The relationship between adult preference and offspring performance in the invasive tephritid species, *Dacus frontalis*, of wild and cultivated cucurbitaceous hosts at different stages of fruit maturity

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Abstract

Dacus frontalis (Diptera:Tephritidae), is an emerging pest that causes damage to fruit in Africa and now represent a threat to Cucurbitaceae production in Europe. Understanding interactions between *D. frontalis* and host plants is important to improve pest management and prevent their invasions in areas where this pest is not yet established. In this study, female preference and larval performance of *D. frontalis* with regard to wild and cultivated Cucurbitaceae species at different stages of fruit maturity (green, intermediate, and ripe) were examined. Host plant quality, species, and fruit maturity play a major role in oviposition preference under both choice and no-choice conditions. They also influence larval performance (larval survival, development time, and pupal weight). Larval survival rates differed significantly between fruit species and different stage of fruit maturity, ranging from 0.2% to 0.7% in the case of ripe melon and green Bitter apple, respectively. Larval performance was higher in fruit with low soluble sugar, such as green bitter apple. Results revealed that *D. frontalis* has distinct ovipositional preferences for the cucurbitaceous host plants tested, with a clear preference for cultivated fruit compared with wild fruit. In cultivated cucurbitaceous fruit, the highest number of eggs was laid on the oviposition device containing green cucumber (48 eggs/female) and the lowest on that containing green melon fruit, where there was no oviposition. Females of *D. frontalis* were able to choose fruit for oviposition that promoted high larval performance, such as cucumber, pumpkin, zucchini, and watermelon particularly at the green stage. This behaviour reveals a positive preference–performance relationship. Predicting the interactions between exotic insects and their potential host plants is important for preventing invasions using Pest Risk Analyses and associated quarantine procedures.

Introduction

Biological invasions of exotic insects represent a major challenge for both natural and human-altered ecosystems. They seriously impact biodiversity (Pimentel *et al.,* 2000), and are considered to be one of the main features of global change (Vitousek *et al.,* 1997). Invasive species represent a growing threat to world food security and the global economy due to their negative effects on agriculture (Eschen *et al.,* 2021). Despite the implementation of strict quarantine measures, numerous tephritid fruit fly invasions have been reported worldwide (Duyck *et al.,* 2022). The Tephritidae family is therefore the subject of many Pest Risk Analyses (PRA). *Dacus frontalis* (Becker, 1922) (Diptera: Tephritidae) is an invasive species affecting fruit production in Africa (AL-Jorany, 2013; El Harym and Belqat, 2017; Hafsi *et al.,* 2015). In recent years, climate warming has reduced climatic barriers to pest establishment. Consequently, *D. frontalis* has gradually spread, expanding its geographical distribution from Mediterranean regions, such as Tunisia and Algeria, to other areas (Elghadi and Port, 2019; Foottit and Adler, 2009; Hafsi *et al.,* 2015). Though not yet established, this tephritid species was recently intercepted recently in Europe and classified as a regulated species in the European Union (Rousse *et al.,* 2024). Global warming creates suitable environmental conditions for the translocation of *D. frontalis* from tropical areas to temperate regions, previously thought to be too cold to allow population persistence. Thus, it has emerged as a serious pest that threatens Cucurbitaceae production in temperate regions (Hafsi *et al.,* 2024, 2015; Rousse *et al.,* 2024).

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In of the event of invasions by phytophagous insects, the question of predicting host range is particularly important (Bellamy *et al., 2013*). The establishment of new exotic phytophagous insects in new regions could mitigated by the successful implementation of integrated pest management (Walsh *et al., 2011*). A better understanding of host specialisation and the varietal susceptibility of the preferred host crops could help predict which plants are likely to be attacked by a given pest. This is particularly important from an applied perspective given that in complex cropping systems, there is often a variety of different available hosts.

In most phytophagous insects, larvae are often less mobile than adults. Thus, the success of larval development depends on the quality of the plant chosen by the adult (Jaenike, 1978). Female have access to many different resources of variable nutritional value for larvae. Therefore, we would expect high selection pressure for female oviposition behaviour to maximise offspring fitness (Jaenike, 1978). This scenario has often been considered in the context of the preference–performance hypothesis (PPH) also known as the 'mother knows best' principle (Jaenike, 1978; Valladares and Lawton, 1991). Although the PPH predicts a positive correlation between female oviposition preference and larval performance, this is not always the case (Keeler and Chew, 2008). Investigating the relationships between the host fruit species and *D. frontalis* oviposition behaviour and offspring performance could further our understanding of the insect–plant interactions underlying successful establishment on a host plant in a new environment.

In the field, female preference and larval performance are affected by a variety of biotic and abiotic factors. These include chemical and visual cues, natural enemy avoidance, plant nutrient compounds, and secondary metabolites, as well as the nutritional requirements linked to the insect life stages (Thorsteinson, 1960; Webster and Cardé, 2017). In tephritid species, host selection behaviour may be affected by the pericarp firmness, fruit odour, colour, and shape (Brévault and Quilici, 2007; Jaleel *et al., 2019*). While visual and tactile stimuli are important in female choice (Balagawi *et al., 2005*; Piñero *et al., 2006*), olfaction is primarily used to locate host plants (Dalby-Ball and Meats, 2000). In addition, the nutritional status, toxins and secondary metabolites of the host can affect offspring fitness and fruit fly development (Balagawi *et al., 2005*; Rattanapun *et al., 2009*; Hafsi *et al., 2016*). Host fruit provide tephritids with an array of vital resources. In particular, carbohydrates and lipids represent key aspects of fruit composition, which are known to affect larval survival in polyphagous and oligophagous tephritid species (Awmack and Leather, 2002; Hafsi *et al., 2016*).

