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Distribution of *Virachola livia* (Lepidoptera: Lycaenidae) Eggs and Influence of Conspecific Aggregation and Avoidance Behavior

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ABSTRACT

The oviposition behaviour and distribution of the eggs of carpophagous *Virachola livia* Klug (Lepidoptera: Lycaenidae) was studied on pomegranate for six years. Taylor's power law and Iwao's mean patchiness regression, and common *k* proved the aggregated distribution of the eggs on pomegranate fruits. The butterflies tend to oviposit one egg per fruit, indicating the existence of conspecific egg avoidance behaviour. The study showed that the selection of oviposition sites was affected by the part of the fruit body and the cardinal direction of the tree canopy. Results suggest that the oviposition behavior of *V. livia* and, consequently, the distribution of the eggs may be regulated by the conspecific aggregation and conspecific egg avoidance. It is apparent that the butterfly integrates these two behaviors to maximize the success of its reproduction.

Keywords: Conspecific egg avoidance, Pomegranate, Oviposition site, Oman.

INTRODUCTION

We studied the temporal and spatial distribution of *Virachola livia* Klug (Lepidoptera: Lycaenidae) eggs in pomegranate plantation and the factors influencing this distribution.

Despite the importance of this pest, we recognized during literature search that the knowledge on its ecology is still poor and the comparable data are very few and rare. This carpophagous species specialized on pomegranate *Punica granatum* (Lythraceae) fruits for reproduction. The females start laying eggs on pomegranate fruits at the beginning of the fruit setting, and continue without interruption during all growth stages (Awadalla, 1966). Such ephemeral host promote the conspecific competition (Heed, 1968; Takahashi *et al.*, 2005). Some behaviours of *V. livia* that play important role in its egg distribution, e.g. the preferential choice of oviposition sites, and the cannibalism behavior in larval stage, were studied by Awadallah (1966). The limited resources cause the rising of the conspecific attraction, which is a form of social information. Attraction to the presence of conspecifics often happens because that may indicates high-quality sites or resources (Raitanena *et al*, 2014). Thus, conspecific attraction results in aggregation of individuals with similar needs and may therefore intensify competition, in particular, at high densities (Atkinson and Shorrocks, 1981). On the other hand, conspecific egg avoidance behavior was reported in many butterfly species and, in this case, the ovipositing females may avoid host plants bearing conspecific eggs (Kellogg, 1985; Marchand and Mcneil, 2004). Conspecific egg avoidance behavior has been reported in *V. livia* females on pomegranate fruits (Awadallah, 1966). In such insects, females apparently avoid host overload by assessing their egg-load and, if necessary, adjusting their oviposition behavior, accepting

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only plants without eggs (Shapiro, 1980). And/or this avoidance could be due to the existence of cannibalism behavior in larval stage (Awadallah, 1966). So, decisions of the ovipositing females are often critical for the fitness of the offspring (Doak *et al*., 2006). This study aimed to determine temporal and spatial distribution of the eggs of *V. livia* on pomegranate, during the period from 2003 to 2008. In addition, the candidate forces that may guide and regulate the egg distribution were to be investigated. The obtained knowledge is necessary for developing successful management for this key pest of pomegranate.

MATERIALS AND METHODS

Area and Locations

This study was performed in 10 different locations in "Al Jabal Al Akhdar", the main area of pomegranates cultivation in Oman. The total number of pomegranate trees in the selected locations was 20,349 trees. The 10 Locations (L) namely are: Alain (L1); Hailalyaman (L2); Kashe (L3); Manakher (L4); Okr (L5); Saiq (L6); S Sallot (L7); SeihKatana (L8); Sherija (L9) and Wadibanihabib (L10). Saiq (UTM: 565362.80 Easting, 2551473.50 Northing) is the center of the studied area and the other locations are located at 2 to 9-kilometer distance around it.

