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Do Egg Pods in the Desert Locust *Schistocerca gregaria* Display as Oogenesis Limiting Factor? III-Effect of Egg Pod Extracts on Egg Pod Biometrics and Biological Aspects of the Offspring

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Abstract: The exposure of solitary and gregary adult females during oviposition period to the contaminated sand of ovipositing sites with their egg pods extracts in hexane or ethanol reduced the number of egg pods, laid eggs, hatching percent and caused malformed eggs and froth. The incubation period of deposited eggs of treated females and the nymphal duration were longer than untreated ones. Therefore, the offspring of treated females were abnormal in both shape, weight and growth.

Key words: Desert locust, egg pod, offspring, hatching, incubation period, malformed eggs, abnormal females

INTRODUCTION

During larval development each ovariole differentiates into a series of ovariole follicles, each containing an oocyte which remain relatively small and develop until adult eclosion[1]. Growth of oocytes occurs, after adult moult, in two stages. First, a period of rapid somatic growth (continues from few days to several weeks). Second, a period of rapid oocytes growth that begins after accumulation of sufficient reserves in the fat body. Oocytes development is divided into previtellogensis, early vitellogenesis and choriogensis[2].

The egg pod foam is produced from the proteinaceous secretion of the accessory glands. This secretion which travels along the oviducts is transformed into froth by an unknown process[3]. After hardening the foam binds the eggs together, prevents collapse of the hole, facilitates gas exchange, reduces water loss and provides a soft, friable material through which the hatching wiggle to surface[4]. The hatched nymphs per female of *Schistocerca gregaria* were significantly diminished by froth and egg mass extracts[5].

MATERIALS AND METHODS

Both phases of *Schistocerca gregaria* were reared under normal condition (32±2°C and 65±5% RH.) at the Locust and Grasshoppers Research Department, Plant Protection Research Institute Dokki, Giza, Egypt. This colony was initiated using progenitors of wild strains indigenous to Aswan. The insects have been reared and handled to satisfy the crowded breeding conditions described by Hunter-Jones[6].

Egg pods of solitary and gregary females were collected for each, then froth were separated. Hexane and ethanol were used to extract active materials (pod factors) from froth and eggs[7].

Oviositing bioassays: The ovipositing females of the desert locust are usually attracted to egg laying sites in which the other females try to put their egg pods. Moreover, these females prefer to lay their egg pods in moist sand contaminated with extracts from egg pod froth and eggs[7]. The present study was carried out to follow up the effect of hexane and ethanol extracts of two parts of egg pods (froth and eggs) on egg pod biometrics and some biological aspects of the offspring. The cups as ovipositing sites were filled with sterilized sand and contaminated with froth and eggs extracts in hexane and ethanol, respectively. Ten days old adult females and males, were exposed to the contaminated cups, each cup received one ovipositing female and male.

The cups and exposed insects were kept under glass cylinders in the rearing laboratory.

Pre-oviposition period and oviposition period: Gregary and solitary females were isolated directly after emerge. Then after at the 10th day the females were treated according to the experimental design, then every female was kept with a male. The days after treatment till first egg deposition were counted and considered preoviposition period. The

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days after that till the last egg pod deposition were considered as oviposition period.

Egg pod characteristics: The weight and length of froth, egg mass, egg and egg pod produced from each treated group were estimated compared to the untreated ones.

Incubation period = Days from egg pod deposition till egg hatching.
Total nymphal development (duration) = Sum of the 1st, 2nd, 3rd, 4th and 5th instar periods in days.

Statistical analysis: All data were subjected to analysis of variance. Means were compared using least significant difference (LSD) at $\alpha = 0.05$ by using Microsoft Excel ware program.

RESULTS AND DISCUSSION

Effects of egg pod extracts on egg pod biometrics

Effect on egg weight: The weight of eggs may be considered as a character reflecting the efficiency of nourishing the primary oocytes with nutrients and consequently pointing to its qualitative potency. The results in Table 1 shows that the weight of egg of solitary females ranged from 0.425-0.86 mg, while those of gregary females were between 0.46-0.78 mg.

