



Is Host Size an Indicator of Quality in The Mass-Reared Parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae)?

Authors: López, Olga P., Hénaut, Yann, Cancino, Jorge, Lambin, Michael, Cruz-López, Leopoldo, et al.

Source: Florida Entomologist, 92(3) : 441-449

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.092.0305>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

IS HOST SIZE AN INDICATOR OF QUALITY IN THE MASS-REARED PARASITOID *DIACHASMIMORPHA LONGICAUDATA* (HYMENOPTERA: BRACONIDAE)?

OLGA P. LÓPEZ¹, YANN HÉNAUT², JORGE CANCINO¹, MICHAEL LAMBIN³, LEOPOLDO CRUZ-LÓPEZ² AND JULIO C. ROJAS²

¹Subdirección de Desarrollo de Métodos, Programa Moscafrut SAGARPA-IICA, Central Poniente No. 14,
Col. Centro, 30700, Tapachula, Chiapas, México

²Depto Entomología Tropical, El Colegio de la Frontera Sur (ECOSUR), Apdo Postal 36, Tapachula Chiapas, México

³Centre de Recherche sur la Cognition Animale, Université Paul Sabatier, 118 Rte de Narbonne,
31062 Toulouse, France

ABSTRACT

Diachasmimorpha longicaudata (Ashmead) is an endoparasitoid of fruit flies reared for augmentative biological control of several species of *Anastrepha* in Mexico. During the production of *D. longicaudata* different sizes of parasitoids are produced depending on the host size. Here, we investigated whether host size influences the biological and behavioral parameters of the wasp that emerged under laboratory conditions. Three different sizes of host (small, medium, and large) were used for the experiments. Host size significantly affected the number of parasitoids emerged as greater number of parasitoids emerged from medium size hosts compared to small and large hosts. The ratio of females to males did not differ among the groups. Host body size influenced life expectancy of parasitoid females and males deprived of food, and parasitoids that emerged from large hosts lived longer. In contrast, host body size did not significantly influence the life expectancy of parasitoid females and males provided with food *ad libitum*. Host body size also affected gross and net fecundity of emerged parasitoids; females that emerged from medium and large host larvae were more fecund. Host size did not affect most of the behavioral parameters evaluated, except the time of landing on source. Females that emerged from large host larvae spent less time before landing on a host source than females from the smaller hosts. Host body size did not affect the different trajectory indices evaluated, except the mean walking speed of *D. longicaudata*. Females developed in large hosts showed an increase walking speed compared to females from medium and small hosts.

Key Words: mass rearing, host body size, biological control, longevity, fecundity, sex ratio, host location behavior

RESUMEN

Diachasmimorpha longicaudata (Ashmead) es un endoparásitoide de las moscas de la fruta usado como un agente de control de varias especies de *Anastrepha* en México. Durante la producción masiva de *D. longicaudata* diferentes tamaños de individuos son producidos dependiendo del tamaño del hospedero. Este trabajo investigó si el tamaño del hospedero influye sobre los parámetros biológicos y comportamentales de los parasitoides emergidos. Tres diferentes tamaños de hospederos (pequeños, medianos y grandes) fueron usados para los experimentos. El tamaño del hospedero afectó significativamente el número de parasitoides emergidos debido a que un mayor número de individuos emergió de las pupas de tamaño medio en comparación con aquellos emergidos de las pupas de tamaño pequeño y grande. La proporción de hembras/machos no fue significativamente diferente en los tres grupos. El tamaño del hospedero influyó en la esperanza de vida de los parasitoides hembras y machos sin alimento, ya que los parasitoides grandes vivieron más tiempo. En contraste, el tamaño del hospedero no afectó la esperanza de vida de los parasitoides a los cuales se les proporcionó alimento *ad libitum*. El tamaño del hospedero influyó en la fecundidad de las hembras emergidas, las hembras provenientes de hospederos medianos y grandes fueron más fecundas. El tamaño del hospedero no tuvo relación con los parámetros comportamentales de los parasitoides emergidos, excepto el tiempo de aterrizaje sobre el hospedero. Las hembras provenientes de hospederas grandes tardaron menos tiempo en aterrizar en comparación con las hembras provenientes de hospederas pequeñas. El tamaño del hospedero no afectó los diferentes índices de trayectoria evaluados, excepto la velocidad promedio de caminar de *D. longicaudata*, las hembras provenientes de hospederos grandes mostraron un incremento en su velocidad de caminar en comparación con las hembras provenientes de hospederos chicos y medianos.

Translation by the authors.

Diachasmimorpha longicaudata (Ashmead) (Hymenoptera: Braconidae) is a koinobiont endoparasitoid native from the Indo-Australian region that attacks late instars of several fruit-infesting tephritid flies (Diptera: Tephritidae) (Wharton & Gilstrap 1983). This parasitoid has been employed in classical and augmentative biological control programs against several fruit flies, including *Bactrocera* spp, *Ceratitidis capitata* (Wiedemann) and *Anastrepha* spp (Bess et al. 1961; Wharton & Gilstrap 1983; Eskafi 1990). During the 1950s *D. longicaudata* was introduced into Mexico (Jimenez 1963), and currently it is mass-reared for augmentative biological control of several species of *Anastrepha* (Sivinski et al. 1996; Montoya et al. 2000). One of the principal reasons for its use as a biological control agent is that its mass rearing has been developed successfully (Wong & Ramadan 1992). For instance, 50 million parasitoids are produced per week in the mass-rearing program in Mexico (Cancino et al. 1996).

