Factors responsible for behavioural and pigmentary gregarization in hatchling desert locust *Schistocerca gregaria* (Orthoptera: Acrididae) (Forskal)

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ABSTRACT

With a view to elucidating the factor(s) responsible for gregarization in locusts, the behavioural and pigmentary characteristics of hatchling *Schistocerca gregaria* (Forskal) have been quantified using logistic regression analysis and colour scores, respectively. Of the three factors reported here, sands previously used for egg-laying by the solitary- and crowd-reared females were not found to induce any gregarization in the progeny, whereas higher densities of the egg pods and ovipositing females were both indicative of having significant gregarizing effects on the offspring hatchlings. Results of this study suggest that the most likely source of the gregarization signal in *S. gregaria* could be the foam produced by the females during oviposition.

INTRODUCTION

Gregarization refers to the process of acquisition of gregarious phase characteristics of solitary phase locusts, eventually resulting in swarming and migration. Locusts show density-dependent changes in phase characteristics such as behaviour, colour, morphometrics, endocrine physiology and reproductive parameters (Pener 1991). A detailed analysis of the distribution of egg pods laid by a part of a large swarm of *Schistocerca gregaria* was first presented by Stower *et al.* (1958), which clearly showed the habit of grouped oviposition by this species. Subsequently, the formation of laying groups was found to be greatly assisted by the gregarious interactions of the locusts (Popov 1958 ; Norris 1963). The habit of oviposition in groups clearly ensures that nymphs of the next generation are in close proximity to each other as soon as they emerge (Uvarov 1977).

Once an apparently suitable site for oviposition is located, a *Schistocerca* female is found to tap the soil with the end of her abdomen and to probe it with the ovipositor. Continued confirmation of the acceptable nature of the site results in the drilling of a hole (Popov 1958). When the hole is completed, the female retracts her abdomen slightly and a foamy secretion from the accessory reproductive glands is produced from the genital opening. Some of this secretion is absorbed by the soil immediately surrounding the hole so that it is lined with the foamy material. The foam is also used to glue the eggs to adhere to each other. The eggs are laid by the contraction of the common oviduct and this is accompanied by abdominal contractions. The eggs are laid in diagonal rows and when they are all laid, the remaining upper portion of the hole is filled with the remainder of the foam. This 'foam plug' protects the eggs from desiccation and provides a route of escape for hatchlings (Uvarov 1996). It has long been speculated as to whether the soil, previously used for oviposition, and/or contaminated with relics of ovipositor ducts, faeces, decaying egg pods, pieces of foam plug and the like, could be a possible source of attraction to other *Schistocerca* females ready to oviposit and also, if this attraction of the female parent could initiate gregarization in her progeny. Despite the findings that oviposition sites remained attractive in this way for several days in the grasshopper, *Zonocerus veriegatus* (McCaffery and Page 1982) and that sand previously used for oviposition attracted females of *Locusta migratoria* (reviewed by Whitman 1990), the correlation between the sand contaminated by egg-laying females and the phase characteristics of their immediate progeny has remained unconfirmed in both species of locusts. It seemed, therefore, that experiments designed to investigate the effects of contaminated sand (specifically the effect of the chemical(s) of the foam absorbed into the sand) as well as that of densities of mature females and their egg pods on the behaviour and colouration of the first-instar nymphs of *S. gregaria* might provide insights into the questions raised in the earlier findings (Islam *et al.* 1994b) concerning the way in which the densities experienced by females at oviposition and the influence of neighbouring egg pods could account for gregarization in locusts. Though the presence of a relatively heat-stable, species-specific contact pheromone that appeared to stimulate grouping by ovipositing females was reported long ago (Norris 1963, 1970), the exact

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relationship between the density of ovipositing females and/or egg pod density on the phase status with respect to the behaviour and colouration of the offspring has never been examined in detail.

MATERIALS AND METHODS

The locusts:

The fourth-generation solitary-reared parents and parents reared in a crowd for many generations were used. Each solitary-reared female was mated at least twice (paired with a male for ≤ 24 h) to ensure that sufficient hatchlings were available for colour scoring and behavioural assays. Random matings occurred among the members of the crowd-reared insects. Egg Pods were collected throughout the mature life of the ovipositing females where needed. For collecting multiple egg pods (see below), mature parents of the same age group were used. All the experimental eggs were collected and incubated in locust rearing room in the Department of Zoology, University of Oxford, UK at 30-40° C and 60-70 % uncontrolled RH under a 12 h: 12 h light: dark photo-regime.

