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SIZE, FECUNDITY, AND GONADIC MATURATION OF *TOXOTRYPANA CURVICAUDA* (DIPTERA: TEPHRITIDAE)

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ABSTRACT

The papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, is an important pest of papaya. It is distributed from Florida, USA, to northern South America. We studied aspects of its biology on papaya, *Carica papaya*. Females and males emerged within a 3-d period with similar numbers emerging daily. Females are heavier than males but had similar longevity. Puparial length, puparial weight, and adult weight did not correlate with adult longevity. First chorionated eggs were recorded 4 d after emergence. Females 6 d old had an average of 44 ± 2.2 (sem) chorionated eggs. Heavier females have a reproductive advantage as they have more chorionated eggs than light females. More than 85% of females lived at least 6 d.

Key Words: egg maturation, longevity, emergence rhythm, *Carica papaya*, Mexico

RESUMEN

La mosca de la fruta de la papaya, *Toxotrypana curvicauda* Gerstaecker, es un insecto plaga de la papaya, *Carica papaya,* que se distribuye desde la Florida en los EUA hasta la parte norte de Sudamérica. En esta ocasión, estudiamos aspectos de su biología en *Carica papaya*. Ambos sexos emergen en un lapso de 3 días con similar número de hembras y machos emergiendo diariamente. Las hembras son más pesadas que los machos pero presentan similar longevidad. No existe relación entre longevidad del adulto y el largo o ancho de la pupa o por el peso del adulto. Los primeros huevos corionados se observaron en hembras de 4 d de edad. En promedio cada hembra madura sexualmente (6 d de edad) presentó 44 ± 2.2 huevos corionados. Las hembras pesadas tienen una ventaja reproductiva ya que presentan más huevos corionados que hembras ligeras. La mayoría de las hembras (> 85%) vivieron al menos 6 días.

Translation provided by the authors.

The papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Diptera: Tephritidae), is one of seven species of the genus *Toxotrypana* (White & Elson-Harris 1992). *Toxotrypana curvicauda* has been reported from south Florida and south Texas, through much of Central America, to northern South America including some Caribbean islands (Knab & Yothers 1914; Eskafi & Cunninghan 1987; O'Doherty & Link 1993).

Several authors have reported on the biology of this species. Knap & Yothers (1914) and Mason (1922) produced the first reports on the life cycle. Landolt (1984) studied ovary and egg development and reported that males are ready to mate on the day they emerge while females have a 6-d premating period. Aluja et al. (1994) evaluated preference for papaya varieties and Landolt & Hendrichs (1983) and Aluja et al. (1997a, b) reported on spatial and temporal distribution of this fly. The sex pheromone of *T. curvicauda* was identified by Chuman et al. (1987). Improvements in trapping techniques with sex pheromone were done by Landolt et al. (1988), Landolt & Heath (1990), and Heath et al. (1996). Castrejón-Gómez et al. (2004) reported the use of food attractants for capturing the papaya fruit fly.

Body size and/or weight have been traditionally considered key determinants of an organism's ecological and physiological properties (Thornill & Alcock 1983; Honěk 1993), because it is strongly correlated with many physiological and fitness characteristics (Reiss 1989; Roff 1992). Female weight is generally accepted as an index of potential fecundity, assuming a positive relationship between the number of oocytes in the ovarioles and the weight of the female. Thus, heavy females have more eggs available for fertilization (Tzanakakis 1989; Fay 1989; Sivinski 1993). Similarly, large size or weight has been associated with greater longevity (Bloem et al. 1994). In mass rearing facilities, weight is an important parameter when evaluating the quality of laboratory populations (Chambers & Ashley 1984).

There is no published information available on puparial morphometry and adult emergence rhythm of the papaya fruit fly. Also, the relationships among puparial weight and number of mature eggs, and gonadic maturation and female age have not been explored. This information is important for understanding the biology of *T. curvicauda* on *C. papaya* and for planning research on the mating system as a tool for management of this papaya pest.

