Life-history traits of *Dacus frontalis* Becker (Diptera: Tephritidae) reared at four constant temperatures

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Abstract *Dacus frontalis* (Diptera: Tephritidae) is an emerging species affecting fruit production in Africa and may pose a serious risk to the Cucurbitaceae fruit producing industry in Europe in response to climate change. To understand how temperature affects the fitness and population dynamics of this species and consequently its invasive potential, we investigated for the first time the survival and development time of immature stages, longevity and fecundity of *D. frontalis* adults in the laboratory at four constant temperatures of 15, 20, 25 and 30 °C. In addition, the lower developmental threshold and thermal constant were calculated using a temperature summation model. Results showed that the rearing temperature has a significant effect on the survival, development, reproduction, and longevity of the pumpkin fruit fly. The highest survival rates of eggs, larvae, pupae, adult females and males were observed at 20 °C. The development time of immature stages and from egg to adult, decreased significantly with increasing temperature from 15 to 30 °C. Females produced a significantly higher number of eggs at 20 °C, and no oviposition was observed at 15 °C. Pupae were able to survive at 15 °C with the longest development time, suggesting that this tephritid species can overwinter as pupae in the field in North Africa. The thermal constant of egg, larval, and pupal stages were 33, 95, and 210 DD, respectively. The minimum temperature threshold of egg, larval, and pupal stages were 4.6, 13.5, and 9.5 °C, respectively. These thermal requirements may explain the seasonality of *D. frontalis* observed in North Africa. Implications for pest management and potential geographical distribution are discussed.

Keywords Cucurbitaceae · Fitness · Reproduction · Survival · Tephritidae · Thermal plasticity

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Introduction

The pumpkin fruit fly, *Dacus frontalis* Becker (Diptera:Tephritidae), is one of the economically damaging fruit fly species that negatively impacts food security in areas where it is established and in newly invaded areas (Elghadi & Port, 2019; Foottit & Adler, 2009; Hafsi et al., 2015a). This fruit fly species originated from South Africa and is widely

distributed throughout Africa and the Middle East (GBIF Secretariat, 2023). In recent years, in response to global warming, that relaxes climatic barriers to establishment, *D. frontalis* has gradually spread and expanded its geographical distribution to new areas, becaming a serious pest threatening the cucurbit fruit industry in these areas. Since the first detection of *D. frontalis* in Libya in 1992, it has spread rapidly to most areas of North Africa, invading Tunisia, Algeria, and most recently Morocco in 2017 (Elghadi & Port, 2019; Hafsi et al., 2015a). This tephritid species was considered locally as a serious pest of fruit species belonging to Cucurbitaceae family (Ekesi et al., 2007; El-Harym & Belqat, 2017; Hafsi et al., 2015a) and could be established as a very serious agricultural quarantine pest.

In Africa, *D. frontalis* is a major pest of commercial and wild cucurbit fruits (Hafsi et al., 2015a), and can infest some solanaceous fruits such as *Solanum melongena* (L.). As a tephritid species, direct damage is caused by the larval stages when feeding in the pulp of fruits, and indirect damage is caused by secondary microorganisms, which are often introduced by adult females when ovipositing, thus causing them to fall to the ground (Badii et al., 2015). Infestation by tephritid species makes the fruit unmarketable, resulting in severe economic losses (Grechi et al., 2022; White & Elson-Harris, 1992). Heavy infestations of cucurbit fruits by *D. frontalis* have been reported in Egypt, Libya, Iraq, and Tunisia, causing devastating losses that can reach to 60–100% in some areas (Al-Jorany et al., 2019; Elghadi & Port, 2019; Shawkit et al., 2011). For example, in Iraq 68% of the total fruit production was damaged (Al-Jorany et al., 2019) and in Libya 100% losses of cucurbit fruit production were observed (Elghadi & Port, 2019).

