



# Maternal age and larval developmental duration impact demographic characteristics of *Ceratitis capitata* progeny

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With 4 figures

**Abstract:** Maternal effects have been documented in several insect taxa. However, the effect of the age of mother and that of immatures developmental duration on adult performance of true fruit flies (Diptera: Tephritidae) has yet to be addressed. The effects of maternal age and that of the variability in larval developmental duration on the demographic characteristics of *Ceratitis capitata* adults were tested. Under constant laboratory conditions, eggs laid by 10 and 40-days old females (mothers) were artificially implanted into apples. Pupae were collected daily, grouped according to larval developmental duration (short and long-developed larvae) and their size was recorded. Emerging adults from short and long-developed larvae, originating from young and old-mothers, were paired in individual cages with *ad libitum* access to adult diet and water to establish four different adult treatments. Adult mortality and female fecundity were recorded daily. Offsprings of old mothers suffered higher larval and lower pupal mortality in comparison with those originating from young mothers. The egg to pupa developmental duration was shorter and the pupae size larger for the progeny of old mothers compared with those of the young mothers. Longevity of adults with short larval development was longer than that of the long-developed ones, regardless of the age of mother. Neither the duration of larval development nor the mother's age affected the fecundity of female progeny. The effects of maternal age and of the variability during immature development on the demographic parameters of the progeny are discussed.

**Keywords:** demography, immature stages, maternal effects, medfly, Diptera, Tephritidae

## 1 Introduction

The nongenetic effects of the maternal phenotype or of the environment on offspring phenotypes, which are gene independent, are known as maternal effects (Mousseau 1991; Mousseau & Dingle 1991). Alexander Graham Bell (Bell 1918) was the first to describe the negative impact of increasing maternal age on offspring fitness, known as the “Lansing effect” (Priest et al. 2002). Apparently, Lansing effects are not observed only in humankind but in many other animal taxa (Butz & Hayden 1962). Indications of maternal effects have been reported in several multivoltine insect taxa including Diptera (Mousseau, 1991).

The age of mother can strongly affect the performance of offsprings (Butz & Hayden 1962; Priest et al. 2002). This is quite common in insects where increase in the age of the mother is associated with a decline in the fitness of progeny (Mousseau & Dingle 1991). Higher mortality, longer larval developmental times and much smaller body size of adult

progeny obtained from older mothers in comparison to those derived from younger mothers have been reported (Mousseau & Dingle 1991, and references therein; Mohaghegh et al. 1998; Ivimey-Cook & Moorad 2020). Effects on embryonic growth via maternal adjustment of egg cytoplasm composition (Mousseau & Dingle 1991) or by maternally controlled differential deposition of mRNAs which can direct early embryogenesis have been documented (O’Farrell et al. 2004).

Prevailing environmental conditions commonly induce plasticity during the development of individuals (Pigliucci 2001). Multifactorial inheritance (Bergland et al. 2008), involving polygenic, epistatic and gene-environment interactions along with epigenetic modifications further contribute to phenotypic plasticity (Maleszka 2008). Growth rate is influenced by the metabolic rate, hence, genes affecting metabolism are supposed to affect larval development, frequently in interaction with thermal conditions (Kvist et al. 2013).

According to Stearns (1992), not all traits can be optimized at the same time because of trade-offs, which are caused by the distribution of limited resources to a specific trait at the expense of another one that uses the same resource (Zera & Harshman 2001, Réale et al. 2010). Strains with shorter larval developmental duration exhibit a higher competitive ability (Bakker 1962; 1968). The longer the larval developmental duration, the higher the probability of facing resource deficiency, which can severely affect fitness traits by reducing body size (Bakker 1962; 1968; Nunney 1996), fecundity (Joshi et al. 1998; Nunney 1996), and mating success (Partridge & Farquhar 1983).

Temperature and host fruits are considered as the main factors affecting the rate of larval development in many endophytic fruit pests including fruit flies (Diptera: Tephritidae) (Carey 1984; Krainacker et al. 1987).

The Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), is considered one of the most destructive agricultural pests of commercial fruits globally (Papadopoulos et al. 2001a and references therein), due to its extreme polyphagy, and aggressive invasiveness (Papadopoulos 2014; Papadopoulos et al. 2001b and references therein). Biological, ecological and demographic traits of several medfly populations have been extensively studied in order to better understand its invasion biology and design effective population suppression measures (Diamantidis et al. 2011). Medfly has also been used as a model organism for demography and ageing research (Carey 2003). Previous studies have shown that several factors operating during the immature development may affect the fitness of emerging adults and their morphological characteristics (Diamantidis et al. 2020; Krainacker et al. 1987; Pieterse et al. 2017).

Prolongation of medfly's larval developmental duration within infested apples facilitates successful overwintering in temperate areas (Papadopoulos et al. 1996). Nutritional contents of different fruits might greatly affect larval developmental time. The higher the protein level in larval diet the shorter the developmental time and the larger the size of the produced individuals. Nonetheless, there is no information regarding the possible effects of the immature developmental duration on the demographic characteristics of emerging adults.

It is a well-known tenet in demography that the first eggs laid by females affect population growth rate far more than do eggs laid later (Carey 1984; Lewontin 1965). However, it's not known whether the age of the mother influences the fitness of progeny in *C. capitata*.

The aim of the present study was to investigate the correlation among (a) mother's age through which the hatched larvae originated, (b) the variability in the duration of immature stages developmental duration and (c) the demographic characteristics of adult progeny of the model organism *C. capitata*.

## 2 Materials and methods

The experiments were conducted from February to October 2019 in the laboratory of Entomology and Agricultural Zoology, at the University of Thessaly, Greece. A small-scale rearing of *C. capitata* was established in the laboratory ( $25\pm 1^\circ\text{C}$ , 45–55% relative humidity, 14:10 Light:Dark photoperiod) from field infested apples collected in a private orchard, approximately 60 km north from the Laboratory of Entomology, in the region of Larissa ( $39^\circ 42' 06.2''\text{N}$ ,  $22^\circ 44' 28.8''\text{E}$ ), Greece. No specific permission was required for the host fruit collection, other than the owner's permission, as no endangered or protected species were involved. The rearing of medfly was performed by keeping approximately 200 adults in wooden, (30×30×30 cm), wire-screened cages. Adults had free access to water and standard diet (yeast hydrolysate, sugar, and water at 1:4:5 ratio – YS). Females deposited eggs on the inner surface of artificial oviposition substrates (plastic dome). Eggs were collected and hatched larvae were reared in artificial medium. Details regarding the rearing methodology is given in Papanastasiou et al. (2019).

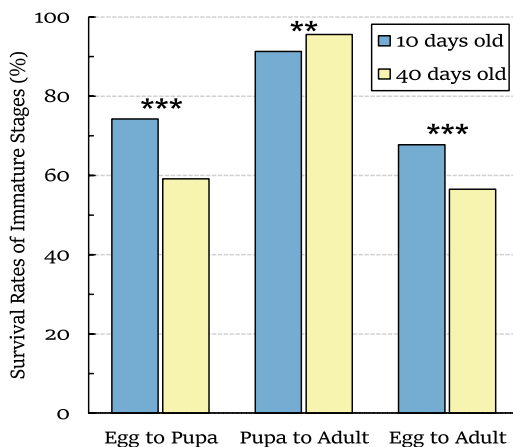
Within 24 hours after adult emergence 10 females and 10 males ( $F_3$  laboratory generation) were transferred in 20×20×20 cm plexiglas cages (10 replicates) and were provided with *ad libitum* water and adult diet (YS). At the age of 10 days, 800 eggs laid by females in artificial oviposition devices (domes) were collected and implanted in 40 apples (Golden Delicious cultivar). Four artificial holes 1.5–2.0 mm in diameter were drilled on opposite sides on the upper part of each fruit and 5 eggs were placed in each hole (20 eggs per apple). Artificially infested apples were transferred individually in plastic bowls on a layer of sterilized sand and were covered with organdie cloth to avoid secondary infestation by drosophilids. Apples were maintained at  $18\pm 1^\circ\text{C}$ , 45–55% relative humidity, 14:10 Light: Dark photoperiod, and were carefully inspected on a daily basis. Each newly formed pupa was collected, pupation date was recorded, and 3 days later it was photographed under a binocular stereomicroscope. Pupae dimensions (length and width) were calculated with the software ImageJ 1.49v. The egg implantation in apples was repeated when females reached the age of 40 days. Depending on the population 40 days is considered an age that marks the progress of aging in wildish medfly populations under constant laboratory conditions (Diamantidis et al. 2009; Papanastasiou et al. 2013). Mortality of flies kept in groups is usually higher; however, no such data have been collected in the current experiment. We kept the parental medflies in 10 cages (5 main cages and 5 for the backup) at a density of 10 females and 10 males in each cage. Dead adults in the 5 main cages were replaced with same age ones kept in additional cages under identical conditions. Overall, 594 pupae were collected from the first implantation of eggs laid by 10-days old mothers and 473 pupae from the second implantation of eggs laid by 40-days old mothers.

