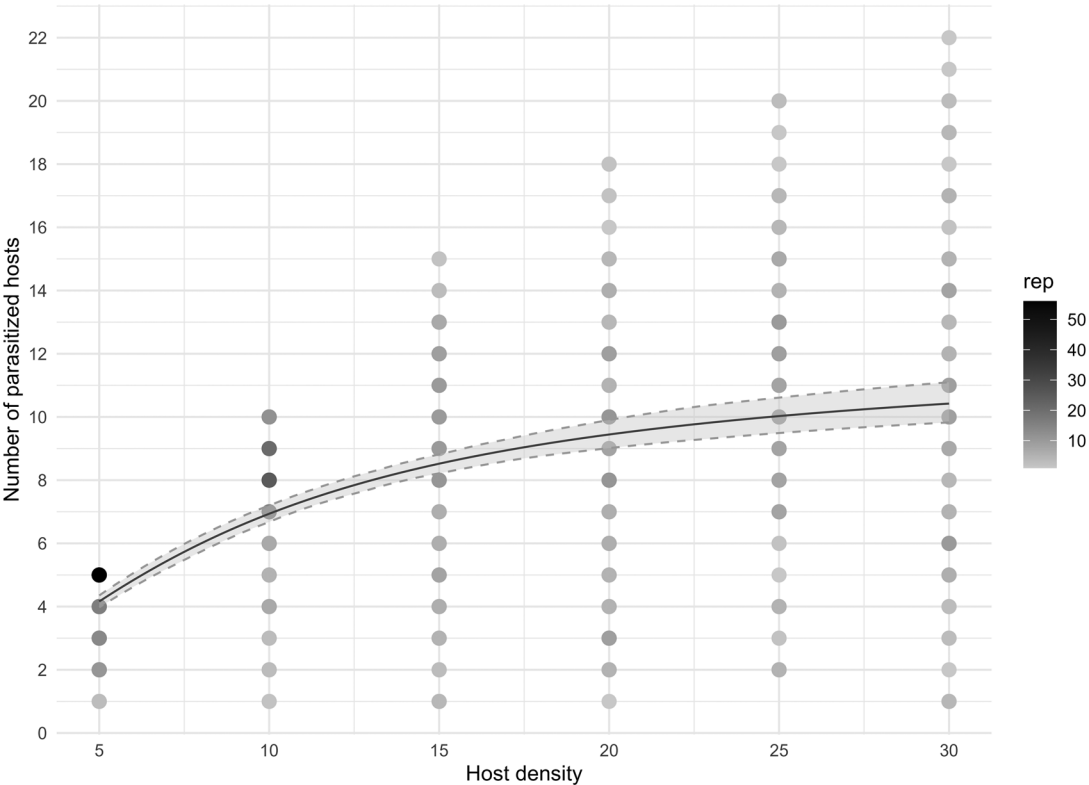


Fig. 2. Functional response curve type II, and 95% confidence intervals, fitted for parasitism of *D. brasiliensis* in relation to different densities of *A. fraterculus* larvae.

the parasitism and emergence curves cross. This value is close to that determined for *Doryctobracon areolatus* (Szepligeti, 1911) (Hymenoptera: Braconidae), where the supply of 10 *A. fraterculus* larvae enabled the emergence of approximately 6 parasitoids (Gonçalves 2016), and *D. longicaudata*, in which the supply of 8 larvae of *Anastrepha ludens* Loew 1873 (Diptera: Tephritidae) per female led to the production of 5 offspring (Montoya et al. 2000).

The results of the model selection conducted using the **frair_test** and **frair_fit** functions indicated a type II functional response. The parameter estimates (and significance levels) for the logistic regression analysis of the proportion of parasitized hosts in relation to the initial host density indicated a type II functional relationship, due to a significant negative first-order term (estimate = -0.07 ± 0.003 , z -value = -25.543 ; $P < 0.0001$), corresponding to a significant decrease in the rate of emerged parasitoids.

