Host influence on life history traits of *Ceratitis capitata* Wiedemann in an arid region of Argentina

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Abstract

The fruit fly *Ceratitis capitata* is a successful generalist due to the trade-off between different variables in its life history traits. The present study aimed to assess some life history traits of *C. capitata* recovered from peach, plum and fig, three key host species, under the climatic conditions of an irrigation oasis in the arid province of San Juan, Argentina. Pupal abundance, sex ratio and morphometric parameters such as pupal and adult weight, pupal volume, wingspan and head-caudal length were influenced by the host in which the larvae were reared. Sexual maturity, measured as the peak of calling (pheromone emission), was homogeneous on the sixth and seventh days after emergence, but males recovered from fig showed early calling activity on the third day after emergence. The plasticity of *C. capitata* to adapt its life history traits to specific nutrient variations within the larval environment allows it to colonise and establish populations where key hosts, as those studied here, are available. The knowledge of the interactions between host fruit trees and *C. capitata* populations provides helpful information for planning the management of local orchards and urban fruit plantations within irrigation oases, taking into consideration the concept of key hosts as peach and fig.

Introduction

Ceratitis capitata Weidemann, the Mediterranean fruit fly or medfly, belongs to the order Diptera, family Tephritidae. It is a species native to sub-Saharan Africa, but has spread to many countries of America and the Mediterranean region, southern Europe, the Middle East, Western Australia and Hawaii due to the presence of hosts, favourable climatic conditions and human activities (De Meyer *et al.*, 2002; Lanzavecchia *et al.*, 2008; Szyniszewska and Tatem, 2014). It is a successful generalist due to the trade-off between different variables in its life history traits, such as low adult survival rates and high fertility rates, together with a short development time (Krainacker *et al.*, 1987). According to White and Elson-Harris (1992), the *r*-strategy traits of *C. capitata* enable it to maintain a high population growth rate across a wide range of temperature regimes, which could explain its establishment on all five continents.

Therefore, polyphagy and its ability to expand the range of host species have implications for its life history traits (Aluja and Mangan, 2008). In the context of life history theory, the main factors determining the overall adaptation of insect species, i.e. survival, development and final size in the adult stage, are the adaptations during the feeding phase within the host and the quality of the host (Krainacker *et al.*, 1987; Fernandes-Da-Silva and Zucoloto, 1997). Depending on the fruit species available and the fluctuations in *C. capitata* populations, two classes of hosts can be recognised: 'key' and 'non-key' host species. It has been determined that around 350 species belonging to 65 families serve as hosts of *C. capitata* (Mau and Kessing, 2007). The primary host species include the citrus group (*Citrus* spp., with the exception of lemon – *C. limon* – and acid lime – *C. aurantifolia*) and stone fruit trees, such as peach (*Prunus persica*), apricot (*Prunus armeniaca*) and plum (*Prunus domestica*). The presence of various key and non-key host species provides a staggered fruiting sequence, which plays a very important role in increasing the abundance of medfly populations (Krainacker *et al.*, 1987). According to its life cycle, the presence of different host species in each season ensures the population's continuity throughout the year, even when temperatures do not favour its development. Therefore, its polyphagous nature and its ability to expand the range of host species have implications for its life history traits.

Knowledge about the species of fruit flies and their respective seasonality related to the phenology of the host plant is crucial to understand the population dynamics of these insects.

It is known, for example, that the degree of fruit ripening during the oviposition period of the fly influences the fruit infestation level (Messina and Jones, 1990). In addition, differences in foraging can be observed when C. capitata attacks fruits in a certain stage of development. In general, the development time, growth and survival of larvae in different host fruits show considerable variation (Krainacker et al., 1987). The nutritional content of different fruits can also greatly affect the larval development time. The nutritional elements, the texture of the pulp and the secondary compounds determine the host suitability for the life cycle development of C. capitata (Kaspi et al., 2002).