To estimate the hatchability of the eggs that were intended for the artificial implantation, we collected additional eggs oviposited by young-10 days and old-40 days mothers (500 and 846 eggs, respectively). Using a painter's soft brush, eggs were carefully placed on black filter paper, saturated with water, in clusters of 100. The eggs were maintained at  $25 \pm 1^\circ\text{C}$ , 45–55% relative humidity and hatched larvae were observed under a binocular stereomicroscope after 2 and 3 days. The number of hatched larvae was recorded, and the percentage of hatchability was calculated for the two age groups of mothers.

To test the effect of both the age of mother and the larval developmental duration, on the fitness traits of the emerging adults, 30 males and 30 females with the shortest larval developmental duration and 60 additional adults with the longest larval developmental duration were selected, which were obtained by eggs laid by 10-days old females. The same numbers of adults that were the progeny of 40-days old females and had short and long larval developmental duration were also selected (see Sup. Materials Figure 1). Males and females were paired and placed in individual cages with an artificial oviposition device (dome) and free access to adult diet (YS) and water. Consequently, four groups of medfly cohorts were established with the following background: (i) 10-days old mothers, short-developed larval stage, (ii) 10-days old mothers, long-developed larval stage, (iii) 40-days old mothers, short-developed larval stage, (iv) 40-days old mothers, long-developed larval stage. Adult mortality and female fecundity were recorded daily.

### 3 Statistical analysis

The effect of maternal age on egg hatchability was tested using the chi-square test. The effect of the age of the mother



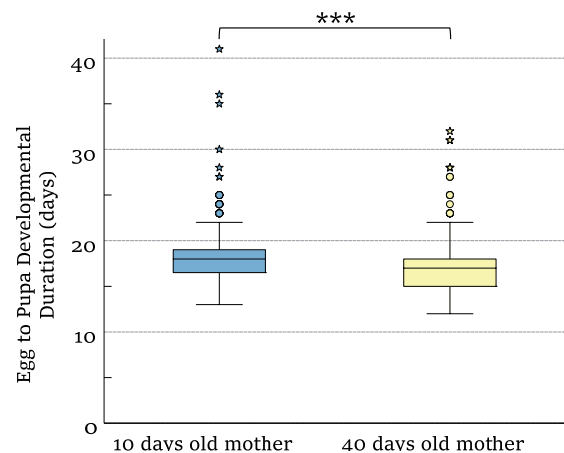
**Fig 1.** Percentage of survival from egg to pupa, pupa to adult and overall immature development – egg to adult. Individuals were obtained from 10-days old females ( $N_{\text{eggs}} = 800$ ,  $N_{\text{pupae}} = 594$ ,  $N_{\text{adults}} = 542$ ) and by 40-days old females ( $N_{\text{eggs}} = 800$ ,  $N_{\text{pupae}} = 473$ ,  $N_{\text{adults}} = 452$ ). Eggs were artificially implanted in Golden Delicious apples and kept at  $18^\circ\text{C}$ .

