SOME FACTORS INFLUENCING PHASE CHARACTERS IN THE NYMPHS OF THE LOCUST, *LOCUSTA MIGRATORIA MIGRATORIOIDES* (R. AND F.)

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Introduction.

Locusts are highly polymorphic species of Acrididae and show large variations in morphometrics, colour and behaviour. When Uvarov (1921, 1928) put forward his phase theory of locusts he pointed out that the extreme forms (phase *gregaria* and phase *solitaria*) represented two very different kinds of natural population. Plotnikov (1927, quoted by Uvarov, 1928) and Faure (1932) showed that the two extremes could be produced in the laboratory by varying the degree to which the locusts were crowded during rearing. When the nymphs of *Locusta migratoria migratorioides* R. and F. are reared in crowds they are orange and black in colour, especially in the later instars, and are similar in appearance to those of swarming populations in the field (Uvarov, 1928 ; Faure, 1932). Dirsh (1951) has shown that in the adults of this species, individuals from swarms (gregarious phase) have low F/C ratios (length of the hind femur/ width of the head), whilst individuals from scattered populations (solitary phase) have significantly higher F/C ratios. Data from laboratory reared *Locusta* (Ellis, 1951) suggest that there is a similar significant difference in the F/C ratios between nymphs reared crowded in cages and those reared isolated in individual jars. The colours of laboratory *Locusta* nymphs reared in isolation and those from scattered field populations are generally a shade of fawn, grey or green.

Under natural conditions, bands of *Locusta* nymphs execute daytime wanderings called marching, which can be induced in the laboratory under suitable conditions of lighting, temperature, etc. In cages, the nymphs march round and round the floor and sides. Previously isolated nymphs show practically no marching when they are first placed in a cage containing a group of previously crowded nymphs. In standard tests under optimal conditions for marching, previously isolated nymphs march for significantly less of the time than crowded ones (Ellis, 1951). There is a certain amount of overlap in colour, F/C ratios and percentages of time spent marching when nymphs reared in the two ways are compared.

When Uvarov (1928) fully elaborated his phase theory he postulated a build-up of *gregaria* characters from generation to generation during periods when populations were high and on the increase. A similar carry-over of *solitaria* characters from generation to generation was suggested for populations that were declining in numbers. Many workers in the last thirty years have assumed a carry-over of *solitaria* or *gregaria* characteristics from generation to generation, but little consideration has been given to the mechanisms involved. In a recent review, Kennedy (1956) pointed out that some of the laboratory work already published illustrated a carry-over of certain phase characters from one generation to the next (notably the work of Albrecht, 1955 ; Albrecht and Verdier, 1956 ; Matthée, 1951 ; Ellis, 1951, 1953), but that studies over many generations had not been reported.

In 1932, Faure produced evidence that the colour of nymphs at hatching was influenced by the degree of crowding of the parents as adults. This has recently been studied in detail by Hunter-Jones (1958) who showed that *Locusta* parents reared in crowds tend to produce dark hatchlings, whilst those kept as single pairs tend to produce pale hatchlings. He classified the first instar nymphs into six main colour groups. Amongst the progeny of adults treated in the same way, there was some individual variation in the colour of hatchlings that may be genetically controlled, since isolated pairs sometimes produced fairly dark hatchlings and occasionally the crowded adults produced pale hatchlings.

Taking pale hatchlings from single pairs and dark hatchlings from crowded parents, Hunter-Jones reared the offspring in two ways. When the offspring were reared in crowds, nymphs that were pale at hatching did not become fully gregarious in colour (bright orange and shiny black) until the fifth instar. Dark hatchlings reached this extreme colour by the third instar and a proportion by the second instar. When the offspring were reared in isolation, those that were pale at hatching were, by the third instar, indistinguishable from those that were dark at hatching. Therefore, as far as nymphal colours were concerned, the rearing density of the parents influenced colour during the early instars, but gradually the density at which the nymph itself was reared became the more important factor. In the case of morphometric ratios, both parental rearing density and the nymphs' own rearing density determined the degree of gregarisation shown.

