

Influence of olive variety on biological parameters of *Bactrocera oleae* (Diptera: Tephritidae)

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Received: 24 June 2016 / Accepted: 24 November 2016 / Published online: 21 December 2016
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Abstract A study was carried out on the impact of several olive *Olea europaea* L. (Lamiales: Oleaceae) varieties (Amfissis, Arbequina, Branquita de Elvas, Carolea, Kalamon, Koroneiki, Leccino, Manzanilla, Mastoidis, Moroccan Picholine, Picholine and Sourani) on the performance of the olive fruit fly *Bactrocera oleae* (Gmelin) (Diptera: Tephritidae). Measurements were made over a period of three successive years monitoring the biological parameters of *B. oleae* (weight of pupa, percentage of emergence, sex ratio, adult size and ovarian maturity) on the varieties of olive tree noted above. These measurements were taken as indices of developmental performance for *B. oleae* on the olive varieties. The results showed that *B. oleae* exhibited the highest performance when it was nurtured on the varieties Manzanilla, Moroccan Picholine, Leccino and Picholine rather than Koroneiki. Specifically, the mean weight of the pupae as well as the length of the developed adults was significantly higher than in those individuals that developed in smaller fruits such as Koroneiki. There were significantly higher recorded percentages of emerged adults (up to 80%), with a tendency to produce more female than male adults, while the developed females produced a significantly higher number of eggs. The highest olive fly performance was shown by individuals developing in Leccino and Carolea, with the females developing in Carolea showing the best reproductive performance compared with all the other varieties. These findings may be of ecological significance, and explain to some extent the observed

variability in fruit infestation among olive varieties in the field.

Keywords Olive fruit fly · Olive varieties · Size · Weight · Emergence · Pupae · Sex ratio

Introduction

The biological parameters of phytophagous insect populations are influenced by various factors, such as abiotic environmental variables (Leather 1995; Leather and Dixon 1982; Ratte 1985), adult weight (Dixon 1987), and larval and adult food supply (Leather 1995; Scriber and Slansky 1981), this being directly related to the nutritional quality of the host plant. In nature, the nutritional quality of plants varies naturally among plant species and varieties within cultivated species (Van Endem 1987). This variation influences both larval performance and the female reproductive output of herbivorous insects (Awmack and Leather 2002; Kaspi et al. 2002). In particular, for most herbivorous insects that are considered capital breeders (species with non-feeding adults), host plant quality is a crucial factor for their fitness (Dawkins 1982), since their reproductive potential is determined by the development of the larval stages (Awmack and Leather 2002; Slansky and Rodriguez 1987). The required nutrients for the larval stage provide energy and building materials for survival, growth and larval development; additionally, stored nutrients can be utilized later, in the pupal stage (Tsitsipis 1989). In addition many authors (Cangussu and Zucoloto 1997; Chan et al. 1990; Tsitsipis 1989; Zucoloto 1991, 1993;) have reported that diet may affect insect performance, not only when provided during the larval stages, but also during the lifetime of the adult

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(during oviposition and egg production; affecting sexual acceptance and adult longevity).

The olive fruit fly *Bactrocera oleae* (Gmelin, 1790) (Diptera: Tephritidae) was used as an indicator phytophagous insect in this study, as it is considered to be a most serious pest of the olive tree *O. europaea* L. in many areas of the Mediterranean basin (Manousis and Moore 1987) as well as in Africa, Asia, and North and Central America (Nardi et al. 2005) for more than 2000 years (Hepdurgun et al. 2009). It is a monophagous frugivorous species, of African origin. It infests fruit of olive trees (Economopoulos 2002). Specifically, although adults of the olive fly may be found resting on other plants (fig trees, locust trees, peach trees, etc.), females oviposit only in the mesocarp of unripe and ripe olive fruits, and the larvae develop only in the pulp of the olive fruit. Fruit infestation is caused by larvae which feed on mesocarp tissue, boring galleries inside the drupe. The formation of galleries within the drupe can lead to infestations of both bacteria and fungi (Athar 2005). Olive fruit fly infestation also causes premature fruit drop, reduces fruit quantity and quality for olive fruit production; and increases olive oil acidity (Manousis and Moore 1987; Michelakis and Neuenschwander 1982).

