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Oviposition strategies and interactions among invasive and native fruit flies (Diptera: Tephritidae) on guava (*Psidium guajava* L.)

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Abstract

Oviposition and agonistic behaviour are important traits for understanding the pattern of coexistence and choice of host fruit shared between natives and invasive species. This study aimed to evaluate the interspecific interactions and the choice of the oviposition sites among three native species of fruit flies of the genus *Anastrepha*: *Anastrepha obliqua* (Macquart), *Anastrepha fraterculus* (Wiedemann), *Anastrepha sororcula* Zucchi, and an invasive species, *Ceratitis capitata* (Wiedemann). The interactions between species were measured by counting the number of eggs laid in semi-ripe and ripe guavas (*Psidium guajava* L.) in intra and interspecific combinations. Additionally, we compared the absolute frequency of agonistic behaviours in interactions between native and invasive fruit flies. The native species of *Anastrepha* did not change their preference for the fruit ripening stage, even in face of the invader *C. capitata*. *Anastrepha* species and *C. capitata* preferred to oviposit in semi-ripe fruits, in all experimental scenarios. We also observed that *C. capitata* avoided interactions with the native species by preferring to oviposit in ripe fruits when in the presence of *Anastrepha* species. All species reduced the number of laid eggs when in the presence of heterospecific females. Aggression was the most frequent agonistic behaviour in all species combinations, followed by display/stalking and avoidance. Finally, our results showed that aggression behaviour was the most frequent in interactions of *Anastrepha* species with *C. capitata*.

KEYWORDS

Anastrepha, *Ceratitits capitata*, exotic species, heterospecific females, host-choice

INTRODUCTION

In pest species of tephritid fruit flies, oviposition performance is an essential factor in understanding attack patterns in commercial and non-commercial crops (Li et al. 2024). As larvae of polyphagous tephritds do not have much mobility to search for food supply, female host choice is essential to successful offspring development (Birke & Aluja 2018; Dias et al. 2017). The main factors influencing oviposition behaviour in fruit flies are host availability, host species, ripeness and variety, chemical cues, presence of other fruit flies, either conspecific or heterospecific, and the habitat (or microhabitat) where they are introduced (Liendo et al. 2020; López-Ley et al. 2016; Nufio & Papaj 2004; Petitinga et al. 2021; Silva et al. 2012).

Female tephritids can recognise and avoid ovipositing in fruits infested by heterospecific or conspecific flies (Devescovi et al. 2015; Liendo et al. 2018). According to Devescovi et al. (2015), fruit flies exhibit different infestation patterns, and this does not necessarily affect the coexistence of native and exotic species.

When the coexistence of both native and exotic fruit flies is not possible, the females may fight by their oviposition site, exhibiting aggressive behaviour (Benelli et al. 2014; Kay & Clarke 2023). As few studies assess competitiveness between native and exotic species in laboratory conditions, the information about aggressive traits in fruit flies is limited. *Bactrocera* spp., commonly known as the most aggressive Tephritidae (Benelli et al. 2014; Duyck et al. 2006; Kay & Clarke 2023), display aggression against heterospecific females, as a way of defending oviposition sites (Ekesi et al. 2009). This aggressive behaviour eventually can lead to the displacement of other species by the larval nutritional source consumption or female defence behaviour (Benelli et al. 2014; Duyck et al. 2006).

The genus *Anastrepha* comprises the most important pests from fruit crops in Brazil and are originally from the Americas (Norrbom et al. 1999). It includes *Anastrepha obliqua* (Macquart), distributed from Mexico to Uruguay (Norrbom 2022a), *Anastrepha fraterculus* (Wiedemann), a cryptic species complex, occurring from Mexico to Argentina (Norrbom 2022b), and *Anastrepha sororcula* Zucchi, widely distributed in South America (Norrbom et al. 1999). The highly polyphagous and invasive *Ceratitis capitata* (Wiedemann), originally from the Mediterranean and widely distributed worldwide, has become one of the main pests of fruit crops in Brazil since it was detected for the first time in 1901 (Ihering 1901). All these species are commonly associated with economically important fruits production, such as mango, guava and citrus (Zucchi & Moraes 2025).

After the introduction of *C. capitata* in several regions, such as Central and South America, many *Anastrepha* species gradually decreased in abundance or changed the use of resources (Duyck et al. 2004). Despite some evidence that *C. capitata* can share the same niche with *Anastrepha* spp. (Liendo et al. 2018), other evidence suggests that native species are displaced by *C. capitata* (De-Sá 2006; Silva et al. 2021).