Materials and Methods

Insects

Insects were collected as larvae from infested papaya fruits obtained from an experimental papaya plantation at the CEPROBI (Centro de Desarrollo de Productos Bióticos) grounds at Yautepec, Morelos, Mexico. Detailed information on localization, native vegetation, and climatic information of the CEPROBI grounds can be found in Aluja et al. (1997a). Mature larvae (100-200) were placed for pupation into a plastic cylindrical container (11 cm high and 8.5 cm diameter) with sterile soil (6 cm deep) and covered with mesh secured with a rubber band. Containers were watered as necessary to keep soil moist. One week after pupation, puparia were recovered and washed under running water and dried on paper toweling. An Ohaus balance (Explorer, 0.0001 g accuracy, made in Switzerland) was used to weigh the puparia. Each puparium was numbered and kept individually in a plastic container (9.5 cm high and 3 cm diameter) with sterile soil until adult emergence. Each puparium was photographed under a Nikon SMZ 1500 stereoscope with a Nikon Coolpix 4500 digital camera. SigmaScan v5 (Systat Software Corporation) was used to measure puparial length and width. Adults were weighed on their emergence day with the same balance noted above. Adults were maintained individually in plastic containers, and fed water and sugar (Sharp & Landolt 1984). Puparia and adults were kept under natural humidity (50-60%), temperature (27 ± 2°C) and light regime (12L:12D). This experiment was carried out from August to September, 2004. For each insect, we recorded puparial weight, length, width; and adult emergence, weight, longevity and sex.

Relationships among Puparial and Adult Weight and Number of Chorionated Eggs

To determine whether puparial and adult weight correlated with the number of chorionated eggs, 40 females (6-8-d-old) were killed by freezing (8 min in a domestic freezer, -20°C). The abdomen was removed from the body and dissected under the stereoscope (described above). Both ovaries were removed, immersed in 1% acetocarmin for 60 s and transferred to clean saline solution. Non-chorionated eggs retain the stain but the presence of the chorion prevents stain absorption (e.g., Fernando & Walter 1999). Unstained eggs were classified as mature and were presumed to be available for oviposition, while stained eggs were classified as immature eggs.

Gonadic Maturation

To determine if there was a relationship between adult age and the number of chorionated eggs, we compared the number of mature eggs contained in one ovary of females at 0, 2, 4, 6, 8, 10, and 12-d of age. We dissected 20 females for each age. Dissection, egg staining, and egg counting followed the methodology described above.

Statistical Analysis

Differences in puparial weight, length and width, as well as adult weight and longevity between males and females were determined with a *t* test. Regression analysis was used to determine the influence of puparial and adult weight on adult longevity and on the number of mature eggs of 6- to 8-d-old females. Analysis of covariance (ANCOVA) followed by a least squared means (LSM) test was used to determine if the number of chorionated eggs was affected by female age. Puparial weight was used as a concomitant variable. All statistical analyses were carried out with SAS (SAS Institute 1996). All data are reported as mean ± standard error.

Results

Female puparia were significantly heavier and longer than male puparia (Table 1). Similarly adult females were significantly heavier than adult males (Table 1). In contrast, puparial width, puparial period and adult longevity were similar for both sexes (Table 1). More than 85% of females

Table 1. Average (± standard error) pupal and adult characteristics of *Toxotrypana curvicauda* on *C. papaya*.

Variable	Females (n = 226)	Males (n = 175)	t	P
Pupal weight (mg)	75.0 ± 0.90	70.2 ± 1.00	3.58	<0.001
Pupal length (mm)	10.3 ± 0.04	9.9 ± 0.05	6.165	<0.001
Pupal width (mm)	2.4 ± 0.05	2.3 ± 0.03	1.75	>0.05
Pupal period (d)	21.6 ± 0.06	21.6 ± 0.07	0.01	>0.05
Adult weight (mg)	48.8 ± 0.60	42.7 ± 0.70	6.639	<0.001
Adult longevity (d)	19.9 ± 1.14	20.0 ± 0.93	0.05	>0.05

lived at least 6 d. However, female and male minimum and maximum longevity were 2-59 and 2–55 d, respectively (Fig. 1).