This fly, a member of the Tephritidae, is able to survive and produce offspring throughout a favourable winter (Tzanakakis 2003), even when there are only a few remaining or unharvested fruits on the trees (Neuenschwander and Michelakis 1979). Therefore, it is able to develop high population levels throughout the whole year. There are more than 1200 cultivated varieties of olives all over the world which vary in morphological and chemical characteristics (Bartolini et al. 2005). Such characteristics of the olive variety and fruits, affect *B. oleae* preference, reproduction and larval development. Though, adult preference as indicated by oviposition sites, larval performance which influence population dynamics are much better in their native range than new regions (Dominici et al. 1986; Donia et al. 1971; Gumusay et al. 1990; Iannotta et al. 1999; Mustafa and Al-Zaghal 1987). This preference and performance is defined mainly by females (Thompson 1988). Neuenschwander et al. (1985) concluded that the ovipositional preference of the fly was positively correlated with fruit weight rather than the colour or hardness of the epicarp. Within a variety, unripe green olives are more susceptible to the fly than ripe red or purple olives (Kombargi et al. 1998; Neuenschwander et al. 1985). Chemical stimuli have been also suggested to play an important role in oviposition behaviour (Dominici et al. 1986; Neuenschwander et al. 1985). An example is the degree of waxiness of the fruit (Kombargi et al. 1998), which varies greatly within and among varieties and negatively influences *B. oleae* preference. Gumusay et al. (1990) described the Cilli olive variety: it is spherical,

with a high water content and soft epicarp, it does not discolour, stays green throughout the season. Also, they reported that it was the most heavily infested by the olive fly among other tested varieties.

Furthermore, the influence of infestation by *B. oleae* on olive oil quality has been shown to increase oxidative and hydrolytic degradation of oil phenolic compounds (Gomez-Caravaca et al. 2008; Montedoro et al. 1992; Tamendjari et al. 2009) as well as the occurrence of off-flavours as a consequence of microbial activity (Bendini et al. 2007). The extent of negative consequences is correlated with the volume of tissue damage by the larvae, as well as the temperature and humidity conditions during fruit storage, and the passage of time between damage formation and oil extraction (Michelakis and Neuenschwander 1982).

The objective of this study was to determine the host suitability of 12 olive varieties infested by *B. oleae*, eight of them cultivated far away from their native range, by measuring specific biological parameters as an index of performance (weight of pupa, percentage of emergence, sex ratio, adult size as well as the ovarian maturity of the adult females).

Materials and methods

Experimental orchard

This study was conducted on the island of Crete in the experimental olive grove of the Institute of Olive Tree and Subtropical Plants in Nerokourou village (1.2 ha, 35°28'39.93"N, 24°02'24.94"E, elevation 52 m) during 2011, 2012 and 2013. Thirty to forty-year-old non-irrigated trees belonging to Amfissis, Arbequina, Branquita de Elvas, Carolea, Kalamon, Koroneiki, Leccino, Manzanilla, Mastoidis Moroccan Picholine, Picholine and Sourani were selected based on vegetative growth and flowering uniformity. Trees were of large size, were spaced about 10 m apart, and pruned annually. The olive varieties Koroneiki, Mastoidis, Kalamon, Amfissis and Carolea, are commonly grown in Greece while Arbequina, Branquita de Elvas, Leccino, Moroccan Picholine, Manzanilla, Picholine and Sourani are only planted in this grove for experimental purposes. The olive varieties in the plantation were arrayed in a randomized block design with each block including one tree of each variety. In all there were seven replications of the blocks. The mean olive fruit production per tree and per field was estimated at ~30, 70 and 50% of the normal yield (about 80–120 kg/tree) in 2011, 2012 and 2013, respectively. However, due to the very low olive fruit yield recorded in 2011, olive fruits were collected only from Amfissis, Branquita de Elvas, Carolea, Koroneiki, Picholine, Mastoidis and Manzanilla and not from Arbequina,

Branquita de Elvas, Kalamon, Leccino, Moroccan Picholine and Sourani.

Plant nutrition needs were provided through chemical fertilizers applied each winter according to soil and foliar analysis. Mean annual air temperature in this area was recorded as 18 °C, relative humidity (RH) was 64% and annual rainfall was 600–800 mm according to the records of the meteorological station of the Institute of Olive Tree, Subtropical Plants and Viticulture, ELGO-DIMITRA.