Efforts to suppress *D. frontalis* populations has always relied on the application of bait sprays containing toxic organophosphate insecticides such as diazinon or fenthion during the fruiting season. Often, the last insecticide treatment is applied when the fruits is ripening, making it difficult which to respect the safety period before harvest (Ba-Angood, 1977). This raises concerns among growers, as chemical treatments do not always prevent fruit damage and fail to suppress the fly population (Hafsi et al., 2015b). Recently, emphasis has been placed on implementing safer environmental measures to control *D. frontalis*, such as the use of entomopathogenic fungi for the biological control (Elghadi & Port, 2019). Therefore, there is a need to explore other control methods to effectively manage this pest and develop an eradication strategy before it spreads to other regions of the world.

Understanding the thermal requirements of insect species is essential for the development of phytosanitary measures and Integrated Pest Management (IPM) programmes (Bale, 2002; Kalaitzaki et al., 2023; Schlesener et al., 2020), especially for invasive pests and in the case of global warming. Studying the thermal requirements of exotic insects can provide also information about insect phenology, population density thresholds and timing of insecticide applications (Wiman et al., 2016). Likewise, it will help to the improve rearing techniques for the implementation of IPM strategies including sterile insect technique (SIT), autocidal and biological control approaches (Pfab et al., 2018; Winkler et al., 2020). In addition, the rapid invasion of *D. frontalis* in North Africa and the Middle East raises questions about its environmental niche breadth and its responses to climate change.

Tephritidae, as ectotherms insect species, are particularly vulnerable to thermal perturbations. The distribution and physiological processes of tephritid species can be affected by extreme temperatures (Pieterse et al., 2017; Terblanche et al., 2011; Weldon et al., 2018), which vary considerably in space and time (Bonebrake & Deutsch, 2012; Gutierrez & Ponti, 2014). Extreme high temperatures can have multiple negative effects on insects, either directly by inducing mortality or sterility associated with cellular and tissue damage (Duyck et al., 2004; Hill et al., 2020; Sinclair et al., 2012; Terblanche et al., 2010), or indirectly by negatively affecting key features of physiological activity (Régnière et al., 2012). Furthermore, low temperature extremes can also have direct consequences (Burikam et al., 1992; Jessup & Baheer, 1990), thus affecting the overwintering survival (Merkel et al., 2019) and insect population dynamics either by reducing growth rate, developmental rate, and reproductive activity (Huang et al., 2020). The response to extreme temperatures may differ between insect families and species. A temperature of 35ºC can induce larval mortality and female sterility in three *Ceratitis* species (Duyck & Quilici, 2002). Moreover, this temperature of 35 °C reduces

the population growth of other tephritid species such as *Ceratitis capitata* (Wiedemann), *Bactrocera dorsalis* (Hendel) and *B. cucurbitae* (Coquillett), suggesting that a temperature range of 35 ºC is more limiting for their establishment in a new area than lower temperatures (Vargas et al., 2000). Given that insect populations can cope with thermal extremes using a variety of mechanisms and strategies (Terblanche et al., 2015), there is need to study and to understand these tolerances and adaptations.

Despite the economic importance of *D. frontalis* in cucurbit crops, little is known about the effects of temperature variation on the *fitness* of this tephritid species. This information can support the success of control strategies against this pest in different regions and ecosystems. It can also help to understand the presence or absence of this insect in a given region and it's invasion success in a such area. Thus, this finding is the first that study the immature life history parameters and estimate the adult performance of *D. frontalis* reared under four constant temperatures.

Materials and methods

Insect rearing

The study was conducted with a laboratory strain of *D. frontalis* that is established in the Entomology laboratory at Higher Agronomic Institute of Chott-Meriem. The strain of *D. frontalis* was initially started from samples of field infested cucumber fruits (*Cucumis sativus* L.) that are collected between september and october 2014 in Kairouan area (Center of Tunisia) (Hafsi et al., 2015a). Larvae were reared on cucumber fruits for three to five generations. However, adults were reared on an optimal diet which contained a mixture of yeast hydrolysate and sugar at 1:3 ratio. Laboratory rearing was conducted under constant conditions in an environmental chamber set at 25 ± 1 °C; 12:12 h (light: dark) photoperiod, and $70 \pm 5\%$ RH. Thermal tolerance experiments were done under four constant temperatures (15, 20, 25, and 30 °C) in a separate environmental chamber (MEMMERT, France) under constant conditions of relative humidity ($70 \pm 5\%$), and photoperiod (L12:D12).