Puparial length increased as puparial weight increased, for both sexes (males: F = 369, df = 1,172, P > 0.0001; females: R^2 = 0.68 and F = 423, df = 1,223, P > 0.0001, R^2 = 0.65). There were no relationships between puparial weight and longevity or for adult weight and longevity for either females (F = 0.007, df = 1,92, P > 0.05; F = 0.25, df = 1,92, P > 0.05) or males (F = 1.1, df = 1,141, P > 0.05 and adult F = 2.57, df = 1,141, P > 0.05), respectively.

Sex Ratio and Emergence Rhythm

Most insects emerged during the first two days at the start of adult emergence (Fig. 2). Similar numbers of males and females emerged in the first (t = 0.452, P = 0.66), second (t = 0.31, P = 0.76) and third day (t = 1.27, P = 0.23). However, significantly more females emerged overall (t = 2.96, P = 0.003), resulting in a 1:1.26 male:female sex ratio.

Relationship between Puparial and Adult Weight, and Number of Chorionated Eggs

Heavier females have a reproductive advantage over light females as heavier females had more chorionated eggs than light ones (Fig. 3A, B).

Gonadic Maturation

No chorionated eggs were obtained from 0- and 2-d-old females. Thus, these data were removed from the statistical analysis. The number of chorionated eggs significantly increased up to 100 eggs as female age increased (Fig. 4). Females at 10 d had more than double the number of chorionated eggs of 4-d-old females (Fig. 4). There was no difference in number of chorionated eggs produced by 10- and 12-d-old females.

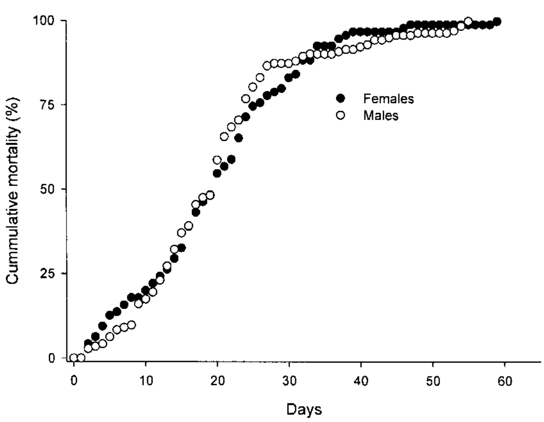


Fig. 1. Cumulative mortality of male and female *T. curvicauda* at 27 ± 2°C, 50-60 RH and, 12L:12D at Yautepec, Morelos, Mexico.

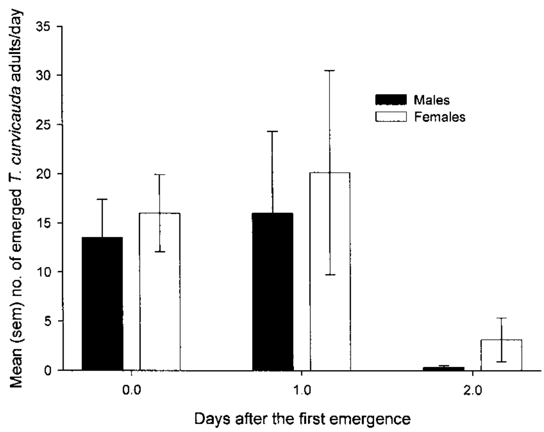
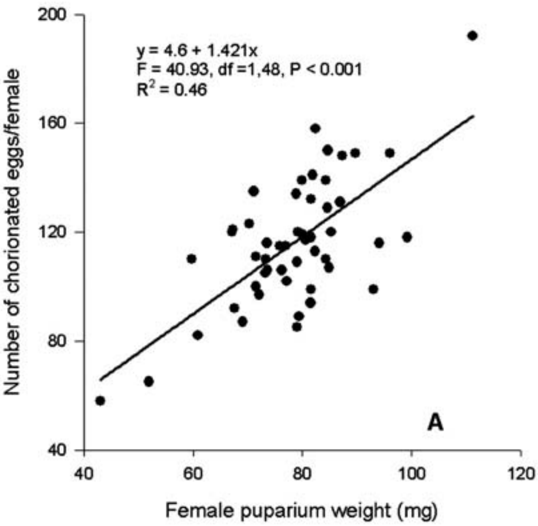


Fig. 2. Mean (± standard error) number of *T. curvicauda* adults that emerged per day starting with first adult emergence; n = 226 and 175 for females and males, respectively.