In Argentina, the Monte desert constitutes the most arid environment. In this region, agriculture is practiced in irrigation oases (Abraham et al., 2009). The only economically important fruit flies present in Argentina are C. capitata and Anastrepha fraterculus (Funes et al., 2017). As a part of an integrated pest management programme, the National Service for Food Health and Quality (SENASA) implements the National Program of Control and Eradication of Fruit Flies with the application of the Sterile Insect Technique (SIT). Knowledge of the host influence on the morphological characteristics and sexual maturity of males of C. capitata on a small scale could provide important information to carry out crop management plans at small agroecological ecosystems such as orchards where the SIT is implemented. Thus, the present study aimed to unravel specific life-history traits of C. capitata recovered from key host species – peach, plum and fig – within the unique climatic conditions of an irrigation oasis in the arid province of San Juan, Argentina. Specifically, we explored how the life history traits of C. capitata are affected by the main hosts in arid environments. No previous studies have investigated these traits in medflies reared in different fruits within such arid conditions. This knowledge could lead to more precise strategies for sustainable pest management, especially in small agroecological ecosystems like orchards in irrigation oases where the SIT is used. Our findings may contribute to developing targeted and effective pest management approaches tailored to the specific dynamics of these agricultural settings.

Materials and methods

Study site and sampling

The study was carried out in San Juan province, which is located in the Monte desert of Argentina, where annual precipitation rainfall is less than 100 mm and the mean monthly temperatures of the hottest (January) and the coolest (June) months are 27 and 8.2°C, respectively (Pucheta et al., 2012). According to its vegetation and physiognomy, the biogeographical province of Monte is defined as a xeric biome (Warner and El-Baz, 1979; Roig-Juñent et al., 2001). In this region, agriculture is confined to irrigation valleys where fruits, vegetables and forage crops are grown under intensive agriculture (Abraham et al., 2009). Sampling was carried out in a family orchard, located in the Department of Chimbas. The orchard represents a small-scale model of pest interaction with different hosts. It has an approximate area of 0.5 hectares, with several species of fruit trees, represented mostly by peach (P. persica), bald peach (P. persica var. nucipersica), flat peach (P. persica var. platycarpa), damascus (P. armeniaca), plum (P. domestica) and fig (Ficus carica). The orchard also has some species of pome fruits, such as apple (Malus domestica) and pear (Pyrus communis), as well as persimmon (Diospyros kaki) and kumquat (Fortunella japonica). No pest control was conducted in the orchard for approximately 2 years prior to the study and during its execution.

Sampling was carried out every 15 days with four sampling dates during December and January, to ensure the availability of infested fruits for the three host species selected. Samples were processed according to each measurement described below.

Pupal abundance

To determine the abundance of pupae, fruit trees were chosen at random. The number of trees sampled for each host species selected was as follows: 25 for peach, 20 for plum and 6 for fig. A total of 120 peaches, 120 plums and 60 figs showing evidence of infestation (i.e. with no evidence of larvae abandonment) were collected. Fruits collected from each host were held in acrylic plexiglass boxes (30 cm × 30 cm × 45 cm) with sterilised sand as a pupation substrate under controlled conditions of temperature and humidity (25°C, 60% RH). The sand was sieved every 3 days and the number of pupae present in each sample was recorded. The samples were discarded after five consecutive sievings in which no pupae were recovered.

Pupal development

Pupae recovered from each host species were obtained from the sand sieved every day and the day and number of pupae per host were recorded in each sieving. Pupal development was evaluated as the time (days) elapsed since the larva emerged from the fruit until adult emergence.

Emergence and sex ratio

Ten pupae from each host were arranged inside a volumetric flask, in a total of 20 flasks per host ($n = 20$), under controlled laboratory conditions of temperature and humidity (25°C and 60% RH). Every 1 or 2 days, the number of emerged flies and their sex were recorded.

Pupal weight and morphometric parameters

Groups of five pupae of each host species were weighed in an analytical balance (mg range). The individual weight was recorded as an average per pupa and 20 repetitions were carried out (100 pupae per host). The length and width of each pupa were measured with a caliper. Twenty repetitions were carried out. Pupal volume was calculated with the ellipsoid formula:

$$\text{Vol} = \frac{4}{3}.a.b^2$$

where a is the longest axis and b is the shortest axis of the pupa.