There is a possible asynchrony between the native species *A. fraterculus* and the invasive *C. capitata*, based on the degree of ripeness of the fruit and host preference can favour the coexistence of both species, in a scenario where the first one was already established (Liendo et al. 2018). Further information on how *Anastrepha* spp. and *C. capitata* interact is needed to understand their distribution.

In this study, we evaluated if *Anastrepha* oviposition choice for ripeness stage is affected by the presence of other *Anastrepha* species or *C. capitata* in guava [*Psidium guajava* L. (Myrtaceae)]. We used as model three pest species of *Anastrepha* from Brazil: *A. obliqua*, *A. fraterculus* and *A. sororcula*, and the invasive *C. capitata*. We measured the number of eggs laid by females in pairwise combinations between each species for semi-ripe and unripe guava. Regarding agonistic interactions, we provided a detailed description and compared the frequency of aggression, avoidance and display/stalking behaviours in each combination.

MATERIAL AND METHODS

Fly sampling and population maintenance

The population of *A. fraterculus* used in the experiments was collected in Bento Gonçalves, Rio Grande do Sul (29°10′15″S, 51°31′8″W) from infested guavas. The specimens of *A. obliqua* were collected in Cruz das Almas, Bahia (12°40′12″ S, 39°6′7″ W) from infested guavas, and the individuals of *A. sororcula* were collected in Parnamirim, Rio Grande do Norte (5°54′56″ S, 35°15′46″ W). The *Anastrepha* species lineages used in the experiments had been maintained under laboratory conditions for 5 years. Specimens of *C. capitata* were derived from a laboratory colony established over 20 years ago, originally collected from infested fruits of *Terminalia catappa* L. in Itaparica, Bahia (12°53′18′ S, 38°40′43′ W). Laboratory-reared flies were used to standardise age and nutritional status across individuals. Previous studies have shown no evidence that long-term laboratory rearing alters intra- or interspecific competition patterns in tephritid species (Duyck et al. 2007; Liendo et al. 2016).

All specimens used in the experiments were maintained under laboratory conditions at the Technological Center of Agriculture of Bahia (CETAB – Salvador) and the Laboratory of Behavioural Ecology of Insects (LECI), Institute of Biology of Federal University of Bahia (UFBA). The cages were kept under controlled conditions of temperature (25 ± 5°C), relative humidity (70 ± 10%), and a photoperiod of 12 h:12 h (light/dark). The adults were maintained on a yeast extract dried diet (Bionis YE MF®, Biorigin), with approximately 63% protein and sugar content at a ratio of 1:3, and water (Silva-Neto et al. 2012). Immature *Anastrepha* species were reared in their preferred hosts: mangoes (*Mangifera indica* L.), Tommy Atkins variety for *A. obliqua*, and guavas (Paluma variety) for *A. fraterculus* and *A. sororcula*, following the methodology described by Silva et al. (2021). The immatures of *C. capitata* were maintained on artificial diets with yeast extract (Silva-Neto et al. 2012).

Preparation of fruits for the experiment

The fruit chosen as host for all experiments was the guava, Paluma variety, as it is a common host for all species investigated (Zucchi & Moraes 2025), is off economic importance in Brazil (Silva et al. 2010) and is available in markets throughout the year. The fruits were purchased in the market from the same supplier. They were washed with soap and water and stored in a refrigerator until use. Fruits of similar size, around 6 cm in diameter and weighing approximately 190 g, were used for the experiments.

In the oviposition preference tests and filming of behaviours, semi-ripe (tip green and still firm) and ripe guavas (yellowish and less firm but not very soft) were used, following the classification of Azzolini et al. (2004) and Silva et al. (2010). This protocol was based on similar studies on the classification of mango ripening of the Tommy Atkins variety (Mouco 2004; Santos et al. 2008).

Oviposition preference tests

Oviposition by flies in the following combinations were tested: AF (*A. fraterculus* + *A. fraterculus*), AF + AO (*A. fraterculus* + *A. obliqua*), AF + AS (*A. fraterculus* + *A. sororcula*), AF + CC (*A. fraterculus* + *C. capitata*), AO (*A. obliqua* + *A. obliqua*), AO + AF (*A. obliqua* + *A. fraterculus*), AO + AS (*A. obliqua* + *A. sororcula*), AO + CC (*A. obliqua* + *C. capitata*), AS (*A. sororcula* + *A. sororcula*), AS + AF (*A. sororcula* + *A. fraterculus*), AS + AO (*A. sororcula* + *A. obliqua*), AS + CC (*A. sororcula* + *C. capitata*), CC (*C. capitata* + *C. capitata*), CC + AF (*C. capitata* + *A. fraterculus*), CC + AO (*C. capitata* + *A. obliqua*), CC + AS (*C. capitata* + *A. sororcula*).

