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# Oviposition Activity of an Invasive Fruit Fly Species at Different Densities in Laboratory

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## ABSTRACT

The carambola fruit fly (CFF) (*Bactrocera carambolae* Drew & Hancock) is one of the most harmful pests of fruit production. It is an exotic species in Brazil, restricted to the northern region (Amapá, Pará, and Roraima States), and a threat to the national fruit production and exportation. The oviposition activity of this pest is not well known, imposing barriers to understanding its host attack in the field. We aimed to evaluate the daily pattern of oviposition in *B. carambolae* and compare the number of eggs at different female densities (one couple, five couples, and 15 couples) from 07:30 a.m. to 5:30 p.m. We also compared their oviposition depth on different substrates (guava and an artificial substrate). Data were analyzed using a generalized linear mixed model (GLMM) on the software RStudio. Our results showed that *B. carambolae* exhibits a distinct pattern of oviposition activity at different densities during the day, with no preferential oviposition period at higher density. However, increasing density did not affect the number of eggs laid per female during the day. We did not find a significant difference when comparing the oviposition depth of CFF on a guava piece and an artificial device. Our results improve knowledge about the oviposition activity of *B. carambolae* and suggest that its species adopt oviposition strategies to ensure their offspring.

## 1 | Introduction

*Bactrocera carambolae* Drew & Hancock, 1994, known as carambola fruit fly (CFF), is a polyphagous tephritid pest belonging to the family Tephritidae. This species is native to Southeast Asia occurring in India, Indonesia, Malaysia, Sri Lanka, Thailand, and Vietnam and is an invasive species in Suriname, French Guiana, and Brazil (CABI 2021). Commonly associated with its preferential host fruit, star fruit (*Averrhoa carambola* L., Oxalidaceae) (Sauers-Muller 2005; Castilho et al. 2020), *B. carambolae* also attacks other hosts, such as mango (*Mangifera indica* L., Anacardiaceae) and guava (*Psidium guajava* L., Myrtaceae) (Lemos et al. 2014; Koswanudin et al. 2018; Castilho et al. 2020; Adaime et al. 2023). In Brazil, *B. carambolae* is officially a quarantine pest in the country's North region, restricted to the states of Amapá, Pará, and Roraima (Soares et al. 2023). So far, in this country, *B. carambolae* attacks 35 host plant species belonging to 14 families; the most frequently infested are star fruit, guava, *Syzygium malaccense* L. ([Merr. & L. M. Perry]., Myrtaceae), and *Malpighia emarginata* DC., Malpighiaceae (Adaime et al. 2023; Costa, Sousa, Jesus, et al. 2023; Costa, Sousa, de Souza-Filho, et al. 2023; Costa et al. 2024; Lemos et al. 2024). Although the number of new hosts of CFF has been well described, the oviposition behavior and daily pattern of oviposition on host fruits in the field are still unclear.

The fruit fly's oviposition behavior is critical to understanding its infestation pattern in noncommercial and commercial hosts (Li et al. 2024). This behavior is influenced by environmental, biological, chemical responses, and nutritional sources (Joachim-Bravo et al. 2001; Akol et al. 2013; Liendo et al. 2020; Cortés-Martínez et al. 2021; Yee 2021; Li et al. 2024). For instance, daylight positively influences the oviposition behavior of fruit flies (Guillén et al. 2022), which may exhibit a preference to lay their eggs during the morning (Flitters 1964; Aluja et al. 1997; Raghu et al. 2002, 2004; Brévault and Quilici 2007; Galvão-Silva et al. 2023; Bayoumy and El-Metwally 2017). In addition to environmental conditions, natural barriers of the host fruit, such as morphology and chemical compounds, also influence the oviposition of Tephritidae fruit flies (Dias, Ongaratto, et al. 2017; Nor et al. 2018). Dias, Ongaratto, et al. (2017) assessed the oviposition deepness of two fruit flies. They observed that the success of the oviposition depends on its relationship with the host and fruit characteristics such as peel thickness, pH, and soluble solids. The authors found that the presence of benzyl isothiocyanate (BITC) on papaya (*Carica papaya* L. [Caricaceae]) affects the deepness of aculeus insertion of *Ceratitis capitata* (Wiedemann, 1824) on the fruit. In the same study, the peel thickness of mangoes (in mm) (0.19 ± 0.03) increased *Anastrepha fraterculus* (Wiedemann, 1830) depth of aculeus insertion on the fruit and oviposition success. On the other hand, two mango cultivars showed resistance against *Anastrepha ludens* (Loew, 1873) and *Anastrepha obliqua* (Macquart, 1835) infestation (Guillén et al. 2017). The authors found that beyond peel firmness and unknown chemical compounds, the resin ducts and sap in the exocarp offer resistance against these two species, suggesting that the resin is an essential component of mango resistance against both fruit flies.

The presence of conspecific females also influences the ovipositional activity of fruit flies, either by cross-recognition of infested fruits or by the stimulant effect of the presence of conspecific females in the oviposition site or environment (Prokopy and Fletcher 1987; Díaz-Fleischer and Aluja 2003; Davis et al. 2011; Liendo et al. 2020). According to Davis et al. (2011), the female–female interactions might reduce the choiceness of the oviposition site of *Rhagoletis juglandis* Cresson, 1920. To *A. ludens* and *Bactrocera tryoni* (Froggatt, 1897), the presence of a conspecific female stimulates its oviposition (Prokopy et al. 1999; Díaz-Fleischer and Aluja 2003).

The oviposition behavior of the invasive species, *B. carambolae*, is poorly known. Few studies have assessed parameters such as fecundity and clutch size (de Jesus Barros et al. 2017, 2018); however, the temporal pattern of oviposition, intraspecific interactions, and oviposition deepness of this species is not well known and may comprise its management in the field. Our study aimed to evaluate whether female density affects the daily oviposition pattern and number of eggs of *B. carambolae*. In addition, we compared the oviposition depth of *B. carambolae* in an artificial oviposition device and in pieces of guava. Similar to other invasive species, such as *C. capitata*, we hypothesized that *B. carambolae* does not have a preferred period of the day for laying its eggs, regardless of female density. However, as assumed by Díaz-Fleischer and Aluja (2003), and Prokopy et al. (1999) for *A. ludens* and *B. tryoni*, of which higher female density increases oviposition, we assume that the greater number of females would increase the number of eggs/female/day laid by *B. carambolae*.