Temporal Egg Distribution

Sampling was carried out during the flight season of females (from May to August). Sampling was started at 1st May when all trees were bearing fruits after the dormancy season. In this study, one pomegranate fruit was selected as a sample unit. Fruits were selected randomly and from all parts of the canopy. The samples were taken from 10% of the total number of the trees in each location to avoid biased estimate of population mean. To maximize detection probability and to minimize the effect of its variation on the population size estimate (Cochran, 1977; Zonneveld *et al*., 2003) fruits sampled twice a week. A primary sampling test was carried out in 2003 season at Saiq to estimate the smallest sample size that provides the desired precision. The primary test was conducted with different levels of sampling (3, 4 and 5 fruits per tree). The Relative Variation [RV= (Standard error×100)/Mean] calculated to evaluate the efficiency of the data (Darbemamieh et al., 2011; Moradi-Vajargah *et al*., 2011). A total number of 1,667,117 fruits were inspected and a total number of 113,471 eggs were counted from 2003 to 2008. Census of eggs performed *in situ* without detaching the fruit to avoid any economic loss. The live eggs were removed after counting directly to avoid exaggerating if they did not hatch until the next census. The weekly egg density was averaged from the two datasets of each week. The gathered data of each year were segmented based on yearly, monthly, and weekly sets to simplify its illustration, and the statistical analysis. Since the numbers of pomegranate trees vary from one location to another, we estimated the egg density as the number of deposited eggs per 100 fruits to correct the unbalanced number of inspected fruits in each location.

Spatial Distribution

The following regression models were used to describe the dispersion pattern (regular-random - aggregated) of the eggs:

***Taylor's Power Law*:** $Log\ s^2 = Log\ \alpha + b\ Log\ m$, where s^2 is the variance and m is the egg density, a and b are the parameters of the regression (Taylor *et al.*, 1978). The intercept (α) is related to sample unit size, and the slope (b) is an index of dispersion that indicates a uniform, random or aggregated dispersion when $b < 1$, $=1$, or > 1, respectively (Southwood, 1978).

Iwao's Mean Patchiness Regression: $m^* = \alpha + \beta m$, where m^* is determined as [$m^* = m + (s^2/m) - 1$]; the slope β reflects the distribution of population in space and is interpreted in the same manner as b of Taylor's power law.

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The mean density m and variance s^2 used to estimate the parameter k, where $k= m^2/(s^2 - m)$. Then, we regressed k on m: $k= c+dm$ (Southwood, 1978; Feng and Nowierski, 1992). The existence of common k (the negative binomial distribution parameter) has been examined.

Eggs Distribution within Fruits

This test was conducted to investigate the distribution of the eggs within the fruits; on different sites (hypothesized) of the fruit body; the orientation of the egg-bearing fruits on the tree canopy, and the number of the eggs per egg-bearing fruit. The government experimental farm (300 trees) in Saiq was selected to conduct this experiment where the trees were planted in regular proper spacing (5×5 m). Thus, it was possible to detect the different cardinal directions of each canopy and their fruits clearly. The egg census was carried out from 25 May to 29 June 2003 in weekly basis covering 200 to 210 trees. Four fruits were randomly selected and inspected from each tree, one fruit from each direction of the canopy. A total number of 5,000 fruits were inspected in this experiment, where a number of 877 fruits were found bearing 1,112 eggs. The investigated parameters of the eggs distribution within fruits were:

Hypothesized Sites of the Fruit Body

Regarding the egg location on the fruit, we divided the fruit body into 7 hypothesized sites: Apex (1); top half (2); lower half (3); bottom (4); calyx (5); edge of the calyx (6); and inside calyx (7).

Orientation in Tree Crown

Concerning the distribution of eggs proportion on the fruits in each cardinal direction (N, E, S and W) of the tree canopy.

Categories of egg-bearing fruits

The egg-bearing fruits were categorized into 10 categories (category1, 2, 3, 4, 5, 6, 7, 8, 9, 10), the category number indicates the number of the eggs on the fruit; e.g. category1 for fruits bearing one egg each, and category10 for fruits bearing 10 eggs each. The Poisson distribution probability was applied to detect the random variability of the categories (Doane and Seward, 2010). The probability was estimated by the following function:

$P(x; \mu)= (e^{-\mu}) (\mu^x)/x,$

Where, μ= The number of the tested category in the sample, x= The actual number of egg-bearing fruits per sample, and e is approximately equal to 2.71828.

