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The disruptive impact of novaluron, a chitin synthesis inhibitor, on the adult performance and reproduction of the black cutworm, *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae)

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ABSTRACT

The black cutworm *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) has a wide range of distribution throughout Africa, Europe, Asia, and the Americas. It is a polyphagous insect attacking nearly all vegetables and many important grains in the world. The present study was carried out to investigate the effect of novaluron (a chitin synthesis inhibitor) on the most important parameters of adult performance and reproductive potential of this insect. Both the 4th instar and 5th instar larvae were treated with a series of novaluron concentrations (50.0, 25.0, 12.50, 06.25 & 03.10 ppm) *via* fresh discs of castor bean leaves. The most important results could be summarized as follows. The adult emergence was considerably blocked, regardless of the treated larval instar. Various adult mortality percentages were recorded. Novaluron failed to affect the adult morphogenesis after treatment of 4th instar larvae, while it exhibited a slight anti-morphogenic effect on the adults after treatment of 5th instar larvae only with 25.00 ppm. The total adult longevity was generally shortened. The pre-oviposition period was remarkably prolonged. The oviposition period was considerably shortened. The post-oviposition period was prolonged or shortened, depending on the concentration and the treated larval instar. The oviposition efficiency was severely inhibited, in a dose-dependent trend. Adult fecundity was drastically prohibited and fertility was dramatically reduced. The embryonic developmental rate was remarkably retarded, since the incubation period of eggs was considerably prolonged. Therefore, novaluron may be an effective IGR being used in the IPM program against *A. ipsilon*.

INTRODUCTION

The origin of the black cutworm *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) is uncertain, though it is now found in many zoo-geographic regions globally (Muştu *et al.*, 2021). It is widely distributed all over the world, particularly in moderate and subtropical countries of the northern and southern hemispheres (Harrison, and Lynn, 2008; Binning *et al.*, 2015; Mishra, 2020; Rodingpuia and Lalthanzara, 2021). It is a polyphagous insect feeding on nearly all vegetables and many important grains, attacking mainly Solanaceae, Cruciferae and Curcubitaceae; however, they can also attack other species of different plant families (EI-Salamouny *et al.*, 2003; Navarro *et al.*, 2010; Fernandes *et al.*, 2013).

In Egypt, *A. ipsilon* has become widely spread in recent years throughout the country attacking all vegetables, including potato and tomato, and many economic field crops, such as clover, wheat, corn and bean and other important grains (Dahi *et al.*, 2009; Fahmy, 2014; Sharaby and El-Nojiban, 2015; Abdou and Abdel-Hakim, 2017; Abdel-Hakim, and El-Mandarawy, 2017). In Egypt, also, control of *A. ipsilon* has become a serious challenge facing applied entomologists nowadays considering the fast development of to almost all available conventional insecticides, resistance and cross-resistance such as organophosphates, carbamates and pyrethroids (Yu *et al.*, 2012; Fahmy, 2014; Mahmoud *et al.*, 2016; Shaurub *et al.*, 2018). In addition, the intensive use of many conventional insecticides led to several dramatic problems, such as serious toxicological hazards to human health (Sharifian *et al.*, 2012; Tiryaki and Temur, 2010; Chowański *et al.*, 2014). They usually, also, exhibit neurotoxicity, teratogenicity and mutagenic effects in non-target animals (Chaubey, 2015).

The serious problems and environmental hazards of the insecticides have led researchers all over the world to search for new control strategies (Laznik and Trdan, 2012) and some alternatives to synthetic insecticides (Glare *et al.*, 2016). These alternative compounds should be eco-environmentally safe compounds (Ansari *et al.*, 2012; Liao *et al.*, 2017; Kunbhar *et al.*, 2018), effective at low concentrations (Gade and Goldsworthy, 2003; Walkowiak *et al.*, 2015) and biodegradable into harmless compounds (Tiryaki and Temur, 2010; Li *et al.*, 2017). Among the alternative control, agents are the insect growth regulators (IGRs), which are a good option for insect pest management because they are less toxic to man and domestic animals, less toxic to natural enemies and non-target organisms, less persistent, and more specific to the target pests than conventional insecticides (Mondal and Parween, 2000; Taleh *et al.*, 2015). In contrast to the classical chemical insecticides, IGRs are not directly neuro-toxic to insects but act selectively on the development, metamorphosis and/or reproduction of the target insects (Zhou *et al.*, 2003; Martins and Silva, 2004) owing to their disruptive effects on the normal activity of endocrine organs and hormonal regulation of insects (Wang and Liu, 2016).

According to the specific mode of action, IGRs had been classified into three categories: (i) juvenile hormone analogues (JHAs, also called Juvenoids), (ii) Ecdysteroid agonists and (iii) Chitin synthesis inhibitors (CSIs) or moult inhibitors (Oberlander and Silhacek, 2000). They had been, also, grouped in CSIs and substances that interfere with the action of insect hormones (i.e. JHAs, and ecdysteroids)(Tunaz and Uygun, 2004). Such compounds have much greater metabolic and are environmentally more stable than earlier analogs and are much better suited to insect pest control (For some detail, see reviews of Dhadialla and Jansson, 2000; Dhadialla *et al.*, 2005). CSIs inhibit the chitin biosynthesis in the larval stage, leading to abnormal endocuticular deposition and abortive molting, thus prevent molting, or produce an imperfect cuticle (Mondal and Parween, 2000; Dhadialla *et al.*, 2005). Currently, different generations of CSIs have been developed and successfully used as important components in integrated pest management (IPM) programs of pest species of different orders (Zhao *et al.*, 2012; Sun *et al.*, 2015).

Novaluron {Rimon EC-10, 1-[chloro-4-(1,1,2-trifluoromethoxyethoxy) phenyl]-3-(2,6-difluorobenzoyl) urea} is a relatively new benzoylphenyl urea CSI (Ishaaya *et al.*, 2007) with molecular formula: C₁₇H₉ClF₈N₂O₄. It inhibits the chitin formation on larvae of various insects (Belinato *et al.*, 2013). It has low mammalian toxicity (Barazani, 2001; Ishaaya and Horowitz, 2002) and is generally selective in favor of non-target organisms, such as natural enemies (Cutler *et al.*, 2006). Also, it has no cross-resistance with conventional insecticides (Ishaaya *et al.*, 2002, 2005). Its residues tend to dissipate with a half-life of 2.08 days and the safe use of it on tomatoes, and possibly on other crops in Egypt was established (Malhata *et al.*, 2014).

As reported in the current literature, novaluron exhibits high toxicity and effectiveness against several dipterous species (Mascari *et al.*, 2007; Bouaziz *et al.*, 2011; Fontoura *et al.*, 2012; Djeghader *et al.*, 2013). Novaluron is, also, a powerful suppressor of lepidopteran larvae of different species (Ishaaya, 2001; Ghoneim *et al.*, 2017a, b; Tanani *et al.*, 2017) and whiteflies known to attack cotton, corn and vegetables (Ishaaya *et al.*, 2002, 2003). Also, it is used effectively to control some species of Hemiptera (Portilla *et al.*, 2012) and Coleoptera (Alyokhin *et al.*, 2009; Arthur and Fontenot, 2012). The present study was carried out to investigate the effect of novaluron on the most important parameters of adult performance and reproductive potential of *A. ipsilon*.

MATERIALS AND METHODS

1. The insect Culture:

A culture of the black cutworm *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) was established under constant conditions ($27\pm 2^{\circ}\text{C}$ and $65\pm 5\%$ R.H.) at Department of Zoology and Entomology, Faculty of Science, Al-Azhar University, Cairo, Egypt. It was originally started by a sample of eggs from the susceptible strain culture maintained for several generations in Plant Protection Research Institute, Doqqi, Giza, Egypt. The rearing technique was carried out according to Abdin (1979) with the improvement of El-Shershaby (2010). The eggs were kept in wide-mouth plastic jars (1000 ml) fitted with filter paper until hatching. Newly hatched larvae were kept into new jars and provided with clean castor bean leaves *Ricinus communis* as food every day. At reaching the 4th instar, larvae were reared in few numbers in separate jars to avoid crowding and cannibalism. The pupae were then placed in plastic jars (10 x 25 cm) fitted with filter paper, as an oviposition site for future moths. After the adult emergence, each jar was provided with a piece of cotton wool soaked in a 10% sugar solution for feeding moths.