## 2 | Materials and Methods

### 2.1 | Insect Collection and Maintenance

The *B. carambolae* individuals used in the present study belong to a laboratory population collected from infested guava in Macapá city (0°02′18.84″ N, 51°03′59.1″ E) and star fruits in Campo Experimental do Cerrado da Embrapa Amapá (00°23′14.31″ N, 51°02′44.45″ E). The colony was maintained at the Laboratory of Entomology at Embrapa Amapá (Macapá, Amapá, Brazil). For colony maintenance, guavas (maturation stage 2—light green) (Azzolini et al. 2004) were offered to sexually mature females (between 20 and 25 days old) for 24 h. The infested fruits were placed in plastic containers (11.6 cm × 8 cm) containing vermiculite. Ten days after the infestation (time to achieve the third instar larvae) (Bariani et al. 2016), the fruits were periodically checked until the collection of puparia. Next, the puparia were placed in small plastic containers (30 cm × 15 cm × 1.92 m) with vermiculite and covered with voil to allow oxygenation and their posterior emergence. To offer better conditions for pupae survival, they were kept in a room with controlled environmental conditions (Temp: 25°C ± 2°C; RH: 70% ± 10%). After the emergence, the adults were kept in plastic rearing cages (57.5 × 39.5 × 32 cm) with water and a diet based on yeast extract (Bionis) and sugar (1:3) (Silva Neto et al. 2012), and kept under controlled conditions (Temp: 25°C ± 2°C; RH: 70% ± 10%), and 12L:12D photoperiod.

### 2.2 | Experiment 1—Daily Oviposition Pattern in *B. carambolae*

To the first set of experiments, copulated adults of *B. carambolae* (25–26 days old) were captured and separated for tests of its daily oviposition pattern. Further, these adults were randomly separated into three groups: (1) 1 couple per cage, (2) 5 couples per cage, and (3) 15 couples per cage (adapted from Díaz-Fleischer and Aluja 2003). Only mated couples were used in this experiment, to ensure that females were fit for oviposition (Díaz-Fleischer and Aluja 2003). Further, males were kept inside the experiment cages, because they play an important role in female oviposition behavior (Li et al. 2024), possibly stimulating oviposition.

Each set of couples (one couple, five couples, and 15 couples) were placed into small plastic cages ([42 × 34 × 23 cm] = experimental unit), with diet (Bionis and sugar 1:3) and water ad libitum for oviposition tests. After 24 h of climatization and adaptation in the experimental cage, an artificial oviposition device (2.5 cm diameter and 1.6 cm thick) (agar-agar +25% artificial guava juice +75% distilled water and red food aniline) (adapted from Roriz

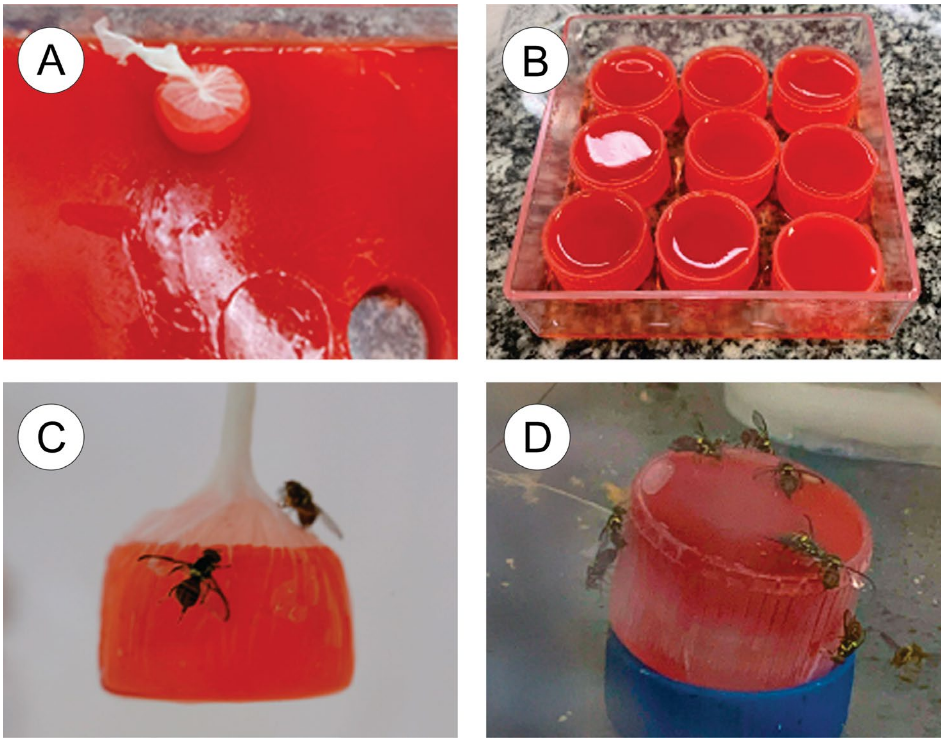

**FIGURE 1** | (A) An artificial device was covered with Parafilm for female oviposition; (B) Oviposition device with extremities covered with Parafilm and the lateral covered with the plastic cap in the oviposition depth tests; (C) *B. carambolae females* landing on the artificial device during oviposition bioassays; (D) *B. carambolae* females exploring the artificial device during the depth oviposition tests.

et al. 2017), was offered to females for oviposition and egg collection (Figure 1A,C).

At each 1-h interval (from 7:30 a.m. to 5:30 p.m.), the oviposition devices were removed and replaced by a new one. We counted the number of eggs laid by each group at each 1-h interval. To evaluate whether density affects oviposition in *B. carambolae*, the number of eggs was divided by the number of females since as more females are in the cage, more eggs will be laid. Fifteen replications were carried out for each group. Overall, 165 oviposition devices were offered for each group density tested in this experiment. Three hundred couples were used in this experiment, divided into three groups (15 for one couple, 75 for five couples, and 225 for 15 couples). The experiments were carried out between February and April 2024. All three groups replicates were made on different days/weeks, using specimens from the 24th to the 26th generation.