The quality of released individuals plays a fundamental role in a successful biological control program (Van Lenteren 1991; Wong & Ramadan 1992). Although some techniques for quality evaluation of *D. longicaudata* have been developed (Messing et al. 1993; Cancino & Yoc 1993; Purcell et al. 1994), the search for new quality indicators is still important because they may contribute information for quality improvement of released parasitoids. The size of puparia of the parasitized host may be a useful quality indicator of the individuals produced because it may have a direct relationship with size of parasitoids. In several parasitoid species, body size is a reliable indicator of parasitoid capacity as a biological control agent (Godfray 1994; Van Lenteren 2002). In various species of *Trichogramma*, large parasitoids are more efficient than small ones (Greenber 1991; Honda & Luck 2001).

The present study was undertaken to assess the effect of the host body size on emergence, longevity, fecundity, and host location behavior of mass reared *D. longicaudata*. We worked with 3 different sizes of a host of *D. longicaudata* reared in laboratory conditions. The results obtained may be important in understanding the significance of host size in relation to the quality control of *D. longicaudata*.

MATERIALS AND METHODS

Biological Material and Wasp Selection

Diachasmimorpha longicaudata and the host *Anastrepha ludens* (Loew) were produced at the "Moscafrut" mass rearing facilities located in Metapa, Chiapas, México according to procedures described elsewhere (Cancino et al. 1996). The parasitoids have been reared for more than 200

generations. Host larvae used for rearing the parasitoids were irradiated with 45 Gy to avoid emergence of adults from unparasitized hosts. Mango fruits (*Mangifera indica* L., var. Ataulfo), used as an odor sources in host location experiments, were selected from trees located in Tapachula, Chiapas, Mexico. Fruits in trees were covered with paper bags to avoid feral infestations. When fruits were $\frac{3}{4}$ ripe, 5 mangoes were placed into a cage ($1 \times 1 \times 1$ m) and exposed for 15 min to 200 mated females of *A. ludens*. Fruits with an average of 20 fruit fly third instars, about 15 d after oviposition, were used in the following experiments, which were conducted at $26 \pm 1^\circ\text{C}$, 75 ± 5 relative humidity, and a 12:12 h light: dark period.

We selected different sizes of *A. ludens* puparia (14-d-old) to be parasitized by *D. longicaudata* in order to obtain parasitoids from different size hosts. Host puparia were selected from different samples, measured, and put through the pupal sizing and separating machine (FAO/IAEA/USDA 2003). The puparia were separated in 3 size groups based on puparial diameter. Hereafter, we called them large (diameter: 2.84 ± 0.028 mm), medium (2.43 ± 0.032 mm), and small (2.02 ± 0.031 mm) puparia. One lot of 30 female parasitoids that emerged from each size group was selected and killed for measuring their hind tibia length with an eyepiece micrometer.

Adult Emergence and Sex Ratio

Samples of 100 parasitized host puparia from each size group were placed in plastic containers (5 cm high \times 7 cm diameter). The containers were checked to determine adult parasitoid emergence and sex-ratio. The experiment was performed 14 times.

Adult Parasitoid Longevity, Fecundity, and Flight Ability

Longevity of parasitoids was evaluated from cohorts of 30 females and 15 males that emerged from each size group; they were placed in Hawaii-type cages ($25 \times 25 \times 25$ cm) (Wong & Ramadan 1992). Adult parasitoid longevity was evaluated under 2 different conditions: those fed *ad libitum* with honey and water or those deprived of food. Longevity of individuals and their sex were recorded at 24-h intervals until the death of all adults. The experiment was replicated 6 times. Life expectative was estimated based on models from Carey (1993).

Female fecundity was evaluated with cohorts of 30 females and 15 males that emerged from each size group, and were placed in Hawaii-type cages, as above. The parasitoids were fed *ad libitum* with honey and water. After the fifth day, 200 *A. ludens* last instars in artificial diet in Petri

dishes (9.5 cm diameter \times 0.5 cm depth) covered with organza cloth were placed into the cage and exposed to the parasitoids for 2 h daily until the last female of the parasitoid cohort died. After exposure, the fruit fly larvae were washed from the diet with water and placed in plastic containers (9 cm high \times 5 cm diameter) with vermiculite for pupation during the next 15 d. We recorded sex and number of parasitoid adults that emerged. The parasitoids that emerged were related with the respective number of females alive each day. The offspring production per female parasitoid was estimated in terms of gross fecundity ($\sum mx$) and net fecundity ($R_o = \sum lxm$) following the procedures described by Carey (1993). The experiment was performed 6 times.

Samples of 100 fruit fly puparia from each size group after exposure to parasitoids were placed inside PVC black cylinders (8 cm height \times 10 cm diameter) to evaluate the flight ability of emerged wasps. The inside walls of the container were coated with neutral powder to prevent parasitoids from leaving the cylinders by walking. The cylinders were placed in screened cages (60 \times 60 \times 60 cm) with a source of light (fluorescent tube, 75 w) 50 cm above the top of the cages. The cages were checked daily and parasitoids that were able to fly out of the cylinders were removed. After 10 d, the number of parasitoid adults that remained within cylinders (walkers) as well as the number of non-emerged puparia were recorded. Flight ability (percentage fliers) was estimated according to Cancino et al. (2002). The experiment was replicated 14 times.