A comparison of the AIC and BIC values indicated that the type II functional response provided the best fit among the models tested (Table 1). Specifically, the type II model showed the lowest AIC (3622.9) and BIC (3631.7) values, in comparison with the type I (AIC = 4377.5; BIC = 4381.9) and type III (AIC = 3624.9; BIC = 3638.1) models. Providing reasonable initial values for the free parameters of the model is essential for optimizing nonlinear models. This process involves some practical rules; for example, for models with a type II functional response, h can be approximated as the inverse of the maximum number parasitized, and T is set to 1 (Bolker 2008). In this study, we used $a = 1$, $h = 0.1$, and $T = 1$. Once the initial estimates and fixed values were provided, the model was optimized using the maximum likelihood estimation. In the **FRAIR** package, the models used a binomial likelihood function that imposes an upper limit (all parasitized hosts) and a lower limit (no parasitized hosts) on the response.

The functional response is represented by an asymptotic curve, with capture rate $a = 2.688 \pm 0.164$ ($Z = 16.39$; $P < 0.0001$) and handling time $b = 0.081 \pm 0.002$ ($Z = 37.48$; $P < 0.0001$) (Fig. 2). Each point represents an observation of the number of emerged parasitoids at a given larval density. The experiment was repeated several times per density level, resulting in vertical columns of overlapping points. The right-side grayscale bar indicates the repetition number (*rep*), with lighter shades representing earlier repetitions and darker shades indicating later ones.

The **FRAIR** package also includes **frair_boot**, which uses a nonparametric bootstrap method based on the **boot::boot** function (Canty and Ripley 2025). This procedure generates several curve estimates and has 95% confidence intervals by default, with $a = 2.7$ (confidence interval: [2.3, 3.3]) and $b = 0.08$ (confidence interval: [0.07, 0.09]).

The type II functional response shown by *D. brasiliensis* when offered different densities of *A. fraterculus* larvae indicated that the number of parasitized hosts increased, as showed in Fig. 2. The type II functional response is the most common for parasitoids, although type III responses have also been reported for the braconid *D. longicaudata*, a parasitoid of the Mexican fruit fly *Anastrepha ludens* Loew, 1873 (Diptera: Tephritidae) larvae (Montoya et al. 2000). On the other hand, type I functional responses have also been reported for the parasitoids *Trichopria drosophilae* (Perkins, 1910) (Hymenoptera: Diapriidae) and *Pachycreoideus vindemiae* (Rondani, 1875) (Hymenoptera: Pteromalidae) in pupae of *Drosophila*

suzukii (Matsumura, 1931) (Diptera: Drosophilidae), another pest that also attacks fruit (Kaçar et al. 2017). Notably, these two parasitoids also parasitized *A. fraterculus*. Thus, fruit fly parasitoids show different functional responses and should be analyzed on a case-by-case basis.

The results obtained for *D. brasiliensis* can directly influence the maximization of its multiplication process in the laboratory, potentially yielding a high rate of parasitism and thus