Few studies have explored interactions between *D. frontalis* and its host plant, and only adult emergence from field-collected fruits has been monitored (AL-Jorany, 2013; Elghadi and Port, 2019; Hafsi *et al., 2015*; White and Elson-Harris, 1992). The present study examined the relationship between female preferences and larval performance in *D. frontalis*, based on a confirmed protocol developed in previous studies (Charlery de La Masseliere *et al., 2017*; Hafsi *et al., 2016*; Lauciello *et al., 2024*). The first step was to study the oviposition behaviour and larval performance of a Tunisian population of *D. frontalis* on wild and cultivated cucurbitaceous fruit present in Tunisia. The phenology and correlated nutrient composition of different cucurbit fruit species on host specialisation of *D. frontalis* was then analysed. The general patterns observed for this specialist phytophagous insect were analysed in the light of the PPH.

Materials and methods

Insect rearing

The initial colony of *D. frontalis* was obtained from infested cucumber fruit (*Cucumis sativus* L.) collected in the field in the Kairouan area (Tunisia) in 2015. Insects were then reared at Laboratory of Entomology at High Agronomic Institute of Chott-Mariem (Tunisia). Prior to the start of the experiments, *D. frontalis* flies were reared for five generations in Perspex rearing cages (90 × 90 × 90 cm). the cage had a cloth sleeve opening at the front and were maintained under controlled conditions (photoperiod:12:12 L:D; temperature: 25 ± 1°C and relative humidity: 70%), in climatic chambers using non-infested cucumber fruit as described in Hafsi *et al* (2024). The adult flies were fed on a protein: sugar mix (3:1) media and water was provided *ad libitum*. Adult flies were provided with fresh non-infested cucumber fruits for laying their eggs. Infested fruit was removed from cages after 24 h, placed in plastic containers with sand at the bottom as a pupation, and kept till pupation. Resulting pupae were sieved using a mesh screen and kept in a new cage for emergence.

Experimental fruit species

Female oviposition and larval performance experiments were conducted to assess the preference–performance relationship using five cultivated (zucchini, cucumber, pumpkin, melon, and watermelon) and two wild Cucurbitaceae (squirting cucumber and bitter apple) host plant species (Table 1). This choice aligned with White and Elson-Harris (1992), who indicated that these host fruit species might be suitable host for egg laying and for the larval development of *D. frontalis*. The chosen cultivated host plant species were planted and grown in a greenhouse on the farm of the High Agronomic Institute of Chott-Mariem (Tunisia), using an organic crop production system to produce healthy undamaged fruit. Plants were watered regularly, as required, and no additional fertiliser was added. We did not use transgenic fruit species in the experiments. No insecticide treatments were applied to seeds or plants. Undamaged wild fruit was collected in the field during the fruiting season and examined in the laboratory for the presence of tephritid larvae and oviposition puncture.

Three classes of each fruit species were categorised as a function of their phenological maturity stage, as described in Table 1. The 'green' category represented all fruit at 3–5 days after fruit setting, and was characterised by lower weights. The 'intermediate' category included all fruit of 15–18 days after fruit setting and was characterised by medium weights. The 'ripe' category regrouped all fruits at ripening stage, characterised by higher weights. For wild Cucurbitaceae fruit species, experiments were only conducted with green and intermediate fruit because ripe fruit could not be collected at that time of year, for logistical reasons. Ten fruit per host species and per phenological stage of maturity (Table 1) were selected and measured for weight, size, water, and sugar content. Fruits were weighed using a standard electronic digital precision balance (Sartorius, CP64). Sugar content was measured from a drop of fruit juice, collected from mixed fruit pulp, using a handheld refractometer (COMECTA® NR 151 Mod. Spain).

Larval performance

The larval performance of *D. frontalis* was studied on seven fruit species using forced infestations. For each replicate, fruit was

Table 1. Weight, water content, and total suspended solids (TSS) ($n = 6$) of the five cultivated and the two wild Cucurbitaceae host–plant species according to their phenological stage of maturity

| Fruit status | Common name | Scientific name | Host fruit maturity | | | | | | | | |
| | | | Green | | | Intermediate | | | Ripe | | |
			Weight (g)	*Water content (%)*	*TSS (Brix)*	*Weight (g)*	*Water content (%)*	*TSS (Brix)*	*Weight (g)*	*Water content (%)*	*TSS (Brix)*
Cultivated	Zucchini	*Cucurbita pepo* L.	23.10 ± 9.8	92.3	3.06 ± 0.38	42.1 ± 13.5	93.85	4.89 ± 0.64	83.8 ± 13.5	94.80	5.56 ± 0.43
	Cucumber	*Cucumis sativus* L.	19.7 ± 5.43	96.7	3.09 ± 0.42	31.5 ± 9.4	95.94	3.82 ± 0.64	65.8 ± 8.7	95.26	4.28 ± 0.78
	Pumpkin	*Cucurbita maxima (Duchesne)*	33.0 ± 2.6	91.6	3.94 ± 0.27	162.6 ± 10.1	96.29	5.22 ± 0.25	382.5 ± 14.6	97.86	5.04 ± 0.28
	Melon	*Cucumis melo* L.	49.7 ± 15.1	94.2	3.34 ± 0.57	115.7 ± 17.2	98.17	4.73 ± 0.15	246.9 ± 28.2	98.46	6.93 ± 0.25
	Watermelon	*Citrullus lanatus (Thunb.)*	50.1 ± 16.4	95.3	3.03 ± 0.46	162.7 ± 20.3	97.13	4.16 ± 0.42	353.1 ± 87.4	97.72	5.78 ± 0.44
Wild	Squirting cucumber	*Ecballium elaterium* L.	6.33 ± 1.4	70.2	3.13 ± 0.45	12.3 ± 2.1	72.75	3.93 ± 0.49	–	–	–
	Bitter apple	*Citrullus colocynthis* L.	24.6 ± 5.5	87.5	2.03 ± 0.75	38.6 ± 15.2	91.29	2.43 ± 0.95	–	–	–

