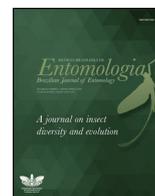




SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
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REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

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Biology, Ecology and Diversity

Biology of *Bactrocera carambolae* (Diptera: Tephritidae) on four hosts

Alison Pureza Castilho^a, Joel Pasinato^b, Jhulie Emille Veloso dos Santos^c,
Analia e Silva da Costa^c, Dori Edson Nava^d, Cristiane Ramos de Jesus^e, Ricardo Adaime  a, e, *



^a Universidade Federal do Amapá, Programa de Pós-graduação da Rede Bionorte, Macapá, AP, Brazil

^b Universidade Federal do Rio Grande do Sul, Programa de Pós-graduação em Fitotecnia, Porto Alegre, RS, Brazil

^c Faculdade de Macapá, Macapá, AP, Brazil

^d Embrapa Clima Temperado, Pelotas, RS, Brazil

^e Embrapa Amapá, Macapá, AP, Brazil

ARTICLE INFO

Article history:

Received 8 March 2019

Accepted 6 September 2019

Available online 17 October 2019

Associate Editor: Leonardo Barbosa

Keywords:

Carambola fruit fly

Fruit flies

Insect

Quarantine pest

ABSTRACT

Bactrocera carambolae is a quarantine pest found in Brazil, restricted to the states of Amapá, Pará and Roraima. This fruit fly can potentially cause extensive socioeconomic and environmental damage in the country, if it disperse into areas where fruit is grown for exporting. The objective of this work was to study the biology of *B. carambolae* on fruits of *Averrhoa carambola* L. (Oxalidaceae), *Psidium guajava* L. (Myrtaceae), *Spondias mombin* L. (Anacardiaceae) and *Eugenia stipitata* McVaugh (Myrtaceae). The following parameters were investigated: duration of egg-larva, pupal, egg-adult, pre-oviposition, oviposition and post-oviposition periods, pupal weight and viability, sex ratio, fecundity, fertility and longevity. All parameters except pupal weight, oviposition and post-oviposition period, egg fertility and sex ratio were influenced by the host plant on which the larvae were reared. The carambola fruit fly completes its development on all those hosts studied here, with the highest fecundities on *A. carambola* and *P. guajava*.

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Introduction

Bactrocera carambolae Drew & Hancock (Diptera: Tephritidae), native to Asia, is an invading species in South America, where it was collected for the first time in 1975 in Paramaribo, Suriname. In Brazil, it was detected for the first time in 1996 in the municipality of Oiapoque, state of Amapá (Silva et al., 2004). *Bactrocera carambolae* is an important impediment to fruit exportation, due to the quarantine restrictions imposed by importing countries on regions where the pest is present (Godoy et al., 2011; Lemos et al., 2014; Ferreira and Rangel, 2015; Miranda and Adami, 2015). This species is currently classified as a quarantine pest present in Brazil, where it is distributed in the states of Amapá, Pará and Roraima and is under official control by the Ministry of Agriculture and Food Supply (Brasil, 2018).

Availability of information on the population dynamics and demography of this fruit fly, as well as range and preference for hosts, are essential for the establishment of control measures (Lemos et al., 2014). *Bactrocera carambolae* is a polyphagous fruit fly with 21 reported host plants in Brazil (Adaime et al., 2016). Despite

existing reports of *B. carambolae* on native plants of the Amazon region, including *Eugenia stipitata* McVaugh, *Pouteria macrophylla* (Lam.) Eyma and *Licania* sp., it should be noted that all reports occurred in environments altered by human activity (Lemos et al., 2014; Almeida et al., 2016). On the other hand, the considerable host range of this pest (Adaime et al., 2016) and their potential for adaptation to other regions of Brazil, such as the São Francisco Valley (Pessoa et al., 2016), put fruit growing at risk (Lima et al., 2018).

Among the reported hosts of *B. carambolae* in Brazil, we chose two primary hosts – carambola [*Averrhoa carambola* L. (Oxalidaceae)] and guava [*Psidium guajava* L. (Myrtaceae)] – and two alternative hosts – yellow mombin [*Spondias mombin* L. (Anacardiaceae)] and araza [*Eugenia stipitata* McVaugh (Myrtaceae)], as mentioned in the literature (Lemos et al., 2010, 2014; Adaime et al., 2016; Almeida et al., 2016; Brasil, 2018).