Olive fruit sampling

Some 300–1000 infested olive fruits (with oviposition sites, tunnels and exit holes) were collected from the trees of each olive variety, in order to record the developmental parameters of the olive fly. Fruits were collected at head height and along the four cardinal points of each tree. They were then immediately transferred to the laboratory for the olive fly measurements as described in the next section.

Developmental parameters of olive fruit fly

In order to study the above parameters of *B. oleae* among olive varieties, the infested olive fruits were collected from each variety during the last week of November 2011, 2012 and 2013 which is the end of the harvest period in Crete. At this time of the year there was a high live olive fruit fly infestation due to the favourable environmental conditions for its development, and also because all bait spray applications for fly control had ended more than 2 months previously.

Each sample of olives was enclosed in a wooden cage (dimensions 300 × 300 × 300 mm) in controlled conditions of 22 ± 2 °C, 60 ± 5% RH and 12:12 (L:D). Pupae were collected from the cages on a daily basis and, after weighing, each one was immediately isolated in a small plastic cage (120 × 90 mm) until adult emergence. The percentage of emergence was estimated as the proportion of adult olive flies adults out of the total number of pupae.

After adult emergence, pairs of flies (depending on the emerged individuals from each variety) were put together in the small cages in order to mate, and provided with food solution (sugar and water) for about 15 days. Water was provided separately. Afterwards, the females were anaesthetized with CO₂ and preserved in 30% alcohol. They were then dissected and examined under a stereomicroscope in order to check for the presence (and number) of mature eggs. Adult body length (of both sexes) as well as the sex ratio of the recorded adults (proportion of females out of the total) was recorded under a stereomicroscope equipped with an ocular micrometer.

The weight of 25 fruits per cultivar as well as the colour of the harvested fruits was recorded before their isolation in the wooden cages in 2012 and 2013.

All records were taken under controlled conditions of 22 ± 2 °C, 60 ± 5% RH and 12:12 (L:D); comparable to those prevalent in the field.

Data analysis

In order to compare differences among varieties, data (weight, length and number of eggs/female) were analyzed by one-way analysis of variance (ANOVA) followed by multiple comparison of means using Tukey's honestly significant difference (HSD). Percentage of sex ratio and emergence were analyzed using the χ^2 test. Means and standard errors based on the original data are presented in the tables. The significance level for all analyses was 0.05. Data analysis was conducted using the statistical package JMP (SAS Institute 2008).

Results

During 2011, mean pupal weight from var. Koroneiki (5.73 mg), was significantly lower than from the other varieties (Manzanilla, Mastoidis, Picholine, Amfissis, Branquita de Elvas and Carolea) ($F = 8.61$; $df = 6, 256$; $p < 0.001$). The percentage of emerged adults for each variety ranged from 79.63% (Koroneiki) to 90% (Branquita de Elvas) ($\chi^2 = 0.73$; $df = 3$; $p < 0.01$), while no adults emerged from pupae developed in Manzanilla, Picholine and Amfissis. The percentage of females out of the total adults emerged from pupae, ranged from 23.33% (Branquita de Elvas) to 59.09% (Carolea) and was significantly influenced by the variety ($\chi^2 = 17.6$; $df = 3$; $p < 0.01$). Significantly larger size (adult length) was recorded in adults which had developed on var. Carolea (6.47 mm) compared to Koroneiki, Mastoidis and Branquita de Elvas (5.56 mm) ($F = 7.60$; $df = 3, 163$; $p < 0.001$). Similarly, the highest mean number of mature eggs was recorded in female adults that had developed in Carolea fruits (18.14 eggs) compared to Koroneiki (9.08 eggs) and Branquita de Elvas (8.00 eggs), while Mastoidis showed no difference ($F = 3.77$; $df = 3, 45$; $p < 0.01$) (Table 1).

The following year (2012), the recorded pupal weights from small-sized varieties of Koroneiki (5.80 g) and Mastoidis (6.11 g) were significantly lower than those from other varieties, while the heaviest specimens were recorded from the medium-sized variety Leccino (7.95 mg) ($F = 25.44$; $df = 11, 1809$; $p < 0.001$). The significantly lowest percentage of emerged adults was recorded from Mastoidis (45.96%) and the highest from Leccino (90.37%) ($\chi^2 = 5.57$; $df = 11$; $p < 0.01$) while the percentage of females out of the total emerged adults ranged from 44.02% (Koroneiki) to 63.16% (Sourani) and was also significantly influenced by olive variety ($\chi^2 = 5.57$; $df = 11$; $p < 0.01$).