Tests were carried out in acrylic cages (49 × 45 × 49 cm). Semi-ripe and ripe guavas were placed in opposite sides of the cages and exposed to mature females (age: ~15 days) for 24 h (placed and removed at 8:00 AM). The flies were supplied with water and diet. Twenty couples were placed in each cage. In experiments with individuals of the same species (control), 20 pairs of the same species were placed in each cage, and in experiments using combinations between the species, two by two, 10 pairs of each species were placed in each cage to maintain the proportion of individuals. Ten replicates were performed for each preference test, which a replicate was a cage. One exception was the combination of *A. sororcula* versus *C. capitata*, in which there were five replicates due to the lack of *A. sororcula* specimens.

The number of eggs of each species, in each combination, were counted under a stereomicroscope and were identified based on their morphological characteristics described in the literature (Figueiredo et al. 2011; Roriz et al. 2015; Selivon & Perondini 1998, 1999, 2023). In controls, the eggs of each cage were divided by two to standardise the number of eggs per female of each species in each cage.

Agonistic interactions

Agonistic interaction experiments were performed with *A. fraterculus*, *A. obliqua* and *C. capitata*. There were not enough specimens of *A. sororcula* to carry out the combinations with this species. Agonistic interactions were evaluated through filming to classify the types and frequencies of agonistic interactions between females of the same species and different species exposed to the same oviposition site. These experiments were performed and adapted according to the methodology standardised by Silva et al. (2021). The design was made by placing six females of each species combined two by two in an acrylic cage (49 × 45 × 49 cm) for the experimental treatments and 12 females for the control treatments (species alone), in the following combinations: *A. fraterculus* versus *A. obliqua*; *A. fraterculus* versus *C. capitata; A. obliqua* versus *C. capitata; A. fraterculus* versus *A. fraterculus*; *A. obliqua* versus *A. obliqua; C. capitata* versus *C. capitata*. Each cage into which the females were placed contained two guava fruits (semi-ripe and ripe). Each female was painted with a different non-toxic colour on the scutum. In previous studies, this colour marking did not influence the behaviour of flies (Benelli et al. 2012). The flies in each cage were filmed for an hour during the morning for further analysis and quantification of behaviours. The observed agonistic interactions were classified as avoidance, aggression or display/stalking (Table 2), and only the behaviours that occurred in fruits were counted since, in frugivorous species of Tephritidae, interactions between females usually occur on the host fruits (Benelli et al. 2015). The behaviours observed in the semi-ripe and ripe fruits within the same cage were counted together. The behavioural units analysed were based on the studies of Pritchard (1969), Benelli et al. (2014) and Benelli (2015).

Fly behaviour was filmed with two Geovision-GV-BX 220D-3.2 M cameras with variable focus lenses at 30 frames/s, positioned on both sides of the cage, with artificial lighting of 1700 lx and relative humidity of 57%. Images were captured using Eagle Vision Pro version 4, and videos were saved in AVI format using Geo Vision 800. Video recordings enable more detailed and complete observations of the number of rapid and subtle movements associated with aggression (Briceño et al. 1999). Ten replicates (replicate = cage) were performed for each treatment.

Statistical analysis

Data from oviposition choice tests and agonistic interactions were analysed using a generalised linear model (GLM), assuming a negative binomial or Poisson distribution. The quality of the model was verified using the half-normal plot from the *hnp* package (Moral et al. 2017). Pairwise comparisons were made using Tukey's test, with Bonferroni corrections. All analyses considered a significance level of 5% and were conducted in R (https://www.r-project.org/), using the packages *MASS* (Ripley et al. 2013) and *multcompView* (Graves et al. 2015).

RESULTS

Oviposition preference tests

The presence of other species had a significant effect on oviposition for each species in cross-species combinations (Table 1). Fruit ripening significantly influenced the oviposition of all species except *C. capitata* (Table 1). The interaction between these two factors was significant only for *A. fraterculus* and *C. capitata* (Table 1).

All species studied showed a noted preference for semi-ripe fruits with conspecific females, except for *A. fraterculus*, which oviposited a similar number of eggs in ripe or semi-ripe fruits in tests with conspecific females (Figure 1). In tests with heterospecific females, there was no change in the original oviposition preference in any of the native species when placed with heterospecific females, except for *A. fraterculus*, which preferred to lay eggs in semi-ripe fruits (Figure 1a–c). Only the invasive species, *C. capitata*, changed its oviposition preference. Unlike native *Anastrepha* species, *C. capitata* preferred ripe guavas when in the presence of *A. fraterculus*, *A. obliqua* and *A. sororcula* rather than semi-ripe guavas (Figure 1d).