Averrhoa carambola is native to tropical Asia and its fruits can be consumed *in natura* or used to make juices and sweets (Cavalcante, 1996). Guava originated in tropical forests in Latin America and is particularly notable for the high nutritional value of its fruit, as well as the multiple forms in which it is used (Gonzaga Neto, 2001). In the Amazon, it grows along rural roads, near native vegetation, due to its ease seed dispersal (Cavalcante, 1996). Yellow mombin is found in the Atlantic Forest and Amazon in upland and floodplain

* Corresponding author.

E-mail: ricardo.adaime@embrapa.br (R. Adaime).

forest environments, and is also present in inhabited areas, albeit in a subsynchronous state. Its fruits are consumed *in natura* or processed into juices, ice creams and popsicles (Sacramento and Souza, 2009; Cavalcante, 2010). Araza is native to the Peruvian Amazon, where it is widely found across practically the entire region (Pinedo et al., 1981). Its pulp is used in the preparation of juices, preserves, creams, jams and sweets, but is rarely consumed *in natura* due to its acidity (Falcão et al., 1988; Cavalcante, 1991).

Despite the undeniable importance of *B. carambolae* to the Brazilian fruit industry, no studies have yet been conducted to investigate its biology on multiple hosts. In light of this, our study aimed to determine the biological parameters of *B. carambolae* on fruits of four plant species under laboratory conditions.

Material and methods

The experiment was conducted in the Plant Protection Laboratory at Embrapa Amapá, where a colony of *B. carambolae* was established in 2013, from guava fruits collected in the state of Amapá. All procedures used for rearing are described in Bariani et al. (2016) and summarized below. Larvae were fed on an artificial diet containing sugarcane bagasse, soybean flour, sodium benzoate, sanding sugar, yeast extract, citric acid, Nipagin and distilled water, and were maintained in a climate-controlled room ($28 \pm 1^\circ\text{C}$; $80 \pm 10\%$ R.H.; no photophase). The puparia obtained were placed in plastic bottles (500 mL) containing vermiculite and kept in a climate-controlled chamber ($26 \pm 1^\circ\text{C}$; 12-h photophase) until adult emergence. The adults were kept in rearing cages in a climate-controlled room ($26 \pm 2^\circ\text{C}$; $70 \pm 10\%$ R.H. and 12-h photophase), and their diet was composed of Bionis® YE MF yeast extract and refined sugar (1:3 ratio), placed on cotton in Petri dishes (5 cm diameter). Water was offered by capillarity, through a 'sponge cloth' (Esfrebom®, manufactured by Bettanin Industrial S.A., Esteio, Rio Grande do Sul, Brazil).

Infestation of fruits

When the adult flies had reached the age of 25–30 days, cages were set up for infestation of fruits of the four host plant species targeted in this study, as follows:

Psidium guajava: two cages were set up (45 cm length \times 30 cm width \times 35 cm height), each containing 50 "green-ripe" fruits and 100 couples of *B. carambolae*. The fruits had a mean weight of 196.46 ± 3.85 g and were obtained in a supermarket in the city of Macapá, vacuum-packed and confirmed to be free of infestation by fruit flies.

Averrhoa carambola: two cages were set up (45 \times 30 \times 35 cm), each containing 50 "green-ripe" fruits and 100 couples of *B. carambolae*. The fruits had a mean weight of 114.70 ± 5.96 g and were obtained at the Experimental Field for the Cerrado at Embrapa Amapá, located in the rural area of Macapá.

Spondias mombin: one cage was set up (45 \times 30 \times 35 cm), containing 135 "green-ripe" fruits and 200 couples of *B. carambolae*. The fruits had a mean weight of 15.86 ± 0.27 g and were obtained from an agricultural property in the city of Porto Grande.

Eugenia stipitata: 30 cages were set up (20 \times 12 \times 12 cm), each containing one "green" fruit and 10 couples of *B. carambolae*. The fruits had a mean weight of 147.0 ± 8.9 g and were obtained from a small domestic orchard in the urban area of Macapá.