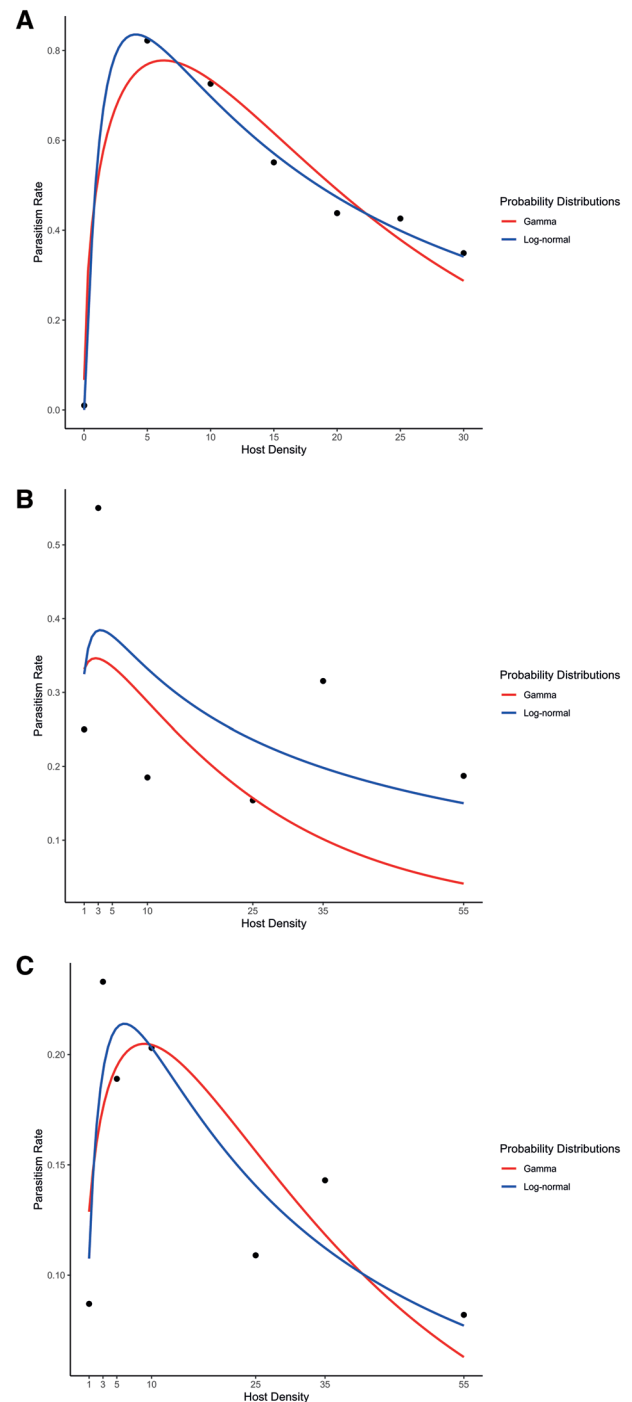


Fig. 3. Observed data of females A) *D. brasiliensis* exposed to larvae of *A. fraterculus*, B) *D. longicaudata* exposed to larvae of *A. fraterculus*, and C) *D. longicaudata* exposed to larvae of *C. capitata*, along with the fitted Log-normal and Gamma models. The points represent the experimental data.

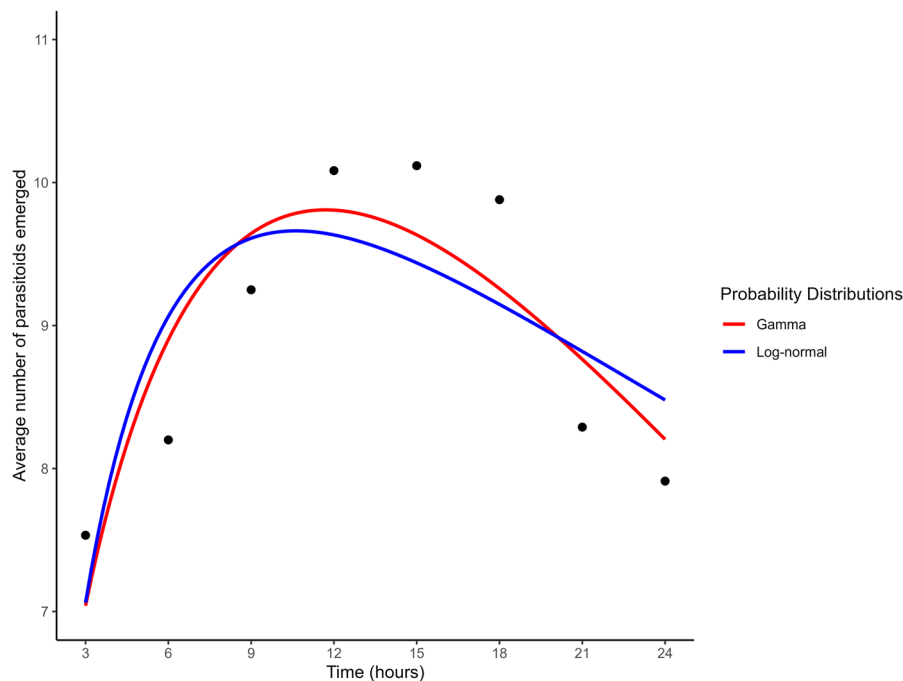


Fig. 4. Number of emerged parasitoids of *D. brasiliensis* reared on *A. fraterculus* larvae subjected to eight different exposure times along with the fitted Log-normal and Gamma models. The points represent the experimental data.