2. Novaluron Concentrations and Larval Treatment:

Novaluron (a chitin synthesis inhibitor) {Rimon EC-10, 1-[chloro-4-(1,1,2-trifluoromethoxyethoxy) phenyl]-3-(2,6-difluorobenzoyl) urea} is a relatively new benzoylphenyl urea chitin synthesis inhibitor (CSI) (Ishaaya *et al.*, 2007) with molecular formula: $\text{C}_{17}\text{H}_9\text{ClF}_8\text{N}_2\text{O}_4$. It was purchased from Milipore Sigma, Burlington, MA 01803, USA Merk Ltd., Egypt. A series of 6 concentrations of novaluron was prepared by diluting with distilled water in volumetric flasks: 100.0, 50.0, 25.0, 12.5, 6.25 and 3.1 ppm.

Bioassay test was carried out against 4th and 5th instar larvae of *A. ipsilon* using the dipping technique. Discs of fresh castor bean leaves were dipped in each concentration for 5 minutes and air dried before the introduction to larvae as food for 24 hr under the aforementioned laboratory conditions. Control larvae were provided with water-treated castor leaves. Thirty larvae in three replicates (10 larvae/replicate) of treated and control larvae were kept separately in plastic vials. After 24 h feeding on treated leaves, larvae were provided with fresh untreated castor bean leaves every day until pupation. No adult could emerge after treatment of 4th instar larvae with the highest concentration of novaluron, but some adults successfully emerged after treatment of 5th instar larvae with this concentration. Just after adult emergence, the most important parameters of adult performance and reproductive potential of *A. ipsilon* were recorded

3. Criteria of Study:

3.1. The Most Important Parameters of Adult Performance:

Adult Emergence: The number of successfully emerged adults was expressed in % according to Jimenez-Peydro *et al.* (1995) as follows:

$$[\text{No. of completely emerged adults} / \text{No. of pupae}] \times 100$$

Adulticidal Activity: Mortality of the successfully emerged adults was determined in %.

Adult Morphogenesis: The imperfectly emerged adult females had been calculated in % and recorded in photos.

Adult Longevity: The longevity of adult females and their major compartments were measured in days: pre-oviposition (gonad maturation) period, oviposition period (reproductive life-time) and post-oviposition period.

3.2. Criteria of the Reproductive Potential:

The successfully emerged adult males and females with perfect morphology were used for the determination of different parameters of the reproductive potential. Three replicates of untreated adult males and treated females, produced from each treatment, were coupled in small plastic jars (1♂:1♀). Each jar was provided with pieces of sterilized cotton soaked in 10% honey solution for feeding and provided with two paper pieces placed at the top and bottom serving as oviposition sites. The laid eggs were counted every day during the oviposition period for determining the oviposition rate, fecundity and hatchability%.

The Oviposition Efficiency: The oviposition efficiency was denoted by the oviposition rate which was calculated as follows:

$$\text{Number of laid eggs per } \frac{\text{♀}}{\text{reproductive lifetime (in days)}}$$

The Reproductive Capacity: The most important parameters of reproductive capacity are fecundity and fertility.

Fecundity: The laid eggs were counted for calculating the number of eggs per female.

Fertility: The hatchability was usually expressed in the hatching percentage of the laid eggs.

Sterility index was calculated according to Topozada *et al.* (1966) as follows:

$$\text{Sterility Index} = 100 - [(a/b / A/B) \times 100]$$

Where: a: mean number of eggs laid per female in the treatment. b: percentage of hatching in the treatment. A: mean number of eggs laid per female in the controls. B: percentage of hatching in the controls.

Incubation period: The deposited eggs were kept in Petri dishes under the same controlled laboratory conditions as previously mentioned. Just after the oviposition, eggs were observed until hatching elapsing an incubation period (in days).

4. Statistical analysis of data:

Data obtained were analyzed by the Student's *t*-distribution, and refined by Bessel correction (Moroney, 1956) for the test significance of the difference between means using GraphPad InStat[®] v. 3.01 (1998).

RESULTS

1. Effect of Novaluron on The Most Important Parameters of Adult Performance of *A. ipsilon*:

The newly molted 4th instar larvae of *A. ipsilon* were treated with 6 concentrations of novaluron *via* fresh clean castor bean leaves (100, 50.0, 25.0, 12.50, 06.25 & 03.10 ppm). At the highest concentration, larvae and pupae completely died. Data of the most important parameters of adult performance were assorted in Table (1). After treatment of the newly molted 5th instar larvae with novaluron, data of these parameters were summarized in Table (2).

1.1. Effect of Novaluron on The Adult Emergence:

It may be important to mention that adult emergence is a prerequisite process in insect life. Depending on the data of Table (1), the adult emergence was considerably blocked, in a dose-dependent course (85.6, 75.5, 69.0, 63.3 & 33.3% emergence, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, in comparison with 100% emergence of control adults) after treatment of 4th instar larvae with Novaluron. Depending on the data of Table (2), treatment of 5th instar larvae with Novaluron led to partial hindering of the adult

emergence, in a dose-dependent course (92.6, 89.7, 86.9, 75.0, 69.5 & 25.0% emergence, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 100% emergence of control adults).

1.2. Effect of Novaluron on Adult Survival:

As shown in Table (1), adult mortality was observed only at three concentrations, after treatment of 4th instar larvae of *A. ipsilon* with Novaluron (9.8, 6.7 & 8.3% mortality, at 06.25, 12.50 & 25.00ppm, respectively, 0.0% mortality of control adults). After treatment of 5th instar larvae with novaluron concentrations, the successfully emerged adults completely died at the highest concentration. Also, adult mortalities were recorded at 06.25, 12.50 & 50.00ppm (9.5, 6.7 & 22.2% mortality, respectively, Table 2).

1.3. Effect of Novaluron on Adult Morphogenesis:

After treatment of 4th instar larvae, novaluron failed to affect the adult morphogenesis, since no deformed adults were observed (Table 1). On the other hand, the tested IGR exhibited a weak anti-morphogenic action on adults only at one concentration (19.40% deformed adults, at 25.00ppm) after treatment of 5th instar larvae with a series of its concentrations (Table 2). As clearly shown in Plate (1), the adult deformities were seen as atrophied mouthparts, curled wings and pupal exuvia attached to the abdomens.

1.4. Effect of Novaluron on Adult Longevity:

After treatment of 4th instar larvae of *A. ipsilon* with Novaluron, data of the total adult longevity and its major compartments were arranged in Table (1). Depending on these data, the total adult longevity was generally shortened, almost in a dose-dependent trend (16.3±1.00, 16.3±1.53, 13.0±1.73, 13.0 & 9.0 days, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 17.0±1.00 days of control adults). The first-time compartment of adult longevity is the pre-oviposition period. This period was remarkably prolonged (3.0±0.58, 5.0±1.0, 5.0±1.0, 6.0 & 4.0 days, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 2.3±0.58 days of control adults). The oviposition period is the second major time interval of adult longevity. It was considerably shortened, in a dose-dependent manner (10.3±0.58, 8.0±1.00, 5.3±1.53, 4.0 & 4.0 days, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 11.7±1.16 days of control adults). The last major compartment of adult longevity is the post-oviposition period. This period was diversely affected, since it was prolonged or shortened, depending on the Novaluron concentration (3.3±0.58, 3.3±1.16, 2.7±0.58, 3.0 & 1.0 days, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 3.0±0.58 days of control adults).