Egg, larval, and pupal development

Eggs were collected from an artificial egg-laying device placed for 2-hours into laboratory *D. frontalis* strain. The device consisted of a half of yellow ball (3 cm diameter) with 100 small holes through which the females laid their eggs. A piece of 5 g of cucumber fruit was placed inside the device so that its odor stimulated egg-laying. Eggs were carefully collected with a camel brush and a sample of 100 eggs were placed on black humid blotting paper inside a petri dish. At each tested temperature, ten replications were maintained with 100 eggs each. Egg developmental duration and survivorship for each temperature were determined by observation of egg hatching every 12 h for 4 days.

Newly emerged larvae (< 4 h) were placed on slit made on the surface of premature cucumber fruit with camel brush for a final density of 1 larva per 10 g of cucumber. This density prevents intraspecific resource competition. After that, each cucumber fruit was placed in a plastic container aerated by meshed openings and layered with dry sand for pupation. In total, ten replications were done at each tested temperature. Every 48 h during 45 days, all containers were examined and pupae were collected and placed individually into a small plastic container containing sand. Towards the end of the pupal stage, the number and the sex of newly emerged adults was recorded daily (Duyck & Quilici, 2002) to determine the time and the percentage of adult emergence. The sex ratio was calculated for each tested temperature as the total number of emerged females/total number of emerged males.

Adult survival, longevity and female fecundity

At each tested temperature, thirty pairs of newly emerged males and females (< 8 h) were held individually in transparent plastic cups of 1 L volume aerated by meshed openings. Adult flies had free access to food (sugar and protein with 1:3 ratio) and water. Half of the yellow ball (3 cm diameter) with 100 small holes containing a small portion of cucumber fruit (5 g) was placed daily in each transparent plastic cup as oviposition substrate (Duyck et al., 2002). The number of eggs oviposited per female per day and the adult mortality were recorded daily, until the death of all adults, to determine the pre-oviposition

and oviposition duration, fecundity, and longevity of *D. frontalis* females and males at each tested temperature.

Temperature summation model

The temperature summation model was used to predict the development rate of individual life stages (Duyck & Quilici, 2002), and was calculated using regression analysis between temperature and development rate. To establish this relationship, the development time of individual life stages (i.e. the time required for 50% of individuals to complete a given biological stage) was determined at a series of constant temperatures. The lower development threshold *t* (i.e. the temperature at which the development rate is zero) was then determined by extrapolation of the regression line back to the x-axis. The thermal constant *K* (i.e. the number of day degrees above the lower threshold required to complete development) was calculated from the regression equation using the relationship $y = K / (x - t)$ (Duyck & Quilici, 2002).

Statistical analyses

All statistical analysis was carried out using R version 3.6.1 (R Development Core Team, 2008) via the interface R studio (version 1.2.5). Survival rate of each life stage was analyzed using a general linear model (GLM) with a binomial error (logit link) as a function of temperature. Development time of each life stages (eggs, larvae, pupae), female and male longevity, and female fecundity were analyzed by analysis of variance (ANOVA) as a function of temperature. The data were checked for normality by

using the Shapiro-Wilk test and student's t-test was used to compare development and survival for each life stage of *D. frontalis* between temperature treatments. A GLM with binomial error (logit link) was used to determine how the sex-ratio of *D. frontalis* were affected by temperature.