Experimental set-up and collection of egg pods:

Egg pods were collected in two sets of experiments. In the first set, sand previously used (henceforth called contaminated sand) by solitary- and crowd-reared insects, was used as an oviposition medium. Clean sand was used as a control. In addition, two egg pods laid within 2-3 days by individual solitary-reared females in an oviposition tube filled in with clean sand were collected. The first set of experiments therefore had a total of five treatments (Treatments 1-5). In the second set of experiments, possible combinations of mature female density and egg pod density were examined in a 2 x 2 design (Treatments 6-9). After collecting, the egg pods were incubated at 30°-34° C for 12-13 days, and then separated in individual plastic containers (30 ml) in which they hatched. The test insects were maintained alone from the time of eclosion (day 0) and fed until used in the behavioural assays on day 1.

Treatment 1 - Clean sand. Unused silver sand thoroughly washed in hot tap-water and then dried in an oven at 140° C was used as an oviposition medium. Solitary-reared females were offered this medium for laying single egg pods in an oviposition tube (10 cm high, 4 cm diameter). Colour scores and the behaviour of 100 hatchlings from 10 egg pods were recorded.

Treatment 2 - Contaminated sand from solitary culture. Sand previously used for laying by solitary-reared females was used for this treatment. The sand was sieved to remove any faeces, foam plug fragments etc. and then used as a medium for oviposition of a single egg pod from a solitary-reared female. Fifty-three hatchlings from four such egg pods were tested.

Treatment 3 - Contaminated sand from gregarious culture. Same as Treatment 2 except that the sand was previously used by crowd-reared females for laying. Forty-two hatchlings from four egg pods were tested.

Treatments 4 and 5 - Two egg pods per oviposition tube. These treatments were designed to test if a fresh egg pod laid by a solitary-reared female would influence the colouration and/or behaviour of the hatchlings from a second egg pod laid within approximately three days in the same oviposition tube by a second solitary-reared female. An attempt was made to collect as many egg pods as possible from individual solitary-reared females for these treatments, but it was noted that by the time the third egg pod was collected, the first egg pod had dried out. The collection of egg pods in a tube that already had a first egg pod was therefore limited to a second egg pod only. Forty-two hatchlings from four 'first laid' egg pods, and 61 hatchlings from six 'second laid' egg pods were assayed.

Treatment 6 - Single egg pod from a solitary-reared female. Single egg pods laid into clean sand by solitary-reared females were collected. From four egg pods, 53 hatchlings were tested.

Treatment 7 - Egg pod from a solitary-reared female laid in a tube containing freshly-laid multiple gregarious egg pod. Attempts to collect multiple egg pods from solitary-reared females were not fully successful (Treatments 4 & 5). So, further experimentation was conducted to verify whether egg pod density alone could influence the phase status of hatchlings emerging from a solitary egg pod. To obtain a maximum effect, tubes containing at least three freshly-laid egg pods from crowd-reared females were offered to ovipositing solitary-reared females. Five solitary egg pods were collected in individual tubes that already had gregarious egg pods in them, and total of 52 hatchlings were tested.

Treatment 8 - Single egg pod from crowding of solitary-reared females. Solitary-reared females were paired, as usual, with solitary-reared males for ≤ 24 h in individual cages. After mating, the females experienced a pre-oviposition isolation of two days, and then the females were kept in two cages, each with four females. Collection of egg pods was limited to one egg pod per oviposition tube. Fortysix hatchlings from three egg pods were assayed.

Treatment 9 - Multiple egg pods from crowding of solitary-reared females. As for Treatment 8, but the females were crowded at oviposition so that three or more egg pods were laid per oviposition tube within 2-3 days. For this treatment, 47 hatchlings from five egg pods were used.

Hatchling colours:

Using five colour categories (see Islam et al. 1994a), the pigmentary phase characteristic of the hatchlings, ranging from 1 (Uniformly green) to 5 (heavily black), was recorded within 6-12 h on the day of eclosion.