## 2.3 | Experiment 2—Oviposition Depth and Firmness of *B. carambolae* on Two Different Substrates

To compare the oviposition depth of *B. carambolae*, pieces of guava (stage 2—light green) (25 ×25 ×20 mm) and an artificial device (37 mm ×37 mm ×1.6 cm) with one extremity covered with Parafilm and the laterals covered by the plastic cap (28 mm ×2.8 cm) were used (Figure 1B,D). Moreover, 20 pieces of guava (25 ×25 ×20 mm) were offered to ≃400 females in a rearing cage (57.5 ×39.5 ×32 cm) for 30 min to assess the oviposition depth. In another cage, with the same female density, 10 artificial devices as described above, were offered to ≃400 females in a rearing cage (57.5 ×39.5 ×32 cm) for 30 min to assess the same parameters. Further, the measurements were made from each piece of guava and the artificial device, totaling 40 (20 observations for each treatment). Considering that the success of oviposition is measured by the complete insertion of the eggs inside the fruit, only oviposition made below the fruit peel, or the first layer of the artificial device was considered. We measured the oviposition depth with a Mitutoyo digital caliper (resolution = 0.01 mm—0.0005″ and accuracy = ±0.02 mm). To measure the firmness of the device and guava piece, we used the analogical perforator (Fruit Hardness Tester, model PTR-100) (insertion depth 10 mm). Five pieces of the device and five guava pieces were used to verify the firmness of each substrate. We also measured the aculeus length of 10 females 24 h after its emergence, from the base to the extreme apex. No correlation analyses were made between firmness and oviposition depth.

## 2.4 | Statistical Analysis

For each female density, a generalized linear mixed model (GLMM) with Poisson distribution, considering replication as random variable, was used to evaluate the temporal pattern of oviposition in *B. carambolae* in different densities, and to compare the number of eggs/female/day among three female densities (one, five, and 15 females). To compare the oviposition depth on guava and the artificial device, we first tested the assumptions of variance, normality and homogeneity using a Shapiro–Wilk and Bartlett test, respectively. Since these assumptions for a linear model were not achieved, we used a generalized linear model (GLM) with Gaussian distribution. Significance was obtained from the F-test or Chi-square ($\alpha = 0.05$). Pairwise comparisons were performed using Tukey's test with Bonferroni

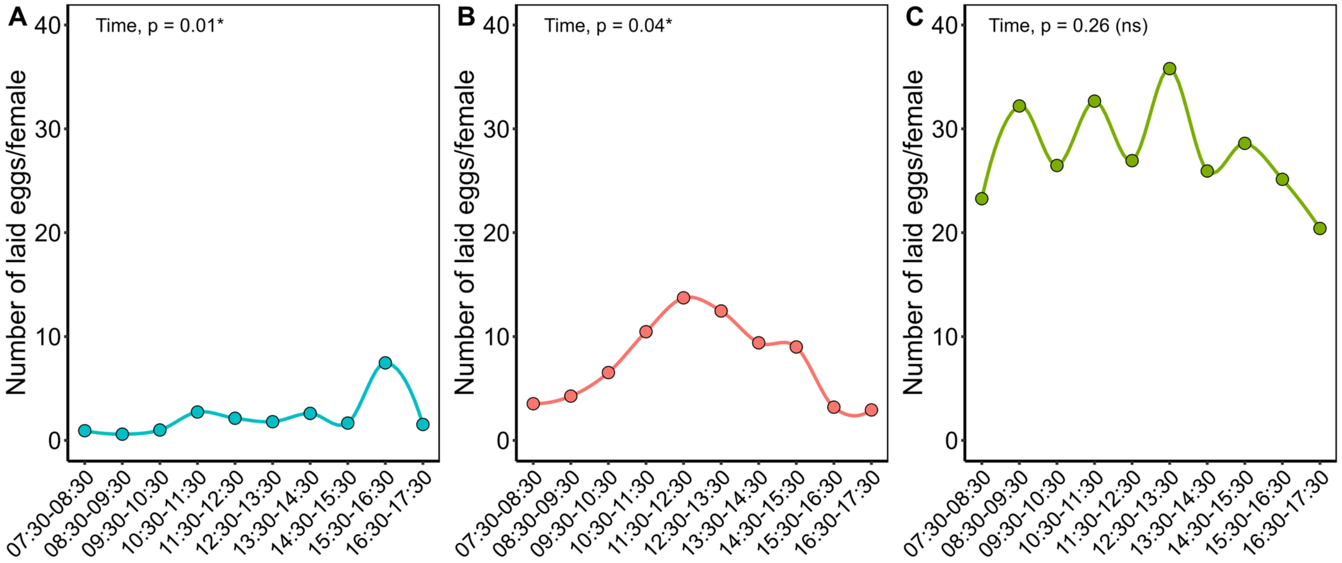

**FIGURE 2** | Temporal oviposition pattern of *B. carambolae* and effects of female densities on its oviposition activity (A: One female; B: 5 females; C: 15 females). *Significantly different. ns, no significant differences.

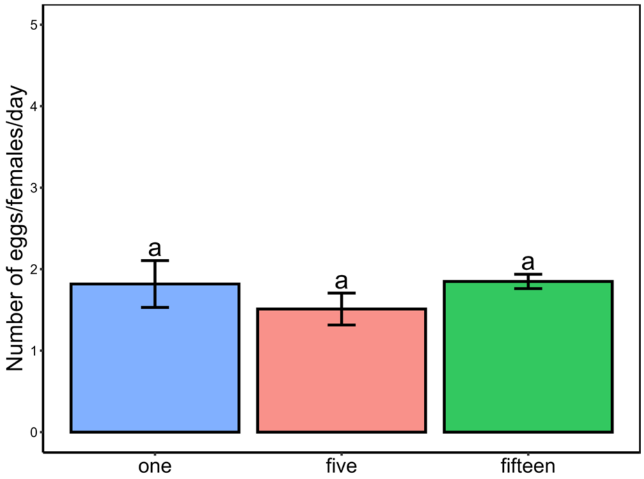

**FIGURE 3** | Comparison of number of laid eggs/females/day at three female densities (one female/cage-blue bars; five females/cage-red bars; fifteen females/cage-green bars). (a) Same letters above error bars indicate no significant difference among densities.

correction ($\alpha = 0.05$), when needed. Model quality was graphically verified using the half-normal plot from the *hnp* (Moral et al. 2017). All analyses were performed in R (version 3.4.1.), using the *lme4* (Bates et al. 2015), *bible* (Bolker et al. 2022), and *emmeans* (Lenth 2022) packages.