weighed and washed, then small incisions (size: $1.5 \times 0.2 \times 0.2$ cm) were made randomly at the surface to allow the introduction of the neonate larvae (<2 h old) into the pulp. The neonate larvae were carefully introduced, using a fine brush and a binocular microscope (Leica® EZ4, Germany). Larvae density was adjusted according to host fruit weight, i.e. one larva per 10 g of fruit, to avoid intraspecific competition according to preliminary data. Each infested fruit species was set in a shallow pan with sand. Pan size different depending on the size of the tested fruit. The pan was then covered with a cloth sleeve to allow pupation. Ten replicates of each fruit species were carried out. Since temperature has a pronounced influence on tephritid larval development (Duyck and Quilici, 2002), all the experiments were conducted in environmental chambers at a constant temperature of 25°C. Larval performance was measured in term of larval survival, larval duration, and pupal weight. Every 48 h, all cups were checked to collect pupae. Larval survival was recorded as the number of pupae recovered from each host. Larval duration was estimated by the time taken from inoculation to pupation. Each individual pupa was weighted using a precision balance (Sartorius® Germany, accuracy: 10^{-4} g). A single performance trait combining the three larval life history traits (survival × pupal weight/developmental duration) (Facon *et al.*, 2021; Lauciello *et al.*, 2024), was used as a measure of larval performance. Thus, we were able to study the correlation between larval performance and fruit nutrient status and compare female preference.

Female preference

The female preference of *D. frontalis* was tested for the seven host fruit species, using choice and non-choice experiments (Charlery de La Masseliere *et al.*, 2017). Female preference was only tested in relation to olfactory cues (volatile fruit emissions), using artificial oviposition devices. These consisted of yellow table tennis balls (4 cm diameter), cut in half and pierced with 48 evenly spaced holes (approximately 0.9–1.2 mm), inserted into a plastic base of suitable diameter. Before each experiment, all devices were washed with a detergent (TFD4, Dominique Dutscher SAS, Brumath, France), rinsed with water, and dried. For oviposition preference, mated females aged 20–30 days were used. Females were fed on a sugar and yeast diet. Water was provided *ad libitum* during the experiments.

Oviposition preference in the non-choice experiment: This trial was performed using five cultivated fruit at three stages of maturity and two wild fruit species at two stages of maturity. For each replicate, five gravid *D. frontalis* females were placed in a cubic cage ($30 \times 30 \times 30$ cm), which contained two egg-laying devices for 24 h. One device contained a piece of fruit, including pulp and peel, while the other was empty and was considered the negative control, since no eggs were found in these devices. A piece of wet yellow sponge was put between the two devices to avoid dehydration. Eggs laid in the different devices were collected after 24 h and counted to assess the oviposition preference regarding the seven host fruit tested. For each fruit species combination, six replicates were conducted.

Oviposition preference in a choice experiment: This trial was performed on the seven cultivated and wild fruit species in the green category. Ten *D. frontalis* females were placed in a cubic cage ($90 \times 90 \times 90$ cm) with seven devices containing a piece of fruit from a different species and an empty device (a negative control). After 24 h, eggs in each device were counted. This experiment was conducted with 12 replicates.

Statistical analysis

All statistical analyses were carried out using R version 3.6.1. (R Development Core Team, 2008). The normality and homogeneity of all data were checked using the Shapiro–Wilk and Bartlett tests, respectively. Larval performance: survival, development time, and pupal weight were analysed using the two-way ANOVA as a function of host fruit species, stage of maturity and interaction between these two variables.

Larval performance and water or soluble sugar contents relationships were fitted with a linear mixed model (estimated using REML and nloptwrap optimiser), including fruit species and maturity stage as random effects.

Female preference: the number of eggs laid in choice and non-choice tests was analysed using the generalized linear model (GLM) with Poisson error (Log link), as a function of fruit species and/or the stage of fruit maturity. The number of eggs laid under no choice conditions was used as an estimate of oviposition preference. A Poisson log-linear model (analysis of deviance with Poisson error), was used to analyse preference–performance relationships between larval performance and female oviposition (expressed by the number of eggs) on the same fruit and maturity. Overdispersion was accounted for using a quasi-Poisson model, rather than a Poisson model in R (O'Hara and Kotze, 2010).

Results

Larval performance

Larval survival rates differed significantly depending on the fruit species ($F_{6, 6267} = 85.1$, $p < 0.001$) and fruit maturity stage ($F_{2, 6267} = 334.6$, $p < 0.001$). The interaction between fruit species and stage of maturity was also significant ($F_{12, 6267} = 16.2$, $p < 0.001$) (fig. 1A). Larvae of *D. frontalis* were able to survive on all tested cucurbitaceous species, with exception of squirting cucumber. *Dacus frontalis* had a larval survival rate ranging from 2% to 75%, with the highest survival rate observed on the two maturity stages of bitter apple. The comparison between the different stages of fruit maturity in the same host fruit species revealed that the highest survival rate for *D. frontalis* was on the green category.