This paper describes some work on a laboratory stock of *Locusta migratoria migratorioides* R. and F. in which the parents were reared for four generations in isolation, except for pairing during the adult stage to ensure fertilisation. Their offspring which were used in the experiments, were reared either in crowds or in isolation. One pattern of the locust nymph behaviour, social aggregation, has been found to be partially related to hatchling colour (Ellis, 1953) and so data on marching behaviour in relation to hatchling colour will also be considered, although the nymphs used in these particular tests generally came from parents that had been reared crowded.

Methods.

Rearing conditions.

The nymphs that were used in tests were reared from soon after hatching until the time of test either in crowds or in isolation. When locust nymphs are reared crowded, a hundred or more are generally kept together in the same cage.

During the experiments on the marching behaviour of nymphs that were dark or pale at hatching, the crowded nymphs were reared in cages of floor area 41 × 41 cms. and 30.5 cms. high, with two walls of zinc gauze and the top of glass. Five to six hundred hatchlings were placed in each cage. By the fourth instar the number had been reduced by cannibalism and by the removal of nymphs for tests to 250-300 per cage. The room temperature was maintained at 28°C, but during the day a lamp placed above each cage increased the temperature inside to 32°C. Isolated nymphs were reared in individual jars of 360 c. cms. capacity. Each jar had a paper screen three quarters of the way round the outside so that, when the jars were stood side by side round a lamp during the day, the nymphs could not see each other.

Throughout the tests on the offspring of the isolated line the constant temperature room was maintained at 30-31°C. About 300 hatchlings were put into each of the cages that measured 30.5 × 30.5 × 30.5 cms. By the fourth instar the number of nymphs had been reduced to 180-200 per cage. During the day a water-bath was placed between the cage top and the lamp, so that the temperature inside the cage did not rise above 33°C.

Nymphs in cages were given fresh grass standing in water each evening and those

in jars small bundles of fresh grass daily. The lamps were turned on for 9-10 hours a day and the caged nymphs spent some part of each day in marching.

Nymphs to be reared in isolation were separated from the others within 24 hours of hatching.

Test conditions and measurements of phase differences

Marching activity was measured in the following way. The experimental nymphs, that were in the middle of the instar, were well fed overnight. The test cage was similar in design to the larger stock cages. It was devoid of food ; a light, surrounded by a black paper screen, was placed centrally above the cage. At room temperatures of 30-31°C this was a 60-Watt lamp and a waterbath was placed between it and the cage top, so as to reduce the amount of radiant heat reaching the nymphs. At room temperatures of 28°C an unscreened 100-Watt lamp was used.

A group of nymphs that had been reared in crowds was allowed to march in the test cage. The experimental nymphs, after being marked with coloured paints, were starved for four hours and were then dropped into the cage of marching nymphs. Several individuals could be tested at the same time. In the experiments with nymphs that were pale or dark at hatching the test animals stayed in the cage for only one hour, and during this time their activities were noted once every two minutes for the last 50 minutes. When nymphs from the isolated line were tested they were observed once a minute for the first, third, fifth and seventh half hours, so that they stayed in the cage for 3,5 hours. The percentage of time spent in marching, that is continuous walking with the antennæ held erect (see Ellis, 1951), by each individual nymph was calculated from the readings.

When the experimental nymphs were in the fourth instar the F/C ratios were calculated from measurements made with calipers. The nymphal colours were classified as below. Although the same classification was used for the second, third and fourth instar nymphs, the older ones tended to have less spotting on the face and the bands of different colour on the face and thorax were more clearly defined than in the younger nymphs.

1°. Face and lower thorax orange. Upper part of the pronotum black. Sometimes an orange keel to the pronotum. Abdomen mainly black. Face often spotted with black or brown pigment. Occasionally nymphs nearly black all over.

2°. Face and lower thorax orange-yellow or reddish-brown, with either brownish-black upper pronotum or some loss of black on pronotum as compared with 1.