Table 1 Biological parameters of olive fly (mean \pm SE) from different olive varieties, 2011

Olive variety	Weight of pupae (mg) (<i>N</i>)	% Emergence (<i>A/T</i>)	% Sex ratio (<i>F/T</i>)	Body length of females & males (mm) (<i>N</i>)	Mean number of eggs per female (<i>n</i>)
<i>Amfissis</i>	7.73 \pm 0.38 a (15)	0	–	–	–
<i>Branquita de Elvas</i>	7.00 \pm 0.27 a (30)	90.00 (27/30)	23.33 (7/30)	5.90 \pm 0.10 b (25)	8.00 \pm 1.41 b (5)
<i>Carolea</i>	7.62 \pm 0.29 a (26)	84.62 (22/26)	59.09 (13/22)	6.47 \pm 0.11 a (22)	18.14 \pm 2.96 a (7)
<i>Koroneiki</i>	5.73 \pm 0.18 b (64)	79.63 (43/54)	55.81 (24/43)	5.89 \pm 0.08 b (41)	9.08 \pm 1.55 b (12)
<i>Picholine</i>	7.50 \pm 0.52 a (8)	0	–	–	–
<i>Mastoidis</i>	6.86 \pm 0.14 a (108)	81.55 (84/103)	55.95 (47/84)	6.12 \pm 0.06 b (79)	12.28 \pm 1.32 ab (25)
<i>Manzanilla</i>	7.42 \pm 0.43 a (12)	0	–	–	–

Means within a column followed by the same letter are not significantly different at the 5% level by Tukey's HSD test

N number of individuals, *A* number of alive individuals out of total, *T* total number of individuals, *F* number of females, *n* number of dissected females

Table 2 Biological parameters of olive fly (mean \pm SE) from different olive varieties and olive fruit characteristics, 2012

Olive variety	Olive		Biological parameters of olive fruit fly				
	Fruit weight (g) (<i>N</i>)	Fruit Colour (<i>N</i>)	Weight of pupae (mg) (<i>N</i>)	% Emergence (<i>A/T</i>)	% Sex ratio (<i>F/T</i>)	Body length of females and males (mm) (<i>N</i>)	Mean number of eggs per female (<i>n</i>)
<i>Amfissis</i>	4.04 \pm 0.10 c (25)	Black (25)	7.15 \pm 0.11 b (267)	81.27 (217/267)	52.07 (113/217)	5.89 \pm 0.04 ab (185)	5.62 \pm 0.43 b (37)
<i>Branquita de Elvas</i>	3.32 \pm 0.11 de (25)	Green (25)	6.96 \pm 0.16 b (126)	82.54 (104/126)	50.96 (53/104)	5.88 \pm 0.05 ab (97)	4.71 \pm 0.40 bc (41)
<i>Arbequina</i>	1.83 \pm 0.08 g (25)	Purple (25)	7.55 \pm 0.13 ab (174)	83.33 (145/174)	50.34 (73/145)	5.78 \pm 0.04 b (138)	3.59 \pm 0.55 bc (22)
<i>Carolea</i>	4.72 \pm 0.07 b (25)	Black (25)	7.61 \pm 0.18 ab (97)	88.66 (86/97)	47.67 (41/86)	6.10 \pm 0.06 a (77)	8.83 \pm 0.61 a (18)
<i>Kalamon</i>	2.95 \pm 0.13 e (25)	Black (25)	7.50 \pm 0.14 ab (153)	82.31 (121/147)	50.41 (61/121)	5.73 \pm 0.05 b (114)	3.29 \pm 0.63 bc (17)
<i>Koroneiki</i>	0.99 \pm 0.04 h (25)	Green (25)	5.80 \pm 0.10 c (329)	55.93 (184/329)	44.02 (81/184)	5.51 \pm 0.04 c (166)	3.20 \pm 0.52 c (25)
<i>Leccino</i>	2.47 \pm 0.06 f (25)	Black (25)	7.95 \pm 0.15 a (135)	90.37 (122/135)	47.54 (58/122)	5.84 \pm 0.05 b (112)	3.76 \pm 0.57 bc (21)
<i>Mastoidis</i>	1.46 \pm 0.06 g (25)	Green (25)	6.11 \pm 0.102 c (229)	45.96 (91/198)	47.25 (43/91)	5.81 \pm 0.06 b (85)	4.92 \pm 0.75 bc (12)
<i>Moroccan Picholine</i>	3.38 \pm 0.09 de (25)	Purple (25)	7.69 \pm 0.17 ab (108)	85.85 (91/106)	57.14 (52/91)	5.85 \pm 0.06 ab (84)	3.91 \pm 0.55 bc (22)
<i>Picholine</i>	3.57 \pm 0.14 d (25)	Green (25)	7.21 \pm 0.22 ab (66)	80.30 (53/66)	54.72 (29/53)	5.81 \pm 0.07 ab (48)	4.62 \pm 0.72 bc (13)
<i>Manzanilla</i>	5.23 \pm 0.16 a (25)	Purple (25)	7.41 \pm 0.19 ab (229)	86.36 (76/88)	51.32 (39/76)	5.79 \pm 0.06 b (72)	5.31 \pm 0.72 bc (13)
<i>Sourani</i>	2.31 \pm 0.07 f (25)	Purple (25)	7.35 \pm 0.25 ab (49)	77.55 (38/49)	63.16 (24/38)	5.78 \pm 0.09 abc (37)	3.70 \pm 0.82 bc (10)