Results

Survival rate of immature stage of *D. frontalis* under constant temperatures

Dacus frontalis successfully survived from egg to adult stage at all studied temperatures (Table 1). The survival rate of each immature stage was significantly affected by temperature (egg: $F_{3, 241} = 10.04$, $P < 0.001$; larvae: $F_{3, 372} = 6.77$, $P < 0.001$; pupae: $F_{3, 372} = 8.59$, $P < 0.001$; Table 1). In the low temperature treatment (15 °C), the egg, larval, and pupal stage had significantly the lowest survival rate. Eggs were the most tolerant to low and high-temperatures with the highest survival rate of 56.80 and 85.20% at 15 and 25 °C, respectively. Among the different tested temperature, the highest survival rate was observed at 20 °C for the larval and pupal stages, but not for the egg.

Developmental time and rate of immature stages of *D. frontalis* and sex-ratio under constant temperatures

Dacus frontalis was able to complete its development from egg to adult at all tested temperatures. The developmental time of each life stage and from egg to adult emergence was found to significantly

Table 1 Survivorship (mean ± SE) of different developments stages and sexes of *Dacus frontalis* at different temperatures (15, 20, 25, and 30 °C)

Temperature (°C)	Survivorship (%)				
	Eggs	Larvae	Pupae	Female	Male
15	56.80 ± 2.47 d	43.42 ± 5.72 c	19.73 ± 4.59 b	44.45 ± 3.25 c	32.90 ± 3.07 b
20	73.90 ± 2.03 c	72.00 ± 4.51 a	70.70 ± 4.57 a	84.86 ± 0.98 a	75.58 ± 1.17 a
25	85.20 ± 1.47 b	64.00 ± 4.82 ab	65.65 ± 4.77 a	70.69 ± 0.98 b	66.27 ± 1.02 a
30	81.40 ± 2.53 a	49.00 ± 5.02 bc	48.48 ± 5.23 ab	76.05 ± 1.46 ab	76.17 ± 1.46 a

Different lowercase letters in each column (stage) denote significant difference among different temperatures after analysis using Tukey's test ($P < 0.05$)

affected by temperature (eggs: $\Delta \text{Dev}_{3,\,244} = 11{,}297$; $P < 0.001$; larvae: $\Delta \text{Dev}_{3,\,375} = 491$; $P < 0.001$; pupae: $\Delta \text{Dev}_{3,\,372} = 459$; $P < 0.001$) (Table 2). In response to an increase in temperature from 15 to 30 °C, there was a reduction in the time required to complete the development of each immature stage and the total development form egg to adult, with the shortest being at 30 °C. The development time from egg to adult ranged from 100.26 days at 15 °C to 23.90 days at 30 °C.

For *D. frontalis*, a strong and positive linear relationship was observed between temperature and development rate of each life stage (Fig. 1, $R^2 = 0.95$, 0.94, 0.93 for egg, larval and pupal stages, respectively; $P < 0.0001$). Lower temperature thresholds for egg, larvae and pupae development were estimated as 4.6, 13.5, and 9.5 °C, respectively. The day degree (DD) requirements to complete the egg, larvae, and pupae development were 32, 95, and 210 DD, respectively.

The proportion of females in emerged *D. frontalis* pupae -were not significantly affected by temperature treatments ($\Delta \text{Dev}_{3,\,140} = 198$; $P = 0.734$).

Adult survival, longevity, and fecundity of *D. frontalis* under constant temperatures

With the exception of a temperature of 15 °C, at which females did not lay eggs, *D. frontalis* successfully survived and laid eggs at all other tested temperatures. The survival rates of females and males were found to be significantly affected by temperature ($\Delta \text{Dev}_{3,\,4546} = 4965$, $P < 0.001$; $\Delta \text{Dev}_{3,\,4546} = 5434$, $P < 0.001$, respectively) (Table 1). Females and males of *D. frontalis* had significantly higher survival at 20 °C with 84.86 and 75.58%, respectively.

Overall, temperature treatments had a significant effect on the longevity of male and female *D. frontalis*. Adult longevity was significantly affected by temperature for both sexes (female: $F_{3,\,84} = 125.59$, $P < 0.001$; male: $F_{3,\,84} = 70.49$, $P < 0.001$) (Fig. 2). At 15 °C, the longevity was significantly shorter compared to all other tested temperatures, not exceeding 11 and 10 days for females and males, respectively. Except for 15 °C, and when the temperature was increased from 20 to 30 °C, the longevity of either female or male adults gradually decreased, suggesting that temperature stress shortens the lifespan of both sexes.