In the case of *A. carambola*, *S. mombin* and *E. stipitata*, the fruits were wrapped in fine mesh fabric at the early stage of development, to avoid infestation by fruit flies. To ensure separation between the fruits and the fabric, plastic garbage bins vented at the bottom were used, forming a cage.

Determination of biological parameters of *B. carambolae*

At the end of the period established for oviposition (48 h), the fruits were removed from the cages and individually placed on a thin layer of sterilized vermiculite in clear plastic containers (8–15 cm diameter, depending on fruit size) covered with organza fabric and a vented lid, under controlled conditions ($26 \pm 2^\circ\text{C}$; $70 \pm 10\%$ R.H. and 12-h photophase). After five days, the vermiculite in each container was examined and any puparia were removed and transferred to plastic vials containing moistened vermiculite. This procedure was repeated daily until disposal of the fruits (approximately 20 to 30 days). The puparia obtained were placed in a climate-controlled chamber ($26 \pm 2^\circ\text{C}$; $70 \pm 10\%$ R.H. and 12-h photophase) until adult emergence. The following parameters were assessed: duration of egg-larva period (days), pupal stage (days) and egg-adult period (days), pupal viability (%), sex ratio (number of females/total number of adults) and pupal weight.

From the adults that emerged, individual couples reared on each host plant were placed in plastic cages (20 \times 12 \times 12 cm) with food and water *ad libitum*. Exactly 25 couples were formed for *A. carambola* and *P. guajava*, 20 for *E. stipitata* and 18 for *S. mombin*. Artificial oviposition devices were placed in each cage, each device containing a fine layer of pulp from the fruit of the corresponding species (see details in Bariani et al., 2016). To ensure the availability of pulp during the experiment, pulp from the fruits of the four plant species was extracted and frozen. The cages were inspected on a daily basis, at which time the number of dead adults and number of eggs in the artificial oviposition devices were counted. The following parameters were determined: daily fecundity (number of eggs/female/day), total fecundity (number of eggs/female during lifetime), pre-oviposition period (days from emergence of female to laying of first egg), oviposition period (days from first to last oviposition), post-oviposition period (days from last egg laid to death of female) and longevity of males and females (period of time from emergence to death of individual). Fertility was assessed by analyzing ovipositions made when couples were approximately 30 days old, the age of peak oviposition for *B. carambolae* reported by Jesus-Barros et al. (2017). Eggs were placed on filter paper in 5 cm Petri dishes containing plant-based sponge material, moistened and kept in a climate-controlled environment ($26 \pm 1^\circ\text{C}$; $80 \pm 10\%$ R. H.; no photophase). The number of eclosed larvae was counted daily.

Data analysis

All data were verified for normality using the Shapiro Wilk test; for homoscedasticity using the Bartlett test; and for independence of residuals through graphical analysis. Box cox transformation was applied to pupal weight and fecundity. Pupal weight, periods of pre-oviposition, oviposition and post-oviposition, fecundity and fertility data were submitted to variance analysis ($p \leq 0.05$) and, in cases of statistical significance, the effects of the hosts were compared by Tukey test ($p \leq 0.05$). Data of duration of egg-larva period, pupal stage and egg-adult did not meet parametric assumptions and were submitted to Kruskal-Wallis ($p \leq 0.05$) and means were compared by Dunn test ($p \leq 0.05$), in cases of statistical significance. Sex ratio was compared using chi-square testing (χ^2) ($p \leq 0.05$). Longevity of females and males was analyzed through survival curves using the Kaplan-Meier estimator, compared by log-rank testing. To analyze pupal viability, arcsine transformation was applied to the data and the means were compared by Tukey testing at 5% probability, as described by Pimentel-Gomes and Garcia (2002). All data analyses were conducted using the R software package (R Development Core Team, 2015).

Table 1
Mean \pm standard deviation and interval of variation of biological parameters of *Bactrocera carambolae* reared on fruits of carambola (*Averrhoa carambola*), guava (*Psidium guajava*), yellow mombin (*Spondias mombin*) and araza (*Eugenia stipitata*).

