Thermal Requirements and Annual Number of Generations of Diachasmimorpha longicaudata (Hymenoptera: Braconidae) Reared in the South American Fruit Fly and the Mediterranean Fruit Fly (Diptera: Tephritidae)

Authors: Meirelles, Rafael Narciso, Redaelli, Luiza Rodrigues, and Ourique, Cláudia Bernardes

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Thermal requirements and annual number of generations of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) reared in the South American fruit fly and the Mediterranean fruit fly (Diptera: Tephritidae)

Rafael Narciso Meirelles, Luiza Rodrigues Redaelli, and Cláudia Bernardes Ourique*

Abstract

Diachasmimorpha longicaudata (Ashmead) (Hymenoptera: Braconidae) is the most widely used parasitoid in biological control of Tephritidae programs around the world. Nevertheless, we have little information about the use of these parasitoids against *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae). This study was conducted to evaluate the thermal requirements for the development of *D. longicaudata* in 2 of its hosts, *A. fraterculus* and *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae). Third instars of each fly species were exposed for 1 h to 50 couples of the parasitoid. Subsequently, the larvae were placed individually in glass jars maintained in chambers at temperatures of 15, 18, 21, 25, 28, and 31 °C, at 60 ± 10% RH and a photoperiod of 14:10 h L:D until the emergence of *D. longicaudata*. The rate of development of *D. longicaudata,* in both hosts, increased as temperature increased. The development period of egg-to-adult phases was used to estimate, by the hyperbola method, the lower development threshold (*Dt*) and the thermal constant (*K*) of *D. longicaudata*. *Dt* and *K* were, respectively, 7.83 °C and 322.58 degree days for individuals that developed in *C. capitata*, and 12.5 °C and 227.27 degree days for those that developed in *A. fraterculus*. Adult longevity was inversely proportional to temperature. The results indicated that *D. longicaudata* may not develop in Rio Grande do Sul in the winter, because it is very common that minimum temperatures in the months of Jun and Jul fall below the *Dt*. In the 4 fruit-producing regions of the state of Rio Grande do Sul, the average numbers of generations of *D. longicaudata* per year were estimated in *A. fraterculus* and *C. capitata*, respectively, as follows: Porto Alegre (11.16 and 13.12), Pelotas (7.97 and 10.89), Bento Gonçalves (6.99 and 10.05), and Vacaria (4.84 and 8.28).

Key Words: *Anastrepha fraterculus*; *Ceratitis capitata*; degree days, lower development threshold; parasitoid; thermal constant

Resumo

Diachasmimorpha longicaudata (Ashmead) (Hymenoptera: Braconidae) é o parasitoide mais utilizado em programas de controle biológico de tefritídeos no mundo. Existem poucas informações sobre o seu desenvolvimento em *Anastrepha fraterculus* (Wiedemann) (Diptera: Tephritidae). Este estudo foi realizado para avaliar as exigências térmicas de *D. longicaudata* tendo como hospedeiros *A. fraterculus* e *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) em diferentes temperaturas. Larvas de terceiro ínstar de cada espécie de mosca foram expostas, por uma hora, para 50 casais do parasitoide. Em seguida, as larvas foram individualizadas em frascos de vidro e mantidas em câmaras nas temperaturas de 15, 18, 21, 25, 28 e 31 °C (60 ± 10% UR e 14 horas de fotofase) até a emergência dos parasitoides. A duração das fases de ovo-adulto foi usada para avaliar, por meio do método de hipérbole, a temperatura basal (*Tb*) e da constante térmica (*K*). A longevidade foi comparada entre as temperaturas. A taxa de desenvolvimento de *D. longicaudata*, nos dois hospedeiros, aumentou com a elevação da temperatura. *Tb* e *K* foram, respectivamente, 7,83 °C e 322,58 graus-dias para os indivíduos que se desenvolveram na *C. capitata*, e 12,5 °C e 227,27 graus-dias em *A. fraterculus*. A longevidade foi inversamente proporcional à elevação da temperatura. Os resultados indicaram que *D. longicaudata* pode não conseguir se manter no Rio Grande do Sul no inverno, quando são comuns temperaturas mínimas abaixo das *Tb*s registradas. O número médio de gerações por ano foi estimado para as cidades de Bento Gonçalves, Pelotas, Porto Alegre e Vacaria; Porto Alegre teve o maior número, enquanto Vacaria teve o menor.