After treatment of 5th instar larvae with Novaluron concentrations, data of the adult longevity and its major compartments were distributed in Table (2). Depending on these data, the total adult longevity was slightly shortened, in no certain trend (17.0±1.00, 16.0±4.00, 15.7±0.58, 16.0±1.41 & 16.0±0.71 days, at 03.10, 06.25, 12.50, 25.00 & 50.00 ppm, respectively, vs. 17.3±1.16 days of control adults). The first major compartment of adult longevity is the pre-oviposition period. This period was significantly prolonged but in no certain trend (6.3±0.58, 4.3±1.16, 6.0±1.0, 5.5±0.71 & 8.0±1.41 days, at 03.10, 06.25, 12.50, 25.00 & 50.00 ppm, respectively, vs. 3.6±0.58 days of control adults). The oviposition period is the second major time interval of adult longevity. This period was considerably shortened but in no certain trend (11.0±1.0, 5.6±3.22, 7.0±1.73, 7.5±0.71 & 4.5±3.54 days, at 03.10, 06.25, 12.50, 25.00 & 50.00 ppm, respectively, vs. 11.7±1.53 days of control adults). The last major time interval of adult longevity is the post-oviposition period. This period was slightly prolonged, in no certain trend (3.7±0.58, 2.1±1.00, 2.7±1.53, 4.0±1.01 & 4.5±1.41 days, at 03.10, 06.25, 12.50, 25.00 & 50.00 ppm, respectively, vs. 2.0±0.01 days of control adults).

Table 1: Adult performance parameters of *A. ipsilon* as affected by treatment of the 4th instar larvae with novaluron.

Conc. (ppm)	Adult emergence (%)	Adult mortality (%)	Adult deformations (%)	Longevity (mean days \pm SD)			
				Pre-oviposition period	Oviposition period	Post-oviposition period	Total Longevity
50.00	33.3	0.0	0.0	4.0*	4.0*	1.0*	9.0*
25.00	63.3	8.3	0.0	6.0*	4.0*	3.0*	13.0*
12.50	69.9	6.7	0.0	5.0 \pm 1.0 b	5.3 \pm 1.53 c	2.7 \pm 0.58 a	13.0 \pm 1.73 b
06.25	75.5	4.8	0.0	5.0 \pm 1.0 b	8.0 \pm 1.00 b	3.3 \pm 1.16 a	16.3 \pm 1.53 a
03.10	85.6	0.0	0.0	3.0 \pm 0.58 a	10.3 \pm 0.58 a	3.3 \pm 0.58 a	16.3 \pm 1.00 a
Control	100	0.0	0.0	2.3 \pm 0.58	11.7 \pm 1.16	3.0 \pm 0.58	17.0 \pm 1.00

Conc.: concentrations. *: only one adult moth Mean \pm SD followed with letter a: insignificant (P >0.05), b: significant (P<0.05), c: highly significant (P<0.01).

Table 2: Adult performance parameters of *A. ipsilon* as affected by treatment of the 5th instar larvae with novaluron.

Conc. (ppm)	Adult emergence (%)	Adult mortality (%)	Adult deformations (%)	Longevity (mean days \pm SD)			
				Pre-oviposition period	Oviposition period	Post-oviposition period	Total Longevity
100	25.0	100	00.0	---	---	---	---
50.00	69.5	22.2	00.0	8.0 \pm 1.41 b	4.5 \pm 3.54 b	4.5 \pm 1.41 a	16.0 \pm 0.71 a
25.0	75.0	0.0	19.40	5.5 \pm 0.71 b	7.5 \pm 0.71 b	4.0 \pm 1.01 a	16.0 \pm 1.41 a
12.50	86.9	6.7	00.00	6.0 \pm 1.0 b	7.0 \pm 1.73 b	2.7 \pm 1.53 a	15.7 \pm 0.58 a
06.25	89.7	9.5	00.00	4.3 \pm 1.16 a	5.6 \pm 3.22 a	2.1 \pm 1.00 a	16.0 \pm 4.00 a
03.10	92.6	0.0	00.00	6.3 \pm 0.58 b	11.0 \pm 1.0 a	3.7 \pm 0.58 a	17.0 \pm 1.00 a
Control	100	0.0	00.00	3.6 \pm 0.58	11.7 \pm 1.53	2.0 \pm 0.01	17.3 \pm 1.16

Conc., ---: no adult moth lived, a, b, : see footnote of Table (1).

2. Effect of Novaluron on The Most Important Parameters Of Reproductive Potential of *A. ipsilon*:

After treatment of 4th instar larvae of *A. ipsilon* with 6 concentrations of novaluron (03.10, 06.25, 12.50, 25.00, 50.00 & 100ppm), the successfully mated adult females were observed only at 03.10, 06.25, 12.50, 25.00 & 50.00ppm. Data of the important parameters of reproductive potential were arranged in Table (3). After treatment of 5th instar larvae, the successfully mated adult females were observed only at 03.10, 06.25, 12.50, 25.00 & 50.00ppm. Data of the important parameters of reproductive potential were listed in Table (4).

2.1. Effect of Novaluron on The Oviposition Efficiency:

The oviposition rate is usually used as a good indicator of the oviposition efficiency of an insect. After treatment of 4th instar larvae, novaluron exhibited a strong extended inhibitory effect on the oviposition efficiency of *A. ipsilon*, since the oviposition rate was tremendously regressed, in a dose-dependent trend (23.7 \pm 2.55, 6.8 \pm 0.82, 2.8 \pm 1.49, 2.3 & 1.5, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 59.6 \pm 3.92 of the control adult females, Table 3). A similar strong inhibitory effect of this chitin synthesis inhibitor was recorded on the oviposition efficiency, after treatment of 5th instar larvae (21.3 \pm 2.92, 12.1 \pm 1.47, 5.2 \pm 0.98, 2.1 \pm 1.20 & 1.6 \pm 0.64, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 63.8 \pm 4.98 of control adult females, Table 4).

2.2. Effect of Novaluron on The Reproductive Capacity:

In insects, the reproductive capacity includes two informative parameters, fecundity (mean number of eggs/ \varnothing) and fertility (egg hatchability, viability, or egg hatching%). After treatment of 4th instar larvae with novaluron of fecundity were listed in Table (3). Depending

on these data, fecundity was remarkably prohibited, in a dose-dependent course (246.0±40.95, 54.0±5.57, 14.3±5.51, 9.0 & 6.0, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 695.3±73.79 eggs/ control female). Depending on data of Table (4), treatment of 5th instar larvae with novaluron led to drastically prohibited fecundity, in a dose-dependent course (254.3±17.50, 82.3±42.83, 35.3±2.08, 17.0±8.49 & 6.0±2.83, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 741.7±90.85 eggs/ control adult females). Another good parameter of reproductive capacity is fertility. After treatment of 4th instar larvae with novaluron, fertility was dramatically reduced, in a dose-dependent course (37.77±3.86, 26.40±1.90, 17.43±4.85, 11.1 & 0.0, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 85.75±3.79% hatching of eggs laid by control adult females, Table 3). Novaluron caused complete sterility after treatment of 4th instar larvae with the highest concentration. Also, increasing sterility was recorded with the increasing concentration level of Novaluron (84.38, 97.60, 99.58, 99.83 & 100% sterility, at 03.10, 06.25, 12.50 & 25.00 ppm, respectively).

Similarly, treatment of 5th instar larvae with novaluron resulted in detrimental reduction of fertility, in a dose-dependent course (51.61±2.27, 35.3±4.86, 30.2±0.46, 17.8±0.57 & 0.0, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively, vs. 85.53±3.82% hatching of eggs laid by control adult females, Table 4). Complete sterility was recorded at the highest concentration of novaluron, and sterility increased with the increasing concentration (79.31, 95.42, 98.32, 99.52 & 100% sterility, at 03.10, 06.25, 12.50, 25.00 & 50.00ppm, respectively).

2.3. Effect of Novaluron on Embryonic Development:

No embryological investigation was conducted in the present study, but the incubation period of eggs can be used as an informative indicator of the embryonic developmental rate, i.e., a longer period usually indicates a slower rate and *vice versa*.