Behavioural assays:

A rectangular arena (35.5 cm x 15 cm x 10 cm) was used to investigate the behavioural responses of the

individual test insects. From a range of behavioural elements consisting of locomotory and non-locomotory movements, and avoidance and/or shock reactions, a total of 14 parameters were derived and included for analysis (see Islam *et al.*1994a for details). Finally, the behavioural phase status of the experimental hatchlings was quantified by subjecting the behavioural data to the logistic regression analysis, which in one of the multivariate statistical techniques used to predict a binary dependent variable from a set of independent variables (Hosmer and Lemeshow 1989). Using the behavioural phase of the insects as a dependent (=response) variable and the 14 behavioural parameters as independent (=explanatory) variables, the predicted probability that a test insect belonged to the fully solitary-reared group was estimated by using the model: *probability (solitary)* $=e^\eta (1+e^\eta)$, where e= the base of natural logarithms (approximately 2.718), $\eta = \beta_0 + \beta_1 X_1 + \beta_2 X_2 ....+\beta_s X_s$, β= regression coefficient and X= independent variables. The model was derived from two extreme treatment groups, assigning *probability (solitary)* =1 for the nymphs derived from fully solitary-reared parents and isolated rearing of them upon hatching and *probability (solitary)*=0 for the behavioural record of the nymphs that had fully crowd-reared parents and were reared in a crowd after hatching. The estimated *probability (solitary)* values, therefore, provided behavioural phase indices of the insects used in the experiments. The method of constructing the model has been detailed earlier (Islam *et al.* 1994a, b).

Statistical analyses:

To weight the relative impacts of the densities of mature females and their egg pods on the behaviour and colouration of the offspring hatchlings, either non-parametric tests (Mann-Whitney U-tests) were employed in all cases where the data did not show normality and/or homogeneity of the variance (Siegel and Castellan 1988) or else the data were ranked and normalized, and the transformed values were subjected to analysis of variance (Conover and Iman 1981). Correlation between the behaviour and hatching colour was estimated by calculating Pearson's product-moment correlation coefficient (r).

RESULTS AND DISCUSSION

The logistic regression model:

The logistic regression model was derived from the hatchlings that emerged from single egg pods laid into the clean sand by 10 individual solitary-reared females (n=100) *versus* those that emerged from multiple egg pods laid into the clean sand by the solitary reared-females crowded during oviposition (n=47). The backward step-wise method was used to construct the model that categorized 80.14% of the 147 insects correctly, and had a model χ^2 of 63.32 (P< 0.001 at 6 df) with the Pearson's χ^2 statistic of

120.15 (P=0.87 at 139 df), indicating a near-perfect goodness of fit. Six variables were retained in the model as significant indicators differentiating the two extreme groups of insects (Table 1). By using this model, *probability (solitary)* value of all the experimental hatchlings were computed.

Effect of contaminated sands on hatchling behaviour:

Compared to clean sand (Fig. 1), contaminated sand from neither solitary (Fig. 2) nor gregarious (Fig. 3) culture was found to induce any degree of behavioural gregarization of the hatchlings that emerged from the egg pods laid in such sand by solitary-reared females (Mann-Whitney U-tests, P=0.6694 and P=0.2004, respectively).

Effect of egg pod density on hatchling behaviour:

Two egg pods, laid close to each other in an oviposition tube by two individual solitary-reared females within 2-3 days, failed to induce significant gregarization of the hatchlings emerging from them compared to a single egg pod (P=0.7302 and P=0.2104, respectively; Figs. 4 and 5). This suggested that the behaviour of the hatchlings emerging from the 'first laid' egg pod was not influenced by the presence of the 'second laid' egg pod (P=0.4462). In contrast, the behaviour of the hatchlings that originated from crowded pods, either gregarious (Fig. 7) or solitary (Fig. 9) in origin, was found to differ significantly from that of the hatchlings derived from single pods ($F_{1,199} = 10.60$, P<0.001, Table 2), laid either in isolation (Fig. 6) or in a crowd (Fig. 8).

Effect of female density on hatchling behaviour:

In comparison to a single solitary-reared female per cage at oviposition (Figs. 6 & 7), a density of four solitary-reared females per cage (Figs. 8 & 9) was found to have a significant gregarizing effect on the resultant progeny. Thus, ANOVA of the *probability*

Table 1. Behavioural parameters retained in the logistic regression model constructed for quantifying the behaviour of hatchling *S. gregaria* in an experiment where the effect of contaminated sands, and densities of mature solitary-reared females during oviposition and their egg pods have been evaluated. The method of constructing the model is elaborated in the text.

Model: $\eta = \beta_0 + \beta_1 X_1 + \beta_2 X_2 ..... + \beta_k \cdot X_k$, with *probability (solitary)*$=e^\eta/(1+e^\eta)$.