## 3 | Results

### 3.1 | Daily Oviposition Pattern of *B. carambolae*

Our analysis showed a significant preference to oviposit in a specific period of the day in the densities of one (df = 9; $F = 2.37$; $p = 0.01$) (Figure 2A) and five couples (df = 9; $F = 1.99$; $p = 0.04$) (Figure 2B). The oviposition at a density of one female showed a slow increase in its oviposition from 07:30 a.m. to 2:30 p.m. The period of highest oviposition was observed at 3:30–4:30 p.m. In the second group (=five couples), a slow growth during the morning and early afternoon was exhibited, with the greatest oviposition from 10:30 a.m. to 12:30 p.m.; as it begins, the oviposition of this group decreased slowly till the end of the day (5:30 p.m.). Regarding the third group (=15 couples), no significant temporal pattern was observed (df = 9; $F = 1.26$; $p = 0.26$) (Figure 2C). Its group's oviposition fluctuated throughout the day, with a slight decrease in the later afternoon. Regarding the effects of densities on the number of laid eggs/female/day, there were no significant differences between the three densities (df = 2; $F = 0.83$; $p = 0.43$) (Figure 3).

### 3.2 | *Bactrocera carambolae* Oviposition Depth and Firmness in Two Different Substrates

The mean (±SD) aculeus length of newly emerged females was 1.32 mm ± 0.006 (Figure 4A). No significant differences were found between the oviposition depth of *B. carambolae* in guava and artificial device (df = 1; $\chi^2 = 4.95$; $p = 0.07$). The *B. carambolae* mean oviposition depth on guava was 2.023 ± 1.013 (Min depth: 0.11 mm; Max. depth: 3.95 mm) (Figure 4B), while on the artificial device, the depth was 2.49 ± 0.756 (Min. depth: 0.7 mm; Max depth: 3.63 mm). The firmness (kg/cm$^2$) mean (±SD) of guava pieces was 7.82 ± 3.749; whereas the firmness mean (±SD) of the artificial device was 2.2 ± 0.198.

## 4 | Discussion

To Tephritidae species, oviposition is one of the most important keys to the success of their offspring (Scolari et al. 2021; Li et al. 2024). The oviposition behavior of this family is considered heterogeneous and might change according to species-specific traits, such as clutch size, duration of the oviposition, and patterns of searching fruits (Scolari et al. 2021). Little is known about the invasive species *B. carambolae* oviposition traits (de Jesus Barros et al. 2017, 2018), especially in Brazil, where the pest has been an invader since 1996.

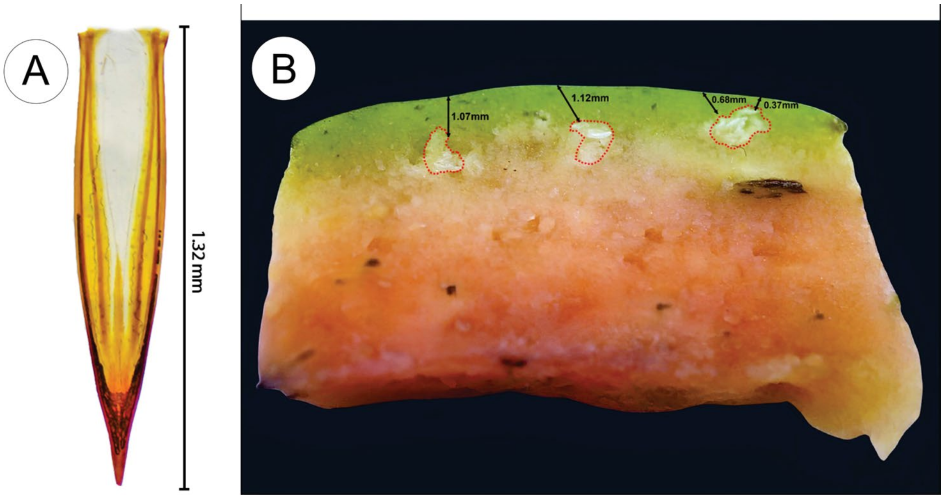

**FIGURE 4** | (A) *B. carambolae* aculeus length; and (B) Cross-section of a piece of guava showing *B. carambolae* clutch eggs. The measure was taken from the puncture found in guava peel to the first egg after the epicarp.

Our first hypothesis predicted that *B. carambolae* does not present a daily oviposition pattern. Moreover, the second hypothesis proposed that high female density would positively influence the ovipositional activity of CFF. Opposite to our first hypotheses, *B. carambolae* showed a clear temporal oviposition pattern in one-couple and five-couple groups. Controversially, when in higher female density (15 couples), the species did not show a temporal oviposition pattern, as observed in *C. capitata*, an invasive species in Brazil (Amaral et al. 2021). Contrary to our second prediction, the oviposition activity (number of eggs) was not influenced by female density. Our results were opposite from those found for *A. ludens* and *B. tryoni* (Prokopy et al. 1999; Díaz-Fleischer and Aluja 2003; Davis et al. 2011). In their work, the authors suggest that the presence of conspecific species can cause a positive stimulus to its oviposition.

Interestingly, in the density of one female (one couple), we observed a species-intrinsic daily pattern of oviposition without the stimuli of conspecific females. In this group, the oviposition activity was significantly slow throughout the day (07:30 a.m. to 2:30 p.m.) compared to the period of the greatest oviposition (3:30 to 4:30 p.m.); close to the end of the day, which is also its preferencial mating period (McInnis et al. 1999). In this group, the absence of a conspecific female and the availability of the oviposition site did not reduce the stimulus to oviposit. Opposite to the results found for *A. ludens*, in which the solitary female tends to visit and oviposit less than when they are with conspecific females (Díaz-Fleischer and Aluja 2003).

A curious positive stimulus from the presence of conspecific species was observed in the second group (=5 couples) affecting the acceptance of the artificial device. The females from this group started to oviposit earlier than the one-female group, beginning its ovipositional activity as soon as the artificial device was provided into the cage at 7:30 a.m. The period with most oviposition activity was observed in the middle of the morning to noon, decreasing its oviposition activity close to 4:30 p.m. Concerning the third group (=15 couples), no oviposition pattern throughout the day was observed, but the data showed a reduction of laid eggs at the end of the day (4:30–5:30 p.m.). As well as the second group (=5 couples), the females from the 15-couple group also accepted the artificial device as soon as it was offered into the cage. For the 15-couple group, we suggest that the increase in female density forced the females to distribute their eggs throughout the day. This behavior is similar to those exhibited by *C. capitata* (Liendo et al. 2020; Silva et al. 2021). Alike *B. carambolae*, *C. capitata* is an invader species in Latin America. These species often change their intrinsic behavior to avoid competition (e.g., by changing the host ripe preference or avoiding previously infested fruits) (Liendo et al. 2020; Silva et al. 2021; Aquino et al. 2025).