Pupal weight differed significantly between fruit species ($F_{5, 1410} = 79.8$, $p < 0.001$) and between the different stages of host fruit maturity ($F_{2, 1410} = 63.2$, $p < 0.001$). The interaction between fruit species and the stage of fruits maturity was also significant ($F_{8, 1410} = 7.2$, $p < 0.001$) (fig. 1B). The lowest pupal weights (75.97×10^{-4} g) were observed on bitter apple, which also had the highest survival rates. In cultivated cucurbitaceous fruit, the pupal weight of *D. frontalis* was highest on melon and zucchini. When comparing the different stages of maturity for the same host fruit species, *D. frontalis* had the highest pupal weight (173.29×10^{-4} g) on the green category of pumpkin, zucchini, melon, and watermelon.

The larval development period differed significantly between fruit species ($F_{5, 1410} = 95.1$, $p < 0.001$) and between the different stages of fruit maturity ($F_{2, 1410} = 66.8$, $p < 0.001$). The interaction between fruit species and the stage of fruit maturity was also significant ($F_{8, 1410} = 11.2$, $p < 0.001$) (fig. 1C). In our trial, *D. frontalis* larvae had significantly longer development time on the wild cucurbitaceous fruit species compared to the cultivated fruit species (fig. 1C), with the exception for cucumber. Regarding the different stage of maturity of the same fruit species, the larval development time (fig. 1C) of *D. frontalis* was significantly shorter for the green category than for the intermediate and ripe categories.
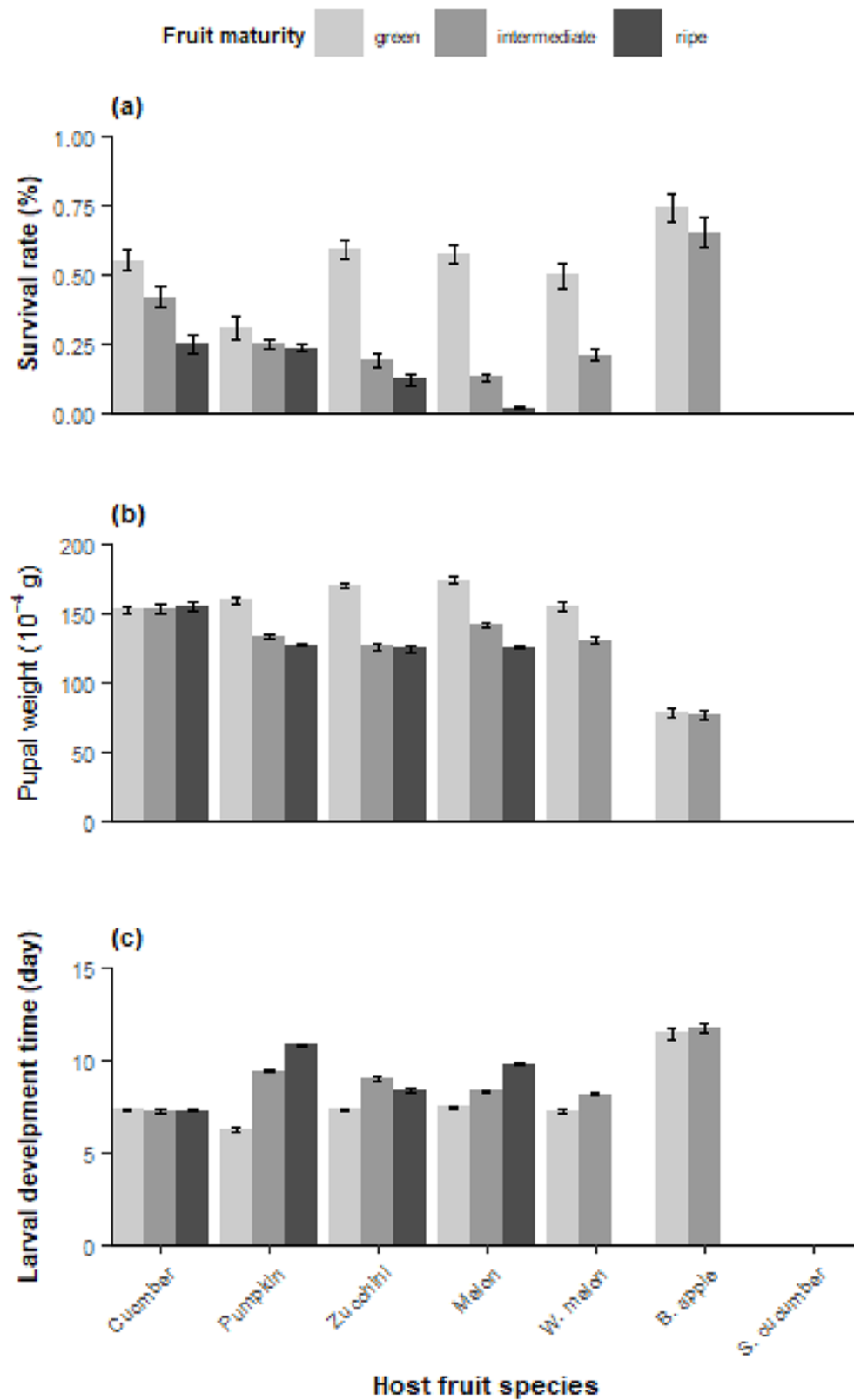
Figure 1. (A) Larval survival, (B) larval development time, and (C) pupal weight (10^{-4} g) of *Dacus frontalis* reared on five cultivated and two wild Cucurbitaceae host plant species. Each cultivated fruit species was tested at three stages of fruit maturity (green, intermediate, and ripe). The two wild fruit species were only tested at green and intermediate stages of maturity. Values are mean ± SE.
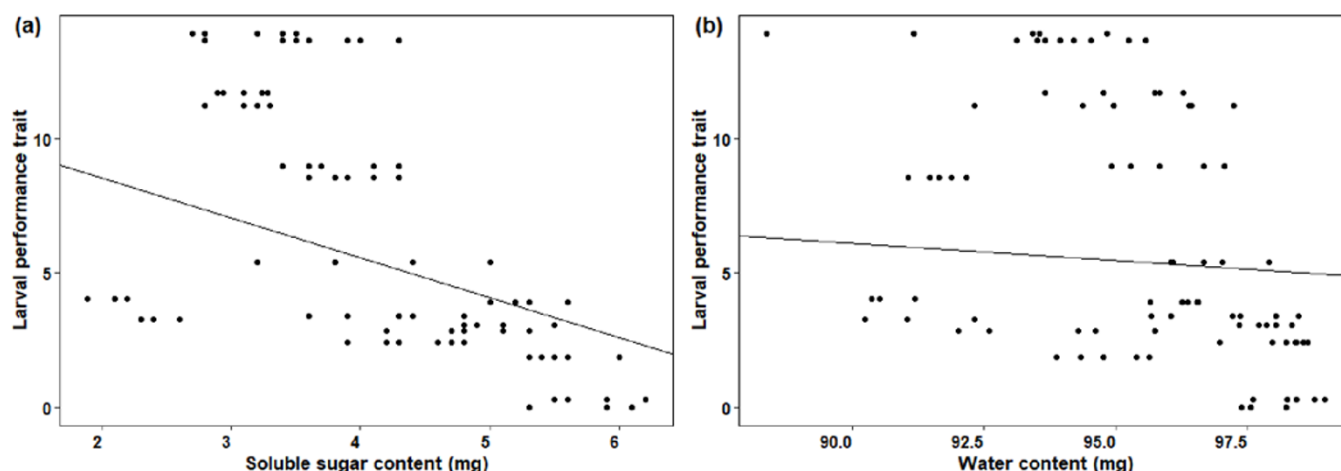
Figure 2. Relationship between larval performance trait (survival × pupal weight/developmental duration) and soluble sugar contents (A) or water contents (B) as predicted by mixed effect regression for *Dacus frontalis* reared on seven cultivated and wild host fruit species belonging to the Cucurbitaceae family at different stages of maturity. We built a linear regression, based on the results of the fitted models where fruit species and stage of maturity were included as random effects for sugar ($p < 0.001$, $R^2 = 0.094$) and water content ($p = 0.410$, $R^2 = 0.003$).