After treatment of 4th instar larvae with novaluron, data of Table (3) showed a general prolongation of the incubation period indicating retarded embryonic developmental rate (4.7±0.58, 5.0±1.0, 5.7±0.58 & 6.0 days, at 03.10, 06.25, 12.50 & 25.00 ppm, respectively, vs. 3.7±0.58 days of eggs laid by control adult females). Similar retardation of embryonic development was recorded after treatment of 5th instar larvae with novaluron, since the incubation period was considerably prolonged, in a dose-dependent course (4.3±0.58, 5.3±0.58, 5.7±0.58 & 6.5±0.71, at 03.10, 06.25, 12.50 & 25.00 ppm, respectively, vs. 3.3±0.58 days of eggs laid by control adult females, Table 4).

Table 3: Oviposition efficiency and reproductive capacity of *A. ipsilon* adults affected by treatment of the 4th larvae with novaluron.

Conc. (ppm)	Oviposition rate (mean ± SD)	Reproductive capacity			Incubation period (mean days ±SD)
		Fecundity (mean no. of eggs/♀±SD)	Fertility (%)	Sterility index (%)	
50.00	1.5*	6.0*	0.0	100.0	---
25.00	2.3*	9.0*	11.1* d	99.83	6.0*
12.50	2.8±1.49 d	14.3±5.51 d	17.43±4.85 d	99.58	5.7±0.58 b
06.25	6.8±0.82 d	54.0±5.57 d	26.40±1.90 d	97.60	5.0±1.0 a
03.10	23.7±2.55 d	246.0±40.95 d	37.77±3.86 d	84.38	4.7±0.58 a
Control	59.6±3.92	695.3±73.79	85.75±3.79	---	3.7±0.58

Conc. ---, *, a, b: see footnote of Table (1). d: very highly significant (P<0.001).

Table 4: Oviposition efficiency and reproductive capacity of *A. ipsilon* adults affected by treatment of the 5th larvae with novaluron.

Conc. (ppm)	Oviposition rate (mean \pm SD)	Reproductive capacity			Incubation period (mean days \pm SD)
		Fecundity (mean no. of eggs/ \pm SD)	Fertility (%)	Sterility index (%)	
50.00	1.6 \pm 0.64 d	6.0 \pm 2.83 d	0.0	100.0	---
25.00	2.1 \pm 1.20 d	17.0 \pm 8.49 d	17.8 \pm 0.57 d	99.52	6.5 \pm 0.71 c
12.50	5.2 \pm 0.98 d	35.3 \pm 2.08 d	30.2 \pm 0.46 d	98.32	5.7 \pm 0.58 c
06.25	12.1 \pm 1.47 d	82.3 \pm 42.83 d	35.3 \pm 4.86 d	95.42	5.3 \pm 0.58 b
03.10	21.3 \pm 2.92 d	254.3 \pm 17.50 d	51.61 \pm 2.27 d	79.31	4.3 \pm 0.58 a
Control	63.8 \pm 4.98	741.7 \pm 90.85	85.53 \pm 3.82	---	3.3 \pm 0.58

Conc.. ---, *, a, b, c: see footnote of Table (1). d: see footnote of table (3).

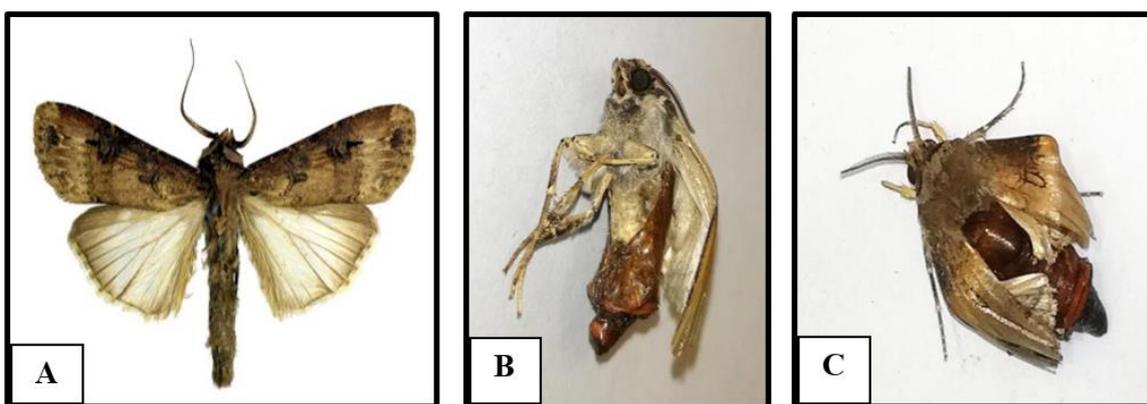


Plate 1: Adult deformities of *A. ipsilon* after treatment of the newly moulted 5th instar larvae with novaluron. A: Normal adult moth. B & C: Adult moths with curled wings, atrophied mouth parts and pupal exuvia attached to abdomens.

DISCUSSION

I. Disrupted Adult Performance of *A. ipsilon* by Novaluron:

1.1. Blocked Adult Emergence:

Depending on the current literature, only a few studies had investigated the effects of IGRs on the adult emergence of *A. ipsilon*, since treatment of 4th instar larvae chlorfluazuron or triflumuron led to a remarkably blocked adult emergence (Fahmy, 2014). A similar result was recorded for chlorfluazuron and flufenoxuron (Shaurub *et al.*, 2018). Also, He *et al.* (2019) recorded significantly reduced adult emergence of *A. ipsilon* after feeding of the newly moulted 3rd instar larvae on an artificial diet mixed with low-lethal concentrations of chlorantraniliprole. Results of the present study were in agreement with these reported results since adult emergence was drastically blocked, in a dose-dependent course, after treatment of 4th instar or 5th instar larvae of *A. ipsilon* with novaluron.

Also, the present results were in accordance with many reported results of partially or completely blocked adult emergence of insects other than *A. ipsilon* after larval treatment with different IGRs, such as the diamondback moth *Plutella xylostella* after treatment with hexaflumuron (Mahmoudvand *et al.*, 2012); the Egyptian cotton leafworm *Spodoptera littoralis* after treatment with novaluron (Ghoneim *et al.*, 2015), cyromazine (Tanani *et al.*, 2015), methoxyfenozide (Khaled and Farag, 2015) and cycloheximide (Basiouny and Ghoneim, 2018); the vinegar fly *Drosophila melanogaster* after topical application of 3rd instar larvae with pyriproxyfen (Benseba *et al.*, 2015); the lesser mulberry snout moth

Glyphodes pyloalis after treatment with lufenuron (Aliabadi *et al.*, 2016); the southern house mosquito *Culex quinquefasciatus* and the Asian tiger mosquito *Aedes albopictus* after treatment with pyriproxyfen (Khan *et al.*, 2016); the pink bollworm *Pectinophora gossypiella* after treatment of larvae with novaluron (Hassan *et al.*, 2017) and after treatment of 1-day old eggs with noviflumuron or novaluron (Tanani and Ghoneim, 2017); the olive leaf moth *Palpita unionalis* after treatment with methoxyfenozide (Hamadah *et al.*, 2017); the yellow fever mosquito *Aedes aegypti* (Braga *et al.*, 2005), the rice moth *Corcyra cephalonica* (Tripathi and Tiwari, 2006), *C. quinquefasciatus* and *Ae. albopictus* (Khan *et al.*, 2016; Bibbs *et al.*, 2017) after topical application of methoprene onto larvae; *C. cephalonica* after treatment of 4th instar larvae with fenoxycarb (Singh and Tiwari, 2016); the parasitic wasp *Encarsia formosa* after treatment of pupae with pyriproxyfen (Wang and Liu, 2016); the false stable fly *Muscina stabulans* after topical application of 3rd instar larvae or prepupae with pyriproxyfen (Hamadah, 2018); *etc.*

Prior to the interpretation of blocked adult emergence of *A. ipsilon* after larval treatment with novaluron, in the present study, it may be important to mention that the adult emergence is a prerequisite process of insect metamorphosis. This crucial physiological process has been regulated by the eclosion hormone. Disturbance of this hormone partially or completely arrests the adults to emerge (Josephraj Kumar *et al.*, 1999). For interpretation of the blocking of adult emergence after treatment of 4th or 5th instar larvae of *A. ipsilon*, in the present study, novaluron might exhibit a disturbing effect on the normal metabolism of insect hormones during the development of the immatures leading to failure of adult emergence (Trigo *et al.*, 1988). In particular, novaluron might disturb the adult eclosion hormone release and/or inhibition of the neurosecretion (Al-Sharook *et al.*, 1991; Josephraj Kumar *et al.*, 1999). On the molecular basis, novaluron might cause misexpression of certain genes, particularly the broad complex (*br-C*) transcription factor gene, leading to symptoms of impaired metamorphosis, like blocking of adult emergence (Wilson, 2004; Nandi and Chakravarty, 2011).