Means within a column followed by the same letter are not significantly different at the 5% level by Tukey's HSD test

N number of individuals per fruit, *A* number of alive individuals out of total, *T* total number of individuals, *F* number of females, *n* number of dissected females

Significantly smaller-sized specimens (adult length) were recorded for individuals that had developed on var. Koroneiki (5.51 mm) with lower mean number of mature eggs in their ovaries (3.20) compared to Carolea (6.10 mm and 8.83

eggs respectively) ($F = 8.03$; $df = 11, 1203$; $p < 0.001$ and $F = 6.80$; $df = 11, 1239$; $p < 0.001$ respectively) (Table 2).

In the final year of the study (2013), the recorded pupal weight from the small-sized variety of Koroneiki

Table 3 Biological parameters of olive fly (mean \pm SE) from different olive varieties and olive fruit characteristics, 2013

Olive variety	Olive		Biological parameters of olive fruit fly			
	Fruit weight (g) (<i>N</i>)	Fruit colour (<i>N</i>)	Weight of pupae (mg) (<i>N</i>)	% Emergence (<i>A/T</i>)	% Sex ratio (<i>F/T</i>)	Body length of females and males (mm) (<i>N</i>)
<i>Amfissis</i>	3.60 \pm 0.09 b (25)	Black (25)	7.40 \pm 0.15 ab (90)	86.41 (89/103)	52.22 (47/90)	5.73 \pm 0.04 abc (90)
<i>Branquita de Elvas</i>	2.62 \pm 0.07 e (25)	Green (25)	6.46 \pm 0.23 cd (50)	80.65 (50/62)	46.00 (23/50)	5.56 \pm 0.06 bcd (50)
<i>Arbequina</i>	1.30 \pm 0.03 gh (25)	Purple (25)	6.27 \pm 0.30 cd (26)	74.29 (26/35)	61.54 (16/26)	5.62 \pm 0.08 abcd (26)
<i>Carolea</i>	4.18 \pm 0.07 a (25)	Black (25)	7.42 \pm 0.11 a (137)	80.59 (137/170)	47.45 (65/137)	5.68 \pm 0.04 abcd (137)
<i>Kalamon</i>	3.22 \pm 0.07 cd (25)	Black (25)	6.70 \pm 0.10 c (157)	76.59 (157/205)	52.23 (82/157)	5.56 \pm 0.03 cd (157)
<i>Koroneiki</i>	0.94 \pm 0.03 h (25)	Green (25)	6.03 \pm 0.08 d (394)	50.90 (394/774)	44.67 (176/394)	5.56 \pm 0.02 d (394)
<i>Leccino</i>	2.60 \pm 0.06 e (25)	Black (25)	7.73 \pm 0.15 a (75)	91.46 (75/82)	60.00 (45/75)	5.85 \pm 0.05 a (74)
<i>Mastoidis</i>	1.48 \pm 0.05 g (25)	Green (25)	6.54 \pm 0.25 bcd (46)	38.02 (46/121)	56.52 (26/46)	5.74 \pm 0.03 abcd (46)
<i>Moroccan Picholine</i>	2.96 \pm 0.07 de (25)	Purple (25)	6.86 \pm 0.14 bc (160)	75.83 (160/211)	40.00 (64/160)	5.57 \pm 0.03 cd (160)
<i>Picholine</i>	3.14 \pm 0.11 cd (25)	Green (25)	7.17 \pm 0.14 abc (114)	79.72 (114/143)	48.25 (55/114)	5.72 \pm 0.04 abc (114)
<i>Manzanilla</i>	3.41 \pm 0.10 bc (25)	Purple (25)	7.21 \pm 0.10 abc (189)	68.98 (189/274)	47.09 (89/189)	5.74 \pm 0.03 ab (189)
<i>Sourani</i>	1.89 \pm 0.05 f (25)	Purple (25)	6.60 \pm 0.40 abcd (5)	83.33 (5/6)	66.67 (4/6)	5.62 \pm 0.18 abcd (5)