The preoviposition period of *D. frontalis* females was significantly affected by temperature treatments ($F_{2,\,67} = 46.70$, $P < 0.001$). Females of *D. frontalis* were not able to produce eggs at low temperatures (15 °C). The duration of preoviposition was shortest at 25 °C (6.23 days) (Fig. 3). Apart from this temperature, preoviposition was significantly prolonged reaching a maximum of 10.35 days at 20 °C. With the increase in temperature, the preoviposition period of *D. frontalis* was first shortened and then prolonged.

The oviposition duration of adults (Fig. 3) and female fecundity (Fig. 4) were significantly affected by temperature treatments ($F_{2,\,67} = 27.43$, $P < 0.001$; $F_{2,\,3371} = 5.84$, $P = 0.015$, respectively). Females of *D. frontalis* were not able to produce eggs at low temperatures ≤ 15 °C. With increasing temperature, the oviposition period of *D. frontalis* was significantly shortened. Regarding female fecundity, during this longest oviposition period, *D. frontalis* females produced significantly the highest number of eggs (14.58 eggs/female/day) at 20 °C. Overall, with the exception of 15 °C, the average number of eggs produced

Table 2 Development time (mean ± SE) of different developments stages of *Dacus frontalis* at different temperatures (15, 20, 25, and 30 °C)

| Temperature (°C)	Development time			
	Eggs (hrs)	Larvae (day)	Pupae (day)	Eggs-adults (day)
15	66.00 ± 0.00 a	49.96 ± 0.14 a	46.73 ± 0.78 a	100.26 ± 1.21 a
20	52.35 ± 0.14 b	14.38 ± 0.15 b	17.70 ± 0.25 b	36.09 ± 1.89 b
25	41.79 ± 0.12 c	09.50 ± 0.15 c	13.68 ± 0.18 c	25.98 ± 1.09 c
30	29.59 ± 0.12 d	05.58 ± 0.15 d	10.47 ± 0.13 d	19.90 ± 0.85 c