Host Location Behavior

In the first experiment, we evaluated female responses to long-range cues in a flight wind tunnel. The tunnel used was constructed of plexiglass and measured 120 cm long, 30 cm high, and 30 cm wide. A fan was used to pull air through the tunnel with a velocity of 0.4 m/s. Activated charcoal filtered intake air. Illumination was provided by 2 fluorescent bulbs mounted 60 cm above the wind tunnel that gave a light intensity of 230 lux. The wasps were individually placed in a 5-cm high plastic release container (4 cm i.d.) and allowed to acclimatize to the wind tunnel room conditions for at least 1 h before being observed. A mango fruit infested with *A. ludens* larvae was used as an odor source, placed in the center of the wind tunnel, 10 cm from the upwind end, and 8 cm above the wind tunnel floor. Each observation began with placing the release cylinder on a 14-cm high platform at the downwind end of the tunnel and 1 parasitoid was released. Tests lasted a maximum of 10 min for each female. We recorded (frequency and time) for taking flight, landing, and probing as defined by Jang et al. (2000). Each female had only 1 flight opportunity and landing was only recorded

in case it was preceded by hovering. Treatments were replicated 50 times for females from small and medium size hosts, and 46 times for females from large hosts. Tests were conducted in a random order. In all experiments 5- to 8-d-old naive female parasitoids were used.

In a second experiment, female response to short-range cues was evaluated in an experimental arena composed of a white plastic box (20 cm long \times 15 cm wide \times 5 cm high). A white filter paper sheet (28 cm long \times 22 cm wide, 127 g/m², Per-felter, Mexico city) was placed over the box (Fig. 1). A rectangular area of 14 \times 10 cm marked in the center of the white filter paper was defined as the observational zone. A video camera (SONY model TRV 530, Tokyo) was focused on this zone before the observations. A plastic container (3.7 cm diameter \times 0.5 cm high) with 20 larvae of *A. ludens* (8-d-old) and 1 g of larval diet was attached underneath the filter paper. This container was placed at one edge of the observational zone. A Petri dish (15 cm diameter \times 0.5 cm high) containing 40 mL of mango juice from infested fruits was placed below the container with larvae. Mango juice was important because without it, wasps left the arena. The wasps of the 3 size groups were individually placed in a plastic vial (5 \times 1 cm) and they were allowed to acclimatize to the arena room conditions for at least 30 min before being observed. Each observation began with placing the vial containing the female in the observation zone at the extreme edge opposite where host larvae were placed. Observation stopped after 10 min or when the parasitoid attempted to oviposit. The movements of the wasp during the observation were recorded by the video camera. The paper filter sheet and the container with mango juice and larvae were changed after each observation. All observations were carried

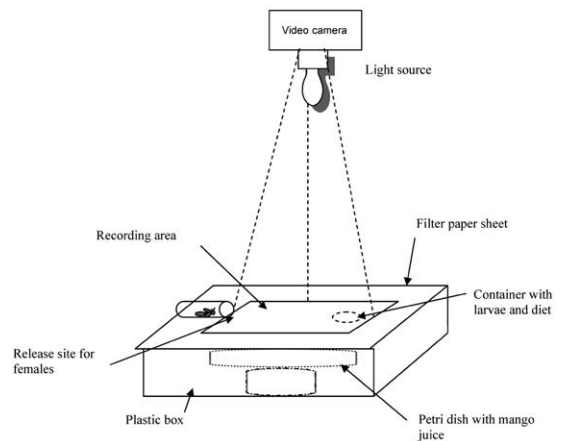


Fig. 1. Schematic view of the arena used for evaluating the response of *Diachasmimorpha longicaudata* females to short-range cues.

out from 10 AM to 2 PM under 245 lux of light intensity. Treatments (parasitoids from small, medium, and large hosts) were replicated at least 10 times and were tested in a random order.

Video images were digitized on a personal computer (1 frame every 40 ms) and the position of the wasp in each frame was considered as point coordinates on an X-Y grid. The image digitalization program was developed by M. Lambin in the Laboratory of Animal Behaviour Cognition of Toulouse Sciences University, France. The digitized search path was used to calculate total length, total duration, duration of stops, mean of stop duration, straightness, diffusion rate, mean walking speed, and total walking speed (Hénaut et al. 2000, 2002).

Statistics

Data were analyzed with the Statistica Software Package (version 6.1) (Stat Soft, Inc., 2003). The relation between diameter and width of puparia and adult size and hind tibia length of emerged parasitoids was analyzed by correlation. Data for adult emergence, longevity, fecundity, and flight ability were analyzed by one-way analysis of variance (ANOVA). Bioassay data for long-range cues (wind tunnel) were analyzed by *G*-test and one-way ANOVA. Prior to statistical analysis, data were checked for ANOVA assumptions and transformed, if needed, to log ($x + 1$) or arcsine. Significant differences were separated by Tukey tests. Variances of sex-ratio data were still heterogeneous after transformation, so randomization one-way ANOVA (Manly 1991) was used to analyze those data. Bioassay data (trajectory data indices) for short-range cues were analyzed by Kruskal Wallis ANOVA by ranks test, and the multiple comparisons between treatments were made by Sprent (1993) procedure.