Twenty adult females and 20 adult males emerged from each host were selected. The adults were treated with the cold shock technique. Groups of five adults of the same sex were weighed in an analytical balance and the individual weight was calculated by taking the average per fly. The wingspan (length from wing to wing) and the head-caudal length (total length) of each fly were measured with a caliper (fig. 1). Twenty repetitions were carried out for weight, wingspan and head-caudal length.

Sexual maturity of males

To record the age at sexual maturity of males, 100 individuals per host with 24 h of emergence were selected and placed individually in 180 cm^3 flasks with water and food *ad libitum* under laboratory conditions (25°C, 60% RH and photoperiod of 12 h light–12 h dark). Food consisted of sugar and hydrolysed yeast (3:1). From the first day and up to 30 days after emergence, the number of calling males was recorded daily every 20 min between 9 a.m. and 2 p.m., which are the peak hours of sexual activity.

Statistical analyses

Emergence percentage, pupal abundance and morphometric traits measured in pupae and adults were analysed with the Kruskal–Wallis test at $P < 0.05$. Pupal length, width and volume were analysed with analysis of variance and the least significant difference test at $P < 0.05$, since these variables were normally distributed. The sexual maturity of males was analysed with Kolmogorov–Smirnov test at $P < 0.05$. Morphometric and weight parameters were subjected to Pearson correlations.

Results

The emergence percentages recorded were 71.5% for peach, with a total of 143 flies emerged, 68.3% for plum, with 143 flies emerged and 62.5% for fig, with 134 flies emerged (fig. 2). The emergence percentage showed no significant differences between hosts (H: 1.30, $P > 0.05$).

Pupal abundance was significantly different between hosts (H: 54.61; $P < 0.0001$). Pupae recovered from peach were the most abundant, whereas pupae recovered from plum were the least abundant (fig. 3).

Emergence occurred over a range of days. In the three hosts, more than 70% of the flies emerged between the sixth and the ninth day after the pupa stage. The maximum emergence peaks for peach, plum and fig were the sixth, seventh and ninth days after the pupa stage, respectively (fig. 4). Although the pupae recovered from peach and plum were the first to emerge, a second emergence peak was recorded on the ninth day for both hosts. Significant differences were found in the pupal development time of females between the three hosts (H: 15.08; $P < 0.0004$). The median time for pupal development was 8 days for males
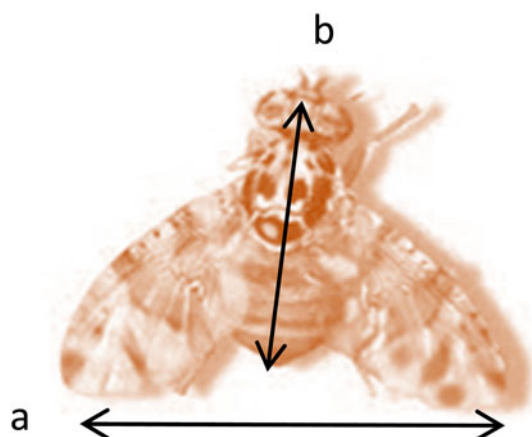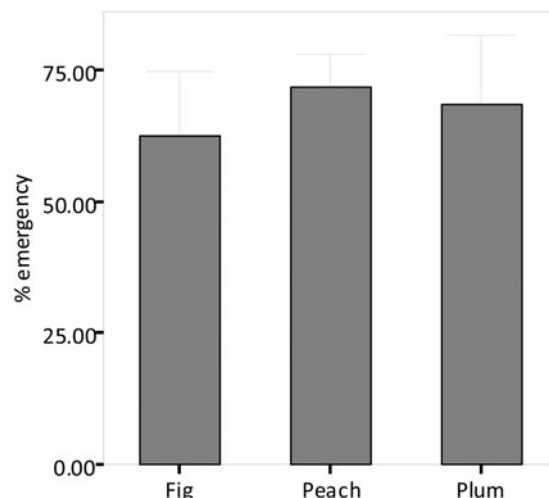

Figure 2. Mean percentage (±SE) of emergence of *Ceratitis capitata* flies from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig).

and females from peach and females from plum, 7 days for males from plum, and 9 days for males and females from fig (table 1).