The larval performance trait decreased significantly with higher soluble sugar contents (estimate $= -1.49$; confidence interval [CI]: -2.26, -0.71; $p < 0.001$; marginal $R^2 = 0.094$; conditional $R^2 = 0.889$). In contrast, it did not differ significantly with regard to fruit water content (estimate $= -0.13$; CI: -0.43, 0.18; $p = 0.410$; marginal $R^2 = 0.003$; conditional $R^2 = 0.888$) (fig. 2).

Female preference

The mean number of eggs laid by *D. frontalis* females in the no-choice assays differed significantly between fruit species ($\Delta Dev_{6, 125} = 1213.8$, $p < 0.001$) and between the different stages of fruit maturity ($\Delta Dev_{2, 125} = 760.3$, $p < 0.001$). The interaction between these two parameters is significant ($\Delta Dev_{12, 125} = 596.29$, $p < 0.001$) (fig. 3A). On the tested fruit species, the lowest number of eggs was observed on oviposition devices containing the wild cucurbitaceous species, with no eggs in the case of bitter apple. In cultivated cucurbitaceous fruits, the highest number of eggs was laid on the oviposition device containing cucumber (48 eggs/female) and the lowest on that containing melon fruit, where there was no oviposition (fig. 3A). Regarding the different classes of the same host fruit species, *D. frontalis* lay the highest number of eggs on the oviposition devices containing fruit belonging to the green category.