In all *Anastrepha* species, we observed fewer eggs in the semi-ripe fruits when females were in the presence of another species (Figure 1d). In *A. fraterculus*, fewer eggs were laid in semi-ripe guava when in the presence of *C. capitata* (Figure 1a). In *A. obliqua*, this reduction was detected when females were placed together with *A. sororcula* (Figure 1b); and in *A. sororcula* when they were in the presence of other *Anastrepha* species. When paired with *Anastrepha*, *C. capitata* (Figure 1c), switched its preference, from semi-ripe fruit to ripe fruits (Figure 1d).

Agonistic interactions

The types of behaviours observed during interactions between the species of fruit flies are shown in Table 2. The behaviours were divided into three types: (1) no interaction between the flies (avoidance), (2) interaction, but without any aggression between them (display and/or stalking), (3) interaction with aggression, resulting or not in the exclusion of any of them (aggression). These analyses were based on and adapted from the studies of Pritchard (1969) and Benelli et al. (2014, 2015).

No difference in fly behaviours was observed in conspecific groups of *A. fraterculus* (Figure 2a) or in combinations of *A. fraterculus* + *A. obliqua* (Table 3; Figure 2d). In conspecific groups of *A. obliqua*, aggression was the most frequent behaviour, followed by display/stalking and avoidance (Table 3; Figure 2b). In conspecific groups of *C. capitata*, the number of aggression and display interactions was significantly higher than avoidance (Table 3; Figure 2c). Aggressive interactions were more frequent than avoidance in combinations of *A. obliqua* and *C. capitata* (Figure 2f), but no differences were observed between avoidance and display, as well as between display and aggression (Table 3; Figure 2f). In the experiments with *A. fraterculus* and *C. capitata*, aggression was more frequent than avoidance and display, but no difference was observed between avoidance and display (Figure 2e).

DISCUSSION

Hierarchy can be a significant factor in interspecific interactions. Even when a species demonstrates greater efficiency in exploiting a particular environment, its occupancy may be restricted in the presence of another species, leading to total or partial displacement. However, interaction can also result in stable coexistence—niche partitioning—when species manage to occupy segments of the environment that are not utilised by competing species (Reitz & Trumble 2002; Duyck et al. 2004, 2006, 2008; Devescovi et al. 2015).

Our results showed that *Anastrepha* species (native) prefer to oviposit in semi-ripe fruit regardless of the presence of other species, whether congeneric or not. The native species also did not avoid niche overlap with the invasive species (David et al. 2017; Masselière et al. 2017), given the maintenance of oviposition preference in semi-ripe guavas by all species of *Anastrepha* used in our study, corroborating previous studies that show the preference of *Anastrepha* species for the fruit still in the early ripening stage (De Oliveira et al. 2015; Diaz-Fleischer & Aluja 2003; Fontellas-Brandalha & Zucoloto 2004).

TABLE 1 Results of the generalised linear model (GLM), assuming Poisson distribution or negative binomial, where the data obtained experiments oviposition choice were analysed.

	A. fraterculus			***A. obliqua***			***A. sororcula***			***C. capitata***		
Factor	***df***	***F***	***p-value***	***df***	***F***	***p-value***	***df***	***F***	***p-value***	***df***	χ^2	***p-value***
Combination	3	53.484	>0.001	3	18.917	>0.001	3	19.503	0.0004	3	125.14	>0.001
Ripening	1	205.871	>0.001	1	86.771	>0.001	1	14.484	0.0002	1	0.11	0.740
Combination: ripening	3	52.909	>0.001	3	9.148	0.027	3	0.206	0.8915	3	542.10	>0.001

Note: Combinations between species and fruit ripening were modelled as explanatory variables, while the number of eggs was considered a response variable. The significance of the model was verified using chi-square or *F* test ($\alpha = 5\%$).