Distribution of Egg-bearing Fruits Categories over the Six Years

The probability (Poisson distribution) of the occurrence of different categories of the egg-bearing fruits over the six years and locations. The probabilities of each category during the oviposition peak in the collected datasets from May and June of each season were examined to detect the pattern of their distribution.

Statistical analysis in the present study were performed by using Minitab 16. Analysis of variance was used to compare means of egg density on yearly, monthly, and weekly basis, and the data were transformed $[(x+0.375)^{0.5}]$ prior to the analysis to stabilize the variances (Zar, 1999). Egg proportions within fruits were transformed using the arcsine square root to normalize the data prior the analysis of variance (Zar, 1999). Means comparison was done by using Tukey 95% Simultaneous Confidence Intervals.

RESULTS

Temporal Distribution

The primary sampling showed that the reliable sample size was 5 fruits per tree

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with Relative Variation (RV) of 8.4%, which is suitable for sampling plan. A total number of 10,174 fruits (from 2,035 trees) was inspected per visit. Flight and oviposition period of *V. livia* on pomegranate takes 15 to 16 weeks. The overall mean of egg density (eggs 100 fruits^{-1}) during the study period was 6.74±0.31 (mean±SEM). Egg density ranged from 4.89±0.57 in 2008 to 10.87±1.33 in 2007 (Figure 1-a). Significant differences was found between 2007 and the other years ($F_{5, 826}$= 8.86, P< 0.001). The monthly data revealed significant differences among months ($F_{3, 826}$= 75.78, P< 0.001). The highest egg density was in May (12.82±0.82), June (7.13±0.47), July (4.00±0.31) and August (0.70±0.07), ranked in the same order (Figure 1-b).

Egg density was significantly different at weekly basis ($F_{15, 826}$= 22.81, P<0.001). The highest egg density was recorded in the 4th week (16.16±1.86), followed by the 3rd (14.82±1.69) and then the 5th (12.96±1.52) weeks, ranked in the same order (Figure1-c). In general, the oviposition pattern showed a sharp increase from the 1st week, reaching the main peak in the 4th week of the season. Thereafter, the oviposition activity gradually decreased until stopped in August.

Spatial Distribution

Both Taylor and Iwao models proved the aggregated distribution of *V. livia* eggs (Table 1). Taylor's power law confirmed a positive significant relationship between variance and mean density during the six years and the slopes (b) were significantly >1. Similarly, Iwao's model showed significant relationship between mean crowding (m^*) and the eggs density (m). Estimates for the density contagiousness coefficient (β), were significantly >1. Moreover, the values of the intercept (α) were < 0, except in 2006. Regression for Taylor's power law and Iwao' patchiness regression are illustrated in Figure 2. Based on values of R^2, Iwao's mean crowding regression fitted the data better than

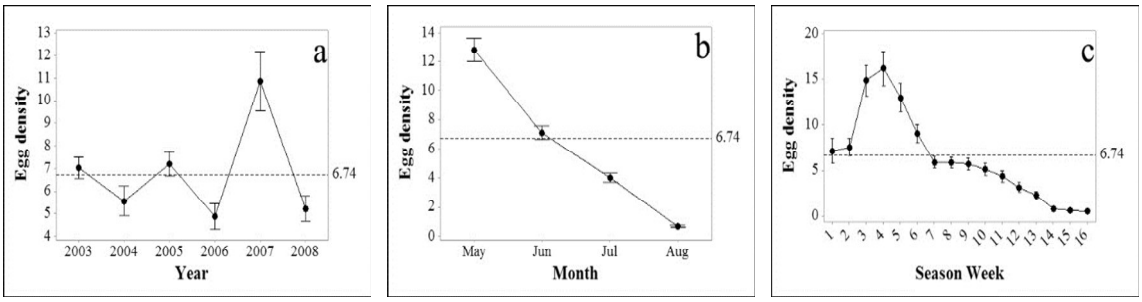

Figure 1. Interval plots show the mean±SEM of the egg density (eggs 100 fruits^{-1}) for *Virachola livia* eggs on pomegranate fruits during the study period, at yearly (a); monthly (b) and weekly (c) basis. The dashed horizontal line represents the overall mean pooled from 827 datasets from 2003 to 2008.