Biological parameters	Hosts			
	<i>Averrhoa carambola</i>	<i>Psidium guajava</i>	<i>Spondias mombin</i>	<i>Eugenia stipitata</i>
Duration of egg-larva period ^a (days)	16.00 \pm 3.30 b (9–28)	15.44 \pm 2.47 c (11–23)	14.10 \pm 0.95 d (10–15)	16.72 \pm 2.42 a (12–28)
Duration of pupal stage ^a (days)	9.79 \pm 1.73 c (4–16)	10.07 \pm 0.73 b (6–13)	11.04 \pm 4.03 a (9–14)	9.81 \pm 1.60 bc (5–12)
Duration of egg-adult period ^a (days)	25.79 \pm 2.37 b (19–32)	25.69 \pm 2.38 b (21–33)	24.10 \pm 0.95 c (20–27)	26.44 \pm 1.82 a (22–30)
Pupal weight ^c (mg)	8.16 \pm 1.79 (5–12)	12.24 \pm 2.47 (8–19)	8.76 \pm 4.03 (4–24)	10.24 \pm 3.58 (5–22)
Pupal viability ^a (%)	56.40 a	57.74 a	37.31 b	40.64 b
Sex ratio ^c	0.54	0.48	0.46	0.60
Duration of pre-oviposition period ^b (days)	28.88 \pm 11.90 a (20–56)	15.20 \pm 8.09 b (9–38)	17.53 \pm 8.26 b (9–42)	21.56 \pm 9.19 ab (12–43)
Duration of oviposition period ^c (days)	47.37 \pm 36.41 (1–119)	39.45 \pm 26.41 (2–107)	63.73 \pm 42.72 (2–144)	45.37 \pm 34.18 (1–102)
Duration of post-oviposition period ^c (days)	15.89 \pm 16.05 (0–46)	13.05 \pm 14.61 (0–49)	13.87 \pm 18.52 (0–51)	16.50 \pm 15.65 (0–47)
Fecundity ^b (No. of eggs)	502.95 \pm 436.88 ab (18–1439)	774.80 \pm 546.72 a (55–2057)	293.93 \pm 311.42 b (6–1097)	176.94 \pm 190.47 b (16–575)
Fertility ^c (%)	38.02 \pm 27.89 (6.67–93.75)	33.52 \pm 28.13 (0–100)	50.51 \pm 31.93 (3.33–100)	43.09 \pm 16.75 (20.0–66.7)

^a Means followed by the same letter in the column did not differ by the Dunn test ($p \leq 0.05$).

^b Means followed by the same letter in the column did not differ by the Tukey test ($p \leq 0.05$).

^c Not significant.

Results

Egg-larva period differed among treatments ($\chi^2 = 155.3$, $df = 3$, $p = 0.001$), being longest for flies reared on *E. stipitata* (16.72 days) and shortest for those reared on *S. mombin* (14.10 days) (Table 1). Pupal stage duration was longer ($\chi^2 = 47.19$, $df = 3$, $p = 0.00012$) for flies reared on *S. mombin* (11.04 days) and shorter for those reared on *A. carambola* (9.79 days). A difference in egg-adult period was also observed ($\chi^2 = 3.97$, $df = 3$, $p = 0.2652$), with the longest period being shown by flies reared on *E. stipitata* (26.44 days) and the shortest by those reared on *S. mombin* (24.10 days); the periods recorded for flies reared on *A. carambola* (25.79 days) and *P. guajava* (25.69 days) were intermediary. There was no difference in pupal weight among treatments. ($F = 0.54$, $df = 3$, $p = 0.464$).

Significant differences were observed in pupal viability on different hosts. Flies reared on *A. carambola* and *P. guajava* were more viable than those reared on *S. mombin* and *E. stipitata* (Table 1). No significant difference in sex ratio was observed ($\chi^2 = 1.9567$, $df = 3$, $p = 0.1024$), with observed ratios ranging from 0.46 (*S. mombin*) to 0.60 (*E. stipitata*).