Un-expectantly, the weight of eggs laid by treated solitary females was heavier than control (0.63 mg) in 5 treatments out of 8 by the two solvents. However, this tendency was not found in gregary phase laying females. This phase dependant response, however did not surpass another one, i.e., the weight of eggs of gregary laying females was always higher than solitary phase (Table 1).

The weight of laid eggs was higher by females treated with ethanol solvent than hexane one, i.e., the former was less effective in controlling this qualitative character than the latter.

Effect on egg length: The length of eggs as a biometric measure for the treatments with egg pod extracts may be an outgrowth of the function of choriogensis dependent on growth of oocytes, or being just reflection of ovariole follicles development. The results of Table 1 contrary to the results of the weight of eggs, length of eggs was reduced nearly to less the half of the control length in the eggs laid by treated solitaries and gregarious. The length ranged from 1.30-5.61 mm, for gregary females treated by hexane and ethanol extracts, respectively. The respective lengths of solitary females were 1.23 to 4.77 mm (Table 1). This tendency may be a result of less control effect of pod factors on the weight of eggs (vitellogenesis) than its effect on choriogensis. This may confirm an assumption that treatment during the preoviposition period have had high controlling action as pointed to in a former paper when compared with the treatment during the oviposition period in which the ovaries of the treated females might escaped the early injurious effect on vitellogenesis. It is worth noting that length of eggs behaved contrary to the weight with respect to solitary females, as the results showed again down rate of measurements in the eggs of treated females than control.

The length of eggs from treated solitaries ranged from 3.40 to 3.93 mm, for hexane (non-polar) and ethanol (polar) solvents, respectively. Compared with 3.41 to 2.10 for, respectively gregarious. The general means for treated solitaries were 3.66 mm and higher than gregary (2.50 mm). However, measurements of control were 4.77 mm for solitary and 5.61 mm for gregary deposited eggs.

Conclusively, the eggs laid by treated females during the preoviposition period in solitary phase exhibited, a phase dependant response towards that egg pod factors and conducted tendency to gregary phase in the quality of eggs.

Hexane treated females laid longer eggs than ethanol, which means that hexane extract was less controlling than ethanol.

Effect on weight of froth: The froth of egg pods is a proteinious secretion from the accessory glands and oviducts. It has an important role in surrounding the eggs with critical physical demands for conduction of successful embryonic development and hatching. In addition, it provides the oviposition sites with soil born factors which have effects on oviposition behaviour. In this study, egg pods were the source of extracted factors. Although the froth and eggs were considered solely, but it is reasonable that froth is the source of these factors rather than eggs. Eggs are coated by froth during this travel through the oviduct.

Results of Table 1 showed that the froth secreted by treated solitary females was lower in weight of all treatments than control, contrary to weight of eggs. Thus, negative relative between egg weight and froth weight was found by treatment.

In gregary the above relation was also found but oppositely exhibited. The froth secreted by gregary females was higher in weight than control while egg weights behaved oppositely. It may be concluded that applying of the pod factors to solitary females caused increase of egg weight and decrease in froth weight as

Table 1: Effect of froth and egg hexane extract on mean weight and length of oocytes and froth in ovipositing females *S. gregaria*