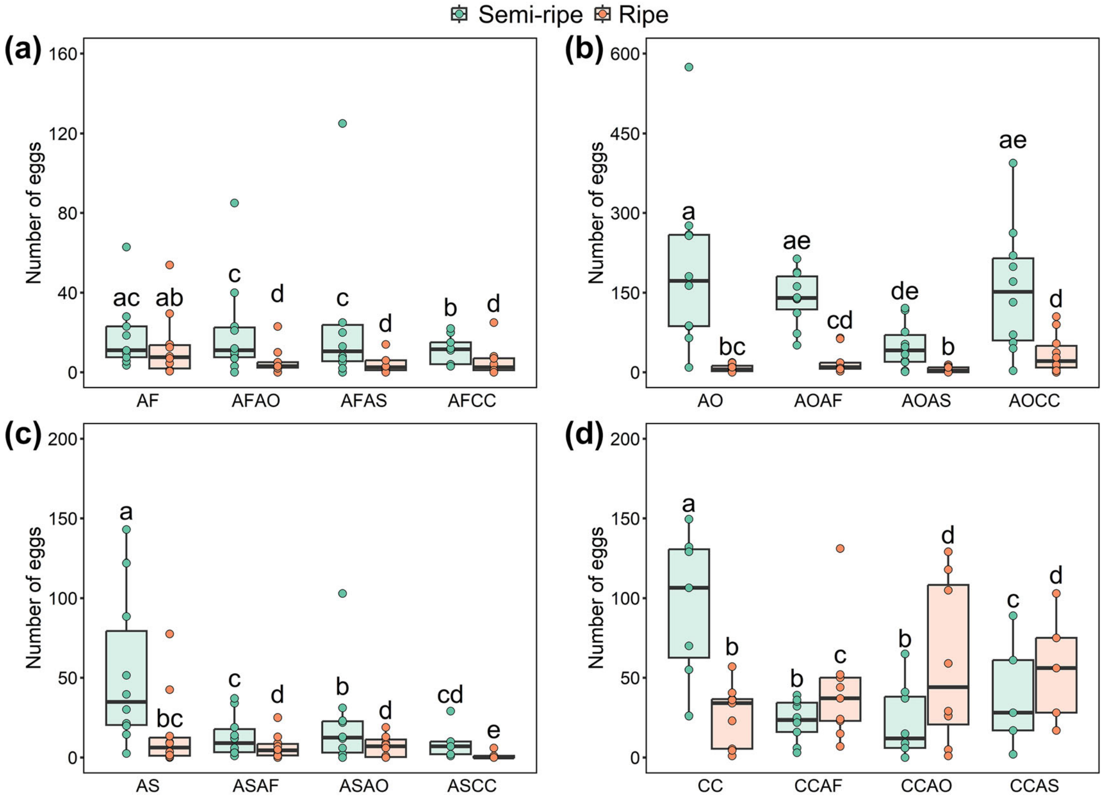

FIGURE 1 Number of eggs laid by females of *A. fraterculus* (a), *A. obliqua* (b), *A. sororcula* (c), and *C. capitata* (d) in intraspecific and interspecific competition scenarios in semi-ripe and ripe guava. The treatments shown in the graph are AF (*A. fraterculus* + *A. fraterculus*), AF + AO (*A. fraterculus* + *A. obliqua*), AF + AS (*A. fraterculus* + *A. sororcula*), AF + CC (*A. fraterculus* + *C. capitata*), AO (*A. obliqua* + *A. obliqua*), AO + AF (*A. obliqua* + *A. fraterculus*), AO + AS (*A. obliqua* + *A. sororcula*), AO + CC (*A. obliqua* + *C. capitata*), AS (*A. sororcula* + *A. sororcula*), AS + AF (*A. sororcula* + *A. fraterculus*), AS + AO (*A. sororcula* + *A. obliqua*), AS + CC (*A. sororcula* + *C. capitata*), CC (*C. capitata* + *C. capitata*), CC + AF (*C. capitata* + *A. fraterculus*), CC + AO (*C. capitata* + *A. obliqua*), CC + AS (*C. capitata* + *A. sororcula*). The data were analysed using a generalised linear model (GLM), assuming Poisson or negative binomial distribution, and the significance of the model was verified using chi-square or *F* test. Comparisons between treatments were made using a Tukey test (α = 5%). Different letters on the top of boxes means statistics differences.

Petitinga et al. (2021) detected a competitive displacement of *A. fraterculus* by *A. obliqua* when both species co-occurred in the same fruit, whether mango or guava. Similarly, Silva et al. (2021) showed that the native species, *A. obliqua*, suffered a partial niche displacement in the presence of the invader *C. capitata* when both competed for the mango at different ripening stages. In the present study, the native species were not displaced by the invader in their preferred host, the semi-ripe guava.

Contrary to *Anastrepha* species, our results showed that *C. capitata* changed its preference for fruit ripening and laid more eggs in the ripe guavas when sharing the fruits with another species.