RESULTS

The diameter of fruit fly puparia was different for the 3 groups used in this study ($F = 705.8$; $df = 2, 89$; $P < 0.001$), with a positive relationship between diameter and width of puparia ($R^2 = 0.94$, $P < 0.001$).

There was a positive correlation between the hind tibia length and the total body length of the parasitoids that emerged from the 3 sizes of hosts ($R^2 = 0.82$; $P < 0.001$), with hind tibia measurements as follows: (small = 1.45 ± 0.02 mm, medium = 1.86 ± 0.02 mm, and large = 2.11 ± 0.01 mm; $F = 307.7$; $df = 2, 83$; $P < 0.001$).

Adult Emergence and Sex Ratio

The size of host influenced the number of wasps that emerged, and percent emergence of *D. longicaudata* was greater in medium size hosts

compared to those that emerged from small and large hosts (65.35 ± 1.53 , 46.25 ± 2.15 , and 49.59 ± 1.75 , respectively, ($F = 33.15$; $df = 2, 39$; $P < 0.001$)). Host puparial size did not affect the ratio of female to male wasps ($F = 0.428$; $df = 2, 39$; $P = 0.134$), although the ratio showed a trend toward more females as size of host increased. Female to male ratio averaged 1.82 ± 0.27 , 2.11 ± 0.12 and 3.22 ± 0.26 for wasps that emerged from small, medium, and large hosts, respectively.

Adult Parasitoid Longevity, Fecundity, and Flight Ability

Host size affected life expectancy of unfed females ($F = 11.21$; $df = 2, 15$; $P = 0.001$), but not unfed males ($F = 0.84$; $df = 2, 15$; $P = 0.44$). Unfed females that emerged from medium and large hosts lived longer than those from small ones (5.25 ± 0.35 , 5.46 ± 0.29 , and 3.63 ± 0.25 d, respectively). Unfed males that emerged from small, medium, and large hosts lived 3.39 ± 0.40 , 4.78 ± 0.34 , 4.56 ± 0.31 d, respectively. Host size did not influence the life expectancy of females ($F = 0.02$, $df = 2, 15$, $P = 0.98$) or males ($F = 1.03$, $df = 2, 15$, $P = 0.38$) with food. Fed females emerging from small, medium, and large hosts lived 19.23 ± 0.79 , 20.13 ± 1.47 , and 19.14 ± 0.72 d, respectively. Fed males emerging from small, medium, and large host lived 13.81 ± 1.40 , 16.13 ± 1.54 , and 16.41 ± 1.05 d, respectively.

The period of fecundity between different size females was similar, 70% of the eggs were produced when females were 7-18-d-old (Fig. 2). However, gross fecundity ($F = 5.24$; $df = 2, 15$; $P = 0.01$) and net fecundity rate ($F = 14.57$; $df = 2, 15$; $P = 0.0003$) were affected by host size, being higher in parasitoids that emerged from medium and large hosts. The rate of gross fecundity was 53.6, 63.7, and 60.5 for wasps that emerged from small, medium, and large hosts, respectively. The rate of net fecundity was 37.4, 45.7, and 46.7 for parasitoids that emerged from small, medium, and large hosts, respectively. The offspring sex-ratio was not affected by the host size ($F = 1.67$; $df = 2, 15$; $P = 0.22$).

Host size did not influence the flight capability of parasitoids ($F = 0.87$; $df = 2, 39$; $P = 0.42$); flying adults averaged 89.1 ± 0.6 , 89.78 ± 0.8 and $90.5 \pm 0.9\%$ for parasitoids emerging from small, medium, and large hosts, respectively.

Host Location Behavior

The frequency and latency of the behavioral activities performed by the 3 groups of parasitoids are shown in the Table 1. None of the activities evaluated were affected by host size (taking off: $G = 1.15$, $df = 2$, $P = 0.56$; hovering: $G = 2.27$, $df = 2$, $P = 0.32$; landing: 2.27 , $df = 2$, $P = 0.32$; and probing: $G = 3.56$, $df = 2$, $P = 0.17$). Latency for taking off ($F = 0.29$; $df = 2, 89$; $P = 0.74$) and probing ($F =$

