Journal of Applied Biological Scien 3(2): 119-125, 2009
ISSN: 1307-1130, www.nobel.gen.tr

Effects of Dietary Fatty Acids on the Fecundity of the Endoparasitoid *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae)

Z. Ülya NURULLAHOĞLU[1] Ekrem ERGİN[2]
[1] Department of Biology, Faculty of Science Selçuk University, Konya, 42031, TURKEY
[2] Nursing High School, Gülhane Military Medical Academy, Ankara, 06018, TURKEY

***Corresponding Author**
e-mail: nulya28@hotmail.com

Received: May 05, 2009
Accepted: June 30, 2009

ABSTRACT

Synovigenic parasitoids rely on adult feeding to increase their reproductive potential. Here, we examined the impact of fatty acid composition in the artificial diet on the fecundity and hatchability of the endoparasitoid *Pimpla turionellae* L. adult females. Females were provided with natural diet (honey and host pupae), a basic chemically-defined synthetic diet, or five different synthetic diets without palmitic, stearic, oleic acid, linoleic acid or linolenic acid separately, or all fatty acids. The effects of dietary fatty acid deficiency on total and age-dependent fecundity and hatchability of the parasitoid were investigated. Females fed with natural diet laid 27.4 eggs throughout a period of 15 d, and 78.96% of these eggs hatched. The highest fecundity was observed with females fed with basic synthetic diet, a stearic-and palmitic acid-free diet or an oleic acid-free diet. Females provided with linoleic acid- and all fatty acids-free diets had the lowest fecundity. The highest egg hatching (84.76%) was observed with females fed with the basic synthetic diet whereas fatty acid-free diet reduced egg hatching to 57.05%. Age-dependent fecundity increased from day 20 to 28 and then decreased on day 31. Egg hatchability of females provided with linoleic or linolenic acid-free diets were similar to those fed with all fatty acid-free diet. Relative to basic synthetic diet, linoleic or linolenic acid-free and all fatty acids-free diets significantly reduced total and diet-dependent egg hatchability. These results have important implications for understanding both the lipid allocation strategy and the impact of fatty acids alone and in combination on reproduction of this parasitoid, which are used as important biological control agent.

Key Words: *Pimpla turionellae*, nutrition, synthetic diet, fatty acids, egg hatching.

INTRODUCTION

Producing high numbers of hymenopteran parasitoids for biological control programs requires development of high quality diets and efficient mass-rearing techniques in laboratory condition. There have been several attempts in rearing parasitoids on artificial diets that are formulated to mimic natural diets [1, 2]. Most adult female parasitoids require both quantitative and qualitative nutrients to ensure reproductive success during their lifespan. Therefore, the amount and the type of food can have significant impacts on the fecundity and egg hatching capacity of females [3-5].

The development of artificial diets for artificial mass-rearing of insects has also stimulated determination of their nutritional requirements, propagating large numbers of insects for biological conrol programs and physiological studies. Nutritional quality of adult diets can be evaluated by many biological and physiological parameters such as survivorship, developmental time, adult longevity, sex ratio, sexual maturity time, egg production and hatchability. Fatty acids are widely used by insects as an energy source for some metabolic functions and as components of structural compounds such as phospholipids.

Most insects require dietary polyunsaturated fatty acids (PUFAs) for successful development to adult stage and reproduction [6, 7]. Parasitoid females need to feed from the host in order to sustain egg production. Endoparasitoid *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae) can be reared on a diet without fatty acids but addition of fatty acids to the diet increased high quality adults and fecundity [8, 9]. *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae) require fatty acids in their diet to produce normal adults [10].

Adults of synovigenic parasitoids usually feed on body fluids of a host to obtain food for growing of their ovaries during preoviposition period and production of large number of eggs [11-15]. However, adult parasitoids not only feed on hosts for obtaining protein [16] but also they require additional amounts of nutritional resources (i.e. floral nectar, honeydew) for egg production. Thus, nutritional value of adult food is also an important factor in hymenopteran parasitoids for egg production beside quality and quantity of larval diet [17-20].