Variables in the Equation	Coefficient β	Significance of change in the log likelihood ratios	Partial correlation coefficients*
Track speed	-17.770	<0.001	-0.235
Turns per time	-35.746	0.001	-0.193
Crouching time-fraction	-2.695	0.056	-0.095
Grooming time-fraction	-22.901	<0.001	-0.194
Jumping frequency	152.037	0.003	0.169
Walking time-fraction	14.887	0.001	0.100
Constant	3.251	<0.001	

*The coefficient describes the partial correlation between the dependent variable and each of the independent variables. It ranges from −1 to +1; positive values indicate that as the variable increases in value so does the *probability (solitary)*; for negative values, the opposite is true. The absolute magnitude indicates the strength of contribution of the variable to the model.
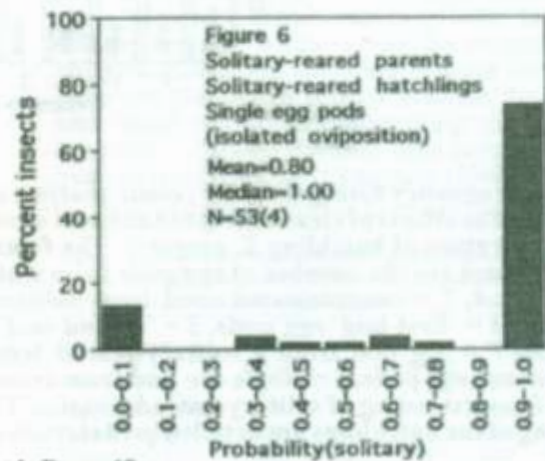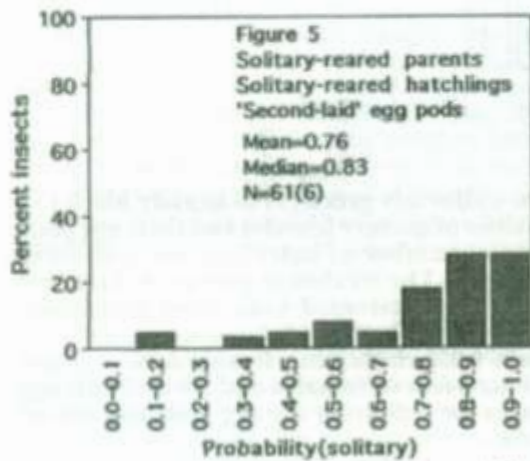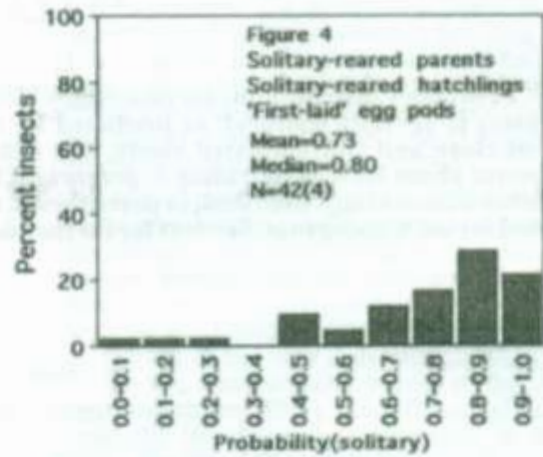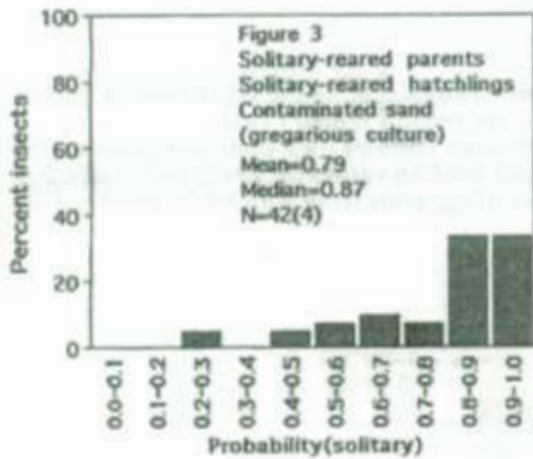
Figure 1
Solitary-reared parents
Solitary-reared hatchlings
Clean sand
Mean=0.81
Median=0.88
N=100(10)

Figure 2
Solitary-reared parents
Solitary-reared hatchlings
Contaminated sand
(solitary culture)
Mean=0.73
Median=0.84
N=53(4)