Table 1. Spatial distribution parameters of *Virachola livia* eggs on pomegranate fruits, estimated by Taylor's power law and Iwao's patchiness regression analysis.

Year	*Taylor' power law*					*Iwao's mean crowding regression*				
	α	b	R^2	t_b	P_b^c	α	β	R^2	t_β	P_b
2003	-1.549	1.15	0.689	5.16	<0.0002	-0.986	1.14	0.853	8.35	<0.0001
2004	-0.665	1.91	0.910	11.04	<0.0001	-1.002	1.38	0.957	16.85	<0.0001
2005	-0259	2.19	0.984	26.80	<0.0001	-1.007	1.46	0.985	22.04	<0.0001
2006	-0.603	1.59	0.923	11.96	<0.0001	0.976	1.32	0.968	13.49	<0.0001
2007	-1.416	1.40	0.918	11.62	<0.0001	-0.998	1.36	0.996	54.82	<0.0001
2008	-0.505	1.98	0.987	30.23	<0.0001	-1.000	1.33	0.997	65.70	<0.0001

^{c}***P**$_b$*= Probability of t of the slope.

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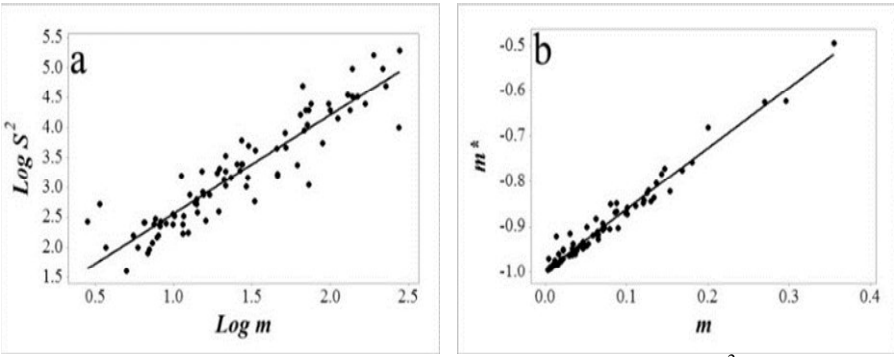

Figure 2. Regression analysis indicating significant relationship for *Log* s^2*= Log 0.9279+1.6425 Log m* (a), and for *m*= -0.9953+1.3431m* (b) for *Virachola livia* egg density on pomegranate fruits.

Taylor's power law model. Iwao's regression clearly provided more even distribution of points along the line and showed no evidence of curvilinearity compared to the plot of Taylor's power law. The regression of the estimated negative binomial parameter *k* on *m* (using all data where the variance exceeded the mean) was not significant in case of years (R^2= 0.022) or locations (R^2= 0.0004) datasets (Figure 3). So, independence of *k* with the mean density *m* suggests the existence of common *k* (k_c) for the negative binomial distribution of the populations (Elliot, 1977; Tsai *et al.*, 2000).

Eggs Distribution within Fruits

Hypothesized Sites of the Fruit Body

There were significant differences between the proportion of oviposited eggs on the fruit body in different sites ($F_{6,\ 70}$= 6.91, P< 0.001) (Figure 4-a). The grouping of means placed the sites into four ranks; the first rank included site no. 4 (Bottom) alone with a number of 288 eggs (25.9%). Then sites no. 3 (lower half), 7 (inside calyx) and 2 (top half) located in the second rank consisted of 247 eggs (22.2%), 208 eggs (18.7%) and 195 eggs (17.5%), respectively. Sites no. 5 (Calyx) and no.1 (Apex) were located in the third rank and comprised 101 eggs (9.1%) and 56 eggs (5.1%), respectively. While site no. 6 (edge of the calyx) was in the fourth rank as the least favoured site for oviposition with only 16 eggs (1.4%). The total number of oviposited egg on sites 4, 3, 2, and 7 was 938 eggs, representing 84.4% of the total number of eggs (1,112 eggs).