Pimpla turionellae L. is a hymenopterous parasitoid species used for biological control of some lepidopteran pest insects. They need consumption of essential nutrients to provide ovariol development before ovipositon after adult emergence [21]. A chemically defined synthetic diet containing amino acids, lipid, water-soluble vitamins, inorganic salt mixtures, sucrose, RNA and miscellaneous was firstly described by Emre [22] for *P. turionellae* adults. The lipid mixture consisted of stearic, palmitic, oleic, linoleic, and linolenic acids [23]. However, there is no evidence showing the effects of dietary fatty acids alone or together that were investigated by omitting, reducing or increasing the amount of the total lipid mixture in the diet. Here, we investigated the effects of fatty acid deficiency in the artificial diet on fecundity and hatchability of *P. turionellae* females relative to basic artificial diet and natural diet.

MATERIALS AND METHODS

Insects

Laboratory colonies of *P. turionellae* and *Galleria mellonella* L. (Lepidoptera: Pyralidae) were established from adults that were collected from an apple garden in Konya, and from beehives in Ayvalık, Turkey, respectively. *P. turionellae* were mass-reared on the pupae of *G. mellonella* as host, at 25 ± 1°C, 60 ± 5% RH and a photoperiod of 12:12 (L:D) h. Adults were daily fed with a 50% (w/v) honey solution and provided with host pupae (one pupa per parasitoid) every 3 d. *G. mellonella* were reared in 2-L glass jars containing an artificial diet [24] at 30 ± 2°C, 60 ± 5% RH and constant darkness.

Feeding Experiments

Studies on the effects of different diets on the number of eggs laid (henceforth referred to as fecundity) and the percentage of eggs hatched (henceforth referred to as hatchability) of *P. turionellae* females were conducted rearing insects with different diets: natural diet (50% honey solution and three host pupae per five parasitoids every 3 d), a basic synthetic diet, or one of five different synthetic diets lacking palmitic, stearic acids, oleic acid, linoleic acid, linolenic acid, or all fatty acids respectively. The synthetic diet described by Emre [22] was used for rearing the adults of *P. turionellae*. The diet consisted of amino acid mixture, lipid, water-soluble vitamin mixture, inorganic salt mixtures, sucrose, and RNA. The lipid mixture is composed of chlosterol, stearic, palmitic, oleic, linoleic and linolenic acids, and Tween 80. Adding the same amount of tween 80, which is an emulsifiying agent, also complemented fatty acid deficieny in each synthetic diet.

Five pairs of *P. turionellae* adults (1-2-d-old) emerged on the same day and of approximately the same size were placed in 1-L glass cups lined with a cloth for each diet. Adults were provided with either 50% (w/v) honey solution and host pupae or one of the synthetic diets placed on a piece of aluminum foil. Males were removed from the cups after 24 h. Ten *G. mellonella* pupae were presented for 1 h to female *P. turionellae* for parasitization beginning on the 16th d after adult emergence and continuing through the 31st d by 3 d intervals. Host pupae were covered with double layers of netting to prevent host feeding by parasitoid. Females were daily fed at the same time in the morning for 1 h and transferred to clean cups to prevent microbial growth. All cups were maintained under the same conditions used for the stock culture of *P. turionellae*. On the following day of each parazitization, paratized host pupae were dissected to obtain eggs. Fecundity (total number of eggs produced per female) for each diet was recorded with dividing the total number of eggs by the number of females. Results from each observation were pooled to determine the total fecundity per female in 16 d for each diet. Eggs were allowed to hatch in the 0.8% NaCl solution [8, 22] and observed daily until hatching. Hatchability was recorded as percentage of eggs hatched for each diet. Experiments were replicated three times with 5 females per replication of each diet.

Statistical Analysis

Data on fecundity and hatchability were evaluated by one-way analysis of variance (ANOVA). Means on diet-dependent fecundity and hatchability were separated using Tukey's Honestly Significant Difference (HSD) tests (SPSS Inc. 1999). Age-dependent fecundity and hatchability for each diet were compared with one-way repeated-measures ANOVA and means were separated with paired samples t-tests. Data for fecundity and hatchability were also subjected to two-way ANOVA to determine the main effects of age, diet, and their interactions. Before analysis, data on the hatchability were arcsine transformed to meet the assumption of normality [25]. Results were considered significant when $P < 0.05$.

RESULTS

Total Fecundity and Hatchability

Diet-related changes in total fecundity and egg hatching ratio of an individual female at the end of the experimental period are given in Table 1. Total fecundity of females (from day 16 to day 31) differed significantly among diets ($F=51.976$; $df=6, 14$; $P<0.05$).