Palavras Chave: *Anastrepha fraterculus*; *Ceratitis capitata*; constante térmica; graus-dia; parasitoide; temperatura basal

Diachasmimorpha longicaudata (Ashmead) (Hymenoptera: Braconidae), which originated in the Indo-Australian region, is a koinobiont endoparasitoid of various tephritid species. It has been introduced into various tropical and subtropical regions for control of *Anastrepha* species (Diptera: Tephritidae) and *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) (Montoya et al. 2000). This parasitoid is considered the most important biological control agent for inundative releases against diverse species of fruit flies in Latin American countries (López et al. 2009).

In 1994 Embrapa (the Brazilian Corporation of Agricultural Research) introduced *D. longicaudata* into Brazil from the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, Florida, USA, and released it in northeastern Brazil, where it is now established in the Recôncavo Baiano region and in the Submé-

Programa de Pós-Graduação em Fitotecnia, Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves 7712, 91540-000. Porto Alegre, RS, Brasil
*Corresponding author; E-mail: rafael.meirelles@ufrgs.br

dio São Franscisco region (Carvalho & Nascimento 2002). Its establishment has been demonstrated in the states of Minas Gerais (Alvarenga et al. 2005) and Rio de Janeiro (Leal et al. 2008). However, there are no records in regards to its release in Rio Grande do Sul.

Fruit flies (Diptera: Tephritidae) are first-order pests in fruit crops in Brazil (Nava & Botton 2010). In Rio Grande do Sul, *C. capitata* and *Anastrepha fraterculus* (Wiedemann) are important pests of exotic fruit crops such as apple and peach (Kovaleski & Ribeiro 2003). *Anastrepha fraterculus* also damages native fruit crops including several Myrtaceae (Gattelli et al. 2008).

Temperature is an important climatic variable that can directly influence the phenology and distribution of insects (Damos & Savopoulou-Soultani 2012). The optimal temperature for the development of a pest species may not be the same as that of its natural enemy (Horn 1998). Determination of the most appropriate temperature for the development of a parasitoid is important for its laboratory production and for planning field releases, and is a fundamental requirement of any program of biological control of pests. Meirelles et al. (2013) determined the development of *D. longicaudata* on *C. capitata* and *A. fraterculus* at a constant temperature (25 ± 1 °C). This study sought to determine the thermal requirements of *D. longicaudata* reared in these 2 host species, to estimate the potential number of generations of *D. longicaudata* per year in 4 fruit-producing regions of the state of Rio Grande do Sul, and to reveal information about the development and possible establishment of this parasitoid in these regions.

Materials and Methods

REARING OF INSECTS

All insects were reared at 25 ± 2 °C, 65 ± 10% RH, and a photoperiod of 14:10 h L:D.

Fruit Flies. Adults of *A. fraterculus* and *C. capitata* were kept in separate cages (45 × 30 × 30 cm). Food—adapted from Salles (1995) including wheat germ, beer yeast, the hydrolyzed protein Biorigin®, crystal sugar (at a ratio of 1:1:1:3), and water—was supplied ad libitum. Adults of *A. fraterculus* received oviposition substrates for 24 h (Salles 1992) composed of agar (5 g), blackberry juice (80 mL), and water (160 mL). The eggs were removed from the substrate and kept in distilled water for 48 h in a climate chamber (25 ± 2 °C, 65 ± 10% RH; in the dark), and then transferred to a larval diet. A 250 mL orange plastic tube was used as a substrate for *C. capitata* oviposition, following the method of FAO/IAEA/USDA (2003). The eggs were removed daily from the substrate and held 24 h before being placed in a climate chamber on the larval diet. The larval diet for both fly species was composed of raw carrot (500 g), cooked carrot (500 g), crystal sugar (500 g), beer yeast (100 g), corn flour (600 g), nipagin (4.4 g), sodium benzoate (4.4 g), citric acid (14.4 g), and distilled water (400 mL) (Terán 1977). The diet was placed on trays, where the eggs were distributed. The trays with larval diet and eggs were wrapped in newspaper and held for 7 d. Then the trays were unwrapped, placed on sterilized sand, and held for an additional 10 d. During this time the larvae exited the diet and pupated in the sand. The sand was then sifted, and the pupae were placed in plastic boxes (15 ´ 15 ´ 5 cm) with sterilized sand until emergence.