Orientation in Tree Crown

The egg proportions on the egg-bearing fruits in relation to the cardinal directions

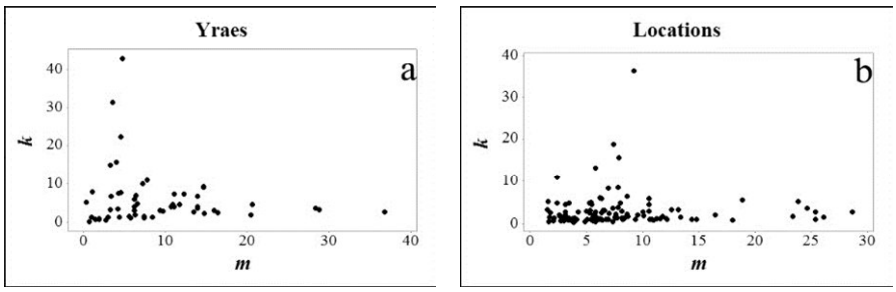

Figure 3. Scatter plots of *k* for *Virachola livia* over mean egg density (*m*) on pomegranate fruits from datasets where the variance exceeded the mean. Regression between *k* and mean *m* were not significant neither of years (R^2= 0.023, P= 0.273) nor of locations (R^2= 0.0004, P= 0.843) data.

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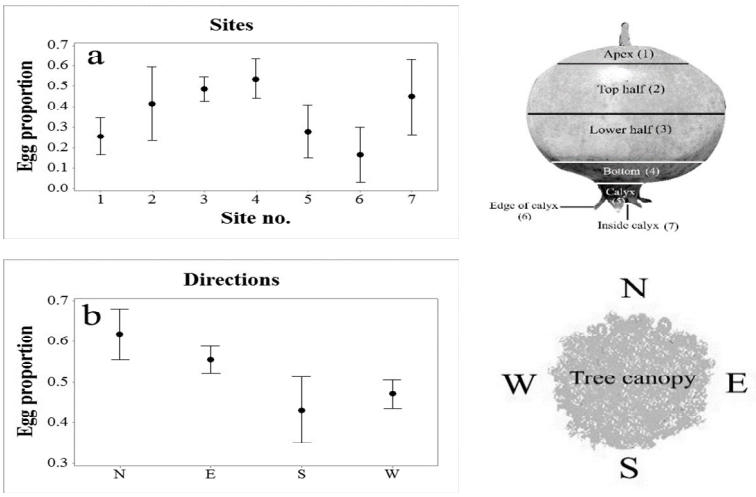

Figure 4. Interval plots for the distribution of *Virachola livia* eggs on the seven hypothesized sites on pomegranate fruit body (a); and on the four cardinal directions of the pomegranate tree crown (b). Total inspected fruits= 5,000; Egg-bearing fruits= 877, and Number of eggs= 1,112.

were significantly different ($F_{3,\ 23}$= 14.23, P< 0.001) (Figure 4-b), where they placed into four ranks (1,2,3,and 4, respectively). The highest number of eggs was recorded on the fruits in north direction as 351 eggs (31.6%), followed by the east direction in the second rank with 313 eggs (28.2%). The fruits in the west direction comprised 235 eggs (21.1%) and placed the third rank; the south direction had the lowest number of eggs i.e. 213 (19.2%) (Figure 4-b).

Categories of Egg-bearing Fruits

This survey was undertaken to estimate the probability of occurrence of different number of eggs on the egg-bearing fruits. The proportion of different categories revealed significant differences ($F_{7,\ 47}$= 148.83, P< 0.001). Category 1 (number of the category is equal to the number of the eggs on the fruit) was in the first rank and included 736 fruits (83.9% of total number of fruits). Category 2 was in the second rank with 95 fruits (10.8%), followed by categories 3 and 4 in the third rank with 28 fruits (3.2%) and 11 fruits (1.3%), respectively. Fruits with five or more eggs were very rare i.e. 7 fruits (0.8%), and placed as the fourth rank. Distribution of egg-bearing fruits categories and the empirical egg counts of the six census dates illustrated in Figure 5. The probabilities of categories distribution (Poisson) were 35.7, 22.6, 9.6, 3.0, 0.8, and 0.20% for categories 1, 2, 3, 4, 5, and > 5, respectively (Table 2).