1.2. Reduced Adult Survival:

As far as our literature survey could ascertain, no information was available on the adulticidal effects of IGRs on *A. ipsilon*. Only a few results had been reported in the current literature regarding the extended toxic effects of IGRs on some other insects after treatment of larvae, such as *S. littoralis* after treatment of larvae with novaluron, especially at the higher concentrations (Hamadah *et al.*, 2015); the onion flies *Delia antiqua* after larval treatment with pyriproxyfen (Zhou *et al.*, 2016); *P. gossypiella* after-treatment of the newly hatched larvae with novaluron (Hassan *et al.*, 2017) and *P. unionalis* after treatment of last instar (6th) larvae with methoxyfenozide (Hamadah and Abo Elsoud, 2018). Results of the present study were, to a great extent, in accordance with those reported results, since treatment of 4th instar or 5th instar larvae of *A. ipsilon* with novaluron resulted in various mortalities of the successfully emerged adults, in a dose-dependent course.

The adult mortality of *A. ipsilon* after treatment of newly moulted 4th and 5th instar larvae with novaluron, in the current study, could be explained by the retention and distribution of this IGR in the insect body as a result of rapid transport from the gut of treated larvae into other tissues, by the direct and rapid transport *via* the haemolymph to other tissues, and/or by lower detoxification capacity of adults against the tested compound (Osman *et al.*, 1984; Smagghe and Degheele, 1992). Also, an extended or chronic lethal effect of novaluron might be due to disturbed adult enzymatic pattern and hormonal hierarchy (Kartal *et al.*, 2003). However, the adult life in insects depends on healthy immature stages. Digestive disorders such as starvation, disturbance in metabolism, degeneration of peritrophic membranes and accumulation of faecal materials at the hindgut may be the cause of untimely adult mortality as a result of CSIs exposure (Soltani, 1984).

1.3. Imperfect Adult Morphogenesis:

As searching the available literature, the effects of IGRs on the adult morphogenesis of *A. ipsilon* have received very little research attention. However, a significantly increased number of deformed adults had been recorded by He *et al.* (2019) after feeding of the newly moulted 3rd instar larvae of *A. ipsilon* on an artificial diet supplemented with low-lethal concentrations of chlorantraniliprole. In the present study on *A. ipsilon*, novaluron failed to affect the adult morphogenesis after treatment of 4th instar larvae but exhibited a slight anti-morphogenic effect on adults after treatment of 5th instar larvae only with 25.00ppm. The adult deformities were seen as atrophied mouth parts, curled wings and pupal exuvia attached to the abdomens.

The present result was, to some extent, consistent with some reported results of impaired adult morphogenesis of different insects by various IGRs, such as *S. littoralis* by tebufenozide and methoxyfenozide (Gobbi *et al.*, 2000; Pineda *et al.*, 2004), flufenoxuron (Bakr *et al.*, 2010), novaluron (Hamadah *et al.*, 2015), chlorfluazuron, flufenoxuron and pyriproxyfen (Shaurub *et al.*, 2020); the red palm weevil *Rhynchophorus ferrugineus* by diofenolan (Tanani, 2001); the eastern spruce budworm *Choristoneura fumiferana* by tebufenozide and methoxyfenozide (Sundaram *et al.*, 2002); the red flour beetle *Tribolium castaneum* and the confused flour beetle *Tribolium confusum* by cyromazine (Kamaruzzaman *et al.*, 2006); the sunn pest *Eurygaster integriceps* by pyriproxyfen (Mojaver and Bandani, 2010); the red cotton stainer *Dysdercus koenigii* by flucycloxuron (Khan and Qamar, 2011); the Mediterranean flour moth *Anagasta kuehniella* by diflubenzuron and hexaflumuron (Ashouri *et al.*, 2014); the corn earworm *Helicoverpa armigera* with hexaflumuron (Taleh *et al.*, 2015); *C. cephalonica* by fenoxycarb (at concentrations 0.05% and 0.025%) (Begum and Qamar, 2016); *P. gossypiella* by teflubenzuron (Said *et al.*, 2017); the false stable fly *Muscina stabulans* by pyriproxyfen (Hamadah, 2018); the tobacco cutworm *Spodoptera litura* by buprofezin (Khatun *et al.*, 2019); *etc.*

In contrast, the present results disagreed with few reported results of IGRs' failure to affect the adult morphogenesis of some insects, such as *P. unionalis* after larval treatment with methoxyfenozide (Hamadah *et al.*, 2017) and *P. gossypiella* after larval treatment with novaluron (Hassan *et al.*, 2017)

For interpretation of the anti-morphogenic action of novaluron on the adult moths of *A. ipsilon*, in the current investigation, this IGR might exert an adverse action on the hormonal balance during the adult differentiation, in particular the disturbance of ecdysteroid titer which led to changes in lysosomal enzyme activity causing overt morphological abnormalities (Josephraj Kumar *et al.*, 1999). In addition, other suggestions can be appreciated, such as the chitin synthase might be inhibited by metabolites of the tested compound (Cohen and Casida, 1980), inhibition of DNA synthesis and/or inhibition of facilitated diffusion and active transport across cell membranes of nucleosides and amino acids (Mayer *et al.*, 1988).

1.4. Influenced Adult Longevity:

1.4.1. Total Adult Longevity:

After the attainment of sexual maturity, insects often show degenerative changes in some tissues and organs which can be called 'senility' or 'aging'. In insects, the affected adult longevity can be considered an informative indicator for adult aging, i.e., prolongation of longevity may denote a delay of aging and *vice versa*, although death is usually the destiny of all creatures (Ghoneim *et al.*, 2017a). The total adult longevity of *A. ipsilon* was reported to be shortened after treatment of larvae with some IGRs, such as flufenoxuron (El-Sheikh, 2002), chlorfluazuron, or triflumuron (Fahmy, 2014) and chlorfluazuron or flufenoxuron (Shaurub *et al.*, 2018). Results of the present study were in accordance with these reported

results since treatment of 4th instar or 5th instar larvae of the same insect with novaluron led to a general shortening of the total adult longevity.

Also, the present results were in agreement with many reported results of shortened adult longevity of different insects after larval treatment with various IGRs, such as *S. litura* after treatment with RH-5849 (ecdysone agonist) (Seth *et al.*, 2004); *S. littoralis* after treatment with lufenuron (Sammour *et al.*, 2008), methoxyfenozide (Pineda *et al.*, 2009) and novaluron (Hamadah *et al.*, 2015); the Oriental fruit moth *Grapholita molesta* (Reinke and Barrett, 2007) and the beet armyworm *Spodoptera exigua* (Luna *et al.*, 2011) after treatment with methoxyfenozide; *G. pyloalis* after treatment with lufenuron (Aliabadi *et al.*, 2016); *P. gossypiella* after treatment with diflubenzuron and chlorfluazuron (Kandil *et al.*, 2005; Rabie *et al.*, 2006; Salem, 2015), methoxyfenozide (Sabry and Abdou, 2016) and novaluron (Hassan *et al.*, 2017), as well as after treatment of 1-day old eggs with noviflumuron or novaluron (Tanani and Ghoneim, 2017); *M. stabulans* after treatment with novaluron (Hamadah, 2018); *etc.*

On the contrary, our results disagreed with those reported results of prolonged adult longevity in some insects by different IGRs, such as *A. ipsilon* after treatment of 3rd instar larvae with chlorantraniliprole (He *et al.*, 2019); *P. gossypiella* after treatment with lufenuron, chlorfluazuron and Chromafenozide (Kandil *et al.*, 2012), hexaflumuron (Kandil *et al.*, 2013), pyriproxyfen (Sabry and Abdou, 2016) and the lowest concentration of novaluron (Hassan *et al.*, 2017); as well as the mustard aphid *Lipaphis erysimi* after treatment with pyriproxyfen (Liu and Chen, 2001) and *P. unionalis* after treatment with methoxyfenozide (Hamadah *et al.*, 2017).