The pre-oviposition period was longer ($F_{3,66} = 7.40$, $p = 0.00023$) for flies reared on *A. carambola* (28.88 days) in comparison to *S. mombin* (17.53 days) and *P. guajava* (15.20 days), but flies reared on *E. stipitata* (21.56 days) did not differ from other treatments (Table 1). No significant difference was observed in the oviposition period ($F_{3,66} = 1.45$, $p = 0.2358$) and post-oviposition period ($F_{3,66} = 0.18$, $p = 0.9071$). Oviposition periods ranged from 39.45 days (*P. guajava*) to 63.73 days (*S. mombin*), and post-oviposition periods ranged from 13.05 days (*P. guajava*) to 16.50 days (*E. stipitata*).

Fecundity was influenced by the host plants used for larval development ($F = 11.07$, $df = 3$, $p = 0.0014$), with the highest number of eggs/female being observed for flies reared on *P. guajava* (774.80 eggs) and the lowest for those reared on *S. mombin* (293.93 eggs) and *E. stipitata* (176.94 eggs) (Table 1). For females reared on *P. guajava*, the rate of oviposition was more strongly concentrated in the first 40 days of life, whereas oviposition by females reared on other hosts was more evenly distributed over time (Fig. 1).

As regards mean longevity of females, a significant difference was only observed for flies reared on *P. guajava* when compared to

A. carambola and *S. mombin* (Fig. 2). Overall, female survival varied among the four hosts, with the shortest survival period being observed for females reared on *P. guajava* and the longest for *S. mombin* (Fig. 2). A statistical difference was found in mean longevity of males reared on different hosts (Fig. 3). Longevity of males reared on *S. mombin* was equal to that of those reared on *A. carambola*, but higher than the longevity of males reared on *P. guajava* and *E. stipitata*. Males reared on *E. stipitata* had equal longevity to those reared on *P. guajava* and lower longevity than males reared on *A. carambola* and *S. mombin*.

There was no significant difference in fertility of eggs ($F_{3,41} = 3.11$, $p = 0.0367$) produced by females whose larvae were reared on different host plants, despite an observed fertility range of 33.52% for *P. guajava* to 50.51% for *S. mombin* (Table 1).

Discussion

The differences detected in duration of egg-larva, pupal and egg-adult periods among different host plants may be associated with the nutritional quality of their fruit. Some hosts may have provided resources for larval development in amounts that were adequate and sufficient for completion of the biological cycle in less time. Fruit size may also have interfered in the duration of biological parameters, as larval development could be accelerated by the lower food availability provided by smaller fruits, as observed for *S. mombin*, whose fruit had a mean weight of 15.86 g, nine times less than *E. stipitata* (147.0 g). Bariani et al. (2016) described rearing techniques for *B. carambolae* in the laboratory and reported that the time needed for egg-adult development is 22.5 days when larvae are reared on guava fruits and 19.5 days for larvae fed an artificial diet, durations that are shorter than those reported here. This indicates that artificial larval diets tend to be more nutritionally adequate for *B. carambolae*.

In Brazil, the existing studies on *B. carambolae* biology are recent. Jesus-Barros et al. (2017) studied the fecundity and longevity of females of *B. carambolae* in the laboratory, fed an artificial diet at the larval stage (brewer's yeast, soybean flour, sanding sugar, Nipagin, citric acid, sodium benzoate, ground and dried sugarcane bagasse, and distilled water) and in adulthood (same diet used in our present study). Pre-oviposition and oviposition periods were