Distribution of Egg-bearing Fruits Categories over the Six Years

The probability of the occurrence of different categories of egg-bearing fruits over the six years and locations were estimated (Figure 6). The highest probability belonged to category 1, either in yearly or location cases. The probability of category 1 was the superior, even under the highest egg density in 2007 i.e. 0.16 compared to 0.015 for category 2. The fruits with more than two eggs were rare, e.g. probability of category 3 was minor (97×10^{-5}), and it was very minor for fruits bearing > 5 eggs (58×10^{-9}) in the same year.

DISCUSSION

The present study provided a description of temporal and spatial distribution of *V. livia* eggs in pomegranate plantation.

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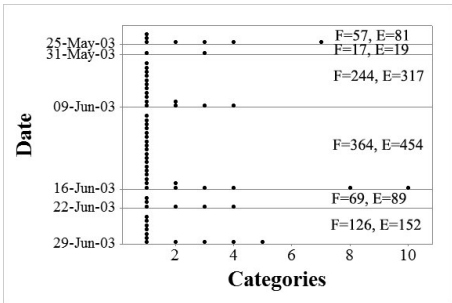

Figure 5. Dot plots showing the actual number of egg bearing-fruits in each category during the high oviposition activity time of *Virachola livia* from 25 May to 29 Jun 2003. Each dot in column represents up to 18 observations. F= Total number of egg-bearing fruits, and E= Total number of counted eggs in each census date.

Table 2. Percentages and probabilities (Poisson) of the egg-bearing fruits categories during the peak c the oviposition period from 25 May to 29 June 2003.

Category	Egg-bearing fruits		
	Number	%	Probability (Poisson)
1	736	83.92	0.3568
2	95	10.83	0.2262
3	28	3.19	0.0956
4	11	1.25	0.0303
5	1	0.11	0.0077
>5	6	0.68	0.0020
Total	877	100	

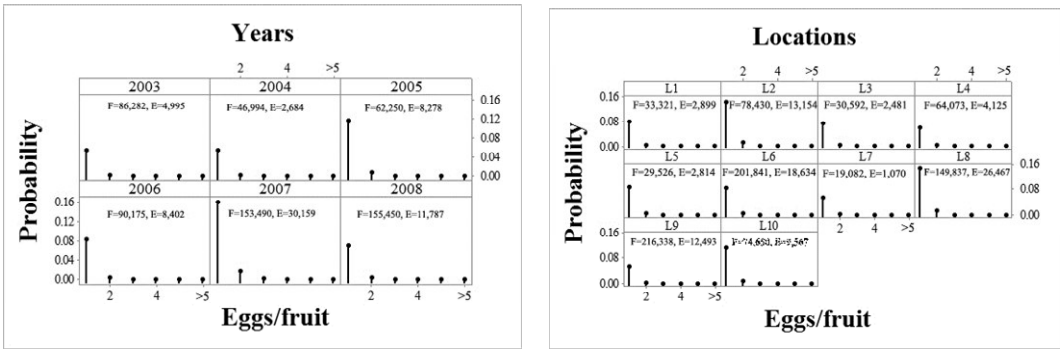

Figure 6. Time series plots illustrate the probability of occurrence of different number of *Virachola livia* eggs per fruit based on the empirical data from 2003 to 2008, and locations. Fruits with zero eggs were excluded from the graph to emphasize the comparison between the egg-bearing fruits categories. F= Number of inspected fruits, and E= Total number of recorded eggs.