The mean number of eggs laid by *D. frontalis* females in the choice trials differed significantly between fruit species ($\Delta Dev_{7, 95} = 529.2$, $p < 0.001$) (fig. 3B). On the fruit species tested, the lowest number of eggs was observed on the oviposition devices containing wild cucurbitaceous species. No eggs were laid in the devices filled with bitter apple (fig. 3B). In cultivated
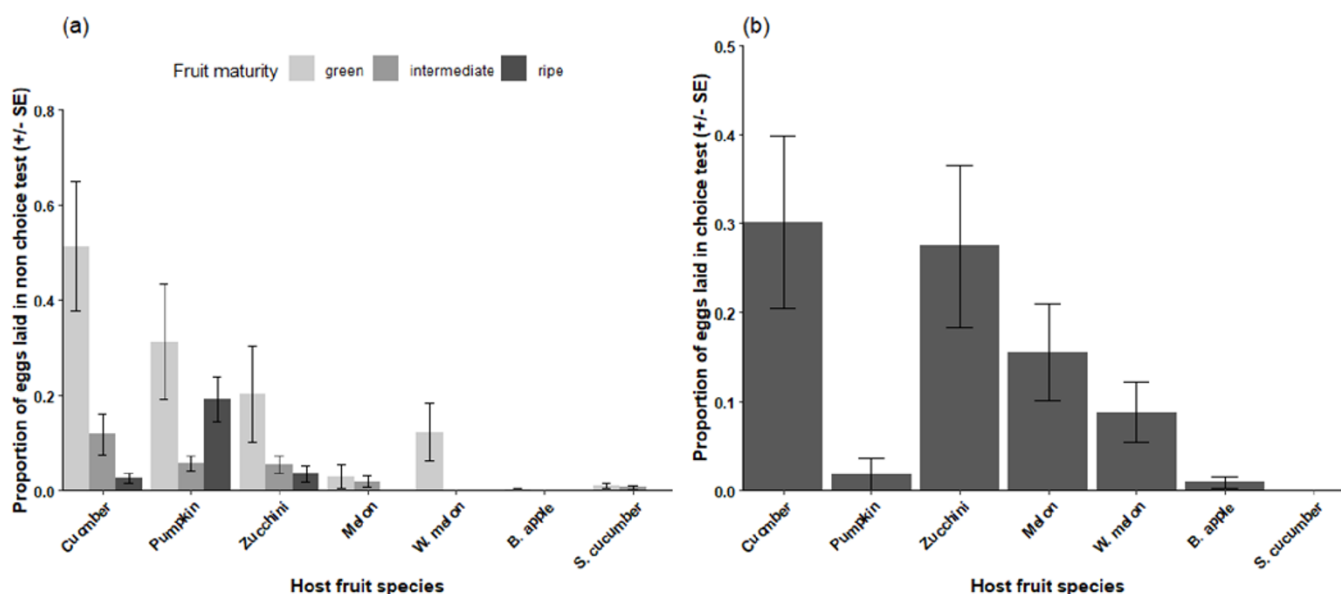

Figure 3. Proportion of eggs laid by gravid females of *Dacus frontalis* in cultivated and wild host fruit species belonging to the Cucurbitaceae family occurring in Tunisia during (A) a non-choice test at different stages of host fruit maturity (green, intermediate, and ripe) and (B) a choice test on green tested fruit.
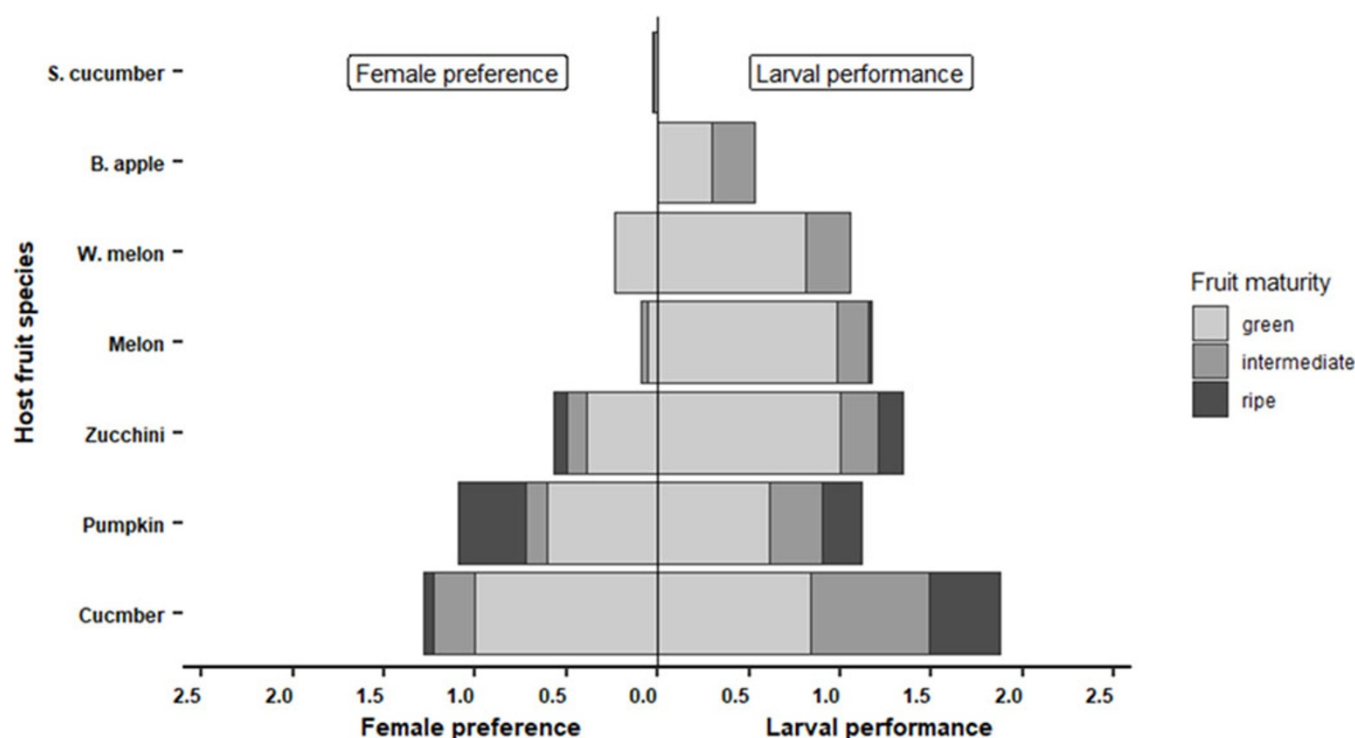
Figure 4. Female preference in non-choice test and larval performance trait (survival × pupal weight/developmental duration) for *Dacus frontalis* at different stages of fruit maturity (green, intermediate, and ripe) for five cultivated and two wild host fruit species belonging to the Cucurbitaceae family and found in Tunisia.