Discussion

Toxotrypana curvicauda females had a 6-d precopulatory period. During the female's precopulatory period, ovaries and eggs increase in length and width (Landolt 1984). Our results show that the first chorionated eggs appeared later than 2 d after emergence, indicating that several days are required to produce mature eggs, as in many tephritids (Williamson 1989). Females that were 6-d-old had more than 45 chorionated eggs per ovary, and 10-d-old females had more than 70 chorionated eggs per ovary. In contrast, Knab & Yothers (1914) indicated that females had around 100 eggs and Rojas (1992) reported 67.8 ovarioles per females. However, none of the preceding authors related the number of eggs or ovarioles with female puparial or female adult weight. Our results indicate that research addressing female fecundity also should consider the positive and linear relationships between puparial and adult weight as well as age and the number of chorionated eggs.

According to Mason (1922), *T. curvicauda* females may lay 2 to 30 eggs during each oviposition. However, Rojas (1992) and Landolt & Reed (1990) reported that on average each female laid 5.4 and 29 eggs, respectively. This indicates that for females to lay their full egg-load, gravid 6-d-old females need to oviposit more than three times a day. According to Landolt and Hendrichs (1983), females may oviposite from 1 to 13 times each. Under laboratory conditions, gravid females may oviposit more than three times in a day



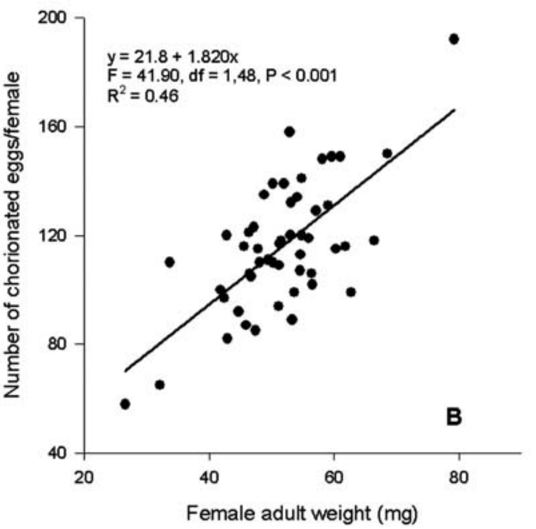


Fig. 3. Relationship between (A) pupal weight and number of chorionated eggs and (B) female adult weight and number of chorionated eggs in *T. curvicauda*.

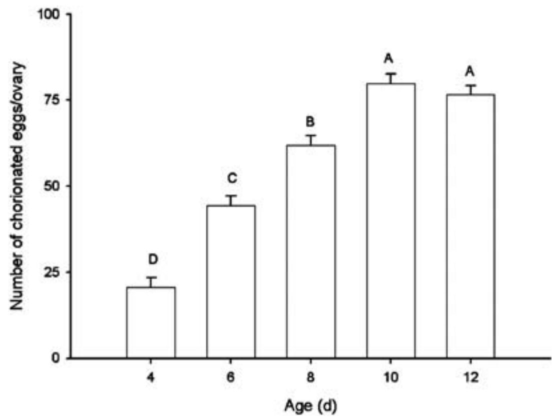


Fig. 4. Mean (± standard error) number of chorionated eggs per ovary of *T. curvicauda* females of different ages. Bars topped with the same letter are not significantly different (LSM; $P = 0.05$).

(A. Jiménez-Pérez, personal observation). This suggests that females may find at least three suitable oviposition substrates daily indicating its importance as a pest.

Knab & Yothers (1914) failed to find immature eggs in mature females and indicated that the oviposition period should be short. However, our observations indicate that mature and immature eggs coexist within the ovary, as indicated by Williamson (1989) for most tephritid species.

A precopulatory period has important implications for populations. It increases pre-reproductive mortality and decreases population growth. A female biased sex ratio may be a mechanism to diminish the effects of pre-reproductive female mortality. Puparial weight can be an additional factor used to assess the number of chorionated eggs. Our results will aid us in planning future research programs on *T. curvicauda*.

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