Treated phase	Solitary ovipositing females				Gregary ovipositing females			
Hexane	Wt. of one oocyte±S.D (mg)	Length of one oocyte±S.D (mm)	Wt. of froth ±S.D (mg)	Length of froth ±S.D (mm)	Wt. of one oocyte±S.D (mg)	Length of one oocyte±S.D (mm)	Wt. of froth ±S.D (mg)	Length of froth ±S.D (mm)
Solitary froth	0.425± 0.5	2.20±0.02	5.6±0.1	41.1±2.2	0.600±0.1	1.73±0.25	6.70±0.3	34.4±7.8
Gregary froth	0.710±0.3	2.33±0.15	7.5±0.4	31.0±1.6	0.670±0.5	2.33±0.04	9.10±0.3	24.5±2.7
Solitary eggs	0.860±0.5	3.40±0.44	3.9±0.8	17.0±3.0	0.560±0.7	3.33±0.10	6.50±0.8	35.0±5.0
Gregary eggs	0.480±0.6	1.23±0.36	4.7±0.9	19.4±4.2	0.710±0.5	3.41±0.60	0.47±0.2	24.5±2.7
Solitary control	0.630±0.2	4.77±0.15	8.4±1.5	28.0±0.5				
Gregary control					0.770±0.1	5.61±0.5	5.40±0.1	27.6±0.9
Ethanol								
Solitary froth	0.81±1.6	2.25±0.42	56.0±0.8	23.7±3.3	0.610±0.2	2.47±0.21	7.00±0.5	38.6±2.3
Gregary froth	0.56±0.8	1.92±0.52	54.0±0.2	19.1±2.5	0.780±1.0	3.67±0.47	5.10±1.0	18.6±4.3
Solitary eggs	0.70±0.4	3.93±0.38	51.0±0.3	37.1±3.1	0.460±0.0	1.30±0.49	7.10±0.3	37.2±3.1
Gregary eggs	0.66±0.4	1.73±0.37	42.0±0.4	25.2±6.3	0.730±0.3	2.10±0.6	4.00±1.0	38.0±1.8
Solitary control	0.63±0.2	4.77±1.50	84.0±1.5	28.0±0.5				
Gregary control					0.720±0.1	5.61± 0.5	5.40±0.1	27.6± 0.9

Table 2: Effect of treating *S. gregaria* ovipositing females with hexane extract on preoviposition, oviposition and incubation period

Treated phase	Solitary ovipositing females			Gregary ovipositing females		
Extracts	Preoviposition period (days)	Ovipositing period	Incubation period (days)**	Preoviposition period (days)	Ovipositing period	Incubation period (days)**
Solitary froth	08.000	6.50 (3.70)	15.70	8.70	8.10 (2.30)	14.75
Gregary froth	09.700	7.85 (3.00)	16.50	9.00	8.23 (3.00)	14.60
Solitary eggs	07.30	7.17 (4.25)	15.30	9.70	9.70 (2.00)	17.60
Gregary eggs	10.70	9.30 (3.00)	20.00	9.30	8.30 (3.00)	14.70
Solitary control	06.00	5.30 (6.00)	15.10	--	--	--
Gregary control	--	--	--	6.50	5.25 (4.00)	13.80

The figures in parentheses indicate the average of egg pod numbers for each indicated group
** Incubation period in days expressed as an average of the incubation period of the produced egg pods from the treated ovipositing sites

Table 3: Effect of treating *S. gregaria* ovipositing females with ethanol extract on preoviposition, oviposition and incubation period

Treated phase	Solitary ovipositing females			Gregary ovipositing females		
Extracts	Preoviposition period (days)	Ovipositing period	Incubation period (days)**	Preoviposition period (days)	Ovipositing period	Incubation period (days)**
Solitary froth	08.00	06.90 (3.50)	14.30	10.70	9.60 (2.50)	14.75
Gregary froth	12.30	11.20 (3.20)	16.25	08.70	8.00 (3.20)	15.50
Solitary eggs	07.70	07.00 (4.50)	14.50	08.30	8.80 (2.20)	16.75
Gregary eggs	12.00	10.00 (4.00)	17.50	09.70	8.80 (3.00)	15.60
Solitary control	06.00	05.30 (6.00)	15.10	--	--	--
Gregary control	--	--	--	06.50	5.25 (4.00)	13.80

The figures in parentheses indicate the average of egg pod numbers for each indicated group
** Incubation period in days expressed as an average of the incubation period of the produced egg pods from the treated ovipositing sites

compared by control (Table 1). In gregary females, the treatment caused decrease of egg weights and increase in froth weights, when compared with control.

Effect on length of froth: The froth secreted by treated solitary females was mostly shorter than control as previously found with respond to weight of froth (Table 1). Also, in accordance with weight, the froth of treated gregary females was elongated when compared with control.

In conclusion, the non-polar fraction of egg pods were more effective in adversing the egg weight and froth weights of both phases than polar ones. These specific effects of both fractions were phase dependent. Applying of the pod factor to solitary females caused increase of egg weight and decrease in froth weight as compared with control. In gregary females, the treatment caused decrease of egg weight and increase in froth weight, when compared with control. The froth of the egg pods, being the source of the tested materials in the current work, is a field of challenge for many workers and still having unsolved concepts. Both the eggs and foam plugs of egg pods from crowd-reared gregarious females appeared to be a source of gregarization factor. McCaffery *et al.*[8] reported hydrophilic gregarizing factors which is produced at the time of oviposition, predisposes hatchling to attain characteristics of the gregarious phase.