Moreover, our results disagreed with those reported results of unaffected adult longevity of some insects after treatment with some IGRs, such as the house fly *Musca domestica* after treatment with diufenolan (Hamadah, 2003), the codling moth *Cydia pomonella* after treatment with tebufenozide or Methoxyfenozide (Saenz-de-Cabezón *et al.*, 2005), *S. littoralis* after treatment with buprofezin (Ragaei and Sabry, 2011) and the tarnished plant bug *Lygus lineolaris* after treatment with novaluron (Portilla *et al.*, 2012).

To explicate the shortening of total adult longevity of *A. ipsilon*, after treatment of 4th instar or 5th instar larvae with novaluron, in the current study, this IGR, as a xenobiotic compound, might exert a general accelerating action on these adult female moths to quickly pass aging ending in death. However, this result can be interpreted by the accumulation of toxic xenobiotics in the body which upsets a complicated balance of factors such as absorption, excretion and detoxification (Abdel-Aal, 1996). This shortened adult longevity of *A. ipsilon* might be due to interference of novaluron with the hormonal regulation of adult longevity because a close relationship between certain hormones and adult longevity was reported in other insects, such as *Drosophila* (Clancy *et al.*, 2001; Simon *et al.*, 2003; Broughton *et al.*, 2005; Carbone *et al.*, 2006). At least one of the *Drosophila* insulin-linked peptides expressed in the median neurosecretory cells (which produce prothoracicotropic hormone) is likely to contribute to the endocrine regulation of longevity (Toivonen and Partridge, 2009). However, the exact mode of action of novaluron on the biochemical sites in adults of *A. ipsilon* is unknown until now. Also, more information on the adult endocrine system of the present insect is required to clarify the mechanism by which this IGR can affect adult longevity.

1.4.2. The Pre-Oviposition Period:

In most insects, the pre-oviposition period can be called the 'ovarian maturation period' and it may be an informative indicator for the ovarian maturation rate, i.e., the shorter period indicates a faster rate and *vice versa*. In the present study, treatment of 4th instar or 5th instar larvae of *A. ipsilon* with novaluron resulted in a remarkably prolonged pre-oviposition period of the successfully emerged and mated adult female moths. The present result corroborated

with some reported results of the prolonged pre-oviposition period of a number of insects after larval treatment with some IGRs, such as *P. gossypiella* after treatment of newly hatched larvae with diflubenzuron, hexaflumuron, or chlorfluazuron (Kandil *et al.*, 2005, 2013), LC₅₀ values of chromafenozide (Salem, 2015), LC₅₀ of teflubenzuron (El-Khayat *et al.*, 2015) and after treatment of newly hatched or full-grown larvae with novaluron (Hassan *et al.*, 2017); *S. littoralis*, after larval treatment with diflubenzuron (Aref *et al.*, 2010); the Mediterranean flour moth *Ephestia kuehniella* after larval treatment with tebufenozide (Bouzera and Soltani-Mazouni, 2014) and *P. unionalis* after larval treatment with methoxyfenozide (Hamadah *et al.*, 2017).

On the contrary, the present result of the prolonged pre-oviposition period in *A. ipsilon* is contradictory to those reported results of the shortened period in *P. gossypiella*, after treatment of newly hatched larvae with diflubenzuron (Rashad *et al.*, 2006) and *D. antique* after larval treatment with a dose of 100 mg kg⁻¹ of pyriproxyfen (Zhou *et al.*, 2016). Moreover, this period was unaffected in *S. litura* after larval treatment with chlorfluazuron and methoxyfenozide (Shahout *et al.*, 2011) and *D. antique* after larval treatment with high doses of pyriproxyfen (Zhou *et al.*, 2016) or not significantly affected after-treatment of the newly molted 4th instar larvae of *A. ipsilon* with chlorfluazuron and flufenoxuron (Shaurub *et al.*, 2018).

In the current investigation, the retarding effect of novaluron on the ovarian maturation rate (as indicated by prolongation of the pre-oviposition period) in *A. ipsilon* might be understood by influenced germ band or the number of germ cells formed in the embryo (Hodin and Riddiford, 1998). However, the exact mode of retarding action of the tested IGR on the pre-oviposition period is unfortunately available right now and its interference with the hormonal regulation needs further investigation in the foreseeable future.

1.4.3. The Oviposition Period:

In respect of the oviposition period (reproductive life-time), few reported results are available in the current literature. The oviposition period of *A. ipsilon* was considerably shortened after-treatment of the 4th instar larvae with chlorfluazuron and triflumuron (Fahmy, 2014), chlorfluazuron and flufenoxuron (Shaurub *et al.*, 2018), or LC₂₅ and LC₄₅ of chlorantraniliprole (He *et al.*, 2019). The result of the present study on *A. ipsilon* was, to a great extent, concomitant to those reported results, since the oviposition period was conspicuously shortened after treatment of 4th instar or 5th instar larvae with Novaluron.

Also, the present result was in agreement with some reported results of shortened oviposition period of some insects, other than *A. ipsilon*, after larval treatment with various IGRs, such as *S. litura* after treatment of 2nd instar larvae with LC₃₀ of methoxyfenozide (Shahout *et al.*, 2011); *P. xylostella* after larval treatment with pyriproxyfen (Mahmoudvand *et al.*, 2015); *P. unionalis* after treatment of newly moulted last instar larvae with methoxyfenozide (Hamadah *et al.*, 2017) and *P. gossypiella* after treatment of newly hatched larvae with chlorfluazuron (Kandil *et al.*, 2005), diflubenzuron (Rashad *et al.*, 2006), hexaflumuron and chlorfluazuron (Kandil *et al.*, 2013) and LC₅₀ of methomyl (El-Khayat *et al.*, 2015) as well as after treatment of newly hatched or full-grown larvae with novaluron (Hassan *et al.*, 2017).

On the contrary, this result disagreed with the reported considerable prolongation of the oviposition period in *P. gossypiella*, after treatment of newly hatched larvae with LC₅₀ of chromafenozide or Diflubenzuron (Salem, 2015) and teflubenzuron (El-Khayat *et al.*, 2015).

In the current work, novaluron exhibited a prevalent enforcing effect on the adult females of *A. ipsilon*, since they quickly laid their eggs during a very short time interval, regardless of the treated larval instar. The exact mechanism of this enforcement action is still

unknown. However, these females might be enforced to lay their eggs quickly to avoid this toxic xenobiotic factor.

1.4.4. The Post-Oviposition Period:

Depending on the currently available literature, very scarce studies have examined the effects of IGRs on the post-oviposition period on insects. In the present study, treatment of 5th instar larvae of *A. ipsilon* with novaluron led to a slight prolongation of the post-oviposition period, in no certain trend. In addition, this period was diversely affected after treatment of 4th instar larvae, since it was prolonged or shortened, depending on the concentration. This result was, to some extent, in accordance with those reported results of a prolonged post-oviposition period of *P. gossypiella* after larval treatment with hexaflumuron or chlorfluazuron (Kandil *et al.*, 2013) but diversely affected by novaluron, depending on the concentration (Hassan *et al.*, 2017). Also, the post-oviposition period of *P. unionalis* was remarkably prolonged after treatment of newly moulted last instar larvae with methoxyfenozide (Hamadah *et al.*, 2017). Unfortunately, we have no acceptable interpretation for the prolongation of the post-oviposition period of *A. ipsilon* after treatment of 5th instar larvae with novaluron right now!!