on the survival during immature development was tested with the binary logistic regression. The Cox proportional hazards model was used to assess the effect of the above factor on the larval developmental duration. Also, the Cox proportional hazards model was used to test the effects of the age of the mother, the immature developmental duration, and the sex on adult longevity. Univariate Analysis of Variance was used to test the effects of mother's age and larval developmental duration on pupal dimensions (length, width). Similarly, differences in fecundity among females that had long or short larval development and obtained from 10-days old or 40-days old mothers were assessed with the Univariate Analysis of Variance. All data analyses were conducted using the statistical software SPSS 25.0 and significance level was set at  $\alpha = 0.05$  (SPSS Inc., Chicago, IL, U.S.A.).

### 4 Results

The survival rates of larvae, pupae and the total immature development (egg to adult) of individuals laid by 10-days old and 40-days old mothers is given in Figure 1. Egg to pupa and egg to adult survival rates were higher for the progeny of 10-days old than those of 40-days old mothers (Wald test  $\chi^2_{\text{egg to adult}} = 21.67$ ,  $\chi^2_{\text{egg to pupa}} = 41.74$ ,  $\text{df} = 1$ ,  $p < 0.001$ ). However, pupa to adult survival rates were slightly higher for the individuals originated by 40-days old females than those laid by 10-days old ones (Wald test  $\chi^2 = 7.42$ ,  $\text{df} = 1$ ,  $p = 0.006$ ). Hatch rates of eggs laid by 10-days old, and 40-days old mothers were similar (87,4% and 85,3% respectively;  $\chi^2 = 1.112$ ,  $\text{df} = 1$ ,  $p = 0.292$ ).

The developmental duration of the larval stage (egg to pupa) for individuals laid by 10-days old and by 40-days old females is given in Figure 2. Immature developmental dura-

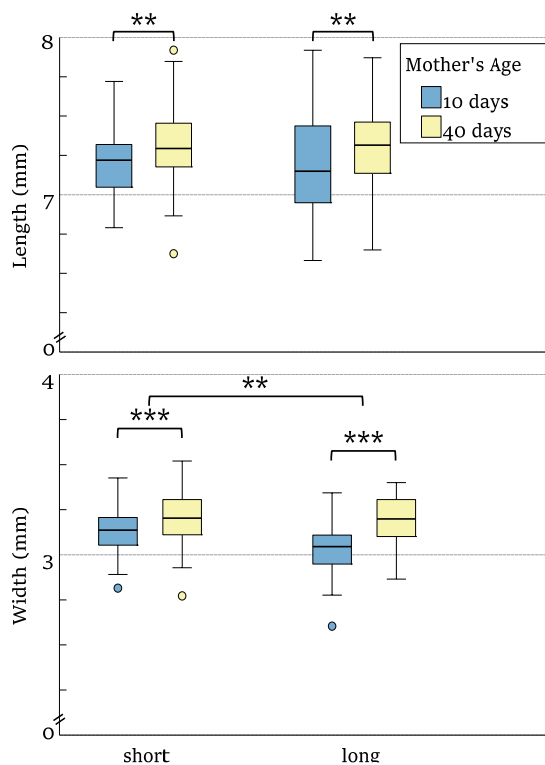


**Fig 2.** Egg to pupa immature developmental duration of individuals laid by 10-days ( $N_{\text{eggs}} = 800$ ,  $N_{\text{pupae}} = 594$ ) and by 40-days old females ( $N_{\text{eggs}} = 800$ ,  $N_{\text{pupae}} = 473$ ). Eggs were artificially implanted in Golden Delicious apples and kept at  $18^\circ\text{C}$ .

tion lasted longer for the offspring of 10-days old females than for those laid by 40-days old female medflies (Wald test  $\chi^2 = 25.631$ ,  $df = 1$ ,  $p < 0.001$ ).

