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FECUNDITY AND MATING PROPENSITY OF *TOXOTRYPANA CURVICAUDA* (DIPTERA: TEPHRITIDAE) ON AN ALTERNATIVE HOST, *JACARATIA MEXICANA* (CARICACEAE)

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ABSTRACT

Adult reproductive biology, including fecundity and mating propensity, may be affected by larval host for insects such as the papaya fruit fly, *Toxotrypana curvicauda* that do not require protein to produce eggs. Although the reproductive biology of papaya fruit flies that were reared on papaya fruit *Carica papaya* L. is known, little is known of flies that develop on alternate host fruit such as *Jacaratia mexicana* (Caricaceae). Therefore, uninfested *J. mexicana* fruit were collected from the field and infested by exposing them to oviposition in the laboratory by papaya fruit flies that were obtained from field-infested papaya. Puparia of females were longer then puparia of males, but there was no difference in either puparial width or weight. Females 6 d old produced 26 eggs/ovary. There was a positive linear relationship between puparial weight and number of chorionated eggs in mature females (6-8 d old), but puparial weight was not correlated with adult longevity. Females produced 2.99 eggs per mg of weight of puparium. Adult females were larger and heavier than adult males. Papaya fruit flies reared on *J. mexicana* are smaller, lighter, and have fewer eggs than reported for flies reared on *C. papaya*.

Key Words: chorionated eggs, *bonete*, *cuaguayote*, puparia weight, mating propensity

RESUMEN

La biología reproductiva, incluyendo fecundidad y propensión al apareamiento puede ser afectada por el alimento de la larva como en la Mosca de la Fruta de la Papaya (MFP), *Toxotrypana curvicauda*, que no requiere alimentarse de proteínas para producir huevos. A pesar de que se conoce la biología reproductiva de esta mosca criada en papaya, poco se sabe de ella en hospederos alternantes como *Jacaratia mexicana* (Caricaceae). Por lo tanto, frutos no infestados de *J. mexicana* fueron colectados en el campo, y fueron infestados (ovipositados) exponiéndolos en el laboratorio a MFP que se obtuvieron de frutos de papaya. Las pupas que dieron origen a machos fueron mas largas que las dieron origen a hembras, pero tuvieron similar ancho y peso. Hay una relación directa y positiva entre el peso de la pupa y el número de huevecillos corionados presentes en hembras sexualmente maduras (6-8 días de edad), sin embargo, el peso de la pupa no correlaciona con la longevidad del adulto. Hembras de 6 días de edad presentan 24 huevos por ovario, y producen 2.99 huevos por cada mg de peso de la pupa. Las moscas obtenidas de *J. mexicana* son mas pequeñas, ligeras y producen menos huevos que las obtenidas de *C. papaya*.

Translation provided by the authors.

The papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker, is a widely distributed pest of papaya *Carica papaya* L. (Baker et al. 1944; Aluja et al. 1994) in subtropical and tropical America (Eskafi & Cunninghan 1987; O'Doherty & Link 1993). Due to its economic importance, researchers have focused on the biology of *T. curvicauda* on papaya (Knap & Yothers 1914; Baker et al. 1944; Mason 1922; Landolt 1984; Chuman et al. 1987; Aluja et al. 1997a, 1997b). Little is known of its biology on alternative hosts. Castrejón (1987) reported another Caricaceae, *Jacaratia mexicana* (A. DC.) (= *Pileus mexicanus* Johnston; *Leucopremna mexicana* Standley) as a *T. curvicauda* host. In addition, *Gonolobus erianthus* Decne (Baker et al. 1944), *G. sorodius* Gray (Castrejón & Camino 1991), *G. niger* (Cav.) R. Br. (Leyva-Vásquez 1992), and *Morrenia odorata* Lindl. (Landolt 1994), all in the Asclepiadaceae, are reported hosts of this fly. All known hosts of *T. curvicauda* produce latex and, except for the commercially grown papaya, are not domesticated.

*Jacaratia mexicana (*bonete or cuaguayote*)* is a dioecious tree reaching 5-12 m in height. The fruit (13-18 cm long) is a hard, green, pendent, 5-locular berry, which becomes yellowish and soft when ripe. The fruit is edible, but less so than papaya. Latex is present in the fruit and other parts of the plant. In Morelos, Mexico, *J. mexicana* fruit is present from Feb to Jun (McVaugh 2001).