Parasitoid. The first specimens of *D. longicaudata* were obtained from the laboratory of the Embrapa Mandioca e Fruticultura research institute (located in Cruz das Almas, Bahia, Brazil) in Oct 2008. The adults, approximately 50 couples, were kept in cages (20 × 15 × 15 cm) covered with voile. Water and food (a mixture of water, honey, sugar, ascorbic acid, and nipagin) were supplied ad libitum. Third instars of *C. capitata* were exposed for 1 h (40 to 50 larvae per parasitism unit) to adults of *D. longicaudata*. Parasitized larvae were placed in plastic boxes (15 × 15 × 5 cm) with sterilized sand until emergence.

EVALUATION OF THE THERMAL REQUIREMENTS AND LONGEVITY OF *D. LONGICAUDATA*

Six sets of 50 pairs of *D. longicaudata*, between 3 and 10 d old, were kept in separate cages (20 × 15 × 15 cm), receiving food and water ad libitum. During several days, each set of *D. longicaudata* was exposed for 1 h to 40 to 50 third instars of *A. fraterculus* (~9 d old). About 18 sets of larvae were used. After exposure, the larvae were placed individually in glass tubes (25 mL) with sterilized sand and damp filter paper, and the tubes were sealed with plastic wrap and distributed evenly in chambers maintained at 15, 18, 21, 25, 28, and 31 °C, at 60 ± 10% RH and a photoperiod of 14:10 h L:D. The insects that emerged at each temperature regime (between 109 and 200 individuals) were placed individually in plastic jars (140 mL) with food and water, and maintained at the same temperature regime until death. Adult emergence and mortality were recorded each morning. The same procedure was repeated exposing parasitoids to larvae of *C. capitata*.

The thermal requirements of the development periods (defined as the period of time from egg to adult emergence) of *D. longicaudata* at the 6 temperatures were estimated through the hyperbola method (Haddad et al. 1999), which calculates the lower development threshold (*Dt*), the thermal constant (*K*), and the optimum temperature range for development. The average development period and the longevity of the parasitoids reared in the same host at different temperatures were analyzed through the Kruskal–Wallis test ($P \leq 0.05$) and Dunn's paired comparisons. The development period of parasitoids reared in the 2 different hosts at the same temperature regimes were compared by the Mann–Whitney test ($P \leq 0.05$) using the program BioEstat® 5.0 (Ayres et al. 2007). The possible number of generations of *D. longicaudata* per year was estimated for the counties of Bento Gonçalves, Pelotas, Porto Alegre, and Vacaria, Rio Grande do Sul, based on the parasitoid's thermal requirements and the mean temperatures of these locations (Applied Meteorology Center of FEPAGRO and the 8th Meteorology District, Porto Alegre), according to Cividanes (2000).

Results

No *D. longicaudata* completed development at either 15 or 31 °C in *A. fraterculus*, or at 15 °C in *C. capitata* (Table 1). The viability (completion of the egg-to-adult cycle) of *D. longicaudata* was greatest at 25 °C when the parasitoid was reared in either host species, and this value was 61.3% in *A. fraterculus* and 58.3% in *C. capitata.* The mean development period of *D. longicaudata* reared in *A. fraterculus* was longest at 18 °C and shortest at 28 °C, and this period was inversely related to temperature and differed among all temperature regimes ($H = 424.54$; df = 3; $P < 0.0001$) (Table 1). When the host was *C. capitata*, the development period varied inversely with temperature among the temperatures of 18, 21, and 25 °C ($H = 603.04$; df = 4; $P < 0.0001$) but was not significantly different between 28 and 31 °C.

The development period of *D. longicaudata* was longer in *A. fraterculus* than in *C. capitata* at all temperatures. Females of *D. longicaudata* took more time to reach the adult phase than males at all temperatures, both in *C. capitata* ($H = 634.96$; df = 9; $P < 0.0001$) and in *A. fraterculus* ($H = 439.62$; df = 7; $P < 0.0001$).

The lower development threshold (*Dt*) of males and females of *D. longicaudata* in *A. fraterculus* (12.5 °C) was higher than in *C. capitata* (7.83 °C) (Table 2). Approximately 99% and 93% of the reduction of the development time at increasing temperatures of *D. longicaudata*

Table 1. Average (± SE) development periods and their ranges (d) of *Diachasmimorpha longicaudata* reared in *Anastrepha fraterculus* [Dl (Af)] and in *Ceratitis capitata* [Dl (Cc)] larvae at 15, 21, 25, 28, and 31 °C, at 65 ± 10% RH and a photoperiod of 14:10 h L:D.