Furthermore, it highlighted the impact of conspecific aggregation and avoidance behavior on laying and distribution of the eggs. The seasonal oviposition activity of *V. livia* comprised one increasing phase (≈ from 1st week of May to 1st week of June) and one declining phase (≈ from 2rd week of June) that continued until the end of the season ≈ in 3rd week of August (Figure 1-c). Formation of these two phases could be possibly due to the availability and/or suitability of the fruits and the competition between the butterflies. The age of the host sometimes becomes a very crucial factor

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affecting the oviposition decision (Sparks *et al.,* 1994; Rabasa *et al*., 2005). Through the growing season, the skin of the pomegranate fruit turns to red in colour and becomes rigid. These changes could give a message (chemical and/or visual cues) to the butterflies that the fruit is about to expire soon, and its offspring would fail to complete their development. Hence, the chance of the butterflies to find younger fruit becomes more difficult day after day. Thus, the butterflies may run out of lifetime and become 'time-limited' before all eggs are laid (Rosenheim, 1999). In this case, the competition rises up, particularly if the ovipositing females show a preference or specificity for some parts in their host (Thompson and Pellmyr, 1991; Schowalter, 2006).

Dispersion of the insect within the host, or the spatial dispersion, is a measure of how the insect population is distributed in space (Taylor *et al*., 1978). Taylor and Iwao regressions, and common *k*, proved the aggregated distribution of *V. livia* eggs on pomegranate fruits. The aggregated distribution (Table 1) means that individuals with similar needs are attracted to the presence of conspecifics because they may indicate high-quality sites or resources (Moradi-Vajargah *et al*., 2011; Raitanena *et al*., 2014). Our study clearly showed that the pest butterfly prefers some sites on the fruit body for egg laying; this also confirms previous field observations by Awadallah (1966). Pomegranate fruit body comprises different characterizations (Wetzstein, *et al*., 2011) which could make some part on the fruit more favoured by the *V. livia*. For instance, the calyx is the hardest part on the fruit body, and it is not easy for the newly hatched larva to penetrate it. Nevertheless, the cavity inside the calyx offers a good harbor and protection for the eggs against sunlight, birds, and other predators. The middle part is the wider diameter of the fruit where the skin (exocarp) is thin. Therefore, the middle part offers the shortest way for the larvae to penetrate and reach the seed through the thin exocarp and thin mesocarp underneath. Data showed superiority of site no. 4 (Bottom), which is relatively less exposed to direct sunlight. In contrast, sites number 1 (Apex) and 6 (Edge of the calyx) were the least favoured sites, which are more exposed to desiccation effect of direct sunlight and to predators. These findings are in agreement with Awadallah (1966), who stated that the middle part of the fruit (equal sites 2, 3, and 4 together in our study) and the inside calyx site (equal site no. 7 in the present study) were the most favoured sites for oviposition by *V. livia.* In addition, the stalk region (equal site no. 1 in our study) was the least favoured site. The lower number of eggs on south side of the tree canopy may be due to the effect of sun. The perpendicular sunbeam in the south making it hotter leading to egg desiccation. The obtained results (Figure 4) and the properties of the different parts of the fruit explain the preferential choice of *V. livia* for oviposition sites in relation to the fruit body and direction of the fruits in the tree canopy.

Hence, it requires the butterflies a compromise between best sites on fruit body and sunlight in order to ensure optimal embryonic development (Janz, 2002; Bancroft, 2005). Egg laying behavior acquires even more importance for species that are endophytic throughout their larval stages. This might be because the larvae are not easily able to switch feeding substrates or migrate to other places following the egg laying (Storey-Palma *et al.,* 2014).

It seems that the butterflies tended to place one egg only over the fruit, and then move to another fruit to lay another one egg and so on. Further, we noted in the field during our work that if more than one egg existed on the same fruit, they were often deposited by more than one butterfly. In such cases, the eggs were distanced on fruit body away from each other with enough space. Iwao's regression showed better fit (Figure 2) with intercept (α) values < 0 in all years, except 2006 (Table 1). The negative intercept indicated that the basic distribution component of population was the individual egg (Sedaratian *et al.*, 2010). The probability