Pupal size (length and width) for individuals laid by 10-days old and 40-days old females is given in Figure 3. Univariate ANOVA showed that 40-days old females yielded longer and wider pupae than 10-days female medflies, regardless of the duration of larval development and the sex of emerging adults ( $F = 9.54$ ,  $40.18$ ,  $df = 1$ ,  $232$ ,  $p = 0.002$  and  $p < 0.001$  respectively). The sex ratio of progeny was 0.90 and 1.08 (females/males) for the 10-days and 40-days old mothers respectively. Also, the developmental duration of larvae and the interaction mother's age by developmental duration were significant predictors of pupae width ( $F_{dev. duration} = 10.01$ ,  $F_{age*dev. duration} = 4.94$ ,  $df = 1$ ,  $232$ ,  $p = 0.002$  and  $p = 0.027$  respectively).

Adults obtained from short immature developmental duration lived longer than flies with long immature development, regardless of the age of mothers (Wald test  $\chi^2_{dev. duration} = 4.56$ ,  $df = 1$ ,  $p = 0.033$ ) (Figure 4). Mother's age did not affect the lifespan of adult progeny, adjusted for larval developmental duration (Wald test  $\chi^2_{mother's age} = 1.42$ ,  $df = 1$ ,  $p = 0.233$ ). Additionally, males lived significantly longer than females (Wald test  $\chi^2_{sex} = 32.20$ ,  $df = 1$ ,  $p < 0.001$ ).

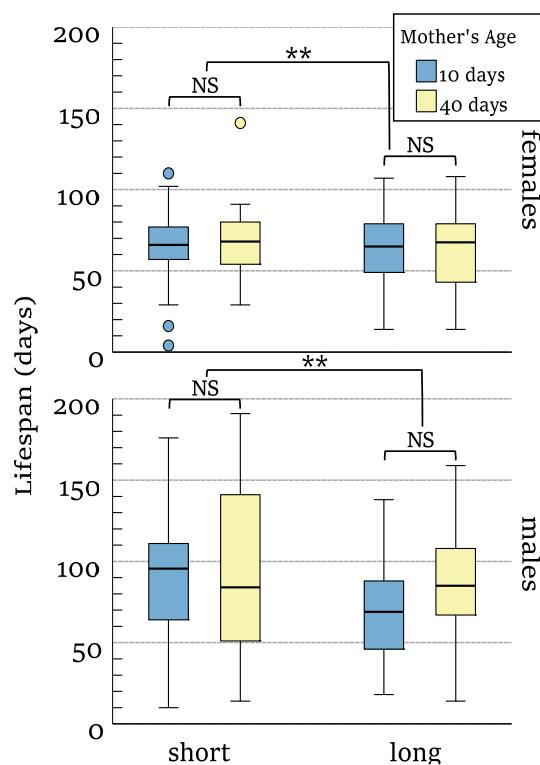


**Fig 3.** Pupal length (above) and width (below) of individuals with short and long larval developmental duration yielded from 10-days ( $N_{pupae} = 120$ ) and 40-days old mothers ( $N_{pupae} = 120$ ).

Neither the duration of larval development nor the mother's age or their interaction were significant predictors of the fecundity of female progeny ( $F_{mother's age} = 3.42$ ,  $df = 1$ ,  $p = 0.067$ ,  $F_{dev. duration} = 0.32$ ,  $df = 1$ ,  $p = 0.0568$  and  $F_{age*dev. duration} = 0.002$ ,  $df = 1$ ,  $p = 0.962$ ) (see Sup. Materials Figure 2).