Figure 3
Solitary-reared parents
Solitary-reared hatchlings
Contaminated sand
(gregarious culture)
Mean=0.79
Median=0.87
N=42(4)

Figure 4
Solitary-reared parents
Solitary-reared hatchlings
'First-laid' egg pods
Mean=0.73
Median=0.80
N=42(4)

Figure 5
Solitary-reared parents
Solitary-reared hatchlings
'Second-laid' egg pods
Mean=0.76
Median=0.83
N=61(6)

Figure 6
Solitary-reared parents
Solitary-reared hatchlings
Single egg pods
(isolated oviposition)
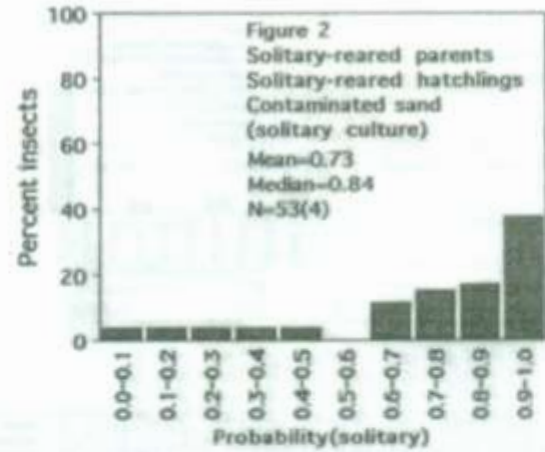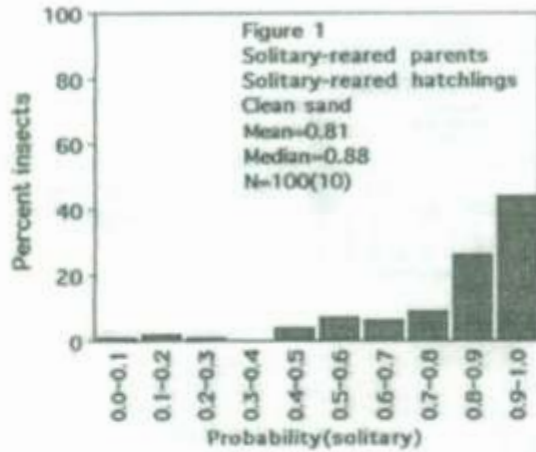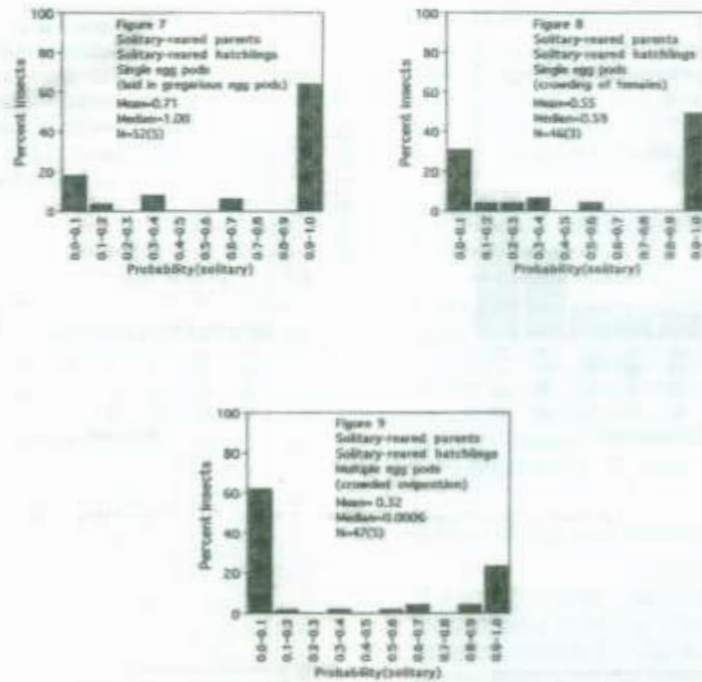Mean=0.80
Median=1.00
N=53(4)