Means within a column followed by the same letter are not significantly different at the 5% level by Tukey's HSD test

N number of individuals, *A* number of alive individuals out of total, *T* total number of individuals, *F* number of females, *n* number of dissected females

(6.03 mg) was significantly lower than that from other varieties, while the heaviest was recorded from the medium-sized variety Leccino (7.73 g) and large-sized variety Carolea (7.42 g) ($F = 18.77$; $df = 11, 1431$; $p < 0.05$). The percentage of emerged adults for each variety ranged from 38.02% (Mastoidis) to 86.41% (Amfissis) while the percentage of females out of the total emerged adults ranged from 40.00% (Moroccan Picholine) to 66.41% (Sourani), and both parameters were significantly influenced by olive variety ($\chi^2 = 34.23$; $df = 11$; $p < 0.01$ and $\chi^2 = 13.17$; $df = 11$; $p < 0.01$, respectively). A significantly smaller size (adult length) was recorded in adults which had developed on var. Koroneiki (5.85 mm) compared with Leccino (5.56 mm) ($F = 6.46$; $df = 11, 1430$; $p < 0.001$) (Table 3).

It should be noted that the size of the fruits differed significantly among varieties in both years; significantly lower mean values of weight were recorded in fruits of var. Koroneiki, Arbequina and Mastoidis compared to var. Carolea and Manzanilla in 2012 ($F = 167.63$; $df = 11, 288$; $p < 0.000$) and 2013 ($F = 153.57$; $df = 11, 288$; $p < 0.001$) (Tables 2, 3).

Discussion

Through our field measurements of *B. oleae* performance among several olive varieties under the same cultural and environmental conditions, we have concluded that the large-sized olive fruits (>3 g/fruit) examined, such as Manzanilla, Moroccan Picholine, Leccino, Picholine, Carolea as well as Kalamon, exhibited the greatest olive fly performance as was indicated by the measurements performed as part of this study on *B. oleae*. The largest olives also exhibited the highest infestation compared to all the other tested olive varieties during the studied years (Garantonakis et al. 2016). Several authors (Dominici et al. 1986; Gumusay et al. 1990; Iannotta et al. 1999; Rizzo and Caleca 2006) refer to the fact that large-sized varieties are more heavily infested than smaller ones, concluding also that within the same variety, the bigger fruits may be preferred over smaller ones by olive flies. Also, there was an intense host preference of the female to large-volume olive fruits, either located in trees within orchards of the same variety, or in specific varieties within orchards with various varieties. This was obvious during 2011, which was a

year of low olive yield. Specifically in varieties with large-volume fruits, the mean weight of the pupae as well as the length of the developed adults was significantly higher than those individuals which had developed in smaller fruits such as Koroneiki. It is important to note that these varieties showed better *B. oleae* performance in all the tested characteristics; there was a significantly higher percentage of emerged adults exceeding 80%, with a significant trend to produce more female than male adults, while the adult females produced significantly higher number of eggs. The best olive fly performance was indicated by individuals that developed in Leccino and Carolea, with females that developed in Carolea showing the best reproductive performance. In contrast, Koroneiki is the only variety which showed clearly the worst olive fly performance, with the lowest recorded values for all the tested characteristics: the mean weight of pupae was significantly lower than for those that developed in other varieties; the adults were significantly shorter (index of size), while the females when dissected had the lowest mean number of eggs in their ovaries. Probably the low flesh quantity of a fruit of Koroneiki variety limits larval development.