increasing the efficiency of rearing and reducing production costs by reducing expenditure on inputs such as diet and labor. However, additional studies are required to characterize the application of these findings in the field and in production systems to understand the population dynamics of the parasitoid and the host (pest) and even their use in applied biological control programs, since laboratory experiments are carried out in confined conditions and parasitoids exhibit different behaviors in the field (Van Lenteren and Bakker 1976). In addition, parasitoid behavior related to learning to locate hosts (Turlings et al. 1993) and variable environmental conditions can interfere with functional responses.

In this study, for the *D. brasiliensis* data, a point near the origin was added to allow the model to capture the rapid increase in parasitism rate at low host densities. For the *D. longicaudata* data, the point (5, 0.1) was removed to allow the log-normal and gamma models to converge. For both experiments, the log-normal distribution provided the best fit to the data, with lower values for all 3 evaluation criteria. Figure 3 illustrates the fits of the distributions.

In studies that estimated the production costs of parasitoids, such as those by Vacari et al. (2012) and Machado et al. (2023), who analyzed the costs of producing parasitoids of the sugarcane borer, the parasitism rate was not considered in the cost calculations. However, in the present study, this factor was considered relevant because a higher parasitism rate indicated a better ratio between the number of hosts offered and the number of emerged parasitoids. Therefore, we aimed to identify the optimal parasitism rate by analyzing its distribution in relation to the number of hosts provided. In a future study, we hope to establish a model to optimize the cost of mass-rearing fruit fly parasitoids.

The gamma and log-normal distributions were used to analyze the average number of parasitoids that emerged after exposure for 3 to 24 h. As shown in Fig. 4, both distributions

showed a good fit to the overall data, but the gamma distribution stood out, particularly in the 12 to 15 h exposure interval, capturing the observed parasitism pattern more accurately. The quality-of-fit indicators corroborated this superiority of the gamma model, showing lower values than the log-normal model: the AIC was 19.1 for the gamma distribution and 22.6 for the log-normal distribution; the BIC was 19.5 and 22.9 for the gamma and log-normal distributions, respectively; and the DPR was 0.5 and 0.6 for the gamma and log-normal distributions, respectively. These results indicate that the gamma model not only fits the data well in general but also offers more robust performance at specific time intervals, reinforcing its suitability for describing parasitism behavior under different exposure conditions.

It is important to emphasize that the functional response and the probabilistic modeling of parasitism rate serve distinct yet complementary roles in our analysis. The functional response describes the mechanistic relationship between host density and the number of parasitized hosts, typically exhibiting nonlinear patterns such as saturation. In contrast, the use of probability distributions (eg log-normal and gamma) aims to model the empirical distribution of parasitism rate observed under different experimental conditions. These models account for features such as skewness and overdispersion in the data, which are common in biological systems. Thus, the probabilistic approach does not intend to replace the functional response framework but rather to provide a flexible and statistically grounded method for describing variability in parasitism outcomes, especially in the context of optimizing rearing strategies.