Fig. 1-9. Contd. Page 48

Figures 1-9. Frequency distributions for *probability (solitary)* values, ranging along the x-axis from 0 (=fully gregarious) to 1(=fully solitary), as predicted by the logistic regression model (Table 1), showing the effects of clean and contaminated sands, and densities of mature females and their egg pods on the behavioural phase state of hatchling *S. gregaria*. The mean and median values for *probability (solitary)*, the number of hatchlings used and, in parentheses, the number of egg pods from which they emerged are presented for each histogram. See text for further detail.
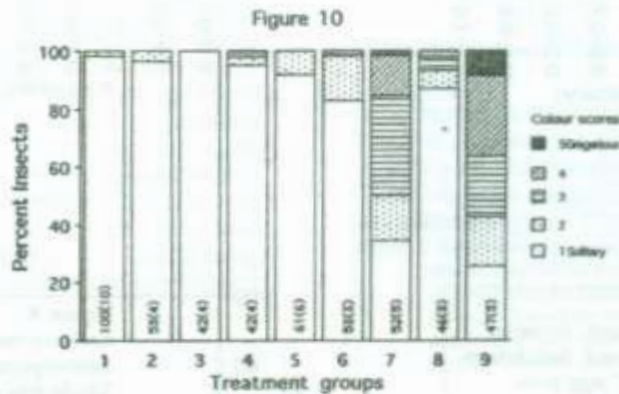

Figure 10. Frequency histograms for colour scores, ranging from uniformly green (1) to heavily black (5), showing the effects of clean and contaminated sands, and densities of mature females and their egg pods on colouration of hatchling *S. gregaria*. The figures indicate the number of hatchlings used, those in parentheses are the number of egg pods from which they emerged. The treatment groups include: 1 = clean sand, 2 = contaminated sand from solitary culture, 3 = contaminated sand from gregarious culture, 4 = 'first-laid' egg pods, 5 = 'second-laid' egg pods, 6 = single egg pod from a solitary-reared female, 7 = egg pod from a solitary-reared female laid in a tube containing freshly-laid multiple gregarious egg pods, 8 = single egg pod from crowding of solitary-reared females and 9 = multiple egg pods from crowding of solitary-reared females. The procedures for collecting the egg pods and colour scoring of the hatchlings are detailed in Materials and Methods.

(*solitary*) values showed that the differences in the behaviour of the hatchlings due to densities of the ovipositing females were highly significant (F_{1191} =30.10, P<0.001; Table 2).

Effects of contaminated sands and densities of solitary-reared females and their egg pods on hatchling colour:

The colour scores of the hatchlings emerging from egg pods laid by the solitary-reared females into contaminated sand of either solitary or gregarious culture were not found to differ statistically from those of the hatchlings derived from egg pods laid into the clean sand (Fig. 10, Treatment groups 1-3; P =0.5144 and P=0.3577, respectively). Similarly, the colour of the hatchlings from the 'second laid' egg pods (Treatment groups 4 & 5; P=0.5230). But in agreement with the behavioural data mentioned above, the colour of hatchlings from egg pods at densities of ≥ 3 pods per tube (Treatment groups 7 & 9) was significantly darker than that of hatchlings from a single pod per tube (Treatment groups 6 & 8). So, it appeared that a high density of egg pods (F_{1191}=137.68, P<0.001) rather than simply a high density of females was effective at promoting gregarious pigmentation in the hatchlings (Table 3; F_{1194}=0.67, P=0.413).

Correlation between the behaviour and hatchling colour:

A significant correlation (r=0.4292; P<0.01) existed between behaviour and colouration of the hatchlings indicating that the darker, black hatchlings behaved more gregariously than the lighter, green counterparts.

The present experiments have considered the possible effects of contaminated sands, and densities of the solitary-reared females during oviposition and their egg pods on the phase state, estimated in terms of behaviour and colouration, of the resultant hatchling *S. gregaria*. It has been shown that chemicals of the egg pod foam absorbed into the sand previously used by egg-laying solitary- and crowd-reared females was unable to induce gregarization in the hatchlings emerging from solitary-reared females when the latter laid their egg pods in such pre-treated oviposition media. It has further been demonstrated that a higher density of ovipositing females as well as a higher density of the egg pods both resulted in the progeny hatchlings which showed a significant gregarious behaviour compared to the controls. A higher density of the egg pods was found to have a pronounced pigmentary gregarization in the progeny than a higher density of the mature females at oviposition.