3°. Face and lower thorax a different colour to the rest of the body. Either black or brown longitudinal stripes on the abdomen or pronotum or on both. Face often spotted with darker pigment. The chief colour combinations were green with a yellow face, golden-yellow with an orange face, yellow-fawn with a yellow face, orange-fawn with an orange face, pink-fawn with a reddish face, grey with a yellow face, reddish-brown with a reddish face.

4°. The same general colour all over, but the face paler than the rest of the body. Black, brown or grey stripes on either the pronotum or abdomen or both. The colours generally one of the following: green, golden, yellow-fawn, orange-fawn, pink-fawn, grey, brownish red.

5°. The same general colours all over as in 4, but stripes were absent or very faint.

From observations on crowded and isolated nymphs, it was clear that these colour groups corresponded roughly with the rearing density: crowded nymphs were generally in the first group, whilst isolated nymphs came into groups four and five.

TABLE 1. — MARCHING BEHAVIOUR OF NYMPHS IN RELATION
PARENTS CROWDED, EXCEPT
Mean Percentages of

Hatchling colour.	Nymph rearing.	Second-instar nymphs.			
Dark	Crowded	52.9	49.1	48.8	50.3
Dark	Isolated	30.7	34.6	24.6	25.6
Pale	Crowded	38.0	46.6	41.1	40.1
Pale	Isolated	15.3	24.7	23.6	24.0

Source variation	D. F.	Sum squares	P	D. F.	Sum squares	P	D. F.	Sum squares	P	D. F.	Sum squares	P
Colour (0).	1	4 919.6	< 0.01	1	1 195.8	< 0.01	1	205.9	> 0.05	1	376.4	> 0.05
Rearing (R).	1	4 623.6	< 0.01	1	1 369.0	< 0.01	1	6 164.8	< 0.01	1	5 749.1	< 0.01
R × 0.	1	11.0	> 0.05	1	498.8	> 0.05	1	156.2	> 0.05	1	236.0	> 0.05
Error.	39	273.5		140	189.5		54	254.1		52	350.1	

(*) The parents of these nymphs were kept in isolation.

Results.

Hatchling colour and marching activity.

The hatchlings of *Locusta* are the same general colour all over, with darker spots. The individuals vary in their general colour from jet-black to yellow-fawn.

In a number of experiments pale and dark hatchlings, all from crowded parents, were reared separately. Pale hatchlings equalled Hunter-Jones' groups 2 and 3. Dark hatchlings equalled Hunter-Jones' groups 5 and 6 (1958). Some of the nymphs were crowded in cages and some were isolated in jars. Marching was measured in one-hour tests and the colours of the nymphs classified. The results for the percentages of time

TO COLOUR AT HATCHING AND DENSITY OF REARING.
WHERE OTHERWISE INDICATED *.
Time Spent Marching.

THIRD-INSTAR NYMPHS.		FOURTH-INSTAR NYMPHS.	
55.6	47.0 (*)	49.5	57.9
19.3	20.0	18.9	26.7
56.6	47.2	40.0	60.5
21.9	15.7	14.3	18.4

D. F.	Sum squares	P	D. F.	Sum squares	P	D. F.	Sum squares	P	D. F.	Sum squares	P
1	24.8	> 0.05	1	840.7	> 0.05	1	400.0	> 0.05	1	69.5	> 0.05
1	7 370.4	< 0.01	1	16 907.8	< 0.01	1	7 563.3	< 0.01	1	12 100.5	< 0.01
1	32.1	> 0.05	1	3 617.8	> 0.05	1	59.76	> 0.05	1	265.8	> 0.05
29	206.3		60	35.8		39	165.42		32	216.0	

spent marching were examined by an analysis of variance. Table 1 shows that the nymphs' own rearing conditions always significantly influenced behaviour: those reared in crowds spent more of the time in marching than those reared in isolation before the test. By the third and fourth instars the nymphs that were pale at hatching were behaving in a way similar to those that were dark at hatching. In two out of the four experiments with second instar nymphs a like result was obtained, but in the other two tests those that were pale at hatching marched for significantly less time than those that were dark.