Another conclusion of the current study is that the adult's increased fitness (ovarian maturity and size) was attributable to emerging from a large pupa, similar to the findings of Forrest (1987) and Visser (1994). It should also be mentioned that a large pupa is linked with the previous development of a large larva, as pupal weight or size is usually used as a measure of larval success in many species of Tephritidae (Averill and Prokopy 1987; Krainacker et al. 1987). Iannotta et al. (1999) reported that although there are several varieties which are preferred by *B. oleae* they did not all subsequently support larval development. Burack and Zalom (2008) reported that there were significant effects of variety on pupal weight and larval developmental time. Specifically, the weight of a pupa developing in Manzanillo and Sevillano olives was higher than those that developed in the less preferred varieties, while the larval developmental duration was significantly shorter in Sevillano olives compared with the other varieties.

Concerning the recorded sex ratio, it was influenced significantly by the variety for each year, although the results are not similar among years, meaning that the variety is not the only factor that determines the sex ratio. Probably there are several biotic (e.g. parasitism) and abiotic factors (e.g. temperature) that influence the mortality of the larva developing in male or a female individual among varieties, other than the choice of the *B. oleae* female. Furthermore, during the fruit olive maturation period, the fruit of each variety or fruits of different varieties suffered numerous physical (firmness, hardness and elasticity) and chemical changes (oil content increase, moisture decrease and fatty

acid release) that probably influence female behaviour and larval development. Goncalves et al. (2012) reported that some of the chemical parameters, such as fatty acid composition, could also be related to the choice of the female olive fly in the selection of the olive variety for laying its eggs. They concluded also that during the harvest period (from September until November), olive fruit fly oviposition was negatively correlated with the water content and positively correlated with the oil content of Madural, Verdeal Transmontana and Cobrancosa olive varieties. The factors other than size of olive associated with variety that may be important in host selection by *B. oleae* may be further investigated by systemic measures of chemical and morphological characteristics of infested olives compared with uninfested olives within a variety.

It is important to note that our measurements concerning the biological parameters of the fly also depend on environmental factors which may influence the performance of the olive varieties in the field in Crete. Though, these field records of *B. oleae* individuals developed on several olive varieties which were adapted to a new environment, are quite valuable for determining its population growth, dynamics and preference with future prospective of their cultivation under large scale fields or on regions of similar environmental conditions.

Despite the fact that this study indicated that Koroneiki and Mastoidis were not the best varieties for female reproduction, in Crete these varieties are the only choice for the olive fly on the island, other than at the research institute. Specifically, both Koroneiki and Mastoidis are grown extensively on the island of Crete (Stefanouadaki et al. 2009) with Koroneiki mainly cultivated in almost all the coastal regions and Mastoidis in the mainland regions, because of its cold tolerance. It is well known that in Crete, *B. oleae* is able to develop high pest densities and more than five generations throughout the year, due to favourable conditions and fruit availability of the mentioned varieties. However, within the same cultivar, there is high variation among cultural practices and climatic conditions which influence, positively or negatively, the fruit which becomes infested by the *B. oleae*.

Understanding the impact of olive variety on infestations of olive fly is not only of scientific but also of practical interest in the production of table olives and oil. Olive cultivars with less susceptibility to olive fly infestation could lead to a reduction in pesticide application in mixed variety plantings of regions with similar climatic conditions. Knowledge about this topic could contribute to a decrease in the cost of olive fly control, improve pest management as well as quality and food safety in olive oil production.

In addition, the determination of the reproductive potential of various olive varieties is essential in

the effort to understand the life history and population dynamics of this species. Further research is needed to verify the effects of physical parameters (fruit weight and volume, flesh/kernel ratio, tissue hardness, etc.), chemical parameters (moisture and oil content of olive fruit) and macroelements (nitrogen, potassium, phosphorus, etc.) of different olive varieties, which may also influence female preference and larval development. The female evaluates all the conditions at its disposal in the selection of a specific fruit, tree, variety, orchard, etc. to choose the best nutritional conditions and other unknown or unpredictable factors for the development of its offspring, as well as to optimize its reproductive success (Moreau et al. 2006).

After investigating all these conditions, the question concerning the most suitable host for olive fruit fly development will clearly be answered.

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