Regarding the proportion of sexes (fig. 5), the number of males emerged was higher than that of females, resulting in a sex ratio of 1.6 males per female for peach, 1.44 males per female for plum and 1.28 males per female for fig. In peach, the number of emerged males was significantly higher than that of emerged females (H: 17.13; $P < 0.0001$).

The weight of males was lower than that of females ($H = 6.9699$; $P = 0.0073$); whereas the weight of females did not show significant differences between hosts ($P > 0.05$), that of males did (H: 6.36, $P = 0.0353$). Males emerged from fig showed the lowest weight (table 2). Morphometric parameters of pupae and adults showed differences between hosts. The length and width of pupae exhibited significant differences between hosts (F: 4.51, $P = 0.0152$; F: 4.01, $P = 0.0234$, respectively). Pupae from peach had the shortest length, whereas pupae from plum showed the

Figure 1. Morphometric parameters taken in adults of *Ceratitis capitata*. (a) Wingspan (length from wing to wing), (b) head-caudal length.
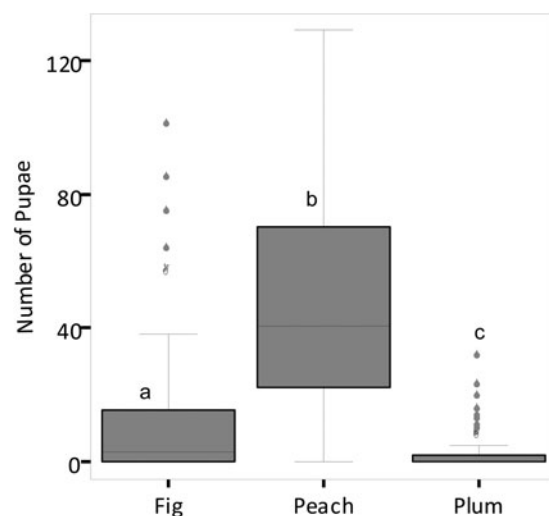

Figure 3. Box plot of number of *Ceratitis capitata* pupae recovered from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig). Symbols over the box plot are outliers.
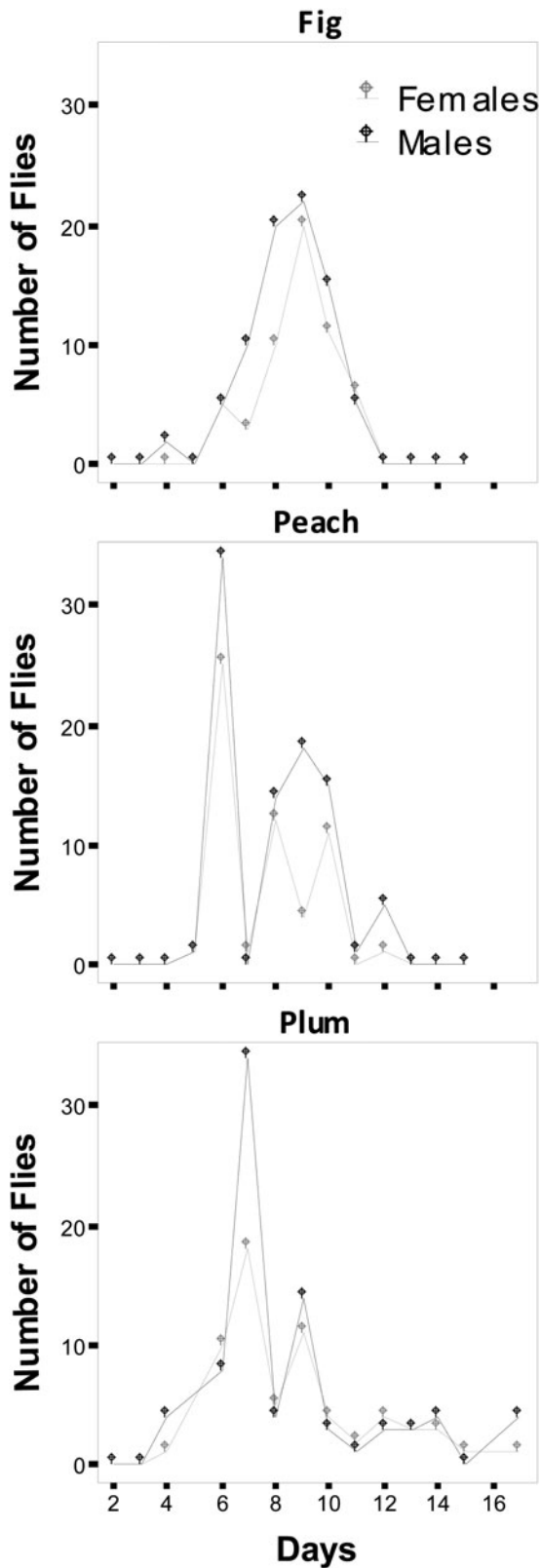
Figure 4. Mean (±SE) number of males and females of *Ceratitis capitata* emerged from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig).