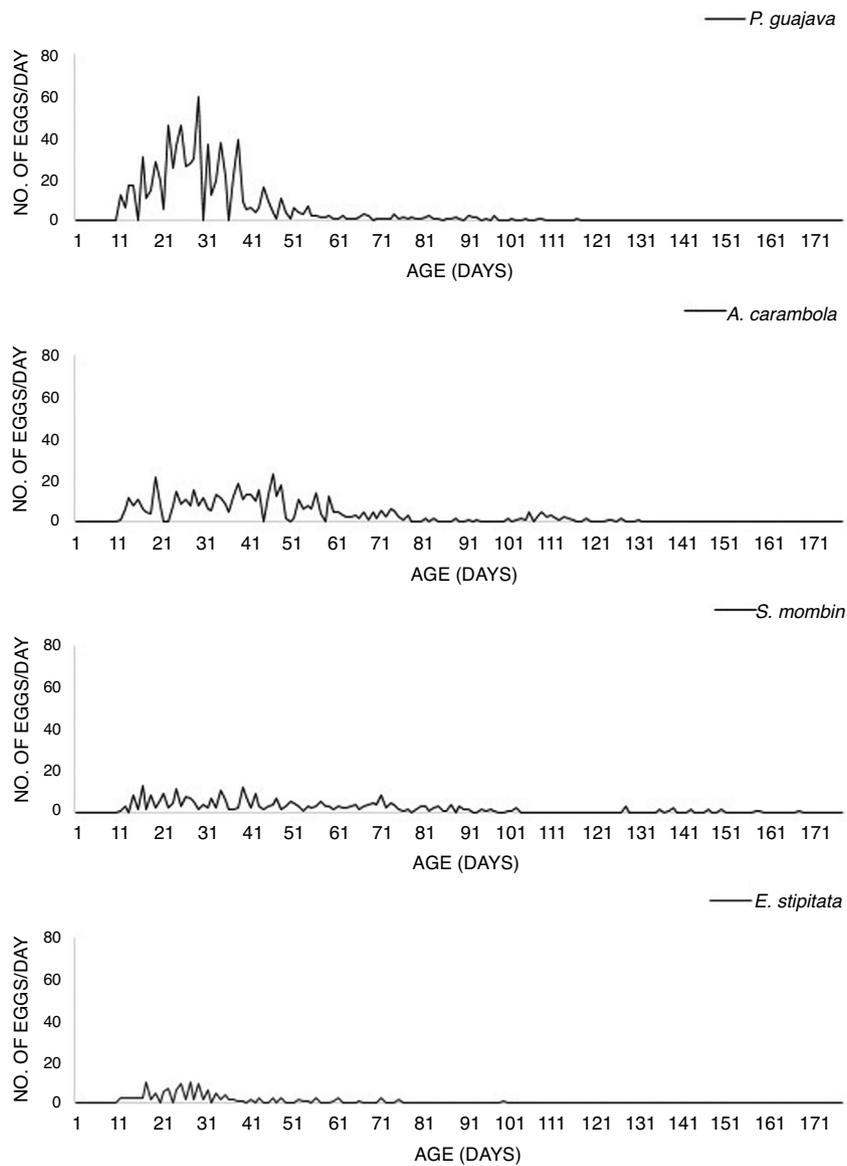


Fig. 1. Daily rate of oviposition of *Bactrocera carambolae* reared on fruits of carambola (*Averrhoa carambola*), araza (*Eugenia stipitata*), guava (*Psidium guajava*) and yellow mombin (*Spondias mombin*).