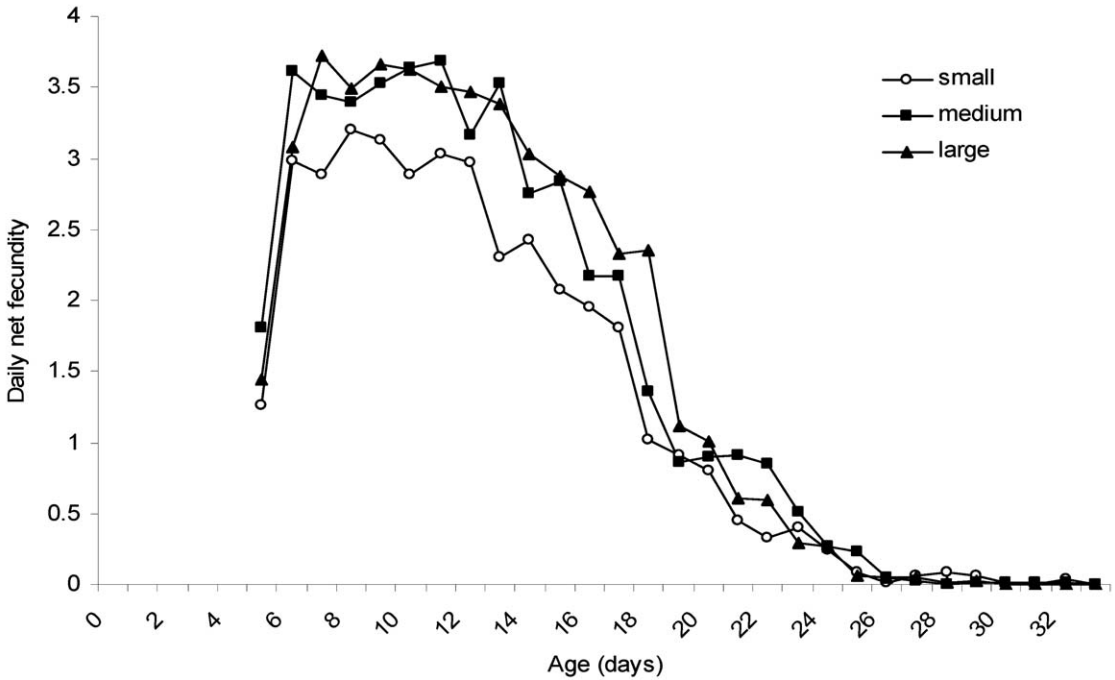


Fig. 2. Daily net fecundity of small, medium, and large *Diachasmimorpha longicaudata* females.

1.06; $df = 2, 82; P = 0.35$) was not influenced by host size. However, latency for landing (time between take off and landing) was affected by host size ($F = 3.13; df = 2, 89; P = 0.048$), with females developing in large hosts spending less time to land on source than those that emerged from small hosts.

There were not clear differences between the results of trajectory recorded (Table 2). The parasitoids emerging from different sizes of hosts had similar response except in the mean walking speed ($H = 7.31; P = 0.02$), with females emerging from large hosts showing an increase in walking

speed compared to females from medium and small hosts.

DISCUSSION

In the present study we found contrasting results about the influence of host size on the biological and behavioral parameters of *D. longicaudata*. The adult emergence ratio was affected by host size and these results agree with those previously reported for this parasitoid species (Wong & Ramadan 1992; Messing et al. 1993). We found significantly more wasps that emerged from me-

TABLE 1. RESULTS OF SEARCHING BEHAVIOR PARAMETERS OF *DIACHASMIMORPHA LONGICAUDATA* FEMALES THAT EMERGED FROM 3 DIFFERENT HOST SIZES.

Size	Take off	Landing	Probing
Frequency (% of response)			
Small	72 a	60 a	52 a
Medium	76 a	70 a	66 a
Large	76 a	74 a	70 a
Latency (sec)			
Small	1.15 ± 0.2 a	0.17 ± 0.0 a	1.97 ± 0.3 a
Medium	1.39 ± 0.4 a	0.14 ± 0.0 ab	1.27 ± 0.1 a
Large	1.05 ± 0.2 a	0.13 ± 0.0 b	1.52 ± 0.3 a

Values followed by the same letter are not significantly different for comparisons within columns.

TABLE 2. COMPARISON OF TRAJECTORY PARAMETERS OF *DIACHASMIMORPHA LONGICAUDATA* FEMALES THAT EMERGED FROM 3 HOST SIZES.

Parameter	Size			P ^a
	Small	Medium	Large	
Total length (mm)	127.01 ± 5.0	120.01 ± 6.0	130.01 ± 5.0	ns
Total duration (s)	89.01 ± 9.0	76.01 ± 13.0	67.01 ± 5.0	ns
Duration of stops (s)	71.01 ± 8.0	61.01 ± 12.0	53.01 ± 5.0	ns
Mean of stops duration (s)	10.72 ± 1.2	9.71 ± 0.8	9.11 ± 0.5	ns
Straightness	0.81 ± 0.0	0.81 ± 0.0	0.81 ± 0.0	ns
Diffusion	0.13 ± 0.0	0.13 ± 0.0	0.15 ± 0.0	ns
Speed (mm.s-1)	1.71 ± 0.2	2.00 ± 0.2	2.32 ± 0.2	ns
Walking speed (mm.s-1)	8.40 ± 0.4 a	8.61 ± 0.4 a	9.91 ± 0.4 b	*

^aIndicates the level of significance of Kruskal-Wallis ANOVA test.

ns, non-significant.

*significant at $P = 0.05$.

dium size hosts compared to those emerging from small and large hosts. The low emergence rates from small size hosts are in agreement with several studies which have shown that small host larvae are not preferred by *D. longicaudata* females and generally a greater proportion of males emerged from such hosts (Messing et al. 1993; Cancino et al. 2002). The low percentage of emergence from large hosts contrasts with results obtained by Messing et al. (1993), who found that larger hosts commonly result in higher emergence rates. The difference between our results and those of Messing et al. (1993) may be due to several factors including methodological and rearing conditions. Host species used for rearing *D. longicaudata* in the studies were not the same and different hosts may provide qualitatively and quantitatively different resources. In *Telenomus lobatus* Johnson & Bin, the percentage eclosion from the eggs of *Chrysoperla* species was higher than that from eggs of *Chrysopa* species (Ruberson et al. 1989). The low emergence of parasitoids from larger hosts in the present study may be due to several factors, such as (1) larger hosts are less abundant within the lot exposed to parasitization and this may affect the probability to be encountered by ovipositing females, (2) larger larvae may have a higher mobility than small and medium size larvae enabling them to escape from parasitization, and (3) larger hosts may be more mature and not as suitable hosts for parasitoid development. Lawrence et al. (1976) found a decline in the suitability of *Anastrepha suspensa* (Loew) larvae for development of *D. longicaudata* when hosts were older than 5 d. Wong & Ramadan (1992) showed that a peak of overall emergence of *D. longicaudata* is achieved sometime during the middle third instar of *Bactrocera dorsalis* (Hendel), after which emergence rates decline again. Large host larvae that are close to pu-

pation may be related to low wasp emergence (Lawrence et al. 1978; Wong & Ramadan 1992).