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Information about the biology of *T. curvicauda* on alternative hosts may provide insight into the phylogenetic relationship between the fly and its host plants. Additionally, information on reproductive behavior and reproductive potential of *T. curvicauda* from alternative hosts is needed to design IPM programs for this pest species. This paper is the first report on the reproductive biology of *T. curvicauda* reared on *J. mexicana*.

Materials and Methods

Insects

Insects were field-collected by methods described previously (Jiménez-Pérez & Villa-Ayala 2006). Larval-infested papayas were obtained from a pesticide-free plantation located on the Centro de Desarrollo de Productos Bióticos (CEPROBI) grounds at Yautepec, Morelos, Mexico. Aluja et al. (1997a) provides detailed information on native vegetation and climate of CEPROBI. Mature larvae were placed in pupation chambers (plastic cylindrical containers, 11 cm high × 8.5 cm diameter) covered with a fine mesh and containing a layer (6 cm) of sterile soil. Chambers were watered as necessary to keep soil moist. Newly emerged adults were separated by sex and placed in single-sex adult chambers (transparent acrylic box, 25 cm^3) covered with a fine mesh. Sugar and water were provided *ad libitum* (Sharp & Landolt 1984).

Jacaratia mexicana Fruits

Fruits of *J. mexicana* were collected early in the morning. Infested fruits are soft at touch and present coagulated latex and exudations. Only uninfested fruits were used for laboratory infestation. They were weighted with an Ohaus electronic scale (Explorer, 0.0001 g accuracy, Nikon Switzerland). Fruit length was measured with a plastic ruler; fruit width was measured with an electronic digital caliper (Truper, 0-150 mm, 0.01 mm precision).

Laboratory Infestation Test

Virgin adults were reared from papaya and were allowed to mate when sexually mature (6 d old) (Landolt, 1984). After mating, 2 females and 2 males were introduced into adult chambers provisioned with a *J. mexicana* fruit as an oviposition substrate, and they were allowed to oviposit over a 3-d time period. Infested fruit was incubated at 50-60 R.H. and 27 ± 2°C. Mature larvae were collected after they exited from the fruit and were placed in pupation chambers. After 1 week, puparial weight, length, and width were recorded (Jiménez-Pérez & Villa-Ayala 2006). Adults were sexed and weighed on the day of emergence (0 d), and longevity was recorded. After measurements were taken, puparia and adults were maintained individually in plastic containers (9 cm x 3.5 cm diameter) covered by fine mesh secured by a rubber band. Adults were fed water and sugar *ad libitum* (Sharp & Landolt 1984). Laboratory infestation tests were conducted in Apr to May 2004, Feb to Apr 2005, and Mar to May 2006.

Female Fecundity and Mating Propensity

The number of chorionated eggs per adult female was determined by dissection with methods reported previously (Jiménez-Pérez & Villa-Ayala 2006). Briefly, maturation of the ovary was assessed, eggs were stained, and number of chorionated (mature) eggs was recorded. The relationship between puparial weight and the number of chorionated eggs was determined from dissections of 40 mature females (6-8 d old). To determine the relationship between egg load and chronological age, the number of mature eggs per ovary was determined for females that were 0, 2, 4, 6, and 8 d old. To test whether mating propensity was associated with female chronological age, females that were 0, 2, 4, 6 and 8 d old were placed with sexually mature males (6 to 13 d old) individually in plastic containers (9 cm × 3.5 cm diameter) and observed for 1 h. If mating occurred, it was recorded and mated individuals were discarded. If mating did not occur, then individuals were separated and retested every 2 d until mating was observed. Sample sizes were 26 to 38 pairs, depending upon insect availability. Mating tests were conducted between 2:00 pm to 4:00 pm, the time of peak mating activity (Aluja et al. 1997a).