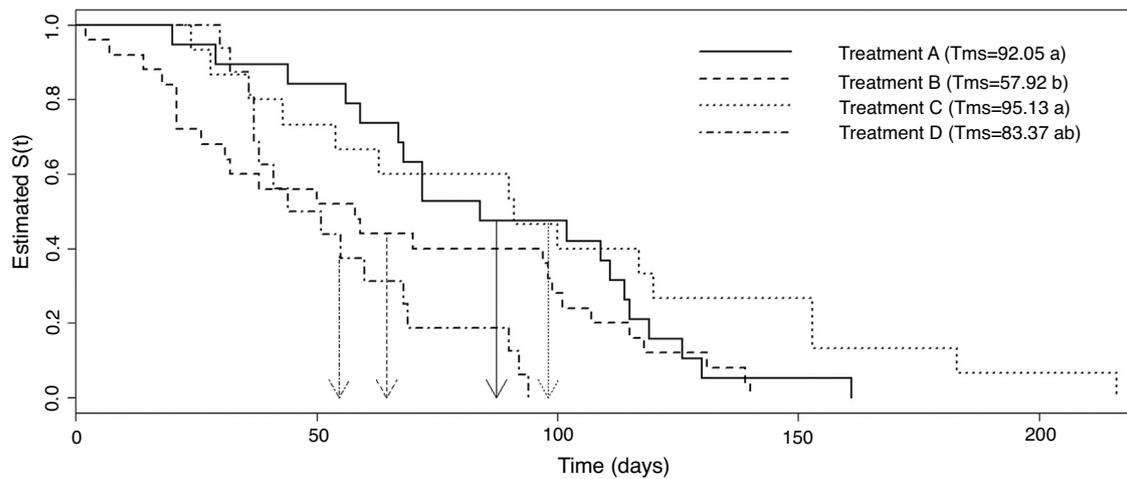


Fig. 2. Survival curve of females of *Bactrocera carambolae*: Treatment A (*Averrhoa carambola*), Treatment B (*Psidium guajava*), Treatment C (*Spondias mombin*) and Treatment D (*Eugenia stipitata*). The arrows indicate the mean survival time (Tms).

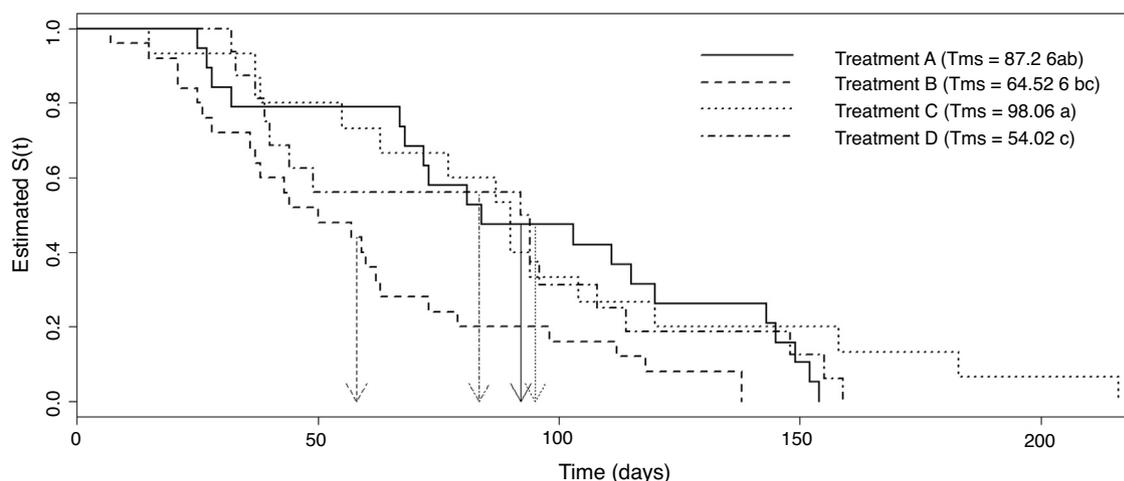


Fig. 3. Survival curve of males of *Bactrocera carambolae*: Treatment A (*Averrhoa carambola*), Treatment B (*Psidium guajava*), Treatment C (*Spondias mombin*) and Treatment D (*Eugenia stipitata*). The arrows indicate the mean survival time (Tms).

25.15 days and 62.73 days, respectively, and the mean longevity of females was 90.70 days. Fecundity varied over time, with peak oviposition on the 28th day and a mean of 1088.26 eggs per female. In a comparison of our work with Jesus-Barros et al. (2017), the only discrepant finding was fecundity. Considering that the adults were fed the same diet in both studies, we can assume that the fruits of the plant species used in this work were probably less nutritionally rich than an artificial diet, possibly interfering in the reproductive performance of the flies.

Pasinato et al. (2019) studied biological aspects of *B. carambolae* reared on table grape ('Italia' cultivar) and acerola, reporting longer egg-larva, pupal and egg-adult periods for flies reared on grape. In that study, diet type had no influence on pre-oviposition, oviposition and post-oviposition period durations. The number of eggs produced per female was higher on grape (1663) than on acerola and was higher than the values reported here, which ranged from 774.80 eggs (on *P. guajava*) to 176.94 eggs (on *E. stipitata*). Among the biological parameters assessed by Pasinato et al. (2019), the strongest discrepancy in relation to our findings here was fertility, which was 5.63% on grape and 12.47% on acerola, lower than the levels obtained in our study. The methodology was the same in both studies and so this parameter may have been influenced by the origin of the flies and aspects related to mating behavior.