Different lowercase letters in each column (stage) denote significant difference among different temperatures after analysis using Tukey's test ($P < 0.05$)
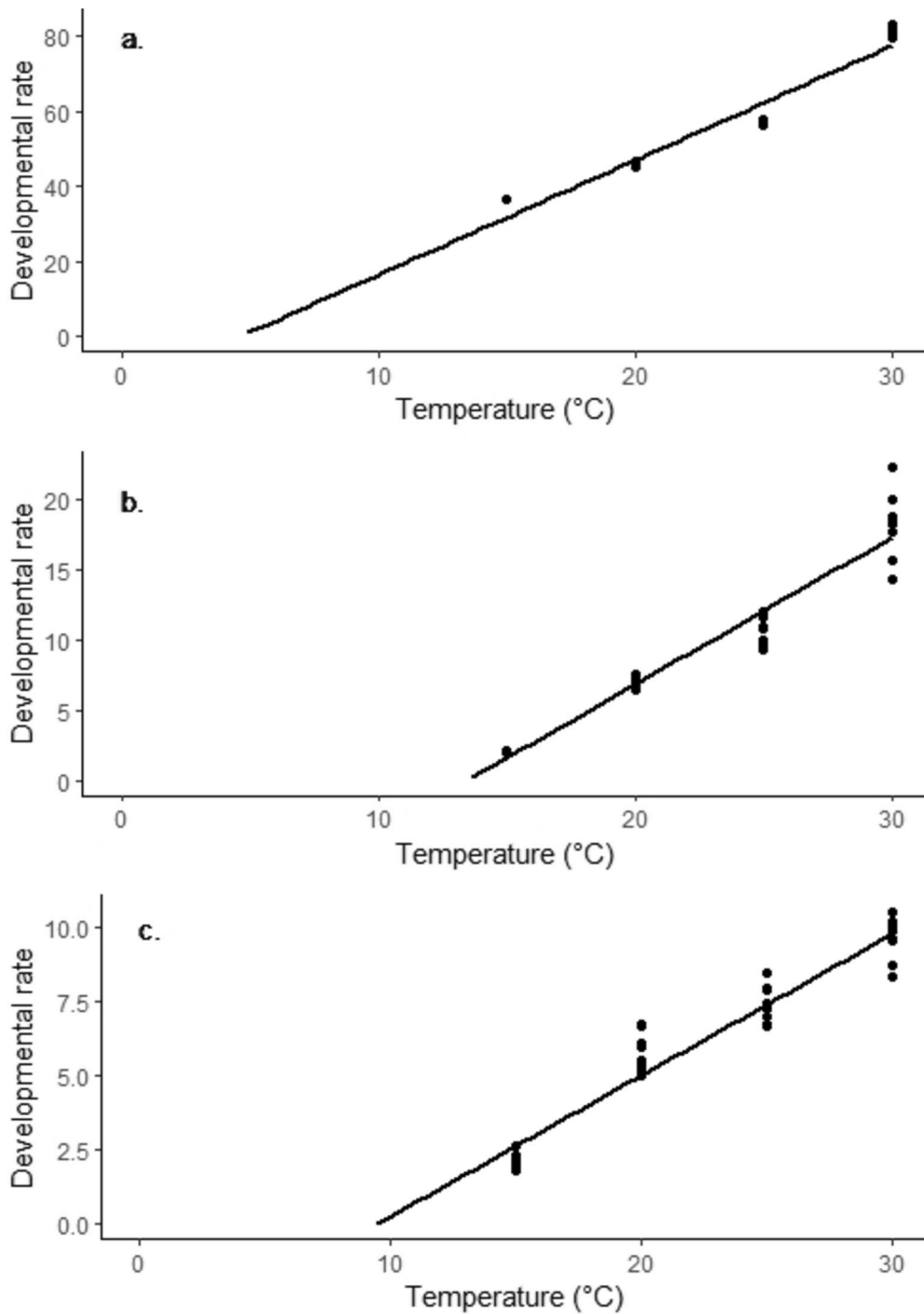
Fig. 1 Effect of constant temperatures on development rates (100/ duration in days) of (**a**) egg, (**b**) larval, and (**c**) pupal stages of *Dacus frontalis* (R² = 0.95, 0.94, 0.93 for egg, larval and pupal stages, respectively; *P* < 0.0001)
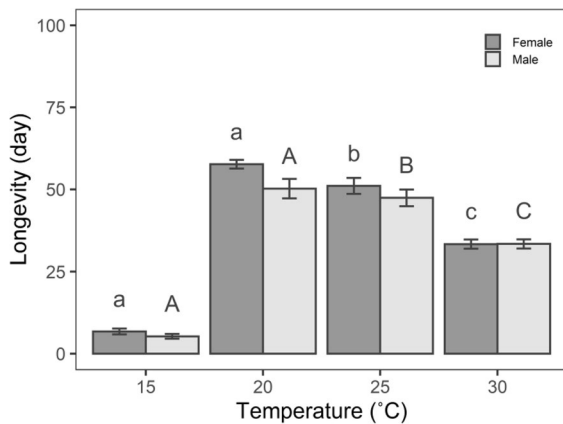
Fig. 2 Longevity (mean ± SE) of *Dacus frontalis* adults under different temperatures (15, 20, 25, and 30 °C). Different lowercase and uppercase letters denote significant difference among different temperatures in female and male, respectively, after analysis using Tukey's test (*P* < 0.05)
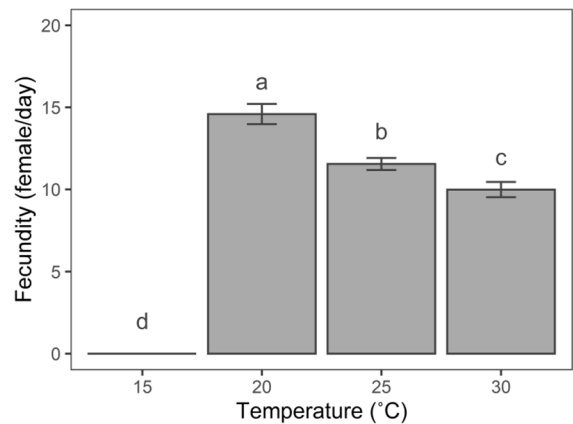
Fig. 4 Fecundity (mean ± SE) of *Dacus frontalis* females under different temperatures (15, 20, 25, and 30 °C). Different lowercase letters denote significant difference among different temperatures after analysis using Tukey's test (*P* < 0.05)
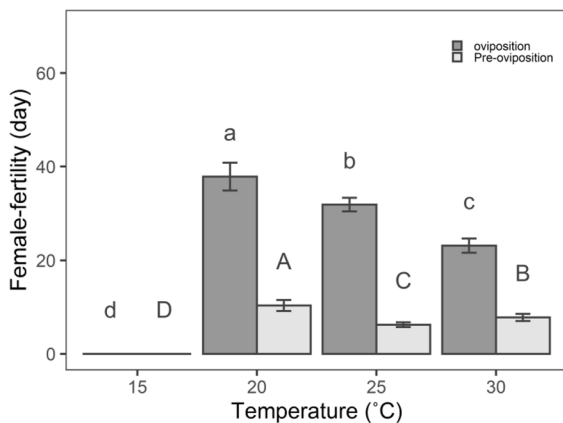
Fig. 3 Preoviposition and oviposition duration (mean ± SE) of *Dacus frontalis* females under different temperatures (15, 20, 25, and 30 °C). Different lowercase letters denote significant difference among different temperatures after analysis using Tukey's test (*P* < 0.05)