This study not only highlights the success of *D. brasiliensis* in parasitizing *A. fraterculus* larvae but also underlines the importance of functional responses in understanding parasitism. The results showed that *D. brasiliensis* exhibited a type II functional response, characterized by the number of parasitized *A. fraterculus* larvae increasing with host density up to a

saturation point. In our laboratory experiment, the Type II functional response is the most appropriate, since the parasitoid has only one host option and parasitism occurs within a previously established timeframe. This finding indicates that *D. brasiliensis* can be used in biological programs to control *A. fraterculus* populations up to a certain density, which should be promising for planning parasitoid releases and management strategies in biological control. These findings will contribute to our understanding of the biology and behavior of *D. brasiliensis*, especially because factors such as handling time and parasitism rate are crucial for determining the competence of natural enemies at different pest densities. This information will also be valuable for the development of future strategies for managing *A. fraterculus*. Our analysis of the distribution of parasitism per host offered and per exposure time of the hosts showed that the log-normal distribution was the best fit for parasitism with host variation, whereas the gamma distribution was the best fit for parasitism over time. This analysis of the distribution of parasitism is important for estimating the cost of rearing parasitoids, since the parasitism rate is a relevant aspect for calculating this cost.

Acknowledgements

This study was supported by the Coordination of Superior Level Staff Improvement (CAPES, Financing Code 001) and Foundation for the Support of Research in the State of Rio Grande do Sul (FAPERGS, Grant No. 24/2551-0001559-0).

Author Contributions

Sonia Poncio (Investigation [equal], Methodology [equal], Writing—original draft [equal]), Pollyane Vieira da Silva (Data curation [equal], Formal analysis [equal], Writing—original draft [equal]), Alexandre Molter (Conceptualization [equal], Formal analysis [equal], Methodology [equal], Validation [equal], Writing—original draft [equal]), and Dori Edson Nava (Conceptualization [equal], Data curation [equal], Investigation [equal], Methodology [equal], Resources [equal], Supervision [equal], Writing—original draft [equal])

Funding

None declared.

Conflicts of Interest

None declared.