Grouped oviposition is characteristic of gregarious phase locust[9] and is assisted by interactions between adults which may involve tactile[10], visual[11] and olfactory[12] stimuli. In the field, oviposition sites of *S. gregaria* containing egg pod densities of 200-800 m^2

Table 4: Duration's (days) of produced offspring from solitary and gregary ovipositing females, treated with hexane egg pod extracts

Treated phase	Duration of solitary stages (days)					
Extracts	1st	2nd	3rd	4th	5th	Total developmental period
Solitary froth	6.6	12.7	7.75	11.0	15	53.05
Gregary froth	6.0	07.5	6.60	09.0	11	40.00
Solitary eggs	7.8	10.6	8.60	07.0	14	48.00
Gregary eggs	5.5	08.0	7.00	05.8	10	36.30
Solitary control	5.0	04.5	4.50	05.6	08	27.60
Treated phase	Duration of gregary stages (days)					
Extracts	1st	2nd	3rd	4th	5th	Total developmental period
Solitary froth	5.7	6.00	08.75	09.30	12.0	41.75
Gregary froth	7.5	7.30	11.50	10.50	12.5	49.30
Solitary eggs	6.6	5.75	08.80	08.90	11.0	41.05
Gregary eggs	7.5	6.80	09.87	10.75	14.5	49.42
Gregary control	4.5	4.50	04.80	04.80	09.2	28.80

Table 5: Duration's (days) of produced offspring from solitary and gregary ovipositing females, treated with ethanol extract

Treated phase	Duration of solitary stages (days)					
Extracts	1st	2nd	3rd	4th	5th	Total developmental period
Solitary froth	9.4	7.5	5.7	9.7	14.0	46.3
Gregary froth	5.9	6.2	6.0	7.2	11.3	36.6
Solitary eggs	8.3	7.5	7.8	8.7	12.2	44.5
Gregary eggs	6.7	5.5	4.9	7.0	10.0	34.1
Solitary control	5.0	4.5	4.5	5.6	8.00	27.6
Treated phase	Duration of gregary stages (days)					
Extracts	1st	2nd	3rd	4th	5th	Total developmental period
Solitary froth	6.4	05.7	07.2	06.4	10.0	35.7
Gregary froth	6.3	10.8	11.6	14.2	13.0	55.9
Solitary eggs	5.5	06.0	05.3	07.6	09.5	33.9
Gregary eggs	6.7	06.8	10.5	12. 8	12.6	49.4
Gregary control	4.5	04.5	04.8	05.8	09.2	28.8

have been recorded[13]. Such behaviour ensures that hatching locusts are in close proximity to each other, thus promoting and maintaining shift towards the extreme gregarious phase[7]. Neighboring egg pods could influence each other by diffusion through the soil a factor that influence development[14]. McCaffery *et al.*[8] discussed the results of Saini *et al.*[7] and Rai *et al.*[15] they reported that these components may play a semiochemical role in attracting females to oviposition sites. They added that there is no evidence to suggest that they alter the phase of the subsequent hatchlings in manner suggested by their findings. They believed that factors affecting hatchling phase described by them act in a wholly different manner and influence embryonic development.

It must be added, according to the current results of pod factors that the factors shown by Saini *et al.*[7] and Rai *et al.*[15] are polar and non-polar extracts of organic solvents while those McCaffery *et al.*[8] are hydrophilic substances extracted without using organic solvents covering any range of polarity.

Effects of egg pod extracts on biological aspects: The offspring of the treated solitary and gregary ovipositing females were maintained under isolation and crowded conditions. The duration of their nymphal instars, body weight, phase coloration and immature stage development period were recorded.

Effects on the pre-oviposition periods: The preoviposition period as days-elapsed form adulthood to oviposition are detailed in Table 2 and 3. The major trends of the data in both phases and by solvents a pronounced prolongation was recorded for all treatment when compared with the controls. These effects were higher in treated solitary (7.0-12.3 days compared with 6.0 days in control). Hexane (non-polar) extract seems to be causing higher prolongation than ethanol (polar) one, while no obvious trend could be related to differences between froth or egg extracts.