The sex ratio of *D. longicaudata* did not significantly vary between the adults that emerged from small, medium, and large hosts, which disagree with previous reports on this species (Messing et al. 1993; Cancino et al. 2002). In contrast to our results, several studies have shown that solitary parasitoid wasps tend to lay male eggs in small hosts and female eggs in large hosts (Godfray 1994; Heinz 1998; Sagarra et al. 2001). Our results may indicate that ovipositing females do not discriminate between the different host larvae quality, here based on host size. However, factors such as mortality, host species, host density, mating, and competence with other foragers may explain the results obtained (Godfray 1994). Ashley & Chambers (1979) found that the sex ratio of *D. longicaudata* did not remain constant and was affected by the age and the density of ovipositing females.

We found that the host body size only affected the parasitoid longevity when they were deprived of food; females from medium and large hosts lived longer than those from small ones. Host body size did not affect longevity of *D. longicaudata* females when food was provided *ad libitum*. Hardy et al. (1992) found that larger individuals of the bethylid parasitoid *Goniozus nephantidis* Muesebeck lived longer than small individuals when supplied with food, but the reverse was true when parasitoids were starved. The fact that females from medium and large hosts lived longer in absence of food may be due to these parasitoids having more energy reserves than those from small hosts. Several studies have reported a high relationship between host size and parasitoid survival (Tillmon & Cate 1993; Jervis & Copland 1996; Sagarra et al. 2001). In parasitoids, as well as other insects, large adult body size is often re-

lated with increased resource carry-over from the larval stage, and this is manifested as higher energy reserves (Riviero & West 2002; Ellers & Jervis 2003).

The duration of the oviposition period of the synovigenic *D. longicaudata* in the present study ranged from 11.8 to 12.1 d and was similar to that found previously for this species (Vargas et al. 2002). Interestingly, the oviposition period was not affected by the body size of females, but body size did affect the fecundity because medium and large females were more fecund than the small ones. In female parasitoids, fecundity is often correlated with body size, a measure of the resources available to the developing larvae (King 1989). It has been discussed that this relationship is particularly evident in proovigenic species, where the maximal number of eggs an individual female can lay is proportional to the amount of stored nutrient reserves obtained during larval stage (Ueno, 1999). In synovigenic species, where egg production should depend on availability of food for adult females (Jervis & Kidd 1986; Heimpel & Collier 1996), body size would not be always a good indicator of female fecundity (Ueno 1999). However, several studies have also shown that there is a positive correlation between body size and female fecundity in synovigenic parasitoids (Godfray 1994).

This study showed that body size of *D. longicaudata* females did not affect most of the activities related to its host finding behavior, except the latency for landing and the walking speed, which are important parameters during host location. Many other studies have shown that parasitoid size influences important behavioral traits such as host searching or host acceptance ability (Bigler 1989; Bouchier et al. 1993; Honda & Luck, 2001). Larger females of *Trichogramma* walk farther per unit of time than their smaller counterparts (Bigler 1989; Honda & Luck 2001) and encounter more hosts (Kazmer & Luck 1995). In contrast, Van Hezewijk et al. (2000) found that the size of *Trichogramma minutum* Riley was not a significant factor affecting either searching or walking speed of wasps.

The lack of relationship between host body size and some of the parameters evaluated in this study may be due to several factors. Firstly, we used females reared in the laboratory for more than 200 generations and adaptation to the mass rearing conditions is inevitable. Cancino et al. (2002) compared the performance of mass reared and wild strains of *D. longicaudata* in laboratory conditions, and found that wild females were bigger, lived longer, and were more fecund than mass reared females. The searching speed of a strain of *T. minutum* did not increase with age as compared with another strain possibly as a result of this trait being lost during more than 100 generations in culture (Van Hezewijk et al. 2000). Sec-

ondly, our study was performed in laboratory; parasitoids may not behave in the same way in the wild where abiotic and biotic factors fluctuate. Thus, further studies are necessary to investigate the performance of mass reared *D. longicaudata* in field conditions.

In conclusion, this study showed that adult emergence, longevity, fecundity, and walking speed of *D. longicaudata* females are affected by host body size. A previous knowledge of these parameters is important in the adequate maintenance of the mass-rearing and the field release of this parasitoid. Thus, host puparia size could be used as an indicator of the quality of emerged parasitoids.

ACKNOWLEDGMENTS

We are grateful with Javier Valle-Mora (ECOSUR) for his statistical help, and Pablo Montoya (Programa Moscafrut) for comments on a previous draft of this manuscript.