Table 1. Pupal development of *Ceratitis capitata* (in days) reared in *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig)

Host	Sex	Median	Min	Max
Peach	♀	8[a]	5	12
	♂	8	5	12
Plum	♀	8[b]	4	17
	♂	7	4	17
Fig	♀	9[b]	6	11
	♂	9	4	11

Different letters within a column show significant differences between hosts at $P < 0.05$.

length of females showed differences between hosts (*H*: 15.08, $P = 0.0005$; *H*: 18.93, $P = 0.0001$). Females emerged from fig showed the smallest wingspan, whereas those emerged from plum showed the shortest head-caudal length (table 2). The head-caudal length of males also showed significant differences between hosts (*H*: 16.02, $P = 0.0003$). The longest head-caudal length was that of males emerged from fig (table 2). The head-caudal length of females correlated negatively with the volume of pupae and wingspan of females ($r = -0.32$, $P = 0.01$ and $r = -0.27$, $P = 0.04$, respectively).

Males emerged from plum and fig showed a peak of phero-mone emission (calling activity) on the fifth day after emergence, whereas males from peach showed a peak of emission on the sixth day after emergence (fig. 6). Males from fig showed two secondary peaks of emission, the first on the third day after emergence and the second on the eighth and ninth days after emergence. However, there were no significant differences in the sexual maturation of males from the different host species ($P > 0.05$).

Discussion

In the present study, we evaluated the influence of cultivated peach, plum and fig as the primary hosts of *C. capitata* in an arid region of Argentina on various life history traits of pupae

longest width (table 2). The volume of pupae also showed significant differences between hosts ($F = 5.13$, $P = 0.0089$). Pupae from plum showed the highest volume. Wingspan and head-caudal
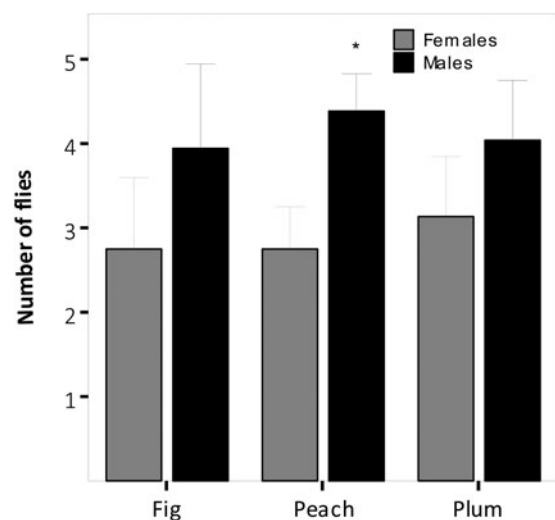

Figure 5. Number of adults of *Ceratitis capitata* emerged by sex from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig).