2. Impaired Reproductive Potential of *A. ipsilon* by Novaluron:

Reproduction in insects is mainly controlled by the juvenile hormone (JH), produced by corpora allata, which is also responsible for protein metabolism and is specifically needed for egg maturation. Many IGRs have been reported to cause sterility of insects or prohibited their fecundity (Ghoneim *et al.*, 2014). It is interesting to categorize the effects of IGRs on insect reproduction into i) reproductive behaviour, ii) oviposition, iii) egg hatchability (ovicidal and embryocidal), and iv) adult sterilization (Mondal and Parween, 2000). On the other hand, ecdysteroids have essential functions in the control of the processes involved in insect reproduction, i.e., vitellogenesis, ovulation of matured eggs and spermatocyte growth (Hagedorn, 1985).

2.1. Prohibited Oviposition Efficiency:

In insects, the oviposition rate can be used as an informative indicator of the oviposition efficiency of adult females (Ghoneim *et al.*, 2014). After treatment of 4th instar or 5th instar larvae, in the present study, novaluron exhibited a strong extended inhibitory effect on the oviposition efficiency of *A. ipsilon*, since the oviposition rate was tremendously regressed, in a dose-dependent trend. This result was, to a great extent, in conformity with the reported results of inhibited oviposition efficiency of some insects after larval treatment with various IGRs, such as *S. littoralis* after treatment with tebufenozide (Bakr *et al.*, 2005), flufenoxuron (Bakr *et al.*, 2010), novaluron (Ghoneim *et al.*, 2014) and dimethyl fluoromalonate, in a dose-dependent course (Ghoneim and Basiouny, 2018); the desert locust *Schistocerca gregaria* after treatment with flufenoxuron and lufenuron (Soltani-Mazouni and Soltani, 1994) or tebufenozide (Al-Dali *et al.*, 2008); the Indian meal moth *Plodia interpunctella* after treatment with the ecdysteroid agonist RH-5849 (Smagghe and Degheele, 1994); the bean beetle *Callosobruchas maculatus* after treatment with cyromazine (Al-Mekhlafi *et al.*, 2011); *P. gossypiella* after treatment with novaluron (Hassan *et al.*, 2017) *P. unionalis* after treatment with methoxyfenozide (Hamadah *et al.*, 2017). In contrast, the present result disagreed with the results of stimulated oviposition of the two-spotted field cricket *Gryllus bimaculatus* by some ecdysteroid agonists (Behrens and Hoffmann, 1983). In the current study, the prohibited oviposition efficiency of *A. ipsilon* adult females, after treatment of 4th instar or 5th instar larvae with novaluron could be explained as a result of the inhibition of ovarian DNA synthesis or the interference of the tested IGR with vitellogenesis via certain biochemical processes. However, novaluron might exert a reverse action to that exerted by the ecdysteroid agonists which stimulate the neurosecretory cells to release a myotropic ovulation hormone (Smagghe *et al.*, 1996; Parween *et al.*, 2001).

2.2. Disrupted Reproductive Capacity:

In insects, fecundity (mean number of eggs/♀) and fertility (egg hatchability, viability, or egg hatching %) are the major parameters of reproductive capacity.

Inhibited Fecundity:

On the basis of the available current literature, fecundity of *A. ipsilon* adult females was conspicuously inhibited after treatment larvae with different IGRs, such as chlorfluazuron and triflumuron (Fahmy, 2014), cyantraniliprole (Xu *et al.*, 2016), chlorfluazuron and flufenoxuron (Shaurub *et al.*, 2018) and chlorantraniliprole (He *et al.*, 2019). The result of the present study was in agreement with those reported results, since treatment of 4th instar or 5th instar larvae of *A. ipsilon* with novaluron led to a drastic prohibition of fecundity, in a dose-dependent course.

Also, this result was in accordance with many reported results of considerably reduced fecundity of different insects, other than *A. ipsilon*, after larval treatment with various IGRs, such as *S. littoralis* after treatment with diflubenzuron (Aref *et al.*, 2010), lufenuron (Gaaboub *et al.*, 2012), methoxyfenozide (Pineda *et al.*, 2009; Khaled and Farag, 2015), novaluron (Ghoneim *et al.*, 2014) as well as chlorfluazuron, flufenoxuron and pyriproxyfen (Shaurub *et al.*, 2020); *P. gossypiella* after treatment of newly hatched larvae with tebufenozide (El-Khayat *et al.*, 2015), diflubenzuron (Kandil *et al.*, 2005; Rashad *et al.*, 2006; Salem, 2015), buprofezin (Al-Kazafy, 2013), hexaflumuron and chlorfluazuron (Kandil *et al.*, 2013), Chromafenozide (Salem, 2015) as well as pyriproxyfen, methoxyfenozide and lufenuron (Sabry and Abdou, 2016), novaluron (Hassan *et al.*, 2017) and tebufenozide (Said *et al.*, 2017); *E. kuehniella* after treatment with tebufenozide (Khebbeb *et al.*, 2008) or diflubenzuron and hexaflumuron (Ashouri *et al.*, 2014); the oblique banded leaf roller *Choristoneura rosaceana* (Sun *et al.*, 2000), the European grapevine moth *Lobesia botrana* (Saenz-de-Cabezón *et al.*, 2005) and *S. litura* (Shahout *et al.*, 2011) after treatment with methoxyfenozide; the mealworm beetle *Tenebrio molitor* after treatment with the ecdysteroid agonist halofenozide (RH-0345) (Taibi *et al.*, 2003); *D. koenigi* after treatment with flufenoxuron (Khan and Qamar, 2011); *P. xylostella* after treatment with Pyriproxyfen (Mahmoudvand *et al.*, 2015); *T. castaneum* (Gado *et al.*, 2015) and *D. antique* (Zhou *et al.*, 2016) after treatment with lufenuron; *C. cephalonica* after treatment with Fenoxycarb (Begum and Qamar, 2016); *D. antique* after treatment with Lufenuron (Zhou *et al.*, 2016); the red-banded leafroller moth *Argyrotaenia velutinana* (Sun *et al.*, 2000), *T. castaneum* (Ali *et al.*, 2016) and the gypsy moth *Lymantria dispar* (Ouakid *et al.*, 2016) after treatment with Methoxyfenozide; *P. unionalis* after treatment with methoxyfenozide (Hamadah *et al.*, 2017); *H. armigera* after feeding of the 3rd instar larvae on diets mixed with LC₁₀ concentration of hexaflumuron, lufenuron and chlorfluazuron (Khorshidi *et al.*, 2019); *Aedes albopictus* mosquito after exposure to pyriproxyfen (Rhyne and Richards, 2020); *etc.* On the contrary, recorded results in the current investigation disagreed with some reported results of failure of some IGRs to affect the fecundity in various insects, such as fenoxycarb against the honey bee *Apis mellifera* (Thompson *et al.*, 2005), methoxyfenozide against *S. exigua* (Christian-Lius and Pineda, 2010) as well as novaluron and diflubenzuron against the brown marmorated stink bug *Halyomorpha halys* (Kamminga *et al.*, 2012). Moreover, feeding of larvae on leaves treated with methoxyfenozide enhanced the fecundity of *S. littoralis* (Ishaaya *et al.*, 1995). However, these diverse effects can be attributed to the different modes of action of IGRs, different susceptibilities of the insect species, time of treatment and other factors.