Statistical Analysis

Mating propensity was analyzed by a G test (Sokal & Rohlf 1994) in Excel (McDonald 2008). Differences in male and female puparial weight, length, and width, as well as adult weight and longevity were determined with t tests (Proc TTEST, SAS Institute 1999). The relationship between number of chorionated eggs and female chronological age was analyzed by a one-way analysis of covariance (Proc GLM, ANCOVA) with puparial weight as a covariate. Significant ANCOVA was followed by a least squares means test ($P = 0.05$) for mean separation. Regression analysis (Proc Reg) was used to test the relationship between number of chorionated eggs per female and puparial weight; and between puparial weight and longevity, with separate analyses for females and males. Summary statistics are presented as mean ± standard error.

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RESULTS

Laboratory Infestation Test

Jacaratia mexicana fruits weighed 479 ± 29 g and were 23 ± 0.53 cm long and 7.1 ± 0.24 cm wide. A total of 745 puparia were obtained from 22 *J. mexicana* fruits (10.5 kg). Thus, there were 0.07 ± 0.008 papaya fruit fly puparia per gram of *J. mexicana*. There were no differences between female and male puparium weight, width, and adult longevity (Table 1). However, puparial and adult weights were greater for females than for males.

Female Fecundity and Mating Propensity

Chronological age of females affected mating propensity (G = 40.33, df = 4, P < 0.001). No newly emerged females (0 d) and few 2-d-old females mated, and mating propensity increased with increasing age (Fig. 1). Mating was observed for over 68% of the sexually mature (≥6 d old females). No chorionated eggs were present in females that were 0 or 2 d old, and these data were removed from subsequent analysis. Non-chorionated eggs were observed in females of all ages, and chronological age affected number of chorionated eggs (F = 81.06; df = 1, 56; P < 0.0001).

There was a linear and positive relationship between number of chorionated eggs per female and puparial weight. Females reared on *J. mexicana* produced 2.99 chorionated eggs per mg (Fig. 2). There is no relationship between puparium weight and adult longevity of either females (F = 0.95; df = 1,114; P > 0.05) or males (F = 0.73; df = 1,97; P > 0.05).

DISCUSSION

Food is considered a key determinant of fecundity in herbivorous insects. Those insects that do not acquire protein or do not feed as adults must obtain all their reserves during their larval stage. Adult female *T. curvicauda* do not require protein as adults to produce eggs (Landolt 1984). Aluja et al. (1997a) observed only 1 and 13 flies out of 1931 and 7230 flies, respectively, feeding in the surface of fruits. They did not observe this fly feeding on bird feces or other protein sources in the field, so the impact of protein feeding by adults on their reproductive biology may be negligible. Larvae of the fly feed on seeds, which are the most nutritious part of the fruit (Mason 1922; Peña et al. 1986) and not on the pulp as do other fruit flies. Host plant composition such as nitrogen, carbon, and other metabolites affects potential and achieved fecundity. This could lead to different reproductive strategies such as modification of eggs size or quantity according to larval host quality and availability (Awmack & Leather 2002).

Knap & Yothers (1914) reported that *T. curvicauda* females have approximately 100 eggs per female while Rojas (1992) reported 67.8 ovarioles and Jiménez-Pérez and Villa-Ayala (2006) reported that sexually mature females (6 d old) had approximately 44 eggs per female per ovary. In contrast, in this study, we found that 6-d-old females had 26 eggs per female per ovary, almost 50% fewer eggs than sexually mature females reared on papaya. However, reproductive potential (measured as number of eggs per female weight) of females reared on *J. mexicana* was greater than that for females reared on papaya (2.99 versus 1.82 eggs per gram, respectively; Jiménez-Pérez & Villa Ayala 2006).

Female reproductive potential has been associated to food quality in the tephritid *Neoceratitis cyanescens* (Bezzi). Females obtained from tomato (*Lycopersicum esculentum* Mill.) fruits (var. Jackal) have a higher weight and have more eggs than those obtained from plants considered its natural reservoirs, such as bugweed (*Solanum mauritianum* Scop) or black nightshade (*Solanun americanum* Mill.) (Brévault et al. 2008). Therefore, populations may build faster in tomato than in the other fruits. In the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), larval host quality determines reproductive capacity. For example, females reared on plum *Prunus americana* Marsh., orange *Citrus sinensis* (L.), and strawberry *Fragaria virginiana* Miller produced 1019.2, 833.3, and 494.5 of eggs/female, respectively, and net reproductive rate (Ro) was 167.1, 83.9, and 49.2 eggs, respectively, (Krainacker et al. 1987) indicating that *C. capitata* populations will increase faster in plum than in the other two hosts.