Table 2. Mean (±SD) weight, and morphometric parameters of pupae (length, width, volume), males and females (wingspan, head-caudal length) of *Ceratitis capitata* obtained from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig)

Host	Pupae				Females			Males		
	Weight (mg)	Length (mm)	Width (mm)	Volume (mm^3)	Weight (mg)	Wingspan (mm)	Head-caudal length (mm)	Weight (mg)	Wingspan (mm)	Head-caudal length (mm)
Peach	8.8 ± 0.8	4.48 ± 0.25[a]	2.02 ± 0.19[a]	77.50 ± 18.46[a]	6.3 ± 0.7	8.04 ± 0.67[a]	5.14 ± 0.46[a]	5.9 ± 1.0[a]	6.95 ± 0.98	4.42 ± 0.32[a]
Plum	9.3 ± 2.0	4.73 ± 0.24[b]	2.19 ± 0.21[b]	96.20 ± 21.69[b]	6.1 ± 1.3	8.23 ± 0.65[a]	4.72 ± 0.42[b]	5.7 ± 0.7[a]	6.96 ± 0.63	4.64 ± 0.45[a]
Fig	8.8 ± 1.6	4.67 ± 0.31[b]	2.06 ± 0.18[a]	83.84 ± 15.69[a]	5.5 ± 1.3	7.27 ± 0.84[b]	5.51 ± 0.50[c]	4.9 ± 1.1[b]	7.30 ± 0.63	4.98. ± 0.39[b]

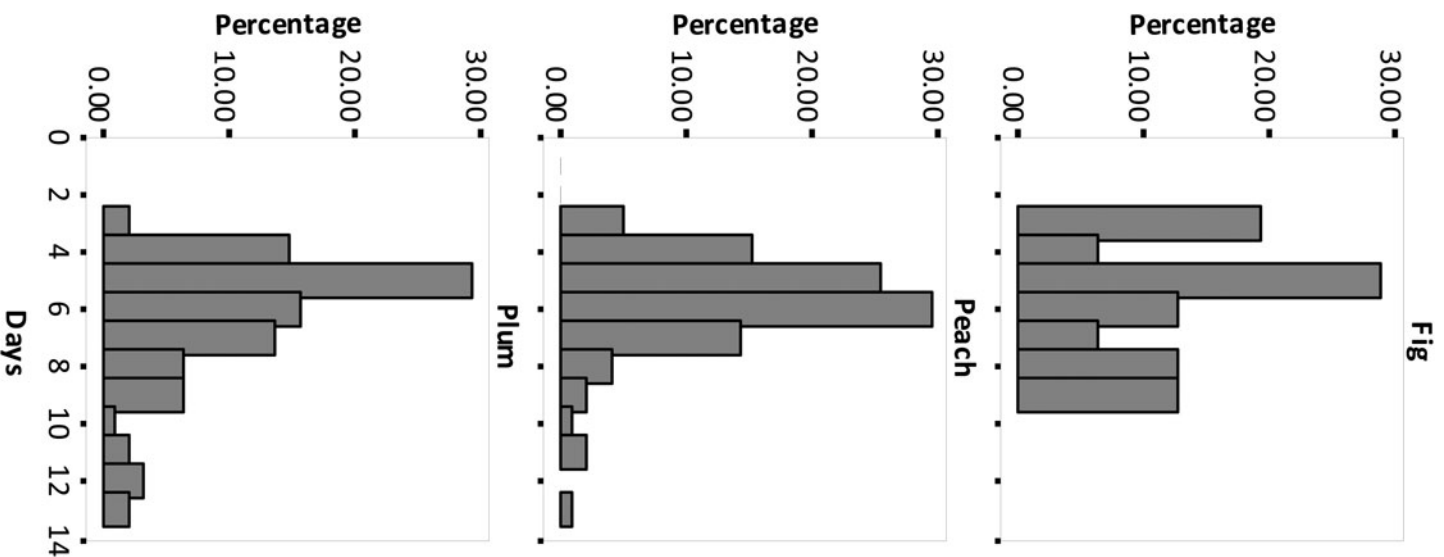Different letters within a column show significant differences between hosts at $P < 0.05$.

Figure 6. Percentage of calling males of *Ceratitis capitata* emerged from *Prunus persica* (peach), *Prunus domestica* (plum) and *Ficus carica* (fig).

and adults. Pupal abundance and development, sex ratio and morphometric parameters were influenced by the host species.