In contrast to the present findings, Lauga and Hatte (1977,1978) demonstrated that when the solitary females were allowed to oviposit in contaminated sand, the egg pods and the eggs laid by the solitary females became more gregarious with respect to egg number per pod and the mean weight of the eggs. In this respect, females of ovipositing

Table 2. Analysis of variance table showing the effects of densities of the mature solitary-reared females at oviposition and their egg pods on the behaviour of hatchling *S. gregaria*

Source of Variation	Sum of Squares	df	Mean Squares	F-ratio	Probability
Egg pod density (E)	9.61	1	9.61	10.60	<0.001
Female density (F)	27.30	1	27.30	30.10	<0.001
Interaction (ExF)	2.98	1	2.98	3.29	0.071
Residual	173.22	191	0.91	-	-

S. gregaria neither aggregated near the sand into which other *S. gregaria* had formerly laid many egg pods nor did they lay a significantly increased number of pods in comparison to unused sand (Norris 1970). However, neither behaviour nor colour patterns of the hatchlings emerging from the egg pods were analysed in the experiments by Lauga and Hatte (1977, 1978). These disagreements could be due to certain species-specific differences, and it is also possible that some attractive material could be left behind by the previous ovipositing females of *L. migratoria* and *Z. variegatus* (see McCaffery and Page 1982). Apparently, *S. gregaria* females either do not produce such a material or even they do, that left behind in the soil is too little to be effective as a gregarizing factor for their progeny.

It has previously been demonstrated that the behavioural and pigmentary phase characteristics of the offspring are determined by the density of the mature females during mating and oviposition, where crowded oviposition in solitary-reared females was found to induce gregarization (Islam *et al.* 1994b). It has now been shown that irrespective of egg pod densities, the density of the ovipositing females alone has a significant effect on the hatchling behaviour in *S. gregaria*. In the present study, the ovipositing females were kept in a crowd of four females per rearing cage. This density of females was equivalent to 400 insects.m², and realistically reflected the field situation where a maximum post-hatching density of *S. gregaria* of 500.m² was recorded (Roffey and Popov 1968). The present results imply that physical contact might elicit release of certain phase specific factor(s) in mature females which could be responsible for gregarization of the offspring. Recent studies have indicated that tactile stimuli override the olfactory and visual stimuli in determining the gregarious behaviour of solitary-reared fifth-instar *S. gregaria* nymphs (Roessingh and Simpson 1994).

Whilst differences due to egg pod densities were

Table 3. Analysis of variance table showing the effects of densities of the mature solitary-reared females at oviposition and their egg pods on the colouration of hatchling *S. Gregaria*

Source of variation	Sum of Squares	df	Mean squares	F-ratios	Probability
Egg pod density (E)	54.66	1	54.66	137.68	<0.001
Female density (F)	0.27	1	0.27	0.67	<0.413
Interaction (ExF)	0.59	1	0.59	1.48	0.226
Residual	77.02	194	0.40	-	-

significant both for behaviour and colour of the experimental hatchlings, those due to female densities were significant only for behaviour but not for colour of the hatchlings. Hatchling colour is therefore much more influenced by egg pod density than the density of mature females at oviposition. A similar result was noted earlier where solitary-reared females crowded during oviposition led to a significantly pronounced gregarious behaviour in the offspring but the same did not produce significantly darker hatchlings (Islam *et al*. 1994b).

Unlike many grasshoppers where egg laying is an individual event unrelated to the activities of other females, the timing and location of oviposition in locusts is strongly influenced by other ovipositing females. It is obvious that the tendency of group oviposition favours the development of gregarious behaviour of the hatchlings since the latter find themselves in crowded conditions from the time of hatching and are less likely to disperse. Field observations have shown that ovipositing females of *S. gregaria* lay their egg pods in dense groups which, on average, might range from $200.m^{-2}$ (Stower *et al*. 1958) to $800.m^{-2}$ (Roffey and Popov 1968). In the present experiment, egg pod densities of approximately $2400-4000.m^{-2}$ were obtained by allowing the females to lay 3-5 egg pods in a 4 cm diameter oviposition tube. Hatchlings from such multiple egg pods (Treatment groups 7 & 9) were found to be gregarized with respect to both colour and behaviour. This strongly suggests that, in addition to female density at oviposition, egg pod density is also responsible for determining the phase of resultant hatchlings. Perhaps, the most likely explanation would be that the foam surrounding the eggs or the foam plug of the egg pod might contain certain chemical(s) that, with increasing densities of the egg pods, affects the embryonic development of the nearby eggs by diffusing through the pod and the soil. The foam produced during egg laying thus appeared to be one of the most likely sources of gregarization signal for locust hatchlings.

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