per female decreased significantly with increasing temperatures.

Discussion

In this study, we investigated, for the first time, the effect of temperature on the development, survival, reproduction, and sex ratio of the invasive tephritid species, *D. frontalis*. We showed a strong and positive linear relationship between temperature and development rate for egg, larval and pupal stages. The temperature infuences significantly the development time of each life stage of *D. frontalis*. This tephritid species is able to develop from egg to adult over a temperature range of 15 to 30ºC, and the development time of each life stage decreases with increasing temperature. Our results are consistent with that of previous studies on other tephritid species (Choudhary et al., 2020; Duyck & Quilici, 2002; Duyck et al., 2004; Tanga et al., 2015).

Considering the survival and development rate of the different developmental stages, our results suggest that 20 and 30 °C represent an optimal temperature for this pest, as *D. frontalis* had the highest survival rate and shorter development time at these temperatures. These parameters are considered as important criteria for mass rearing of tephritid species (Duyck & Quilici, 2002; Duyck et al., 2004; Krainacker et al., 1989). In addition, our resultswere consistent with those observed in the field where larvae of *D. frontalis* were found in cucumber and zucchini crops only when field temperatures ranged from 17 to 30 °C in Iraq and in Tunisia (Al-Soltany et al., 2020; Hafsi et al., 2015a). The ability of eggs of *D. frontalis* to tolerate low and high experimental temperatures (15 and 30 °C) compared to larvae and pupae is expected because eggs are often laid close to the peel of the host fruit and exposed to more extreme temperatures

compared to the larvae, which are able to move inside the pulp of the fruit, protecting them from extreme low or high temperatures (Grout & Stoltz, 2014; Pieterse et al., 2017).

The positive response of immature stages of *D. frontalis* to different thermal environments may explain its current distribution, but also suggests that it can adapt, and invade new areas. In addition to tropical climates, *D. frontalis* is present in colder climates such as in South Africa and the Mediterranean area. The lower developmental threshold for egg, larval and pupal stages of *D. frontalis* was estimated in our study as 4.6, 13.5, and 9.5 °C, respectively, compared to 11.6, 10.2, 11.2 °C for *C. capitata* (Duyck & Quilici, 2002) that is able to establish under different climatic zones (White & Elson-Harris, 1992) including Mediterranean areas. The invasion of *D. frontalis* in new areas of Mediterranea and Europe can be expected as the minimum temperature threshold of this species are lower than those of *C. capitata*, particularly during egg stages.