Unlike pupal abundance, adult emergence was not influenced by the host. The highest pupal abundance was recorded for peach and fig. These results are in accordance with those of Segura *et al.* (2004), who identified peach as a key host of *C. capitata* and as the host that contributed the most to the pupal population. These authors also identified fig as the second largest contributor

to pupal abundance (Segura et al., 2004). In Argentina, fig is one of the last available and one of the most preferred hosts in the summer season. This fruit could serve as a source of energy for metabolic processes necessary for the transition to autumn and winter, when the population is synchronised with a lower availability of hosts.

The short periods of pupal development here recorded for peach, plum and fig are notably different from those reported by Carey (1984). However, our results agree with those of Krainacker et al. (1987) for the same hosts as well as with those of Beddiaf et al. (2022) for fig. Pupal development is influenced by the larval diet (Kaspi et al., 2000). The nutrients acquired from the diet are essential for development and determine how organisms can maximise their fitness (Nash and Chapman, 2014). Larvae fed on fruits with a higher concentration of proteins experience a shorter development period (from egg to adult), whereas larvae fed on hosts with a higher concentration of sugars undergo a longer development period. In the present study, the pupae recovered from plum and peach presented shorter development and a greater number of emerged individuals, whereas those from fig showed the longest pupal development and a lower number of emerged adults, suggesting that pupal viability in fig was lower. The main sugars in fig are glucose and fructose (Veberic and Mikulic-Petkovsek, 2015). Previous studies in Juglans australis have shown that the sugar content in this fruit correlates with the larval development of C. capitata and that the glucose content specifically affects adult emergence and infestation (Oroño et al., 2019). On the other hand, peach is a rich source of amino acids such as asparagine, aspartic acid, glutamic acid, alanine and glutamine (Zhang et al., 2022). These amino acids, along with other essential and non-essential amino acids, have been shown to impact the survival, larval development and fecundity of C. capitata (Chang, 2004). Thus, proteins and amino acids contributed by peach have a great effect on the survival of the larval stage, while carbohydrates, as those from fig, influence survival during the pupal stage (Nash and Chapman, 2014).

Under experimental conditions, the sex ratio of C. capitata is influenced by temperature, shifting the 1:1 ratio of males to females in favour of the latter (Muñiz and Gil, 1984). In the present study, males and females emerged from peach showed significant differences in favour of males. In C. capitata, the shift from the 1:1 male:female ratio in favour of the former is an expected result under certain temperature conditions. Previous studies have shown that, when the temperature at the onset of meiosis is reduced from 26 to 18°C, the proportion of males increases significantly (Shahjahan et al., 2006). On the other hand, our results do not agree with those of Beddiaf et al. (2022), who found that the sex ratio of C. capitata from fig, pomegranate and mandarin is higher for females. A sex ratio favouring males, as here observed in peach, may suggest the need to increase the number of sterile males to be released. This is due to the fact that, in competition with wild males, sterile males generally exhibit lower sexual competitiveness (Shelly et al., 2004; Jofre Barud et al., 2022). Therefore, achieving an effective balance in the population of sterile males released becomes critical to ensure a sufficient representation of these males to successfully compete for mating opportunities with wild females. Thus, the release of sterile males during the peach season in agroecosystems such as that studied here should consider this concept.

Host fruit influences the morphology of insects. The distances between corresponding landmarks on the wings of C. capitata are highly significant among individuals that were reared on nectarine, plum, apple and pear. In addition, C. capitata presents sexual dimorphism for the wing shape (Pieterse et al., 2017). In our study, females had a longer wingspan than males, and the host fruits influenced the wingspan of females. These data agree with those found by Navarro-Campos et al. (2008, 2011), who showed that the wing size of C. capitata varies according to the fruit used as host (apricot, peach, plum and orange) and differs between males and females. The changes in wing shape might be a function of the plasticity of the species and might be related to the host influence on mating success and male competitiveness (Pieterse et al., 2017).