cucurbitaceous fruit, the highest number of eggs was laid in the oviposition devices containing cucumber and the lowest in those with pumpkin fruit. However, *D. frontalis* females exhibit significant ($\Delta Dev_{7,95} = 529.2$, $p < 0.001$) oviposition preferences between the cucurbitaceous species tested. In choice trials, *D. frontalis* females preferred oviposition devices with cucumber and zucchini for egg laying. No preference was observed in the case of squirting cucumber (fig. 3B).

Preference–performance

The larval performance trait (survival × pupal weight/development duration) differed significantly different between host fruit species ($F_{6,6285} = 54$, $p < 0.001$), host fruit maturity ($F_{2,6285} = 579$, $p < 0.001$) and the interaction between the two factors ($F_{12,6285} = 18$, $p < 0.001$) (fig. 4). There was a significant correlation between female preference and larval performance ($R^2 = 0.350$, $p = 0.002$) (fig. 5). Females of *D. frontalis* were able to choose fruit that promoted high larval performance, such as cucumber, pumpkin, zucchini, and watermelon, particularly at the green stage. The highest correlation between larval performance and oviposition preferences for *D. frontalis* was on cucumber fruit, which was used to rear flies in the laboratory.

Discussion and conclusion

Our results revealed that the larval performances and oviposition preference of *D. frontalis* depends on the host fruit species and stage of fruit maturity. Females preferred laying eggs on oviposition devices that contained green and intermediate fruit rather than ripe fruit. Larval growth was superior in green fruit. There was a strong positive correlation between the female oviposition preference of

D. frontalis and offspring performance at immature stages development. The best larval performance was observed on most preferred host, cucumber, particularly on the green and unripe fruit, which tend to be characterised by a low carbohydrate content (Handley *et al.,* 1983).

Larvae of *D. frontalis* were able to survive on cultivated and wild fruit belonging to different species in the Cucurbitaceae family, except in the case of squirting cucumber. l = Larval performance varied depending on the host plant species and fruit maturity. These finding have already been shown in laboratory studies for other specialist and generalist Tephritidae species (Clarke *et al.,* 2005; Duyck *et al.,* 2008; Ekesi *et al.,* 2014; Hafsi *et al.,* 2016). The host plants in our trial were not equally suitable for larval development. They can be classified from poor to good hosts as follows: bitter apple, zucchini, melon, cucumber, watermelon, pumpkin, and squirting cucumber. It is clear that the host plant's stage of maturity influences the larval performance of *D. frontalis*. Green cultivated Cucurbitaceae fruit are the best host with the highest survival rate for *D. frontalis*. Similar findings have been reported for other tephritid species (Rattanapun *et al.,* 2009). These results suggest that the high survival rate of *D. frontalis* on green and unripe fruit may allow this fruit fly to develop earlier, thus avoiding competition from other species (Tephritidae or other species).

Although many host plants can sustain the full development of *D. frontalis*, host quality plays a major role in differential larval survival (Hafsi *et al.,* 2016; Krainacker *et al.,* 1987). *Dacus frontalis* larvae were reared under constant laboratory conditions on seven host fruit (wild and cultivated), with different nutritional compositions. Larval performance differed significantly between fruit species, suggesting that fruit nutritive value impacted the individual fitness of *D. frontalis*. The nutritional content of the larval diet has a significant effect on larval performance. It also has an impact
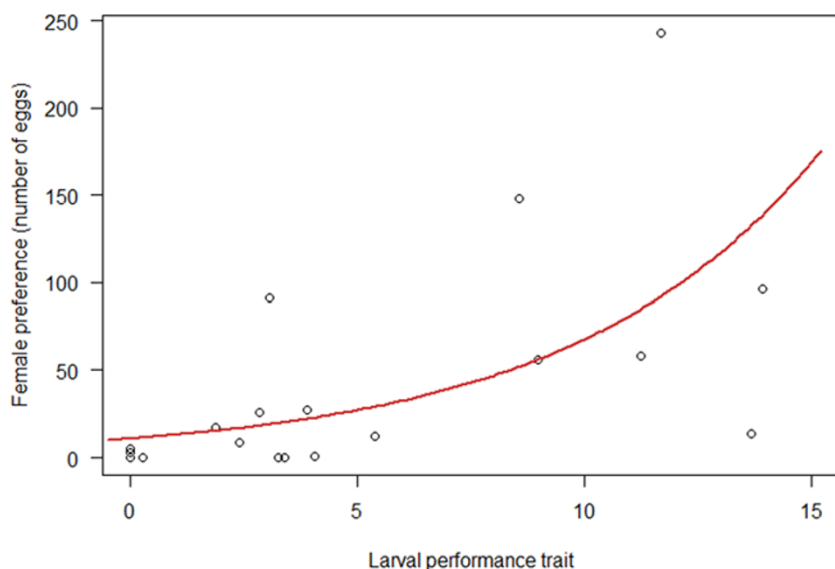
Figure 5. Relationship between female preference (number of eggs laid in non-choice test) and larval performance trait (survival × pupal weight/developmental duration) ($R^2 = 0.350$, $p = 0.002$) for *Dacus frontalis* at different stages of fruit maturity (green, intermediate, and ripe) for five cultivated and two wild host fruit species belonging to the Cucurbitaceae family and found in Tunisia.

on the number of adult fruit flies produced (Hafsi *et al.,* 2016; Roeder and Behmer, 2014) and can explain the differential trophic niche for the fruit fly community in the same area (Hafsi *et al.,* 2016).