Females fed on natural diet normally laid 27.40 eggs in 15 d, which was also similar with the number of eggs laid by those fed on linolenic acid-free diet. The maximum number of eggs was laid by females fed the basic synthetic diet, followed by the stearic and palmitic acid-free diet, and then the oleic acid-free diet. Females provided with linoleic acid- and fatty acids-free diets had the lowest fecundity. Egg hatching ratio of an individual female under different feeding regimes was also significantly different (F=217.814; df=6, 14; P<0.05). Females provided with natural diet had 78.96% eggs hatched at the end of 15 d. Egg hatching ratio of a female (84.76%) fed on basic synthetic diet was the highest whereas with fatty acid-free diet the ratio decreased to 57.05%.

Table 1. Diet-related changes in fecundity and egg hatching ratio of *P. turionellae* females.

Diet	Fecundity (mean[a] ± SE)[b]	Egg hatching ratio (%)[b, c#]
Natural	27.40 ± 0.53a	78.96a
Basic synthetic	31.10 ± 0.21b	84.76b
Stearic and palmitic acid-free	30.80 ± 0.25b	71.91c
Oleic acid-free	30.70 ± 0.26b	72.04c
Linoleic acid-free	23.77 ± 0.60c	64.68d
Linolenic acid-free	28.17 ± 0.50a	61.84d
Fatty acid free-free	23.10 ± 0.66c	57.05e

[a] Data are means ± standard errors/female of three replicates using 5 females per replicate.

[b] Values followed by the same letter in the same vertical column are not significantly different from each other (Tukey's HSD test; P > 0.05).

[c] Data are the pooled ratios of the number of eggs hatched /female in three replicates using 5 females per replicate.

Age-related Fecundity and Egg Hatching Ratio

Age-related fecundity of female wasps fed with different diets is given in Table 2. Two-way ANOVA indicated that the effect of diet on the fecundity of females was diet- (P<0.05) and age- (P<0.05) dependent. The relationship between diets and fecundity of females (R^2 = 0.98) was significantly influenced by the age of females (P<0.05) (Table 3).

Throughout all dietary treatments, fecundity of females differed significantly by the age of the females (Table 2). The highest number of eggs (8.00) was laid by females fed on oleic acid-free and basic synthetic diets on days 25 and 28, respectively. In general, the number of eggs laid by an individual female in all diets plateaus for a period between 22 to 28 d before declining. Fecundity at all times tested also differed significantly among diet groups (Table 2) day 16 (F=29.711; df=6, 14), 19 (F=10.909; df=6, 14), 22 (F=57.667; df=6, 14), 25 (F=94.708; df=6, 14), 28 (F=129.737; df=6, 14), and 31 (F=74.844; df=6, 14) (P<0.05).

Two-way ANOVA indicated that the effect of diet on the egg hatching ratio of females was also diet- (P=0.000) and age- (P=0.000) dependent, and the relationship between diets and egg hatching ratio of females ($R^2 = 0.99$) was significantly influenced by the age of females (P=0.000) (Table 3). The ratio of eggs hatched under each feeding regime differed significantly by the age of the females (Table 4). Younger females (16 to 22 d) fed on natural and synthetic diets had a rather high ratio of egg hatching. The only exception to this trend was with wasps fed on fatty acid-free diet in which the maximum ratio of egg hatching observed as 71.27% on day 31. Egg hatching ratio under different feeding regimes was also significantly different on day 16 (F=235.528; df=6,14), 19 (F=479.879; df=6,14, 22 (F=78.141; df=6,14, 25 (F=61.703; df=6,14), 28 (F=110.586; df=6,14) , and 31 (F=437.711; df=6,14) (P<0.05). The maximum ratios of egg hatching were seen with females provided with natural or basic synthetic diets at all ages. However, the one exception appears to be with regard to the highest egg-hatching ratio observed on day 16 with females fed on stearic and palmitic acid free diet (Table 4).

DISCUSSIONS

It has been previously reported that adult parasitoids require lipid sources for egg production in addition to dietary nutrients obtained during the larval stages [26]. Insect ovaries synthesize lipids in very small quantities and some of oocyte lipids are obtained from vitellogenins [6, 27]. Therefore, the majority of lipids used by oocytes are derived from fat body lipid stores [28]. In most females, vitellogenins are synthesized in fat body cells and then transported to ovaries for egg production [29, 30]. If some nutrient types are scarce in the diet, larva reserves and uses these nutrients throughout adult emergence to compensate for egg production [31, 32]. This confirms our results that females provided with fatty acid-free diet were able to lay eggs in the whole experimental period. In cases of food deprivation, parasitoids may produce fewer eggs or eggs with poor yolk, in an attempt to economise metabolic resources [33]. The decrease in fecundity and egg hatchability of *P. turionellae* females fed on fatty acid-free diet may also be attributed to inadequate quality of food.