Some studies presume that the oviposition preference of the female is associated with the fruit type or ripening stage that provides better development for the offspring (Birke & Aluja 2018; Costa et al. 2011; Joachim-Bravo et al. 2001; Joachim-Bravo & Silva-Neto 2004; Ruiz et al. 2015; Sarwar et al. 2013). Previous findings have shown that *Ceratitis capitata* develops; faster than *Anastrepha* species (Bolzan et al. 2017; Duyck & Quilici 2002; Galvão-Silva et al. 2024), which may explain why the native one does not change the preference for semi-ripe fruits, once it would provide their offspring better conditions and food resources. In addition, oviposition in less suitable hosts can occur when the more generalist species are not able to chemically distinguish different fruits as well as the specialist species (Aluja & Mangan 2008; Bernays 2001) or to avoid competition (Akol et al. 2013; Liendo et al. 2018). The present findings on *C. capitata* align with the latter factor regarding interspecific interactions, as this generalist and invasive species has demonstrated the ability to modify its selectivity across different ripening stages. This observation concurs with Williamson (1996), who proposed that invasive species exhibit a broader range of suitable oviposition sites when in the presence of other species.

Despite not changing their oviposition preference, in the present study, *Anastrepha* species tended to decrease oviposition in the presence of other species. This behaviour followed a specific order: *A. obliqua* reduced the number of eggs in the presence of *A. sororcula*; *A. fraterculus* reduced the oviposition in the presence of *C. capitata*; and *A. sororcula* reduced the number of eggs

TABLE 2 Description of agonistic behaviours performed by female fruit flies (*A. fraterculus*, *A. obliqua* and *C. capitata*) in intraspecific and interspecific competition.

Category/ account	Behaviour	Description
Avoidance	Avoidance/Escape	The female approaches the opponent, which was already in the fruit, often facing each other, and then the second to arrive at the oviposition site moves away.
	Avoidance after a failed fight	After the occurrence of one of the aggressive behaviours described below in the table, which does not result in the expulsion of one of the females, the fly that attempted to fight, moves to another location.
	Avoiding those who are threatening	The female turns away from the opponent threatening her (threat position on display).
Aggression	Opens her wings and pushes with her head	The female spreads her wings as a threat and pushes the opponent with her head (she can push the other's head or ovipositor).
	Wing × Wing (AxA)	The female flaps her wing on the opponent's wing.
	Wing × Head (AxC)	The female flaps her wing on the opponent's head.
	Wings × Trunk (AxT)	The female flaps her wings on the opponent's chest.
	Beating with the ovipositor	The female positions herself facing the opponent, poses a threat, and throws her ovipositor over her chest against the opponent.
	Pushes with head and wing	The female pushes with her head and wing (hitting) the opponent.
	Head × Head (CxC)	The female touches or pushes her head on the opponent's head.
	Head × Trunk (CxT)	The female pushes her opponent's chest with her head.
	Flies toward the opponent	The female flies toward the opponent.
	Leans the front leg against the head of the other	The female touches the front leg to the opponent's head.
	Expulsion	The female expels the opponent through some behaviour described above.
Display/ stalking	Stalking	The female approaches the fleeing opponent, possibly to perform a display and/or aggressive behaviour.
	Flapping the wings	When meeting the opponent, the female flaps her wings and flaps its wings and walks to one side and the other simultaneously, like a crab. This behaviour was also described by Pritchard (1969) and may be followed by the 'Movement of attack without touching', described by the same author.
	Attack movement without touching	The female makes an attack movement (e.g., throwing her head forward) without touching the opponent.
	Threat position	The female faces the opponent and spreads her wings perpendicular to the oviposition site (host), lifting the ovipositor.
	Head rotations	The female locates herself facing the opponent and performs rotational movements with her head.

laid in the presence of *A. fraterculus* and *A. obliqua*. Petitinga et al. (2021) observed the same reduction in oviposition when assessing two native species (*A. fraterculus* and *A. obliqua*) in guava and mango, and similar results were described by Silva et al. (2021) which investigated the interaction between *C. capitata* and *A. obliqua*.

The competition for oviposition sites occurs when adults influence each other, altering the occurrence of oviposition behaviour (Davis et al. 2011). This can happen when individuals directly harm one another through agonistic interactions (Denno et al. 1995; Shelly 1999) or indirectly inhibit the oviposition of other females by marking fruits with a deterrent pheromone (Nufio & Papaj 2004). Our study found that agonistic interactions of the display/stalking and aggression types were the most common in interactions between native species and/or between native and invasive species, which were demonstrated by females at similar intensity in all tested combinations. Such results corroborate the hypothesis proposed by Christenson & Foote (1960) that species interact and defend the occupied territory more through aggression than avoidance.