## 5 Discussion

Future generations' performance, fitness and behavior can be highly affected by parental experience (Baker et al. 2019; Dias & Ressler 2014). The data obtained in the current study document the effect of mother's age and larval developmental duration on some biological traits of *C. capitata*. The higher mortality observed in the progeny of 40 days old mothers during the immature developmental period might be a corollary of a senescence-induced decline in the condition and functional state that can be invested to progeny through cytoplasmic factors, (e.g. yolk quantity, hormones and mRNAs) in the egg which may directly (through maternal programming) or indirectly (through progeny responsiveness to maternally induced factors) affects progeny development (Mousseau & Fox 1998) and specifically the proportion of vitellogenin in the eggs of old mothers. The



**Fig 4.** Lifespan of females (above) ( $N_{females} = 120$ ) and males (below) ( $N_{males} = 120$ ) with short and long larval developmental duration, yielded from 10-days and 40-days old mothers.



variation in the amounts of vitellogenin (the major egg yolk protein provider, which comprises a source of nutrients for the embryos of oviparous invertebrates and vertebrates during early stages of embryo development) (Price 2017) in the eggs of old mothers may be substantial. Hence, this could explain the difference in the survival of immatures of old mothers in comparison with that of the younger ones. Nevertheless, the proportion of larvae hatched from eggs laid by young and old mothers was similar. In the cowpea weevils (*Callosobruchus maculatus*), immature survival decreases as mothers get older, but it increases in the eastern spruce budworm (*Choristoneura fumiferana*) (Harvey 1977; Wasserman & Asami 1985). On the other hand, the age of mother may not affect survival of progeny but their developmental parameters, such as in *Podisus maculiventris* where offsprings of young parents completed development faster and were larger compared with those from older parents (Mohaghegh et al. 1998). Hence, maternal effects in juvenile stages do not affect in the same way every insect taxon. Apart from the amount of vitellogenin, the microbiota of females may decline with senescence and may affect performance of progeny, considering that in tephritids, females bear a symbiont-rich organ known as ovipositor diverticulum, through which they smear the egg surface with symbionts prior to egg deposition (Estes et al. 2009). Indeed, female medflies not only settle bacteria on the surface of newly produced eggs, but they also equip them with lysozyme and antibacterial polypeptides which cause the elimination of pathogens and facilitate the development of beneficial bacteria (Ami et al. 2010 and references within; Marchini et al. 1991). As mothers get older, they possibly invest less on the smearing of egg surface with such microbiota and substances, leading in lower percentage of egg hatchability, lower pupal production or a higher number of partially (i.e. deformed) emerged adults. The hatchability of eggs laid by axenic mothers was significantly lower in insect species such as *Bactrocera tryoni* and *Hylobius abietis* (Nguyen et al. 2020 and references therein). Whether a linkage exists between the amount of essential egg surface substances with mother ageing on *C. capitata* is not yet demonstrated.

Maternal effects may also influence the developmental duration of juveniles (Mousseau & Dingle 1991). Indeed, our results demonstrate that mother's age affected the larval developmental duration of offspring since larvae of young mothers prolong their feeding activity. In *Hylemya antiqua*, shorter immature developmental duration for late yielded progeny compared to young-produced ones was reported for one tested population (Goth et al. 1983). Furthermore, progeny of old tsetse flies females had shorter developmental duration than that of young ones (McIntyre & Gooding 1998). Before making any comparison with tsetse fly, we should consider the uncommon life cycle of this insect which reproduces by adenotrophic viviparity (Hagan 1950) enabling the developing larva to feed with a milky substance secreted via a modified gland called (milky gland) inside the mother's

body (Tobe & Langley 1978), unlike the majority of other oviparous flies such as *C. capitata* where larvae feed on plant hosts. The variability among species regarding effects of the age of the mother on larvae developmental duration cannot be easily explained and more elaborated studies considering maternal investments on offsprings and the biology of the different species should be conducted.

Similar to our findings Goth et al. (1983) reported that pupae formed by late-born progeny were the largest in one out of the three populations considered in their study. Furthermore, McIntyre & Gooding (1998) reported a correlation between maternal age and offspring size on tsetse flies, but in this case old mothers produced smaller progeny. It is known that the progeny of young mothers usually differ from those of old mothers in characteristics that are important for fitness such as morphology, physiology and life history (Mousseau & Dingle 1991). Most studies that reveal negative correlations between the age of mother and fitness of progeny used autogenous species of Coleoptera or Lepidoptera (Fox 1993). Here, we found that older mothers yielded larger pupae in an endophytic dipteran species (*C. capitata*). Interestingly, there was no correlation between the size of pupae with adult demographic traits such as female fecundity.