REFERENCES CITED

- ASHLEY, T. R., AND CHAMBERS, D. L. 1979. Effects of parasite density and host availability on progeny production by *Biosteres* (Opus) *longicaudatus* (Hym: Braconidae), a parasite of *Anastrepha suspensa* (Dip: Tephritidae). *Entomophaga*. 24: 363-369.
- BIGLER, F. 1989. Quality assessment and control in entomophagous insects used for biological control. *J. Appl. Entomol.* 108: 390-400.
- BESS, H. A., VANDENBOSCH, R., AND HARAMOTO, F. H. 1961. Fruit fly parasites and their activities in Hawaii. *Proc. Hawaii. Entomol. Soc.* 17: 367-378.
- CANCINO, J., AND YOC, M. 1993. Methods proposed to apply quality control in mass rearing of *Diachasmimorpha longicaudata*, pp. 37-47 *In* N. G. Benuzzi and M. Leppla [eds.], *Proc. 7th Workshop of Quality Control of Mass Reared Arthropods*.
- CANCINO, J., DE LA TORRE RUIZ, F. MORENO, E. HERNÁNDEZ, AND ZENIL, M. 1996. Establecimiento de la producción masiva de *Diachasmimorpha longicaudata* in Metapa de Domínguez, Chiapas, México, pp. 82-83 *In* Proc. 2nd Meeting of the Working Group on Fruit Flies of the Western Hemisphere, Villa del Mar, Chile.
- CANCINO, J., CANCINO, J. L., MARTINEZ, M., AND LIEDO, P. 2002. Quality control parameters of wild and mass reared *Diachasmimorpha longicaudata* (Ashmead), a fruit fly parasitoid, pp. 84-94 *In* N. C. Leppla, K. A. Bloem and R. F. Luck [eds.], *Quality Control for Mass-Reared Arthropods*, Institute of Food and Agricultural Science, University of Florida, USA.
- CAREY, J. 1993. *Applied Demography for Biologists with Special Emphasis on Insect*, Oxford University Press, New York, 206 pp.
- ELLERS, J., AND JERVIS, M. 2003. Body size and the time of egg production in parasitoid wasps. *Oikos* 102: 164-172.
- ESKAFI, F. M. 1990. Parasitism of fruit flies *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae) in Guatemala. *Entomophaga* 35: 355-362.