In Tephritidae, the highest frequency of agonistic behaviours occurs among males, as females expend significant energy on oviposition (Aliniazee 1974). Consequently, females adopt behavioural strategies to secure a unique oviposition site, increasing the likelihood of successful egg development by reducing larval competition for food (Aliniazee 1974; Dukas et al. 2001). One such strategy involves the deposition of pheromones after oviposition, signalling an occupied site (Edmunds et al. 2010). However, females also compete for oviposition sites by displaying agonistic behaviours toward other females (display/stalking and aggression types,

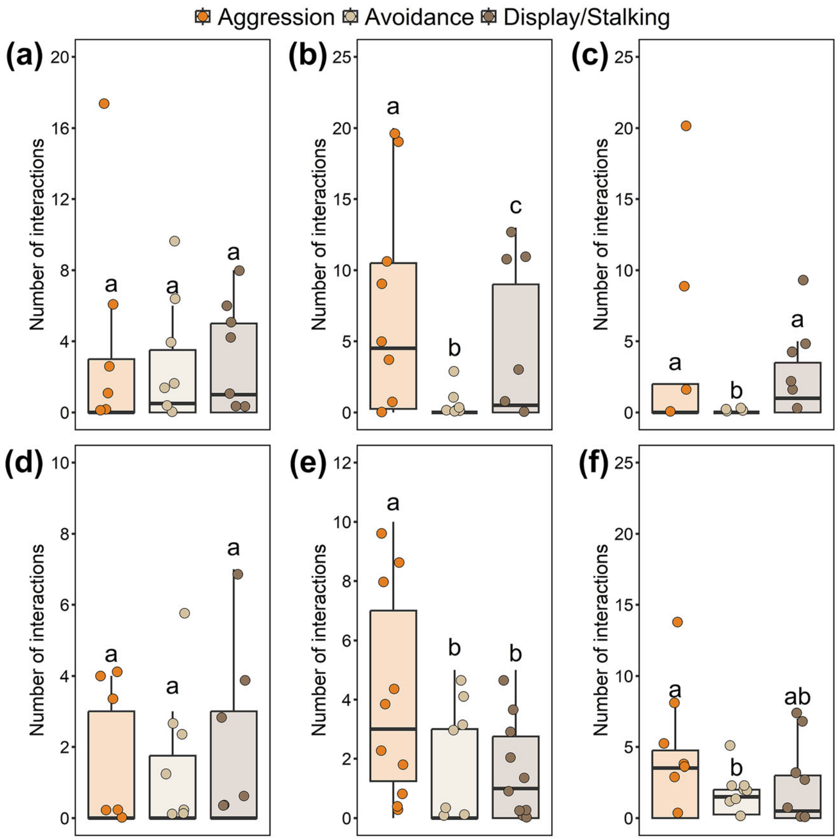

FIGURE 2 Number of intra and interspecific agonistic interactions among females' fruit flies in guava. (a) Conspecific *A. fraterculus*; (b) conspecific *A. obliqua*; (c) conspecific *C. capitata*; (d) *A. fraterculus* + *A. obliqua*; (e) *A. fraterculus* + *C. capitata*; (f) *A. obliqua* + *C. capitata*. Data were analysed using a generalised linear model (GLM), assuming Poisson or negative binomial distribution, and the significance of the model was verified using a chi-square (α = 5%). Pairwise comparisons were made using a Tukey test (α = 5%). Different letters on the top of boxes mean statistical differences between behaviour types in the same combination.

TABLE 3 Results of the generalised linear model (GLM), assuming Poisson or negative binomial distribution, in which the data of agonistic interactions was analysed.

Combination	*df*	χ^2	*p*-value
A. fraterculus + *A. fraterculus*	2	0.883	0.643
A. obliqua + *A. obliqua*	2	70.300	>0.001
C. capitata + *C. capitata*	2	47.454	>0.001
A. fraterculus + *A. obliqua*	2	0.906	0.635
A. fraterculus + *C. capitata*	2	15.777	>0.001
A. obliqua + *C. capitata*	2	11.161	0.003

Note: Combinations between species was modelled as explanatory variables, while the number agonistic interactions were considered a response variable. The significance of the model was verified using a chi-square (α = 5%).

Table 2), often resembling those observed in males (Benelli et al. 2014).

Evidence of agonistic interactions among adults leading to species displacement has been documented. One example is the study by Camargo et al. (1996), in which *A. obliqua* (native species) displaced *C. capitata* (invasive species) from mango in 60.4% of encounters. This displacement may have occurred due to *A. obliqua* being larger than *C. capitata*, as body size influences competition success (Denno et al. 1995). Alternatively, mango may serve as a preferred host for *A. obliqua* (Weens Jr. et al. 2015), conferring a competitive advantage over the invasive species. In another instance, the invasive species (*Bactrocera invadens*) outcompeted the native species (*Ceratitis cosyra*) (Ekesi et al. 2009). In the referenced study, fewer individuals of *C. cosyra* landed and oviposited on mango in the presence of *B. invadens*.