The drastically prohibited fecundity of *A. ipsilon*, after treatment of the 4th instar or 5th instar larvae with novaluron, in the present study, might be due to the interference of this IGR with one or more processes, from the ovarian follicle development to egg maturation or might be due to its direct disruptive effect on some physiological and reproductive

behavioral aspects (Desneux *et al.*, 2007; Magierowicz *et al.*, 2019). In some detail, this fecundity inhibition could be explained by some reasons, as follows. (1) The tested IGR might cause some disorders in the ovaries, including cell death in the germarium, resorption of oocytes in the pre-vitellarium and vitellarium, formation of vitellin envelopes and undue proliferation of follicle cells sometimes resulting in malformation of the whole ovary (Lucantoni *et al.*, 2006; Khan *et al.*, 2007; Zhou *et al.*, 2016; Shaurub *et al.*, 2018). (2) The tested IGR might inhibit the development of some ovarioles and/or synthesis and metabolism of proteinaceous constituents during the oogenesis (Salem *et al.*, 1997) or interfered with vitellogenesis (Perveen and Miyata, 2000; Shaurub *et al.*, 2018). (3) The present IGR might exert an inhibitory action on the ecdysone activity, the threshold of which is essential for normal oogenesis (Terashima *et al.*, 2005). (4) On the basis of hormonal regulation of insect reproduction, the present IGR might disturb the production and/or function of the gonadotropic hormone (juvenile hormone, JH) responsible for the synthesis of vitellogenins (yolk precursors) and vitellogenesis (Di Ilio *et al.*, 1999). (5) Eggs might develop normally in ovaries, but they could not be lay, owing to the adversely deformed ovipositor of adult females or to the reduced mechanical strength (Moreno *et al.*, 1994). (6) It might be acceptable to suggest that the prohibited fecundity of *A. ipsilon*, in the current study, might be due to an inhibitory effect of the tested IGR on the synthesis of both DNA and RNA, suboptimal nutrition owing to reduced feeding, altered mating behaviour as a result of sublethal intoxication, or a combination of factors.

Reduced Fertility:

Fertility (egg hatching % or egg viability) is another important parameter of the reproductive capacity in insects. As reported in the available literature, treatment of 4th instar larvae of *A. ipsilon* with chlorfluazuron or triflumuron led to egg hatchability ranging from zero - 8% (Fahmy, 2014). After treatment with *A. ipsilon* larvae with cyantraniliprole, the egg hatching percentage was significantly declined (Xu *et al.*, 2016). After treatment of the newly molted 4th instar larvae of *A. ipsilon* with chlorfluazuron and flufenoxuron, the egg hatching was severely reduced (Shaurub *et al.*, 2018). The result of the present study was consistent with these reported results since fertility of *A. ipsilon* was dramatically reduced, in a dose-dependent course, after treatment of 4th instar or 5th instar larvae with novaluron. Novaluron caused complete sterility by its highest concentration and increasing sterility by other concentrations.

Also, the present result was in accordance with many reported results of reduced fertility of different insects by various IGRs, such as *P. gossypiella* by lufenuron, methoxyfenozide and chromafenozide (Kandil *et al.*, 2012), methoxyfenozide (Sabry and Abdou, 2016) or novaluron (Hassan *et al.*, 2017); *S. litura* by diofenolan (Perveen and Miyata, 2000) and chromafenozide (Shahout *et al.*, 2011); *E. kuehniella* by tebufenozide (Khebbeb *et al.*, 2008) and hexaflumuron (Ashouri *et al.*, 2014); *D. koenigi* by flufenoxuron (Khan and Qamar, 2011), *C. maculata* by cyromazine (Al-Mekhlafi *et al.*, 2011), *L. dispar* by methoxyfenozide (Ouakid *et al.*, 2016); *P. unionalis* by methoxyfenozide (Hamadah *et al.*, 2017); *T. molitor* by Halofenozide (Taibi *et al.*, 2003); *T. castaneum* by novaluron (Kostyukovsky and Trostanelsky, 2004); *D. koenigi* by flufenoxuron (Khan and Qamar, 2011), *C. maculata* by cyromazine (Al-Mekhlafi *et al.*, 2011), *H. armigera* by hexaflumuron, lufenuron and chlorfluazuron (Khorshidi *et al.*, 2019); *S. littoralis* by chlorfluazuron (Sammour *et al.*, 2008), methoxyfenozide (Pineda *et al.*, 2009), diflubenzuron (Aref *et al.*, 2010), lufenuron (Gaaboub *et al.*, 2012), triflumuron (El-Naggar, 2013), novaluron (Ghoneim *et al.*, 2014), methoxyfenozide (Khaled and Farag, 2015) or chlorfluazuron and flufenoxuron (Shaurub *et al.*, 2020); *etc.*

For explicating the fertility reduction in *A. ipsilon* by novaluron, in the current study, some suggestions could be provided herein. (1) Maturation of the eggs depends basically on

the vitellogenins, precursor materials of vitellins including proteins, lipids and carbohydrates, all of which are necessarily required for embryonic development (Chapman, 1998; Shaurub *et al.*, 2018). These materials are synthesized primarily by the fat body during the immature stages or by the ovary *in situ* (Indrasith *et al.*, 1988; Telfer, 2009). The present IGR might disturb the production and/or accumulation of these materials in the adult females of *A. ipsilon* resulting in the reduction of fertility (Taibi *et al.*, 2003; Pineda *et al.*, 2006; Osorio *et al.*, 2008). (2) The present IGR might indirectly affect fertility via its disruptive effect on opening "potency" of the intracellular spaces in the follicular epithelium or generally inhibited the role of JH (gonadotropic hormone) responsible for the regulation of vitellogenin deposition into oocytes (Davey and Gordon, 1996). (3) The reduction in fertility might be due to the penetration of residual amounts of novaluron in *A. ipsilon* mothers into their eggs and disturbance of embryonic cuticle synthesis. So, the fully mature embryos had weakened chitinous mouth parts that were insufficiently rigid to perforate the surrounding vitellin membrane and free from the eggs (Sallam, 1999; Sammour *et al.*, 2008) or this residual novaluron, in the ovaries of mothers, might exhibit an ovidical or embryocidal effect or retarded the developing embryos at certain stages, as recorded in decreasing hatching percentage. (4) Because some molecular studies revealed the effects of some IGRs on insect reproduction owing to the perturbation of gene expression in the hierarchy cascade of vitellogenesis and/or choriogenesis (Sun *et al.*, 2003), novaluron might interfere with the gene expression resulting in a reduction of the developed embryos in *A. ipsilon*, in the present study. (5) Moreover, the developing embryos in eggs of *A. ipsilon* suffered some morphological deformations and incomplete development of some body parts after larval treatment with novaluron. However, the exact mode of action of novaluron on the fertility of *A. ipsilon* is still debatable and needs further investigation in the future.

2.3. Retarded Embryonic Development:

No embryological investigation was conducted in the present study, but the incubation period of eggs can be used as an informative indicator of the embryonic developmental rate, i.e., a longer period usually indicates a slower rate and *vice versa*. In the present study, the embryonic developmental rate was remarkably retarded, since the incubation period of *A. ipsilon* eggs was considerably prolonged, in a dose-dependent course, after treatment of 4th instar or 5th instar larvae with novaluron. The present result corroborated with the scarcely reported results in the available literature concerning a similar retarding action of some IGRs on the embryonic development of some insects, such as *P. gossypiella* after treatment with lufenuron, chlorfluazuron and chromafenozide (Kandil *et al.*, 2012) or novaluron (Hassan *et al.*, 2017), *C. maculatus* after treatment with cyromazine (Al-Mekhlafi *et al.*, 2011); *S. littoralis* after treatment with novaluron (Ghoneim *et al.*, 2014) and *P. unionalis* after treatment with methoxyfenozide (Hamadah *et al.*, 2017). The delayed embryonic development in *A. ipsilon* after treatment of larvae with novaluron, in the present study, might be due to its disturbing effect on the ecdysteroid level responsible for the regulation of embryogenesis at certain stages, especially those originating from the ovary *in situ* (Chapman, 1998).

Conclusion:

Depending on the present results, novaluron exhibited a drastic blocking effect on the adult emergence of *A. ipsilon*, strong adulticidal effect, remarkably inhibitory effect on the oviposition efficiency of the adult females, strong reducing effect on both the fecundity and fertility, as well as retardation of the embryonic development in the laid eggs. Since inhibiting the fecundity and reducing the egg hatchability are both important factors for success in pest management, novaluron may be an effective IGR being used in the IPM program against *A. ipsilon*.

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