The egg-adult periods reported here for flies reared on *A. carambola* and *P. guajava* are similar to those observed by Pasinato et al. (2019) on grape (25.8 days). For *Ceratitidis capitata* (Wiedemann), Krainacker et al. (1987) observed that nutritional quality of the fruit is the main factor affecting larval performance. In addition, studies have shown that nutritional quality may vary within a single fruit and this factor is most expressive at high levels of infestation, which leads to the ingestion of less nutritious parts of a fruit (Dukas et al., 2001).

Pupal viability was higher for insects reared on carambola and guava, however, this parameter can also be influenced by external factors related to the environment, such as humidity, as observed by Zart (2008).

Individuals reared on *A. carambola* exhibited longer pre-oviposition periods than those reared on *S. mombin* and *P. guajava*. This difference may be related to various factors, including maturation of sexual organs, which requires the ingestion of a protein source, as female tephritids are synovigenic and therefore require a protein-rich diet to promote oocyte maturation over the course of their lives (Tsiropoulos, 1983; Zucoloto, 2000).

The pre-oviposition period duration recorded here for *B. carambolae* appears to be similar to that of other species in the same group. Females of *B. carambolae* obtained from carambola, grape and acerola plants and maintained under the same laboratory conditions also exhibited long pre-oviposition and oviposition periods (Jesus-Barros et al., 2017; Pasinato et al., 2019), supporting the results obtained in this study.

The oviposition pattern observed in this work is similar to that reported by Jesus-Barros et al. (2017) and by Pasinato et al. (2019) for this same species, indicating that the long oviposition period of *B. carambolae* can expressively increase its damage in the field, and also gives it enough time to thoroughly exploit its ecological niche.

According to Godoy et al. (2011) and Malavasi et al. (2013), females of *B. carambolae* can lay 1000–3000 eggs over their lifetime in the laboratory, and from 1200 to 1500 under field conditions. The mean fecundity of females in this study was lower than the levels described for the species, but nevertheless followed the same pattern of producing an elevated number of eggs. Considering that artificial substrates containing fruit pulp were used for oviposition, the results suggest that guava is more attractive to *B. carambolae*. For Tephritidae, Broufas et al. (2009) reported that host quality affects the dynamics of oviposition and ovarian maturation.

The high longevity observed in this study for flies reared on all the studied hosts (Fig. 2) suggests that the carambola fruit fly is able to survive for long periods, during which it can not only cause damage, but also leave a great number of descendants. Our results are supported by Jesus-Barros et al. (2017), who reported survival up to 150 days for females of *B. carambolae*, and by Pasinato et al. (2019), who observed longevities of up to 200 and 127 days for this species when reared on acerola and grape, respectively.

This work has shown that *Bactrocera carambolae* completes its development on all four of the investigated hosts (*Psidium guajava*, *Averrhoa carambola*, *Spondias mombin* and *Eugenia stipitata*), confirming the results published by Adaime et al. (2016). Also, our results show that these fruits are suitable for the development of *B. carambolae*, contributing to the maintenance and growth of populations of this pest species.

Further studies of this nature need to be carried out in order to broaden the knowledge of the carambola fruit fly biology and ecology. Additionally, results such as those obtained in our work are useful for directing actions to combat this important quarantine pest.

Authors' contribution

APC, RA, DEN, and CRJ conceived and designed the experiments and wrote the manuscript; APC, JP, JEVS, and ASC performed field and laboratory work and reviewed the manuscript.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

To the Brazilian Federal Agency for the Support and Evaluation of Graduate Education (CAPES) for the Master's Degree Scholarship granted to Alison Pureza Castilho, and to the National Council for Scientific and Technological Development – CNPq, for the Research Productivity Fellowship granted to Ricardo Adaide. To Alexandra Peter Krüger, M.Sc., and Tiago Scheuemmann, M.Sc., for assistance with statistical analysis. To technical assistant Jacivaldo Barbosa da Costa for support during field and laboratory work. To the Ministry of Agriculture and Food Supply for authorizing publication of data pertaining to the carambola fruit fly, as provided in Normative Rule No. 52/2007.

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