Our observations showed that the *B. carambolae* females often displace other females from the oviposition site (Galvão-Silva. F.L., personal observation). Our findings suggest that to avoid competition for the oviposition site at higher density, *B. carambolae* changes its oviposition activity and waits/searches for a new non-oviposited device/fruit. In *R. juglandis*, the pattern of social stimulation of oviposition was described as a response to increasing competition for a resource (Davis et al. 2011). Nonetheless, the authors highlight that the competition only occurs when the oviposition site (an artificial sphere) is small, forcing the species to compete for its oviposition site. In this referred study, the authors used an artificial sphere like those used in our experiment. Then, we assume that *B. carambolae* chooses avoidance over aggressive competition to guarantee its offspring. Although we did not assess the role of the males in our experiments, according to recent studies (Terzidou et al. 2022, 2023), laboratory males can exhibit a reduction in locomotor activity and a likely mismatch with the females during mating time.

According to the literature, the oviposition activity of Tephritidae fruit flies occurs during the morning–afternoon (Aluja et al. 1997; Sugayama et al. 1997; Yee 2002; Brévault and Quilici 2007; Vayssières et al. 2013; Bayoumy and El-Metwally 2017; Amaral et al. 2021). In this work, even though the distinct pattern of ovipositional activity was found in the tested groups, it was clear that the oviposition activity of *B. carambolae* is highly influenced by the daytime period. In all groups, independently of female density, the ovipositional activity occurred in the morning till the end of the day, suggesting a diurnal activity. Other fruit flies, such as *Anastrepha* *curvicauda* (Gerstaecker, 1860), *A. fraterculus*, *A. obliqua*, *C. capitata, Bactrocera zonata* (Saunders, 1842), and *Rhagoletis indifferens* Curran, 1932, show the same trend and exhibit a diurnal oviposition behavior (Aluja et al. 1997; Sugayama et al. 1997; Yee 2002; Brévault and Quilici 2007; Bayoumy and El-Metwally 2017; Galvão-Silva et al. 2023).

The number of laid eggs per female was not affected by density. Our findings showed that the number of laid eggs was consistent through the groups, with an average of ±1.5 eggs laid per female during the day. Similar results were described by de Jesus Barros et al. (2017). The authors registered an average of 1088.26 ± 167.82 eggs per female. It was also suggested that *B. carambolae* adopt high fecundity as a reproductive strategy. Based on our results, the type of fruit or artificial device does not change its strategy. In our tests, we observed that *B. carambolae* distributed its eggs over time, which could be a strategy to overcome high densities.

Observing the oviposition depth of CFF, we found that the different oviposition sites (a piece of guava and an artificial device) did not affect the oviposition deepness of *B. carambolae*; for both oviposition sites, the deepness shows an average of ±2.0 mm. Similar results were found by Xu et al. (2012). The authors found that in fresh grapes, *B. dorsalis* laid its eggs ±1–2 mm beneath the fruit skin. However, due to the difference between the surface of the oviposition sites (guava and artificial devices) used in this work, the puncture achieves only the epicarp and rarely the fruit's mesocarp. In the native *A. fraterculus* and the invasive *C. capitata*, the mean oviposition depth in guava was up to 5 mm for both species (Dias, Nava, et al. 2017). However, in their work, the authors did not describe the guava maturity stage. In our work, we used guava in stage 2—light green (Azzolini et al. 2004). According to Mahmood (2004), the aculeus length of CFF has an average of 1.51 mm, which is close to the measurement found in our work (1.32 mm).

Host quality (i.e., size, color, degree of ripeness, chemical compounds, among others), aculeus length, and oviposition depth are important factors that influence oviposition success in tephritids (Aluja and Mangan 2008). For polyphagous species, such as *C. capitata*, a short aculeus does not prevent the female from laying eggs in fruits with hard skin, such as guava and orange. Instead, females may choose their host fruit with previous damage (e.g., holes) to deposit their eggs (Díaz-Fleischer and Aluja 2003; Aluja and Mangan 2008; Clarke et al. 2011).

In our tests, the oviposition depth of *B. carambolae* in both oviposition sites was above 2.0 mm and the *B. carambolae* aculeus size was about 1.32 mm, similar to the mean size found by Mahmood (2004). Although we did not evaluate the strategies of females to deposit their eggs, we do not exclude the hypothesis that *B. carambolae* can exhibit the same strategy used by *C. capitata*, depositing its eggs in preexisting holes in the host fruits. Furthermore, we observed that CFF laid its eggs mainly in clutches, sometimes exceeding 15 eggs per clutch, as observed by de Jesus Barros et al. (2018). These oviposition traits might influence the oviposition depth of the species on guava, pushing the eggs downward in the pericarp throughout the oviposition process and possibly increasing their egg viability.

## 5 | Conclusion

The main finding of this study is that the daily oviposition pattern of *B. carambolae* is highly affected by female density, exhibiting different strategies to lay its eggs. The species tends to lay eggs during the diurnal period, as much as it finds hosts or oviposition sites. In Northern Brazil, where this species occurs, surveying and monitoring the pest should consider the broad period of oviposition activity displayed by the pest.

### Author Contributions

**Fábio L. Galvão-Silva:** conceptualization (lead), data curation (lead), investigation (lead), formal analysis (equal), software (equal), visualization (equal); writing – original draft (lead); and writing – review and editing (equal). **Jessica P. M. Oliveira:** conceptualization (equal), methodology (equal), investigation (equal), visualization (equal), and writing – review and editing (equal). **Alexandre S. Araújo:** conceptualization (equal), formal analysis (lead), software (lead), visualization (equal), and writing – review and editing (equal). **Tatiana P. dos Santos:** conceptualization (equal), methodology (equal), and investigation (equal). **Bianca D. G. de Lima:** methodology (equal); investigation (equal). **Willian Ramon L. Figueiredo:** methodology (equal), and investigation (equal). **Dori Edson Nava:** funding acquisition (lead), supervision (equal), visualization (equal), project administration (lead), and writing – review and editing (equal). **Ricardo Adaime:** funding acquisition (lead), visualization (equal), supervision (equal), project administration (lead), resources (lead), and writing – review and editing (equal).