	Dl (Af)			Dl (Cc)		
Temperature (°C)	Development period (d)	*N*	Range (d)	Development period (d)	*N*	Range (d)
15	nd	—	—	nd	—	—
18	39.3 ± 0.48Aa	109	33–62	34.8 ± 0.29Ab	118	31–42
21	28.1 ± 0.31Ba	116	23–39	25.3 ± 0.17Bb	200	22–33
25	17.9 ± 0.13Ca	114	15–23	18.5 ± 0.15Cb	109	17–26
28	14.6 ± 0.11Da	123	13–20	14.8 ± 0.08Db	132	14–18
31	nd	—	—	15.4 ± 0.15D	109	13–19

Means followed by the same uppercase letter within a column (Kruskal–Wallis test, $P = 0.05$) or lowercase letter within a row (Mann–Whitney test, $P = 0.05$) are not significantly different. *N*, number of observations; nd, no development.

reared in *A. fraterculus* and *C. capitata*, respectively, was explained by the increase in temperature (Table 2). The optimum temperature range for development of *D. longicaudata* was 16.37 to 22.48 °C in *A. fraterculus* and 11.56 to 21.86 °C in *C. capitata*.

An inverse relationship between the mean longevity of *D. longicaudata* and temperature was found. When *D. longicaudata* was reared in *A. fraterculus*, the longest development period was recorded at 18 °C (52.7 d) and the shortest at 28 °C (9.2 d). The longevities at 21 °C (29.5 d) and 25 °C (27.0 d) were statistically similar (Table 3). With *C. capitata* as its host, the parasitoid had statistically similar longevities at 18 °C (53.3 d) and 21 °C (39.4 d), intermediate longevity at 25 °C (29.5 d), and the shortest longevities at 28 °C (11.3 d) and 31 °C (11.5 d). Individuals developing in *C. capitata* lived longer at 21 °C ($U = 4742.0$; $P < 0.0001$) than those developing in *A. fraterculus*, i.e., 39.4 d vs. 29.5 d. There was no statistically significant difference between the longevities of *D. longicaudata* reared in the 2 hosts at 18, 25, or 28 °C.

The estimated number of generations of *D. longicaudata* per year for the 4 counties (Table 4) when the host was *A. fraterculus* varied from 4.84 to 11.16, and the corresponding values for *C. capitata* as the host varied from 8.28 to 13.12. Thus *D. longicaudata* has the potential for more generations per year in *C. capitata* than in *A. fraterculus.*

Discussion

The failure of *D. longicaudata* to produce adults at 15 °C in both host species may be attributed to the existence of a dormancy phase stimulated by low temperature. Diapause in larvae of *D. longicaudata* collected in regions of Hawaii, USA, with winter temperatures varying between 2 and 10 °C, was recorded by Clausen et al. (1965). However, the method utilized in our study did not permit us to observe this phenomenon. The failure of the parasitoid to develop at 31 °C in *A. fraterculus* deserves further studies using individuals more experienced on that host. In *C. capitata*, at 28 and 31 °C, emergence of *D. longicaudata* was similar to that recorded in *Anastrepha suspensa* (Loew) (Diptera: Tephritidae) by Ashley et al. (1976). The results obtained in our study may be associated with the fact that the parasitoid had been reared for many generations in *C. capitata*. The rearing of this parasitoid in Brazil has been conducted in *C. capitata* ever since its introduction in 1994. If *D. longicaudata* had been reared for many generations in *A. fraterculus*, it seems possible that its *Dt* value would be different from that reported here.

Vacaria has an annual average temperature (15.2 °C) that is unfavorable to the parasitoid, regardless of the host, when compared with other regions; thus, fewer generations would be expected per year in this region. Among the 4 counties, Porto Alegre had the largest estimated number of generations per year. We expect that in warmer regions, or in periods with mean temperatures above 25 °C, *D. longicaudata* would develop more rapidly, as the time necessary to double its population at 25 °C is 3.92 and 4.73 d in *A. fraterculus* and *C. capitata*, respectively (Meirelles et al. 2013). Perhaps the success of *D. longicaudata* in regions of many countries where it has been introduced as a biological control agent can be explained in part by higher mean temperatures in these regions compared with the fruit-growing counties of Rio Grande do Sul.