Table 2. Age-dependent changes in fecundity of *P. turionellae* females provided with different diets[a].

Diets[b] \ Ages[c]	Day 16	Day 19	Day 22	Day 25	Day 28	Day 31	Statistics (ANOVA) F	df	*P*
Natural	4.27 ± 0.15abcd v	4.80 ± 0.17abcd v	5.67 ± 0.08b v	6.13 ± 0.18bc v	3.93 ± 0.08cd v	2.60 ± 0.10d v	132.182	5, 10	0.00
Basic synthetic	3.50 ± 0.06a w	4.60 ± 0.12b v	4.47 ± 0.13abc w	6.03 ± 0.03c v	8.00 ± 0.12d w	4.50 ± 0.06ab w	284.679	5, 10	0.00
Stearic + palmitic acid-free	2.80 ± 0.12a xy	4.23 ± 0.13ad vw	6.43 ± 0.09bc x	6.00 ± 0.12bd v	7.27 ± 0.18c x	4.07 ± 0.07a wx	186.273	5, 10	0.00
Oleic acid-free	2.27 ± 0.13a x	4.13 ± 0.15b vw	5.63 ± 0.09c v	8.00 ± 0.12d w	5.80 ± 0.12bc y	5.13 ± 0.13c y	287.029	5, 10	0.00
Linoleic acid-free	2.23 ± 0.15a x	3.67 ± 0.24ac wx	5.70 ± 0.17b v	5.13 ± 0.07ad x	4.07 ± 0.12ad vz	2.97 ± 0.12cd v	103.244	5, 10	0.00
Linolenic acid-free	3.37 ± 0.09a wy	4.17 ± 0.17abc vw	4.80 ± 0.12bc w	6.17 ± 0.20bc v	5.70 ± 0.15b y	3.97 ± 0.09ac x	73.198	5, 10	0.00
Fatty acid-free	3.37 ± 0.20a wy	3.27 ± 0.09a x	3.80 ± 0.12ab y	3.80 ± 0.12a y	4.67 ± 0.17b z	4.20 ± 0.12ab wx	30.407	5, 10	0.00

[a] Three replicates with 5 females per replicate.

[b] Values (mean ± SE) in the same horizontal row followed by the same letter (a-d) are not significantly different from each other

(Paired sample t-test, P > 0.05).

[c] Values (mean ± SE) in the same vertical columnfollowed by the same letter (v-z) are not significantly different from each other

(Tukey's HSD test, P > 0.05).

Our results indicated that fecundity and egg hatching ratio of females fed on diets with varying fatty acid content displayed considerable differences. The fact that females fed on fatty acid free-diet had the lowest fecundity and egg-hatching ratio are indications of the importance of fatty acids in oogenesis and egg viability of *P. turionellae*. This prediction, however, is in contrast to the observations of Emre and Yazgan [23], in which they reported that omission of lipids from artificial diet had no significant effect on the reproduction capacity of *P. turionellae*. However, supplementing the diet of another ichneumonid parasitoid, *Diapetimorpha introita* (Cresson) (Hymenoptera: Ichneumonidae) with lipid extracted from host pupae [1] increased fecundity. Similar to these results, we observed linoleic and linolenic acid-free diets decreased egg production and hatchability of *P. turionellae* suggesting that essential role for fatty acids in egg production in *P. turionellae*. Similarly, Casas et al. [2] reported that lipids play a functional role for production of maximum number of eggs like other nutrients such as sugars and proteins obtained from the diet.

A considerable decline in fecundity was also observed with female wasps that fed on linoleic acid-free diet. Egg hatching ratio of females provided with linoleic acid- and linolenic acid-free diets were similar to those fed only on fatty acid-free diet.

Collectively, these results suggest that both dietary linoleic and linolenic acid are important determinants of the reproduction capacity of adult females.

It is likely that female wasps reared on a diet fortified with fatty acids that are already present in host pupae [10, 34] enhance egg production and viability in *P. turionellae*. The observed loss in reproductive output for females when feeding on fatty acid-free diets along with host deprivation determines the nutritional need for PUFAs for adult parasitoids as they are considered essential fatty acids for many insect species.

Table 3. ANOVA of the effects of diet, age, and their interaction on fecundity and egg hatching ratio of *P. turionellae* females provided with different diets.