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The dataset that supports the results of this research is openly available on figshare.com at https://figshare.com/s/5922b741e7e2999f59ef.

### References

Adaime, R., J. D. B. Pereira, M. S. M. Sousa, C. R. Jesus, M. F. Souza Filho, and R. A. Zucchi. 2023. "Moscas-das-frutas, suas plantas hospedeiras e parasitoides no estado do Amapá." In *Moscas-Das-Frutas no Brasil—Conhecimento Básico e Aplicado—Volume II*, edited by R. A. Zucchi, A. Malavasi, R. Adaime, and D. E. Nava, 51–68. FEALQ.

Akol, A. M., C. Masembe, B. E. Isabirye, C. K. Kukiriza, and I. Rwomushana. 2013. Oviposition Preference and Offspring Performance in Phytophagous Fruit Flies (Diptera: Tephritidae): The African Invader, *Bactrocera invadens*. https://nru.uncst.go.ug/handle/123456789/5234.

Aluja, M., A. Jiménez, J. Piñero, et al. 1997. "Daily Activity Patterns and Within-Field Distribution of Papaya Fruit Flies (Diptera: Tephritidae) in Morelos and Veracruz, Mexico." *Annals of the Entomological Society of America* 90, no. 4: 505–520. https://doi.org/10.1093/aesa/90.4.505.

Aluja, M., and R. L. Mangan. 2008. "Fruit Fly (Diptera: Tephritidae) Host Status Determination: Critical Conceptual, Methodological, and Regulatory Considerations." *Annual Review of Entomology* 53, no. 1: 473–502. https://doi.org/10.1146/annurev.ento.53.103106.093350.

Amaral, T. S., A. E. L. Ribeiro, R. D. S. Bulhões, F. R. Sujimoto, and E. L. D. Araujo. 2021. "Sexual and Oviposition Behaviors of *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) in Cashew Apple (*Anacardium occidentale* L.)." *Biology and Life Sciences Forum* 2, no. 1: 28. https://doi.org/10.3390/BDEE2021-09473.

Aquino, J. C., A. S. Araújo, F. L. Galvão-Silva, A. S. do Nascimento, and I. S. Joachim-Bravo. 2025. "Oviposition Strategies and Interactions Among Invasive and Native Fruit Flies (Diptera: Tephritidae) on Guava (*Psidium guajava* L.)." *Austral Entomology* 64: 1–11. https://doi.org/10.1111/aen.70017.

Azzolini, M., A. P. Jacomino, and I. U. Bron. 2004. "Índices Para Avaliar Qualidade Pós-Colheita de Goiabas em Diferentes Estádios de Maturação." *Pesquisa Agropecuária Brasileira* 39: 139–145. https://doi.org/10.1590/S0100-204X2004000200006.

Bariani, A., C. R. de Jesus-Barros, J. P. Carvalho, et al. 2016. Técnicas PARA Criação da Mosca-da-Carambola (*Bactrocera carambolae* Drew & Hancock) em Laboratório Para Pesquisa Científica. http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/1064948.

Bates, D., M. Machler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. https://doi.org/10.18637/jss.v067.i01.

Bayoumy, M. H., and M. M. El-Metwally. 2017. "Daily Flight Activity Rhythms of the Peach and Mediterranean Fruit Flies Using Sexual and Olfactory Attractants." *Acta Phytopathologica et Entomologica Hungarica* 52, no. 2: 227–244. https://doi.org/10.1556/038.52.2017.022.

Bolker, B., I. Giné-Vázquez, and R Development Core Team. 2022. *Package 'bbmle'. Tools for General Maximum Likelihood Estimation*. R CRAN Repository. https://cran.r-project.org/web/packages/bbmle/bbmle.pdf.

Brévault, T., and S. Quilici. 2007. "Influence of Habitat Pattern on Orientation During Host Fruit Location in the Tomato Fruit Fly, *Neoceratitis cyanescens*." *Bulletin of Entomological Research* 97, no. 6: 637–642. https://doi.org/10.1017/S0007485307005330.

CABI. 2021. *Invasive Species Compendium: Bactrocera carambolae (Carambola Fruit Fly)*. CAB International. https://doi.org/10.1079/cabicompendium.8700.

Castilho, A. P., J. Pasinato, J. E. V. D. Santos, et al. 2020. "Biology of *Bactrocera carambolae* (Diptera: Tephritidae) on Four Hosts." *Revista Brasileira de Entomologia* 63: 302–307. https://doi.org/10.1016/j.rbe.2019.09.002.

Clarke, A. R., K. S. Powell, C. W. Weldon, and P. W. Taylor. 2011. "The Ecology of *Bactrocera tryoni* (Diptera: Tephritidae): What Do We Know to Assist Pest Management?" *Annals of Applied Biology* 158, no. 1: 26–54. https://doi.org/10.1111/j.1744-7348.2010.00448.x.

Cortés-Martínez, F., L. Cruz-López, P. Liedo, and J. C. Rojas. 2021. "The Ripeness Stage but Not the Cultivar Influences the Attraction of *Anastrepha obliqua* to Guava." *Chemoecology* 31: 115–123. https://doi.org/10.1007/s00049-020-00332-2.

Costa, J., M. Sousa, M. F. de Souza-Filho, and R. Adaime. 2023. "*Chrysophyllum cainito* L. (Sapotaceae): Novo Hospedeiro da Mosca-da-Carambola no Brasil." *Agrotropica* 35, no. 2–33: 161–164. http://www.alice.cnptia.embrapa.br/alice/handle/doc/1164709.

Costa, J. V., M. D. S. de Sousa, M. F. Souza-Filho, et al. 2024. "First Record of Papaya as Host of Carambola Fruit Fly in Brazil." *Entomological Communications* 6: ec06024. https://doi.org/10.37486/2675-1305.ec06024.

Costa, J. V. T. A., M. S. M. Sousa, C. R. Jesus, et al. 2023. "New Findings on Carambola Fruit Fly Hosts in South America." *Florida Entomologist* 106, no. 3: 161–174. https://doi.org/10.1653/024.106.0303.