References

- Aguiar-Menezes EL, Menezes EB. 1997. Natural occurrence of parasitoids of *Anastrepha* spp. Schiner, 1868 (Diptera: Tephritidae) in different host plants, in Itaguaí (RJ), Brazil. *Biol. Control* 8:1–6. <https://doi.org/10.1006/bcon.1996.0485>
- Aitchison J, Brown JAC. 1957. *The lognormal distribution*. Cambridge University Press.
- Akaike HA. 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19:716–723.
- Altafini DL, Redaelli LR, Jahnke SM, et al. 2021. Functional response and preference of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) in *Ceratitidis capitata* and *Anastrepha fraterculus* (Diptera: Tephritidae). *An. Acad. Bras. Cienc.* 93:e20190935. <https://doi.org/10.1590/0001-3765202120190935>
- Arioli CJ, Botton M, Carvalho GA. 2004. Controle químico da *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae) na cultura do pessegueiro. *Cienc. Rural* 34:1695–1700. <https://doi.org/10.1590/S0103-84782004000600005>
- Bates DM, Watts DG. 1988. *Nonlinear regression analysis and its applications*. Wiley.
- Bolker BM. 2008. *Ecological models and data in R*. Princeton University Press.
- Botton M, Machota Junior R, Arioli CJ. 2023. Controle químico das moscas-das-frutas e uso de tecnologias “atrai-mata”. In: Zucchi RA, Malavasi A, Adaime R, Nava DE. (Org.), editors. *Mosca-das-frutas no Brasil: conhecimento básico e aplicado*. 1 ed. v. 1. FEALQ. p. 491–511.
- Canty A, Ripley BD. 2025. boot: Bootstrap R (S-Plus) Functions R. R package version 1.3-18. <https://doi.org/10.32614/CRAN.package.boot>, <https://CRAN.R-project.org/package=boot>
- Dias NP, Montoya P, Nava DE. 2022. A 30-year systematic review reveals success in tephritid fruit fly biological control research. *Entomol. Exp. Appl.* 170:370–384. <https://doi.org/10.1111/eea.13157>
- Dias NP, Zotti MJ, Montoya P, et al. 2018. Fruit fly management research: a systematic review of monitoring and control tactics in the world. *Crop Prot.* 112:187–200. <https://doi.org/10.1016/j.cropro.2018.05.019>
- Duan JJ, Messing RH. 1997. Effect of two Opiine parasitoids (Hymenoptera: Braconidae) introduced for fruit fly control on a native Hawaiian Tephritid, *Trupanea dubautiae* (Diptera: Tephritidae). *Biol. Control* 8:177–184. <https://doi.org/10.1006/bcon.1997.0503>
- Garcia FRM, Ovruski SM, Suárez L, et al. 2020. Biological control of tephritid fruit flies in the Americas and Hawaii: a review of the use of parasitoids and predators. *Insects* 11:662. <https://doi.org/10.3390/insects11100662>
- Gonçalves RS. 2016. *Técnicas de criação, bioecologia e competição interespecífica de parasitoides (hymenoptera: Braconidae) de moscas-das-frutas (diptera: Tephritidae)*. Tese, Universidade Federal de Pelotas.
- Gonçalves RS, Nornberg SD, Nava DE. 2023. Bioecologia e técnicas de criação de parasitoides das moscas-das-frutas. In: Zucchi RA, Malavasi A, Adaime R, Nava DE. (Org.), editors. *Mosca-das-frutas no Brasil: conhecimento básico e aplicado*. 1ed. FEALQ, v. 1, p. 371–385.
- Holling CS. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385–398. <https://doi.org/10.4039/Ent91385-7>
- Kaçar G, Wang XG, Biondi A, et al. 2017. Linear functional response by two pupal *Drosophila* parasitoids foraging within single or multiple patch environments. *PLoS One*. 12:e0183525. <https://doi.org/10.1371/journal.pone.0183525>
- Machado AVA, Bermúdez NC, Vacari AM, et al. 2023. Use of alternative host and production costs of the sugarcane borer parasitoid *Tetrastichus howardi*. *BioControl* 68:471–481.
- Marinho CF, Souza-Filho MF, Raga A, et al. 2009. Parasitoides (Hymenoptera: Braconidae) de moscas-das-frutas (Diptera: Tephritidae) no estado de São Paulo: plantas associadas e parasitismo. *Neotrop. Entomol.* 38:321–326. <https://doi.org/10.1590/S1519-566X200900300004>
- Montoya P, Liedo B, Barrera JF, et al. 2000. Functional response and superparasitism by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae), a parasitoid of fruit flies (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 93:47–54. [https://doi.org/10.1603/0013-8746\(2000\)093\[0047:FRASBD\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0047:FRASBD]2.0.CO;2)
- Montoya P, Ruiz L, Pérez-Lachaud G, et al. 2013. Field superparasitism by *Diachasmimorpha longicaudata* attacking *Anastrepha* spp. larvae on mango fruits. *Biol. Control* 64:160–165. <https://doi.org/10.1016/j.biocontrol.2012.10.015>
- Munyaneza J, Obrycki JJ. 1997. Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to colorado potato beetle eggs (Coleoptera: Chrysomelidae). *Biol. Control* 8:213–224. [https://doi.org/10.1603/0013-8746\(2000\)093\[0047:FRASBD\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0047:FRASBD]2.0.CO;2)