With respect to the results in hand, it could be claimed that prolongation of the preoviposition period is merely a reflection of the disturbance and delay in the processes of vitellogenesis and oogenesis.

Effects on the oviposition periods: The results shown in Table 2 and 3 are proper reflection of the results reached with the preoviposition period. The solitary control females consumed 5.30 days to produce 6.0 egg pods.

When treated with ethanol extracts of gregary froth it took 11.2 days to deposit 3.2 egg pods (Table 3). The gregary control females needed 5.25 days to deposit 4.0 egg pods, by treatment with hexane solitary egg extract, they consumed 9.70 days to deposit only 2.0 egg pods (50% of the control) (Table 2).

The results shown in Table 2 and 3, provide information about the effects of the pod factors and confirm the previous results that those factors display a limiting action on oogenesis and consequently on egg production. This limiting action had dual effect on the quantitative aspect (the quantity of egg pods) and on the biological aspect (the time consumed for production, which is of physiological bearing).

Effects on the incubation period: The incubation period is the time required for accomplishing the embryonic developmental events to produce the hatch. In this critical period, the fate of the developing system is mapped off. The immature stage organs do not only occupy this map of the forthcoming individual but also by the imaginal ones. Simply this period may be considered, under the running experimental work, as an estimate for the morphogenesis of the eggs resulting from the treated females.

There are a phase dependent variation in this parameter, these periods were 15.10 and 13.80 days for eggs of the solitary and gregary control, respectively (Table 2 and 3). This line was also the case with all treatments with both extracts as the incubation periods of the eggs of treated gregary females were in all cases shorter than their solitary counterparts.

Treating with the extract of pod factor caused, in general, retardation in the embryonic development of both phases with both extracts, as compared with control. It may be concluded that these pod factors manifested its effects far beyond the oogensis and quality of eggs, as previously shown, to the events of the morphogenic development. So, it could be claimed that these pod factors have had a morphogenetic effects based on these reactions of the embryonic events.

The question then arises as to how embryonic developments are affected in such a way that the behaviour and colour of the offspring vary according to the treatment before oviposition. One obvious possible explanation is that the female locust produces a casual factor that influences the states of hatchling and which presumably acts by regulating embryonic gene expression[8]. Such a factor could drive from the reproduction tract of the female and affect the subsequent development in the egg at any time from oogenesis to embryonic development. By virtue of its derivation from the reproductive tract at the time of oviposition and its intimate contact with the eggs, the egg foam could provide an ideal vehicle for exposure of eggs to any factor. It was shown that egg pod foam of *S. gregaria* contains factors that influences the development of locust eggs and leads to production of hatchling with the characteristic shown by the current results.

Effects on the nymphal duration: Metamorphosis from the biological point of view may be considered a valuable parameter to verify whether the pod factors extended their effects to the morphogenesis or not. These factors were shown, by reducing fecundity, to throw considerable percentage of oocytes out of function and play a limiting role on quality and quantity of many physiological parameters of the treated locust females.

The time consumed in the nymphal development involves in each instar a network of factors, which interact to give moulted individual a step towards the expression of its morphogenetic potency, mapped out in its biomass. This time factor, consequently, may be used as a measure for the effect of treatments on the morphogenesis of the resulting offspring.

Characters of the gregarious and solitaries phase of the desert locust *S. gregaria* have been long known to be transmitted form one generation to the next[16]. This phenomenon makes the expression of phase characters accumulative process, where characteristic of both phases are acquired over several generations of a crowded or solitary lifestyle[17]. For the process of transmission to be successful, it is necessary that the female integrates her experiences of population density and that it possesses a mean of passing on the information about her crowding environment to her offspring. Females are able to react to the state of crowding even very shortly before they lay their eggs and a significant increase in gregarious offspring characteristic have been found when solitaries females experience crowded condition as late as at the time of egg laying itself[18].

Characters which vary between phases include colour, hatching weight, morphometric characters, ovariole numbers, metabolic activity and last but not least behaviour[19,20].