Davis, J. M., C. R. Nufio, and D. R. Papaj. 2011. "Resource Quality or Competition: Why Increase Resource Acceptance in the Presence of Conspecifics?" *Behavioral Ecology* 22, no. 4: 730–737. https://doi.org/10.1093/beheco/arr042.

de Jesus Barros, C. R., W. S. de Oliveira, J. P. Carvalho, et al. 2018. "Tamanho Das Posturas de *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae) em Carambola." *Entomotropica* 33: 25–29. http://www.alice.cnptia.embrapa.br/alice/handle/doc/1145068.

de Jesus Barros, C. R., L. O. M. Júnior, A. S. Costa, J. Pasinato, and R. Adaime. 2017. "Fecundidade e Longevidade de *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae)." *Biotemas* 30, no. 4: 7–13. https://doi.org/10.5007/2175-7925.2017v30n4p7.

Dias, N. P., D. E. Nava, M. S. Garcia, F. F. Silva, and R. A. Valgas. 2017. "Oviposition of Fruit Flies (Diptera: Tephritidae) and Its Relation With the Pericarp of Citrus Fruits." *Brazilian Journal of Biology* 78, no. 3: 443–448. https://doi.org/10.1590/1519-6984.167661.

Dias, N. P., S. Ongaratto, M. S. Garcia, and D. E. Nava. 2017. "Oviposition of Anastrepha Fraterculus and *Ceratitis capitata* (Diptera: Tephritidae) in Citrus Fruits, and Development in Relation to Maturity of Orange Fruits." *Florida Entomologist* 100, no. 2: 468–473. https://doi.org/10.1653/024.100.0209.

Díaz-Fleischer, F., and M. Aluja. 2003. "Influence of Conspecific Presence, Experience, and Host Quality on Oviposition Behavior and Clutch Size Determination in *Anastrepha ludens* (Diptera: Tephritidae)." *Journal of Insect Behavior* 16: 537–554. https://doi.org/10.1023/A:1027307424150.

Flitters, N. E. 1964. "The Effect of Photoperiod, Light Intensity, and Temperature on Copulation, Oviposition, and Fertility of the Mexican Fruit Fly." *Journal of Economic Entomology* 57, no. 6: 811–813. https://doi.org/10.1093/jee/57.6.811.

Galvão-Silva, F. L., A. S. Araújo, B. S. Moreira, C. P. Oliveira, and I. S. Joachim-Bravo. 2023. "Oviposition Behavior of *Anastrepha obliqua* (Maquart, 1835) (Diptera: Tephritidae) and Preference Between Two Mango (*Mangifera indica* L.) Varieties." *Entomological Communications* 5: ec05019. https://doi.org/10.37486/2675-1305.ec05019.

Guillén, L., R. Adaime, A. Birke, et al. 2017. "Effect of Resin Ducts and Sap Content on Infestation and Development of Immature Stages of *Anastrepha obliqua* and *Anastrepha ludens* (Diptera: Tephritidae) in Four Mango (Sapindales: Anacardiaceae) Cultivars." *Journal of Economic Entomology* 110, no. 2: 719–730. https://doi.org/10.1093/jee/tow279.

Guillén, L., J. L. Monribot-Villanueva, J. A. Guerrero-Analco, et al. 2022. "Influence of Sunlight Incidence and Fruit Chemical Features on Oviposition Site Selection in Mango by *Anastrepha obliqua*: Implications for Management." *Insects* 13: 141. https://doi.org/10.3390/insects13020141.

Joachim-Bravo, I. S., O. A. Fernandes, S. A. Bortoli, and F. S. Zucoloto. 2001. "Oviposition Behavior of *Ceratitis capitata* Wiedemann (Diptera: Tephritidae): Association Between Oviposition Preference and Larval Performance in Individual Females." *Neotropical Entomology* 30: 559–564. https://doi.org/10.1590/S1519-566X2001000400008.

Koswanudin, D., A. Basukriadi, I. M. Samudra, and R. Ubaidillah. 2018. "Host Preference Fruit Flies *Bactrocera carambolae* (Drew & Hancock) and *Bactrocera dorsalis* (Drew and Hancock) (Diptera: Tephritidae)." *Jurnal Entomologi Indonesia* 15, no. 1: 40. https://doi.org/10.5994/jei.15.1.40.

Lemos, L. D. N., R. Adaime, C. R. De Jesus-Barros, and E. Da Glória De Deus. 2014. "New Hosts of *Bactrocera carambolae* (Diptera: Tephritidae) in Brazil." *Florida Entomologist* 97, no. 2: 841–843. https://www.jstor.org/stable/24362585.

Lemos, L. N., E. V. Pantoja, C. E. Chucre, et al. 2024. "New Host Records for Carambola Fruit Fly and *Anastrepha* spp. in Brazil." *Entomological Communications* 6: ec06026. https://doi.org/10.37486/2675-1305.ec06026.

Lenth, R. 2022. Package 'lsmeans'. R CRAN Repository. https://cran.r-project.org/web/packages/lsmeans/lsmeans.pdf.

Li, X. L., D. D. Li, X. Y. Cai, D. F. Cheng, and Y. Y. Lu. 2024. "Reproductive Behavior of Fruit Flies: Courtship, Mating, and Oviposition." *Pest Management Science* 80, no. 3: 935–952. https://doi.org/10.1002/ps.7816.

Liendo, M. C., M. A. Parreño, A. G. Pietrek, et al. 2020. "Infestation of Fruit by Conspecific and Heterospecific Females Deters Oviposition in Two Tephritidae Fruit Fly Species." *Journal of Applied Entomology* 144, no. 8: 701–709. https://doi.org/10.1111/jen.12791.

Mahmood, K. 2004. "Identification of Pest Species in Oriental Fruit Fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) Species Complex." *Pakistan Journal of Zoology* 36, no. 3: 219–230. Available from: 0030-9923/2004/0003-0219.

McInnis, D. O., P. Rendon, E. Jang, A. van Sauers-Muller, R. Sugayama, and A. Malavasi. 1999. "Interspecific Mating of Introduced, Sterile *Bactrocera dorsalis* With Wild *B. carambolae* (Diptera: Tephritidae) in Suriname: A Potential Case for Cross-Species Sterile Insect Technique." *Annals of the Entomological Society of America* 92, no. 5: 758–765. https://doi.org/10.1093/aesa/92.5.758.

Moral, R. A., J. Hinde, and C. G. B. Demétrio. 2017. "Half-Normal Plots and Overdispersed Models in R: The hnp Package." *Journal of Statistical Software* 81, no. 10: 1–23. https://doi.org/10.18637/jss.v081.i10.