During the winter in Rio Grande do Sul, during the months of Jun through Aug, temperatures may restrict or impair the establishment of *D. longicaudata*. Studies of population fluctuations of *A. fraterculus* in states of southern Brazil point to a reduction in populations during the months of Jun and Jul (Kovaleski et al. 2000), when the mean minimum temperatures are frequently below the development threshold for this parasitoid. The primary hosts of the South American fruit fly in Rio Grande do Sul are species of fruit trees in the Myrtaceae and Rosaceae (Zucchi 2000), which do not have mature fruits in Jun and Jul (Simão 1971; Donadio 2000; Manica 2002; Lira Júnior et al. 2007). Between the maturation of fruit of feijoa (pineapple guava) (*Acca sellowiana* (O. Berg) Burret; Myrtales: Myrtaceae) in May, and the maturation of fruit of Brazilian cherry (*Eugenia* species; Myrtales: Myrtaceae) and loquat (*Eriobotrya japonica* [Thunb.] Lindl.; Rosales: Rosaceae) in Aug, there could be a significant scarcity of hosts for fruit flies and consequently for *D. longicaudata*. Individuals of *D. longicaudata* originating from *C. capitata* had a lower thermal threshold than those reared in *A. fraterculus*. The development rate of this parasitoid, reared in both hosts, increases with an increase in temperature. It is likely that in some regions of southern Brazil, *D. longicaudata* would have difficulty surviving through the winter, making necessary the releases of this parasitoid early in spring.

Table 2. Lower development threshold (*Dt*), thermal constant (*K*) in degree days (DD), linear equation of development speed (1/D), and determination coefficient (R^2) of the biological cycle (egg to adult) of *Diachasmimorpha longicaudata* reared either in *Anastrepha fraterculus* or in *Ceratitis capitata* at 15, 18, 21, 25, 28, and 31 °C, at 65 ± 10% RH and a photoperiod of 14:10 h L:D.

Host	*Dt* (°C)	*K* (DD)	Regression equation	R^2	*F*	*P*
A. fraterculus	12.5	227.27	$y = -0.0550 + 0.0044x$	0.99	288	<0.0001
C. capitata	7.83	322.58	$y = -0.0243 + 0.0031x$	0.93	46.6	0.0064

Table 3. Average (± SE) longevities and their ranges (d) of *Diachasmimorpha longicaudata* reared either in *Anastrepha fraterculus* [Dl (Af)] or in *Ceratitis capitata* [Dl (Cc)] at 18, 21, 25, 28, and 31 °C, at 65 ± 10% RH and a photoperiod of 14:10 h L:D.

	Dl (Af)			Dl (Cc)		
Temperature (°C)	Mean (d)	*N*	Range (d)	Mean (d)	*N*	Range (d)
18	52.7 ± 2.49Aa	109	4–112	53.3 ± 3.05Aa	111	2–145
21	29.5 ± 1.25Ba	116	6–68	39.4 ± 1.69Ab	120	8–107
25	27.0 ± 1.64Ba	108	3–76	29.5 ± 1.76Ba	109	1–77
28	9.2 ± 0.46Ca	123	1–28	11.3 ± 0.75Ca	111	3–34
31	No adults	—	—	11.5 ± 0.70C	109	1–30

Means followed by the same uppercase letter within a column (Kruskal–Wallis test, $P = 0.05$) or lowercase letter within a row (Mann–Whitney test, $P = 0.05$) are not significantly different. *N*, number of observations.

Table 4. Estimated number of generations of *Diachasmimorpha longicaudata* per year in 4 fruit-producing counties in Rio Grande Do Sul, Brazil, based on annual average temperatures (°C) and annual accumulated degree days (DD), for *D. longicaudata* developing in *Anastrepha fraterculus* [Dl (Af)] (*Dt* of 12.5 °C for the egg-to-adult period) or *Ceratitis capitata* [Dl (Cc)] (*Dt* of 7.83 °C for the egg-to-adult period).

		Dl (Af)		Dl (Cc)	
Counties	Annual average temperature (°C)	DD accumulated	No. of generations/year	DD accumulated	No. of generation/year
Bento Gonçalves	16.8	1,590.2	6.99	3,241.7	10.05
Porto Alegre	19.5	2,535.8	11.16	4,231.8	13.12
Pelotas	17.5	1,812.2	7.97	3,513.3	10.89
Vacaria	15.2	1,100.1	4.84	2,670.2	8.28

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