Contrary to generalists, specialist tephritid species are less impacted by the toxicity of their host plant's secondary metabolites (Ali and Agrawal, 2012). This could explain why *D. frontalis* larvae survive in bitter apple (with lowest pupal weight) which is known to contain toxic compounds and secondary metabolites that are harmful to animals that are harmful for animals (Kandibane *et al.,* 2020; Li *et al.,* 2022) such as flavonoids, alkaloids, and phenols (Hussain *et al.,* 2014). The same tendency was observed in another specialist tephritid species, *Neoceratitis cyanescens* (Bezzi, 1933) (Brévault *et al.,* 2008). The ability to exploit toxic hosts may cause harm to insects. For example, secondary metabolites, particularly steroid alkaloids, are known to interact with the ecdysteroid: Juvenile Hormone balance, with a negative impact on larval survival and pupal weight (Erbout *et al.,* 2009; Thummel and Chory, 2002). This was shown for the generalist tephritid species, *Ceratitis fasciventris* (Bezzi) (Erbout *et al.,* 2009). It was also demonstrated in our study on *D. frontalis*. This species can exploit toxic hosts, such as bitter apple, but their pupae are lighter. This characteristic of may allow *D. frontalis* may allow the species to avoid competition, predation, and parasitism on its host plant.

The results revealed that *D. frontalis* females had clear ovipositional preferences for cultivated cucurbitaceous fruit, especially cucumber compared to the wild fruit species tested. The oviposition preference depended on the stage of host fruit development. We observed that females preferred laying eggs on young green and unripe cultivated Cucurbitaceae fruit than on intermediate and ripe fruit. This pattern was observed in other *Dacini* species, which are also cucurbitaceous fruit specialist that are found in the same area. In some cases, these species are even capable of laying their eggs in either the vegetative part of the plant (stems) or in the floral organs (Ryckewaert *et al.,* 2010; Vayssières and Carel, 1999; Vayssières *et al.,* 2008).

Host specialisation has been studied in tephritid species. Results show that the relationship between preference and performance increases with diet specialisation (Charlery de La Masseliere *et al.,* 2017; Facon *et al.,* 2021; Fitt, 1986; Lauciello *et al.,* 2024). Studies reveal that the specialised species belonging to the *Dacus* genus prefer laying eggs on hosts suitable for their larval development (Fitt, 1986). Consistent with the optimal oviposition theory (Jaenike, 1978a), our results demonstrated that *D. frontalis* females preferred to oviposit on young fruit species to optimise larval performance. This preference for young green host fruit, which are often softer and contain sufficient nutrients for larval development, indicates that *D. frontalis* females may have the capacity to choose suitable novel host plants. This supports the 'mother knows best' hypothesis.

Our finding indicates that cucumber is highly preferred by *D. frontalis* and that larvae performed perform well on cucumber, particularly in young fruit, compared to the other crops tested. This is consistent with historical field evidence, which shows that cucumber was the first host plant attacked by this tephritid species when it invaded Tunisia (Hafsi *et al.,* 2015). Flies may appear as soon as host plant start flowering. This pattern was observed in other cucurbitaceous tephritid species in the laboratory and in the field (Atiama-Nurbel *et al.,* 2010; Vayssières and Carel, 1999). Results from laboratory trials have shown that these fruits do not constitute an efficient alternative host for *D. frontalis* in the field because females are unable to oviposit on the fruit pericarp due to its firmness. However, bitter apple and squirting cucumber may be important multiplication reservoirs, if mammals or birds accidentally damage the fruit, leaving openings for egg laying (Tracey *et al.,* 2007). In this case, presence of bitter apple as a host plant between cropping periods may be problematic. Bitter apple can support the larval development of *D. frontalis* and, thus, contribute to its renewed establishment in the field in the following season. The presence of wild host plants is an important consideration when developing pest management programmes for tephritids.

By examining the ecosystems where a species has become successfully established, it is possible to demonstrate that the availability and abundance of suitable host plants is important. It is undeniably the most crucial preliminary factor that will allow an exotic phytophagous insect to survive in a new habitat, on condition that it can tolerate the new climate (Niemelä and Mattson, 1996). Our study documents the fundamental dietary niche of *D. frontalis* and demonstrates that a good host for larvae is also the female's preferred host. Our findings confirm the positive

preference–performance relationship that has been demonstrated for specialist tephritid species (Charlery de La Masseliere *et al.*, 2017; Lauciello *et al.*, 2024). We suggest that *D. frontalis* females prefer a low risk site with the best quality food to ensure that their offspring can develop to optimum fitness. Predicting the interactions between insects and their fundamental host range is essential for predicting invasions using PRA and associated quarantine procedures. It could help limit the consequences of invasions, by proposing adequate management techniques to control future invasive pests.

Competing interests. The authors declare no conflict of interest.

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