The post embryonic period was lower in solitary nymphs (27.6 days) than in gregary ones (28.8 days). The total developmental periods were pronouncingly prolonged in the offspring of the treated females in both phases and by both solvents as compared with control (Table 5). The nymphal stadium durated in one case shown in Table 5 is two fold that of the control (treating by solitary froth hexane extracts reached 53.05 compared with 27.6 days for control) (Table 4).

The effect of hexane extract was more effective in prolongation of the nymphal duration's than the ethanol one and this effect prevailed in all nymphal stages.

Comparing the development of the nymphs resulting from treated females show that: when the nymphs of the solitary offspring of control treatment reached the fifth instar after 27.0 days, the nymphs of treatments were still in the third nymphal instar; an example is shown by comparing the offspring control and treated solitary females.

Thus, it may be concluded that the offspring of treated females in all treatments manifested a state of lagged morphogenesis when compared with their control counterparts. This effect may be extentention of that which happened to the parents or being instant effect of the factors in the contaminated sand.

Whereas the classical view of the role of the accessory glands as providing the only source of material for foam plug formation in *S. gregaria* has been challenged by Sozopa[3], which concluded that accessory glands contribute a major part of its material. The accepted functions of the foam plug include providing protection from desiccation, an easy escape route for the emerging hatchlings[14] and lately an oviposition aggregation pheromone has been reported from it as well[6,14]. In other insect species accessory glands have been shown to produce antibacterial peptides[21], an oviposition deterring pheromone[22] or even virus-like partials which selectively destroy host immune responses[23]. The accessory glands also play a major role in the transfer of behavioural gregarious phase characteristics from mother to offspring in *S. gregaria*. These finding are in accordance with the previously reported evidence for a gregarizing factor present in the egg pod foam of gregarious *S. gregaria*[8].

Although the current data strongly implicate the accessory glands in affecting reproductive potential quantitatively and qualitatively, the nature of their involvement remains to be discovered. In the simplest case it could be supposed that a single factor is secreted and released by the accessory glands and then interacts with a single receptor system in the developing oocyte. More complex scenarios could include multiple, interacting components, not, all of which are produced by the accessory glands, acting on several receptors sites in the egg.

Effects on the daily weight of nymphs: The previous aspects about the biological performance affected by treatment with pod factors manifested an obvious morphogenetic effect. An additional evaluation may be traced by recording the daily body weight through the days of the developmental time. Information's confirming the concept of extended effect of pod factors may be available. Growth as a component of development representing the achievement of the indispensable biomass required for moulting may be used as comparative parameter for the treatments and to verify the extent the pod factors pursued the post embryonic development processes.

The growth rate of 5th instar of solitary offspring was increased by the application of solitary froth and egg extracts than the control and solitary females. It is obvious that the prolongation of the duration of each instar resulted in high growth, but solitary extracts were the most effective against their own phase. On the other hand, the growth of the offspring of solitary females with hexane extracts of gregary egg pod was delayed and the total developmental period was prolonged. So, solitary extracts were effective, than gregary extracts against the ovipositing solitary females.

Generally, growth and durations were highly affected with the application of hexane or ethanol egg pod extracts of their own phase. The durations may be prolonged due to the suppression of growth of the resulting offspring, which were not able to ecdyce to the adult stage except about 20%, which never put any egg pods. Moreover, these results supported the previous results about the durations of the resulting offspring, which were prolonged.

It could be concluded that the daily weight showed the following trends:

- It must be mentioned that these affects on nymphal growth and/or development may be an after effect of treating parents or being equally or additionally the effect of sand born factors from contamination with the non-polar and polar extracts affecting the egg pods itself.
- There exist a phase dependent response as in the treated solitary females the offspring achieved generally lower weights in treatments than in control. In gregary opposite trend was found and the gregary nymphal weight of control females surpassed generally those of treatment.
- Generally, when the nymphal duration prolonged, the weight was increased. This relation was prevailing in solitaries rather than in gregarious. All these parterres are interacting to work in interwoven balance must undoubtedly be reflected on the developmental time and growth as shown in the relation between growth and nymphal duration after treating the parents with pod factors. In the light of the tendency of nymphs to prolong the immature duration to stay longer unable to ecdyce; the juvenile hormone might be responsible for such developmental retardation.

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