	Source	df	MS	F	P	R^2
Fecundity	Diets	6	5.708	111.167	0.000	0.98
	Age	5	24.025	491.213	0.000	
	Diets x age	30	1.088	52.500	0.000	
	Error	84	2.142			
Egg hatching ratio	Diets	6	0.229	407.582	0.000	0.99
	Age	5	0.017	31.578	0.000	
	Diets x age	30	0.056	100.221	0.000	
	Error	84	0.0005			

Table 4. Age-dependent changes in egg hatching ratio of *P. turionellae* females provided with different diets[a].

Diets[b] \ Ages[c]	Day 16	Day 19	Day 22	Day 25	Day 28	Day 31	Statistics (ANOVA)		
							F	df	*P*
Natural	55.00a v	85.35b v	91.53bcd v	72.93ac v	87.37bd v	89.36d u	161.484	5, 10	0.00
Basic synthetic	79.33ab w	87.90ab v	88.81a v	87.96a w	85.46ab v	76.22b v	32.246	5, 10	0.00
Stearic + palmitic acid-free	87.91a x	73.09ac w	86.84a v	52.53b x	59.02bc w	81.01a w	149.858	5, 10	0.00
Oleic acid-free	77.79ab w	79.68a x	65.09ab w	70.58ab vy	67.76b x	78.12a vw	52.267	5, 10	0.00
Linoleic acid-free	55.15a v	66.73b y	60.17ab wx	59.74a xz	70.64ab x	71.27b x	56.409	5, 10	0.00
Linolenic acid-free	66.63a y	70.08a wy	65.97ab w	63.35ab yz	67.84a x	33.03b y	196.978	5, 10	0.00
Fatty acid-free	84.05a z	38.98b z	56.01ab x	64.00ab yz	58.58b w	48.85b z	145.012	5, 10	0.00

[a] Three replicate with 5 females per replicate.

Percentages of hatchability were arcsine-transformed to meet the assumption of normality before applying one- or two-way ANOVA

followed by Paired sample t-test and Tukey's HSD comparison of means. Results are shown untransformed to ease interpretation.

[b] Values (mean ± SE) in the same horizontal row followed by the same letter (a-d) are not significantly different from each other

(Paired sample t-test, $P > 0.05$).

[c] Values (mean ± SE) in the same vertical columnfollowed by the same letter (v-z) are not significantly different from each other

(Tukey's HSD test, $P > 0.05$).

The fatty acids studied here were previously found to comprise a large proportion of the fatty acid composition of another parasitoid species *Apanteles galleriae* Wilkinson (Hymenoptera: Braconidae) and the fatty acid composition of the wasp was qualitatively similar to that of its host *Achoria grisella* Fabr. (Lepidoptera: Pyralidae) [35]. Linoleic acid is a structural component of membranes and a precursor to arachidonic acid that is a precursor to the eicosanoids. Eicosanoids have significant physiological activities such as the stimulation of oviposition [36]. Most insects are unable to synthesize long-chain PUFAs and sterols *de novo* and they have to take them from exogenous sources by feeding to develop and reproduce successfully [5, 37]. Developmental requirements for PUFAs have also been reported for other ichneumonid species [17, 19].

The availability of nutrients during oogenesis of synovigenic species is a major limiting factor in their successful reproduction [38]. Adult parasitoids with longer lifespans depend on host feeding to compensate for this energy intensive activity.

Sandlan [21] reported that newly emerged *P. turionellae* females contained only immature oocytes in their ovaries and they had a 3 to 6-d pre-ovipositional period. During this period they need to acquire nutrients for oogenesis. During the first ovipositional experience, females of *P. turionellae* display host-feeding behavior, which in turn, allows the females to produce mature eggs essentially until death [21].

Reproductive biology of parasitoids should be well understood for improving the efficacy of these organisms in biological control programs. A comprehensive study of the reproductive output that parasitoid species display under different regimes would also help us to determine their dietary requirements, ultimately improving the mass rearing of parasitoids used in biological control applications. By changing and balancing levels of the compounds in their synthetic diet, we may be able to enhance the fecundity and egg vialibity of parasitoids before their releasing into field for biological control purposes. Here, we concluded that the reproduction capacity of *P. turionellae* could be improved by synthetic diet that contains the essential fatty acids.

ACKNOWLEDGEMENTS

We express sincere appreciation to David B. Rivers for reviewing an earlier draft of this manuscript.

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