In our study, display/stalking and aggression behaviours occurred more frequently when females were searching for oviposition sites (Aquino J., personal observation). Thus, once in the fruit, either the two ended up ovipositing and sharing the same resource (Benelli et al. 2015; Dukas et al. 2001; Kravitz & dela Paz Fernandez 2015) or the female who arrived later left the fruit, avoiding competition (Benelli et al. 2015; Dukas et al. 2001). Another personal observation (Aquino J.), which corroborates Dukas et al. (2001), is that females, even when encountering another nearby female on-site, preferred to continue this process, as ovipositing is probably more advantageous than expending energy on fights. Probably, in Tephritidae, host marking with deterrent pheromones (HMPs) after oviposition, which serves to inhibit further oviposition by other females (Nufio & Papaj 2001), is likely a more effective strategy for maximising the success of competing species, as it allows them to avoid conflicts and conserve energy for oviposition (Aliniazee 1974; Dukas et al. 2001). Additionally, pheromone marking may function not only to deter individuals of the same species but also to repel other species (Edmunds et al. 2010). In contrast, species that do not employ host marking via pheromones exhibit much more intense interactions among females (Shelly 1999). Thus, in these species, female interference may primarily occur through chemical signals, with active site defence (involving physical displays or direct contact) being less frequent (Fletcher & Prokopy 1991).

In the scientific literature, there is extensive evidence of competition between different species, particularly between invasive and native species, with the former often successfully displacing the latter (David et al. 2017; Davis 2003, 2009; Devescovi et al. 2015; Duyck et al. 2004, 2006; Ekesi et al. 2009).

Following the introduction of *C. capitata* in various regions, such as Central and South America, many species within *Anastrepha* gradually declined in abundance or altered their host utilisation patterns (Duyck et al. 2007; White et al. 2000).

In Brazil, studies analysing the Tephritidae fauna across different regions demonstrate that the comparative abundance relationship between *C. capitata* and *Anastrepha* species is influenced by factors such as geographic location, study periods, proximity to forested areas, and the predominant fruit crops in the studied regions. In guava orchards across different areas of the country, most studies conducted in the early 2000s reported a predominance of *Anastrepha* species over *C. capitata* (Aguiar-Menezes et al. 2008; Azevedo et al. 2010; Bonfim et al. 2007; De Souza et al. 2020; Dutra et al. 2009; Garcia & Lara 2006). Collections near forest fragments (Monteiro et al. 2018; Rabelo 2010; Uramoto et al. 2008) and mixed orchards also showed a predominance of *Anastrepha* species (Santos et al. 2011; Silva et al. 2021). Conversely, in coffee orchards, *C. capitata* was the dominant species (Nascimento et al. 2023; Souza-Filho et al. 2023; Uramoto et al. 2023). However, long-term monitoring in commercial orchards of the São Francisco Valley (Bahia/Pernambuco), the largest irrigated fruit production hub in Brazil, has revealed significant shifts in the relative dominance of these species over time (Nascimento et al. 2023). Data from 1989 to 1997 indicated that *Anastrepha* species and *C. capitata* accounted for approximately 75% and 25% of collected flies, respectively (Haji & Miranda 2000). More recent trap monitoring indicates that 99% of the collected flies belong to *C. capitata* (Paranhos et al. 2023). Supporting these findings, an infestation surveys of fruits from six different species in the São Francisco Valley region, conducted in 2018, demonstrated a significant predominance of *C. capitata* emergence over *Anastrepha* species (Paranhos et al. 2023).

These trends highlight the importance of expanding long-term faunistic analyses across different regions of Brazil to better understand the potential displacement of *Anastrepha* species by *C. capitata* in the field. Experiments such as ours can contribute to clarifying potential interactive behaviours between these species when competing for the same oviposition sites and may reveal emerging ecological trends.

In summary, our findings indicate that *Anastrepha* species exhibit a preference for ovipositing in semi-ripe guavas, maintaining this preference regardless of the presence of conspecifics or *C. capitata*, suggesting that they do not actively avoid niche overlap with the invasive species. Conversely, *C. capitata* demonstrates greater flexibility in its oviposition preference, potentially shifting its choice to mitigate competition with native fruit fly species (Liendo et al. 2018; Silva et al. 2021; Dias et al. 2023). The plasticity exhibited by *C. capitata* may confer a competitive advantage, reinforcing its invasive potential. All species predominantly defend oviposition sites through aggression and stalking behaviours. Additionally, in *Anastrepha* species, interspecific interactions resulted in a reduction in oviposition on their preferred fruit, likely due to agonistic encounters and possibly the deposition of deterrent pheromones, a characteristic trait of this taxonomic group.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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