- FAO/IAEA/USDA. 2003. Manual for Product Quality Control and Shipping for Sterile Mass-Reared Tephritid Fruit Flies, Version 5, International Atomic Energy Agency, Vienna, Austria, 85 pp.
- GODFRAY, H. C. J. 1994. Parasitoids Behavioral and Evolutionary Ecology, Princeton University Press, Princeton, USA, 473 pp.
- GREENBERG, S. M. 1991. Evaluation techniques for *Trichogramma* quality, pp. 138-145 In F. Bigler [ed.], Proc. 5th Workshop of the Global IOBC Working Group Quality Control of Mass Reared Organisms, Wageningen, The Netherlands.
- HARDY, I. C. W., GRIFFITHS, N. T., AND GODFRAY, H. C. J. 1992. Clutch size in a parasitoid wasp: a manipulation experiment. *J. Anim. Ecol.* 61: 121-129.
- HEIMPEL, G. E., AND COLLIER, T. R. 1996. The evolution of host-feeding behaviour in insect parasitoids. *Biol. Rev.* 71: 373-400.
- HEINZ, K. M. 1998. Host size-dependent sex allocation behaviour in a parasitoid: implications for *Catolaccus grandis* (Hymenoptera: Pteromalidae) mass rearing programmes. *Bull. Entomol. Res.* 88: 37-45.
- HÉNAUT, Y., ALAUZET, C., FERRAN, A., AND WILLIAMS, T. 2000. The effect of larval diet on adult predation behavior in *Orius majusculus* (Reuter) (Heteroptera: Anthocoridae). *J. Econ. Entomol.* 93: 252-255.
- HÉNAUT, Y., ALAUZET, C., AND LAMBIN, M. 2002. Effects of starvation on the search path characteristics of *Orius majusculus* (Reuter) (Heteroptera: Anthocoridae). *J. Appl. Entomol.* 126: 501-503.
- HONDA, J. Y., AND LUCK, R. F. 2001. Interactions between host attributes and wasp size: a laboratory evaluation of *Trichogramma platneri* as an augmentative biological control agent for two avocado pests. *Entomol. Exp. Appl.* 100: 1-13.
- JANG, E. B., MESSING, R. H., KLUNGNESS, L. M., AND CARVALHO, L. A. 2000. Flight tunnel responses of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) to olfactory and visual stimuli. *J. Insect Behav.* 13: 525-538.
- JERVIS, M. A., AND KIDD, N. A. C. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biol. Rev.* 61: 395-434.
- JERVIS, M. A., AND COPLANT, M. J. W. 1996. The life cycle, pp. 63-160 In M. A. Jervis and N. A. C. Kidd [eds.], *Insect Natural Enemies: Practical Approaches to their Study and Evaluation*, Chapman & Hall, London.
- JIMÉNEZ, J. E. 1963. Avances y resultados del control biológico en México. *Fitófilo.* 38: 34-45.
- KAZMER, D. J., AND LUCK, R. F. 1995. Field tests of size fitness hypothesis in the egg parasitoid *Trichogramma pretiosum*. *Ecology* 76: 412-425.
- KING, B. H. 1989. Host-size-dependent sex ratios among parasitoid wasp: does host growth matter? *Oecologia* 78: 420-426.
- LAWRENCE, P. O., BARANOWSKI, R. M., AND GREANY, P. D. 1976. Effect of host age on development of *Biosteres* (= *Opius*) *longicaudatus* a parasitoid of the Caribbean fruit fly, *Anastrepha suspensa*. *Florida Entomol.* 59: 33-39.
- LAWRENCE, P. O., GREANY, P. D., NATION, J. L., AND BARANOWSKI, R. M. 1978. Oviposition behavior of *Biosteres longicaudatus*, a parasite of the Caribbean fruit fly, *Anastrepha suspensa*. *Ann. Entomol. Soc. America* 7: 253-256.
- MANLY, B. F. J. 1991. Randomization and Monte Carlo Methods in Biology, Chapman & Hall, London, 120 pp.
- MESSING, R. H., KLUNGNESS, L. M., PURCELL, M., AND WONG, T. T. Y. 1993. Quality control parameters of mass-reared opine parasitoids used in augmentative biological control of tephritid fruit flies in Hawaii. *Biol. Control* 3: 140-147.
- MONTOYA, P., LIEDO, P., BENREY, B., CANCEINO, J., BARRERA, J. F., SIVINSKI, J., AND ALUJA, M. 2000. Biological control of *Anastrepha* spp. (Diptera: Tephritidae) in mango orchards through augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 18: 216-224.
- PURCELL, M. F., DANIELS, K. M., WHITEHAND, L. C., AND MESSING, R. H. 1994. Improvement of quality control methods for augmentative releases of the fruit fly parasitoids *Diachasmimorpha longicaudata* and *Psytalia fletcheri* (Hymenoptera: Braconidae). *Biocontrol Sci. Tech.* 4: 155-166.
- RIVIERO, A., AND WEST, S. A. 2002. The physiological cost of being small in a parasitic wasp. *Evol. Ecol. Res.* 4: 407-420.
- RUBERSON, J. R., TAUBER, C. A., AND TAUBER, M. J. 1989. Development and survival of *Telenomus lobatus*, a parasitoid of chrysopid eggs: effect of host species. *Entomol. Exp. Appl.* 51: 101-106.
- SAGARRA, L.A., VINCENT, C., AND STEWART, R. K. 2001. Body size as an indicator of parasitoid quality in male and female *Anagyrus kamali* (Hymenoptera: Encyrtidae). *Bull. Entomol. Res.* 91: 363-367.
- SIVINSKI, J., CALKINS, C. O., BARANOWSKI, R. M., HARRIS, D., BRAMBILA, J. DÍAZ, J., BURNS, R. E., HOLLER, T., AND DONSON, G. 1996. Suppression of a Caribbean fruit fly *Anastrepha suspensa* (Loew) (Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biol. Control* 6: 177-185.
- SPRENT, P. 1993. Applied Nonparametric Statistical Methods, Chapman & Hall, London, 342 pp.
- STAT SOFT, INC. 2003. STATISTICA (data analysis software system), version 6. www.statsoft.com.
- TILLMAN, P. G., AND CATE, J. R. 1993. Effect of host size on adult size and sex ratio of *Bracon mellitor* (Hymenoptera: Braconidae). *Environ. Entomol.* 22: 1161-1165.
- VARGAS, R. I., RAMADAN, M., HUSSAIN, T., MOCHIZUKI, N., BAUTISTA, R. C., AND STARK, J. D. 2002. Comparative demography of six fruit fly (Diptera: Tephritidae) parasitoids (Hymenoptera: Braconidae). *Biol. Control* 25: 30-40.
- UENO, T. 1999. Host size dependent sex ratio in a parasitoid wasp. *Res. Popul. Ecol.* 41: 47-57.
- VAN HEZEWIJK, B. H., BOURCHIER, R. S., AND SMITH, S. M. 2000. Searching speed of *Trichogramma minutum* and its potential as a measure of parasitoid quality. *Biol. Control* 17: 139-146.
- VAN LENTEREN, J. C. 1991. Quality control of natural enemies: hope or illusion, pp. 1-14 In F. Bigler [ed.], *Proceedings of the 5th Workshop of the Global IOBC Working Group Quality Control of Mass Reared Organisms*, Wageningen, The Netherlands.
- VAN LENTEREN, J. C. 2002. Status of quality control for natural enemies in Europe, pp. 9-21 In N. C. Leppla, K. A. Bloem, and R. F. Luck [eds.], *Quality Control*

- for Mass-Reared Arthropods, Institute of Food and Agricultural Science, University of Florida, USA.
- WHARTON, R. A., AND GILSTRAP, F. E. 1983. Key to and status of opiine braconid (Hymenoptera) parasitoids used in biological control of *Ceratitis* and *Dacus* species (Diptera: Tephritidae). *Ann. Entomol. Soc. Amer.* 76: 721-742.
- WONG, T. T. Y., AND RAMADAN, M. M. 1992. Mass reared biology of larval parasitoids (Hymenoptera: Braconidae: Opinae) of Tephritidae flies in Hawaii, pp. 405-426 *In* T. E. Anderson and N. C. Leppla [eds], *Advances in Insect Rearing for Research and Pest Management*, Westview Press, Oxford England.