Generally, in oviparous animals, maternal effects can have a high impact on egg size and early development. However, these effects progressively fade away and become imperceptible since the progeny's maturation begins (Bernardo 1996; Fox 1994; Mousseau & Dingle 1991) because of the offspring developmental plasticity (Fox & Savalli 1998). It seems that for some species natural selection probably favors the fastest developing genotype in every environment. A higher competitive ability is exhibited in strains and individuals with shorter larval developmental duration (Bakker 1962; 1968). Short developmental duration is quite important, especially in field conditions, where larvae exploit rather a small amount of available resources which are rapidly depleted, particularly when densities are high (Sevenster 1992; Wertheim et al. 2000) rather than in lab-conducted experiments. The longer the larval developmental duration, the higher the probability of facing resource deficiency (due to the inevitable gradual collapse of fruit induced by larval feeding activity), which can severely affect fitness traits like adult longevity in the present study (Nunney 1996). Consequently, in interspecific and even in intraspecific competition, individuals expressing a short developmental duration are expected to acquire an advantage compared to the individuals which prolong their developmental duration, as long as their rapid consumption allows them to consume a disproportionately large portion of the available resources. Furthermore, short developmental duration entails short generation time, which enhances the intrinsic population growth rate, allowing "fast" individuals to exploit short-lasting peaks in resource abundance (Sevenster & van Alphen 1993). The correlation between larval developmental period and adult

lifespan is not well established. In our study adults obtained from individuals experiencing shorter developmental duration experienced longer lifespan. However, the age of mothers had no apparent effect on the life span of produced adults. Apparently, the relationships between immature development and adult lifespan needs to be further investigated testing also hypotheses related to rate of isomorphy including the adult stage as well (Jarošík et al. 2002). Finally, results in this study regarding the significantly longer lifespan of adult males in comparison to females are in agreement with older studies on adult demographic traits of medfly (Carey 1995; Diamantidis et al. 2009).

The higher survival rates of immatures obtained from younger mothers that we found in our study support the current practice followed in most mass rearing facilities designated to produce sterile males for the management of the Mediterranean fruit fly using the Sterile Insect Release technique. Nonetheless, the increased productivity of males may be slightly offset by the longer developmental period and the smaller size of the produced pupae. Because the effects of mother's age are multidimensional as we demonstrated here, a broader age base of the mother colony for the production of sterile males should be considered.

In conclusion, the present study reveals that both maternal age and larval developmental duration have an effect on demographic traits of medfly's progeny. Additional studies are required to shed light on the mechanisms underlying on the effects of the age of mother and that of larval developmental duration on the demographic traits of *C. capitata*. Generally, it has been found that pre-adult survival in 257 out of 272 populations (93%) consisting of 97 species from different animal taxa and environments is affected by maternal age effects (Ivimey-Cook & Moorad 2020). In their majority, evolutionary genetic models of ageing presume unquestioningly that DGEs (*direct genetic effects*) are the unique path for the evolutionary change (Ivimey-Cook & Moorad 2020 and references therein), but Moorad & Nussey (2016) have suggested that there is also an influence of the maternal contribution of IGEs (*indirect genetic effects*). Despite the lack of studies on age-specific maternal IGEs, there is promising evidence to advocate that maternal effects and IGEs are common and essential in nature and that the age of mother is a robust predictor for a variety of progeny's characteristics (Moorad & Nussey 2016 and references therein; Ivimey-Cook & Moorad 2020 and references therein). Former studies have demonstrated that age-specific maternal effects could be a significant factor of the evolution of senescence (Ivimey-Cook & Moorad 2020 and references therein). However, it is obvious that further research is needed, considering the complexity of the ageing process, to acquire a profound and holistic understanding which will enable us to disentangle the maternal age effects on medfly's progeny and whether there is actually a contribution of the IGEs or another potentially important factor in this whole process.

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