Our results on adult longevity, female oviposition, and pre-oviposition period of *D. frontalis* revealed that these parameters varied with temperature, suggesting that 20 °C is an optimal temperature for best adult performance. However, the determinal effect of prolonged exposure to low temperatures was observed in adult flies, which were unable to reproduce and live for more than 11 days at 15 °C. This suggests that even mild winter temperatures are detrimental to the adult survival and reproductive potential of this tephritid species and the low temperatures (15 °C) may affect ovarianmaturity in females. During winter, sexually mature female flies will resorb developing oocytes and become sexually and ovipositionally inactive (Fletcher, 1975). Thermal tolerance studies on *Ceratitis* and *Bactrocera* tephritid species, showed no ovarian maturation of some adults when reared at 15 °C (Duyck & Quilici, 2002; Duyck et al., 2004). This finding showed that thermal requirements are higher for oviposition than for survival and development of immature and adult life stages. Such results are often observed in *Bactrocera* species, which were considered to be reproductively "diapausing" (Fletcher, 1987). Therefore, thermal requirements can explain the seasonality of *D. frontalis* observed in the field in North Africa (Al-Soltany et al., 2020; Hafsi et al., 2015a), where no adult flies and no fruit damage were observed during the winter season. It

is possible that lower temperatures experienced during winter may limit the reproduction success during this period. However, survival rates and lower temperature thresholds may allow a slow development of egg and larvae during winter and may have probably contributed to favouring its invasion in Mediterranean areas.

Pupae are also able to survive at low temperature with long period of development time, suggesting that this species can overwinter as pupae in the field. In insects, diapause is recognized as the most common mechanism of overwintering (Clarke et al., 2019), which can occur most commonly in the egg or pupal stage (Denlinger, 2002; Tauber & Tauber, 1976). In Dacini fruit flies, the winter diapause is often unknown (Clarke et al., 2019). Dacini species are known as tropical and subtropical species and are generally not associated with temperate regions, but, some species have successfully extended their geographic range into seasonally cold climates where winter temperatures may be limiting (Clarke et al., 2019). This is the case for *Bactrocera olea* and *Bactrocera minax*, which are able to overwinter as diapausing pupae (Dong et al., 2013; Tzanakakis, 2003). Given the importance of this phenomenon in the successful tolerance of insects to low temperatures and in population dynamics, it should be taken into account as one of the important parameters in the biosecurity risk assessment and in the implementation of the pest management strategy of this tephritid species.

For practical implications, the results of this study provide useful information on the effect of temperature on the development and survival of *D. frontalis* under laboratory conditions, which is a first step before analysing more complex ecological relationships. For example, our data can be integrated among other parameters to improve the modelling system of fruit fly population dynamics in order to implement better monitoring and pest management, and to determine the quarantine risk associated with these flies (Ahn et al., 2022; Rossini et al., 2020). Also, our data provide information that may be useful to improve rearing methods of *D. frontalis*, as temperature plays a key role in the rearing process of tephritid species (Brévault & Quilici, 2000). A compromise between a short development time and a high survival rate would be to rear eggs, larvae, and pupae at 25 °C. However, adults should be reared at 20 °C to produce more eggs. In addition, knowledge of optimal

temperatures is important to maintain natural enemies population which might be reared (Brévault & Quilici, 2000) on *D. frontalis* as part of an IPM strategy or for mass rearing of this tephritid species for sterile insect technique (SIT) programs that could be implemented for their control and eradication.

Author contributions   A.H., K.A., and B.C. contributed to the study conception, design and/or writing of the manuscript. Material preparation, data collection and analysis were performed by A.H. and K.A. Statistical analysis was approved by P-F.D. The first draft of the manuscript was written by A.H. All authors reviewed and edited the final manuscript.

Declarations

Competing interests   The authors declare no competing interests.

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