In the present study, pupae from plum showed the highest weight and largest volume, whereas the adults had an intermediate weight and an intermediate wingspan compared to the adults of other hosts. The negative correlation between pupal volume and female wingspan indicates that pupal volume was not a good predictor of larger adult size. Here, we found that larger adults (as indicated by the head-caudal length) were those from fig. The effects of the diet on body size could be mediated through alterations in the quantity of nutrients stored as lipids and proteins prior to pupariation (Nash and Chapman, 2014). Critical weight, which is a point reached during the exponential growth rate of the final larval instar, when the process of pupation begins, allows an insect to adapt the rate of its development to different nutritional environments to optimise key adult traits, such as body size. This trade-off between development time and body size is consistent with the endocrinological control model of holometabolous development (Nash and Chapman, 2014). In addition, the body size of C. capitata is influenced by temperature, with lower temperatures producing larger adults (Navarro-Campos et al., 2011). Thus, the body size variation here observed in C. capitata could be the outcome of the influence of the host fruit species and the temperature during larval development since peach and plum are fruits of midsummer while fig is available at the end of the summer season.

Regarding the sexual maturity of C. capitata, Kaspi et al. (2002) found that the male size does not influence the onset of calling. However, they also found that the calling age is influenced by the protein and sugar concentrations of the larval diet (Kaspi et al., 2002). Males fed protein diets start calling earlier than males fed diets with sugar and deprived of protein. In the present study, males from fig showed a peak of calling activity on the third day after emergence. However, most of the males from the three hosts were sexually mature at the same age (fifth and sixth days after emergence). According to previous studies, the larval diet determines the adult mating success, since adults reared on poor diets suffer reduced fitness (Nash and Chapman, 2014). However, the adult foraging ability to find protein sources also influences the mating success. Males with access to protein resources are more likely to participate in leks than males deprived of proteins (Kaspi et al., 2000). Given the importance of protein in the sexual maturity of males, it seems that a nutritional threshold is needed and that nutrients can be derived from both the larval and adult diets (Kaspi et al., 2002). The sexual maturity of sterile males is important for sexual competitiveness and must be considered when a pest management programme based on the SIT is implemented. Sterile males typically start calling on the fourth day after emergence (Kaspi et al., 2002; Jofré-Barud et al., 2022). Given the multivoltinism of C. capitata, where individuals of different ages coexist under field conditions, it becomes important to adhere to a schedule of two releases per week. This becomes especially important when key

host fruits, as those studied here, are taken into account, emphasising the significance of management measures tailored to the specific life history traits (i.e. sexual maturity and pupal abundance) associated with these crucial hosts.

Effective management of this pest requires a multifaceted approach, as relying on a single method is insufficient. Integration of various methods, including mechanical, cultural, behavioural, chemical and biological control, as well as host plant resistance mechanisms, is essential (Ganie *et al.*, 2022). Successful control of *C. capitata* is achieved through collaborative efforts between orchard owners and official measures. In Argentina, orchard owners play a crucial role in implementing mechanical and cultural control measures. On the other hand, official programmes, such as area-wide integrated pest management, address the broader pest control context by focusing on behavioural, chemical and biological control and using the SIT. Coordination between these complementary strategies enhances the overall efficacy of *C. capitata* control programmes. The results found in the present study highlight the importance of adopting a specific and localised approach for fruit fly control in the arid regions of Argentina. Focusing management strategies on key hosts, especially on peach and fig, can maximise the effectiveness of interventions, addressing critical points of reproduction and development. This tailored approach may optimise control and may have positive implications for production and associated costs in family orchards in irrigation oases and similar areas.

In summary, a deeper understanding of the interactions between host fruit trees and *C. capitata* populations is crucial to formulate effective strategies in local orchards within irrigation oases. The plasticity of *C. capitata*, due to its generalist nature, allows it to exploit a wide range of host trees. However, the identification of key hosts is crucial to ensure successful development while adapting to specific nutrient variations within the larval environment. Understanding the life cycle and key traits of *C. capitata* may facilitate targeted interventions that enable pest management practices during critical stages, such as larval development, thereby gaining advantages over population growth. Recommendations may include timing insecticide applications, removing infested fruits, and adopting cultural practices to disrupt the life cycle of the fly. By incorporating the concept of key hosts such as peach and fig into management strategies, orchard owners can optimise pest control efforts, improving production and reducing associated costs.

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