TABLE 1. AVERAGE (± STANDARD ERROR) PUPARIUM WEIGHT, LENGTH, WIDTH, AND ADULT WEIGHT AND LONGEVITY OF FEMALE (N = 179) AND MALE (N = 167) *TOXOTRYPANA CURVICAUDA* ON *JACARATIA MEXICANA*.

Variable	Females	Males	t	P
Puparium weight (mg)	47.4 ± 1.1	45.9 ± 1.1	0.96	>0.05
Puparium length (mm)	9.2 ± 0.1	8.9 ± 0.1	4.24	<0.001
Puparium width (mm)	2.3 ± 0.1	2.4 ± 0.1	0.94	>0.05
Adult weight (mg)	31.3 ± 0.7	28.7 ± 0.9	2.29	0.02
Longevity (d)	18.8 ± 0.9	18.5 ± 0.8	0.19	>0.05

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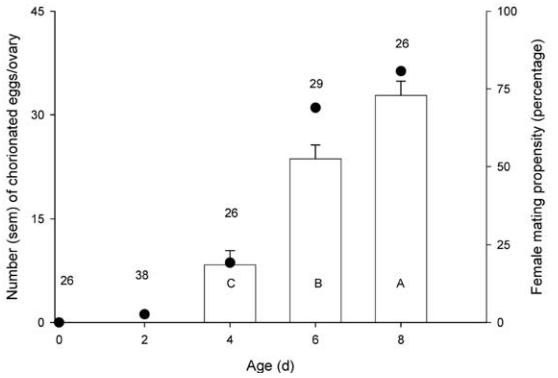


Fig. 1. Number (mean ± standard error) of chorionated eggs per ovary (open bars) and mating propensity (%, solid dots) of *Toxotrypana curvicauda* females. Bars with the same letter are not significantly different (P = 0.05). The sample size for female mating propensity is given above the solid dot for each female age.

Landolt (1984) reported 71% mating for 6-d-old *T. curvicauda* females, which is similar to the percentage we found in this study. Landolt (1984) considered d 1 when females were from 6 to 30 h old, which we defined in our study as d 0. However, while Landolt (1984) reports 15, 60, and 71% mating for 4-, 5- and 6-d-old females, whereas our results show 22, 72, and 82% for 4-, 6- and 8-d-old females, suggesting that females from *J. mexicana* tend to mate earlier than females from papaya. Adult females were heavier than males; however, longevity was similar for both sexes, indicating that being heavier or larger does not confer greater longevity. A similar situation was reported for insects reared on papaya (Jiménez-Pérez & Villa-Ayala 2006).

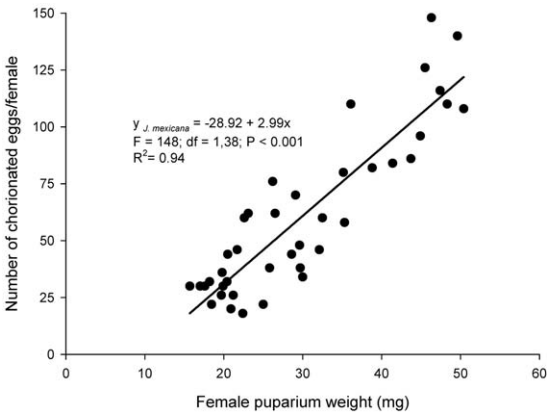


Fig. 2. Relationship between female puparial weight (mg) and the number of chorionated eggs found in ovaries of mature *Toxotrypana curvicauda* females (6-8 d) reared on *Jacaratia mexicana*.

Our results were obtained from laboratory-infested fruits and may not accurately reflect insect attributes of flies obtained from field-infested *Jacaratia mexicana*. Additional studies on reproductive biology of adults obtained from natural infestations are needed. However, this study is the first report of the biology of this species on this host. Information on reproductive potential of this species in an alternative host is relevant when planning control strategies.

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