- Nava DE, Botton M. 2010. *Bioecologia e controle de anastrepha fraterculus e ceratitis capitata em pessegueiro*. Embrapa Clima Temperado, 29p. (Embrapa Clima Temperado, Documentos, 315).
- Nunes AM, Costa KZ, Faggioni KM, et al. 2013. Dietas artificiais para a criação de larvas e adultos da mosca-das-frutas sul-americana. *Pesq. Agropec. Bras.* 48:1309–1314.
- Nunes AM, Muller FA, Gonçalves RS, et al. 2012. Moscas frugívoras e seus parasitoides nos municípios de Pelotas e Capão do Leão, RS, Brasil. *Cienc. Rural* 42:6–12. <https://doi.org/10.1590/S0103-84782012000100002>
- Ovruski SM, Bezdjian LP, Van Nieuwenhove GA, et al. 2011. Host preference by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) reared on larvae of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae). *Fla. Entomol.* 94:195–200. <https://doi.org/10.1653/024.094.0211>
- Paranhos BJ, Alvarenga CD, Adaime R, et al. 2023. Controle biológico das moscas-das-frutas. In: Zucchi RA, Malavasi A, Adaime R, Nava DE. (Org.), editors. *Mosca-das-frutas no brasil: conhecimento básico e aplicado*. 1 ed. FEALQ, v. 1, p. 387-417.
- Poncio S, Nunes AM, Gonçalves RDS, et al. 2016. Biology of *Doryctobracon brasiliensis* at different temperatures: development of life table and determining thermal requirements. *J. Appl. Entomol.* 140: 775–785. <https://doi.org/10.1111/jen.12308>
- Poncio S, Nunes AM, Gonçalves RDS, et al. 2018. Strategies for establishing a rearing technique for the fruit fly parasitoid, *Doryctobracon brasiliensis* (Hymenoptera: Braconidae). *J. Econ. Entomol.* 111: 1087–1095. <https://doi.org/10.1093/jee/toy058>
- Pritchard DW, Paterson RA, Bovy HC, et al. 2017. Frail: An R package for fitting and comparing consumer functional responses. *Methods Ecol. Evol.* 8:1528–1534. <https://doi.org/10.1111/2041-210X.12784>
- R Core Team 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>
- Raga A, Prestes DAO, Souza Filho MF, et al. 2004. Fruit fly (Diptera: Tephritoidea) infestation in citrus in the State of São Paulo, Brazil. *Neotrop. Entomol.* 33:85–89. <https://doi.org/10.1590/S1519-566X2004000100015>
- Rogers D. 1972. Random search and insect population models. *J. Anim. Ecol.* 41:369–383. <https://doi.org/10.2307/3474>
- Royama T. 1971. A comparative study of models for predation and parasitism. *Popul. Ecol.* 13:1–91. <https://doi.org/10.1007/BF02511547>
- Schwarz G. 1978. Estimating the dimension of a model. *Ann. Stat.* 6:461–464. <http://www.jstor.org/stable/2958889>
- Sivinski J, Pinero J, Aluja M. 2000. The distributions of parasitoids (Hymenoptera) of *Anastrepha* fruit flies (Diptera: Tephritidae) along an altitudinal gradient in Veracruz, Mexico. *Biol. Control* 18:258–269. <https://doi.org/10.1006/bcon.2000.0836>
- Suárez L, Biancheri MJB, Murúa F, et al. 2023. Medfly population suppression through augmentative release of an introduced parasitoid in an irrigated multi-fruit orchard of Central–Western Argentina. *Insects* 14:387. <https://doi.org/10.3390/insects14040387>
- Taveira ADP. 2017. Uma modelagem estatística aplicada ao controle biológico da praga que ataca a cultura do algodão. Dissertação (Mestrado) Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo.
- Turlings TCJ, Wäckers FL, Vet LEM, et al. 1993. Learning of host-finding cues by hymenopterous parasitoids, In Papaj DR, Lewis AC, editors. *Insect learning: ecological and evolutionary perspectives*. Chapman and Hall, pp. 51-79.
- Vacari AM, De Bortoli SA, Borba DF, et al. 2012. Quality of *Cotesia flavipes* (Hymenoptera: Braconidae) reared at different host densities and the estimated cost of its commercial production. *Biol. Control* 63:102–106.
- Van Lenteren JC, Bakker K. 1976. Functional responses in invertebrates. *Neth. J. Zool.* 26:567–572.
- Wong T, Ramadan M, Mcinnis D, et al. 1991. Augmentative releases of *Diachasmimorpha tryoni* (Hymenoptera: Braconidae) to suppress a Mediterranean fruit fly (Diptera: Tephritidae) population in Kula, Maui, Hawaii. *Biol. Control* 1:2–7. [https://doi.org/10.1016/1049-9644\(91\)90094-G](https://doi.org/10.1016/1049-9644(91)90094-G)