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distribution of the number of eggs on egg-bearing fruits (Figure 5; Table 2, and Figure 6) demonstrate the tendency of *V. livia* butterfly to lay a single egg per fruit and it avoids the oviposition on the fruit with conspecific eggs. Category 1 was superior despite the high competition during the peak of *V. livia* abundance in May and June (see Figure 1-b). Likewise, Awadallah (1966) found in the field study that most of the pomegranate egg-bearing fruits carried only one egg, thereby supporting evidence of conspecific egg avoidance in this species. However, we can explain the tendency of the females to lay a single egg per fruit as follows:

The females might be able to recognize the presence of conspecific eggs on potential host plants apparently through visual, olfactory, gustatory and mechano-sensory cues by themselves or in combination with each other (Schäpers *et al*., 2015). Thus, they avoid host overload by assessing their egg-load. Consequently, the females may adjust their oviposition behaviour, accepting only host without eggs to ensure enough food for the hatched larva (Rausher, 1979; Shapiro, 1980).

The female might follow this behaviour to minimize the cannibalism risk. Cannibalism behaviour has been reported within the larvae of *V. livia* (Awadallah, 1966), and in its family (Lycaenidae) (Scoble, 1995; Duarte and Robbins, 2009). Situation of overcrowding of eggs means more opportunity of larval cannibalism.

In General, several factors may contribute to the distribution of *V. livia* eggs on the pomegranate fruits as follows:

a) Factors causing aggregation such as resource limitation involving short season of pomegranate fruiting; suitability of the fruit physical status for oviposition during the relatively short life of the butterfly females; and high competition on preferable oviposition sites.

b) Factors causing avoidance such as carrying capacity of the pomegranate fruit; and cannibalism behaviour in larval stage.

In the first glance, it seems that the aggregation and the avoidance in the same time and space are conflicting behaviours. The distribution of *V. livia* eggs within pomegranate fruits depend on the site selection decision made by the ovipositing females. The decision to accept or avoid the fruit and site for oviposition is a contextual response (Thompson, 1988, Janz, 2002). However, there remains the further question of the average density of eggs experienced by the fruits. This, which may be referred to as the 'exploitation pressure', comes out at 1.3 eggs per fruit (1112 eggs on 877 fruits, see Figure 5), reflecting the fact that most of the fruits support only one egg (neglecting the fraction). Nevertheless, the butterfly may avoid those fruits bearing conspecific eggs as long as egg-free fruits are available as alternatives. Once all or most of the available pomegranate fruits have been taken, then the females may cease their discriminatory behavior and oviposit on plants with conspecific eggs instead of not laying eggs at all leading to suboptimal oviposition decisions (Kellogg, 1985; Bernays,1999). It is concluded that conspecific aggregation and avoidance behaviors are decisive factors that have important implications for regulation of *V. livia* population on pomegranate fruits and should be taken into account for designing the management program.

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پراکنش تخم لیویا (بال پولک داران) *Virachola livia* (Lepidoptera: Lycaenidae) و اثر تجمع همگونه و رفتار اجتنابی

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چکیده

در این پژوهش، رفتار تخم گذاری و پراکنش تخم های پروانه میوه خوار *Virachola livia* Klug (Lepidoptera: Lycaenidae) روی انار به مدت شش سال بررسی شد. قانون نمایی تیلور و رگرسیون لکه ای ایواو (Iwao's mean patchiness regression) و مقدار *k*، پراکنش تجمعی تخم ها روی میوه انار را اثبات کردند. نتایج نشان داد که پروانه ها تمایل داشتند در هر میوه یک تخم بگذارند که این امر به رفتار اجتناب از تخمگذاری همگونه اشاره می کرد. این بررسی نشان داد که

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انتخاب مکان تخمگذاری تحت تاثیر بخش های مختلف میوه و جهت های اصلی (cardinal direction) درخت ها قرار داشت. نتایج حاکی از آن است که رفتار تخمگذاری *V. livia* و در نتیجه توزیع و پراکنش تخم ها با تجمع همگونه واجتناب از تخمگذاری همگونه قابل تنظیم است. به نظر می رسد که پروانه مزبور برای بیشینه کردن موفقیت در تولید مثل، این دو رفتار را در هم می آمیزد.

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