Nor, S. M., S. Mohamed, M. H. Sajili, and N. Ngah. 2018. "Ovipositional Behavior Preference of Oriental Fruit Fly, *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) on Different Host Fruits." *Journal of Agrobiotechnology* 9: 173–181.

Prokopy, R. J., and B. S. Fletcher. 1987. "The Role of Adult Learning in the Acceptance of Host Fruit for Egg Laying by the Queensland Fruit Fly, *Dacus tryoni*." *Entomologia Experimentalis et Applicata* 45, no. 3: 259–263. https://doi.org/10.1111/j.1570-7458.1987.tb01092.x.

Prokopy, R. J., M. C. Romig, and R. A. Drew. 1999. "Facilitation in Ovipositional Behavior of *Bactrocera tryoni* Flies." *Journal of Insect Behavior* 12: 815–832. https://doi.org/10.1023/A:1020909227680.

Raghu, S., A. R. Clarke, and J. Bradley. 2002. "Microbial Mediation of Fruit Fly–Host Plant Interactions: Is the Host Plant the "Centre of Activity"?" *Oikos* 97, no. 3: 319–328. https://doi.org/10.1034/j.1600-0706.2002.970302.x.

Raghu, S., R. A. Drew, and A. R. Clarke. 2004. "Influence of Host Plant Structure and Microclimate on the Abundance and Behavior of a Tephritid Fly." *Journal of Insect Behavior* 17: 179–190. https://doi.org/10.1023/B:JOIR.0000028568.90719.2a.

Roriz, A. K. P., H. F. Japyassú, and I. S. Joachim-Bravo. 2017. "Incipient Speciation in the *Anastrepha fraterculus* Cryptic Species Complex: Reproductive Compatibility Between *A.* sp. 1 aff. *fraterculus* and *A.* sp. 3 aff. *fraterculus*." *Entomologia Experimentalis et Applicata* 162, no. 3: 346–357. https://doi.org/10.1111/eea.12526.

Sauers-Muller, A. V. 2005. "Host Plants of the Carambola Fruit Fly, *Bactrocera carambolae* Drew & Hancock (Diptera: Tephritidae), in Suriname, South America." *Neotropical Entomology* 34: 203–214. https://doi.org/10.1590/S1519-566X2005000200008.

Scolari, F., F. Valerio, G. Benelli, N. T. Papadopoulos, and L. Vaníčková. 2021. "Tephritid Fruit Fly Semiochemicals: Current Knowledge and Future Perspectives." *Insects* 12, no. 5: 408. https://doi.org/10.3390/insects12050408.

Silva, D. R. D. B., A. K. P. Roriz, C. S. C. D. A. Petitinga, I. V. G. Lima, A. S. do Nascimento, and I. S. Joachim-Bravo. 2021. "Competitive Interactions and Partial Displacement of *Anastrepha obliqua* by *Ceratitis capitata* in the Occupation of Host Mangoes (*Mangifera indica*)." *Agricultural and Forest Entomology* 23, no. 1: 70–78. https://doi.org/10.1111/afe.12406.

Silva Neto, A. M., V. S. Dias, and I. S. Joachim-Bravo. 2012. "Comportamento Reprodutivo de *Ceratitis capitata* Wiedemann (Diptera: Tephritidae): Efeito do Tamanho dos Machos Sobre o seu Sucesso de Cópula." *EntomoBrasilis* 5, no. 3: 190–197. https://doi.org/10.12741/ebrasilis.v5i3.182.

Soares, G. K. A., E. G. Fidelis, E. S. Farias, G. S. Rodrigues, and J. L. A. Paes. 2023. "Range Expansion and Population Dynamics of *Bactrocera carambolae* in Roraima, Brazil." *Crop Protection* 165: 106167. https://doi.org/10.1016/j.cropro.2022.106167.

Sugayama, R. L., E. S. Branco, A. Malavasi, A. Kovaleski, and I. Nora. 1997. "Oviposition Behavior of *Anastrepha fraterculus* in Apple and Diel Pattern of Activities in an Apple Orchard in Brazil." *Entomologia Experimentalis et Applicata* 83, no. 3: 239–245. https://doi.org/10.1046/j.1570-7458.1997.00178.x.

Terzidou, A., N. Kouloussis, G. Papanikolaou, and D. Koveos. 2022. "Acoustic Characteristics of Sound Produced by Males of *Bactrocera oleae* Change in the Presence of Conspecifics." *Scientific Reports* 12, no. 1: 13086. https://doi.org/10.1038/s41598-022-16888-8.

Terzidou, A. M., D. S. Koveos, N. T. Papadopoulos, J. R. Carey, and N. A. Kouloussis. 2023. "Artificial Diet Alters Activity and Rest Patterns in the Olive Fruit Fly." *PLoS One* 18, no. 2: e0274586. https://doi.org/10.1371/journal.pone.0274586.

Vayssières, J. F., A. Sinzogan, A. Adandonon, P. Van Mele, and S. Korie. 2013. "Ovipositional Behaviour of Two Mango Fruit Fly Species (Diptera: Tephritidae) in Relation to *Oecophylla cues* (Hymenoptera: Formicidae) as Compared to Natural Conditions Without Ant Cues." *International Journal of Biological and Chemical Sciences* 7, no. 2: 447–456. https://doi.org/10.4314/ijbcs.v7i2.3.

Xu, L., C. Zhou, Y. Xiao, P. Zhang, Y. Tang, and Y. Xu. 2012. "Insect Oviposition Plasticity in Response to Host Availability: The Case of the Tephritid Fruit Fly *Bactrocera Dorsalis*." *Ecological Entomology* 37: 446–452. https://doi.org/10.1111/j.1365-2311.2012.01383.x.

Yee, W. 2021. "Temperature Effects on Oviposition by *Rhagoletis indifferens* (Diptera: Tephritidae) Vary in Different Developmental Stages of Sweet Cherry." *Environmental Entomology* 50, no. 3: 514–522. https://doi.org/10.1093/ee/nvab003.

Yee, W. L. 2002. "Daily and Seasonal Activity Patterns of *Rhagoletis indifferens* (Diptera: Tephritidae) in Washington State." *Annals of the Entomological Society of America* 95, no. 6: 701–710. https://doi.org/10.1603/0013-8746(2002)095[0701:DASAPO]2.0.CO;2.