In one of the experiments with third instar nymphs the parents had been isolated (S_3, see page 28). The nymphs' own rearing conditions significantly influenced marching behaviour, but those that were pale at hatching behaved as did those that hatched dark.

TABLE 2. — CHANGES IN NYMPHAL COLOUR WITH REARING CONDITIONS FOR NYMPHS THAT WERE PALE OR DARK AS HATCHLINGS. THE SAME NYMPHS WERE OBSERVED DURING THE 2ND, 3RD AND 4TH INSTARS. THERE WERE 9 NYMPHS PER GROUP.

HATCHLING COLOUR.	NYMPHS REARING.	INSTAR.	NUMBER OF NYMPHS PER COLOUR CLASS.				
			1	2	3	4	5
Dark	Crowded	2	8	1			
		3	9				
		4	8	1			
Pale	Crowded	2	2	4	2	1	
		3	5	3			
		4	7	2			
Dark	Isolated	2	1	3	4	1	
		3	1	2	3	3	
		4		1	3	3	3
Pale	Isolated	2			2	7	
		3		1	2	5	1
		4			3	3	4

The changes in nymphal colours during rearing for one of the tests with fourth instar nymphs is illustrated in table 2. Nymphs that were reared in isolation were more like *solitaria* in colour than those reared in crowds. When reared in isolation the second and third instar nymphs that had been pale at hatching produced a higher proportion of *solitaria* coloured individuals than those that were dark as hatchlings. When the nymphs were reared in crowds a similar difference related to hatchling colour was present up to the fourth instar. These results agree in general with those of Hunter-Jones (1958), who concluded that, although hatchling colour was largely determined by parental rearing density, in older nymphs their own rearing density gradually became the more important factor in determining colour. Table 1 suggests a similar conclusion for marching behaviour, but in this case the nymphs' own rearing conditions operated more rapidly, so that by the third instar, nymphs that were pale at hatching marched as well as those that were dark, although they could still be distinguished by colouring.

These experiments dealt entirely with correlations between behaviour and hatchling colour in locust nymphs of similar parentage. The possibility exists that parental rearing conditions still influence the behaviour of their offspring in a way that is not as easily masked by the nymphs' own rearing conditions as is the nymphal colour.

The influence of parental rearing in isolation for successive generations on marching behaviour,F/C ratios and colour of the offspring.

Some experiments on marching and social aggregation in *Locusta* (Ellis, 1951, 1953) have suggested that parental rearing conditions influence the behaviour of their offspring. In the present tests the offspring were either reared crowded in cages or isolated in jars from birth until the time of the tests when they were in the fourth instar. There were 3 possible parentages and so 6 nymphal groups in all.

Crowded (C) parents were from the normal stock of the Anti-locust Research Centre that have been reared crowded for some 45 generations.

S_1 parents had C parents, but were themselves reared singly as nymphs,

TABLE 3. — THE PERCENTAGES OF TIME SPENT MARCHING, THE F/C RATIOS AND THE COLOUR CLASSES FOR FOURTH INSTAR CROWDED AND ISOLATED NYMPHS OF VARYING PARENTAGE. * *See text for descriptions.*

PARENTS	NYMPHS OWN REARING.	SEX.	NUMBER TESTED.	% OF TIME MARCHING.		F/C RATIOS.		% PER COLOUR CLASS *.				
				Mean	Standard Devia-tion ±	Mean	Standard Devia-tion ±	1	2	3	4	5
C	Crowded	Male	38	55.3	16.618	2.59	0.1182	72	12	16		
		Female	30	57.6	16.787	2.53	0.0762	87	11	2		
S_1	Crowded	Male	15	36.0	18.584	2.75	0.0824	7	13	60	20	
		Female	16	42.3	19.847	2.71	0.1014	6	12	7	75	
S_3	Crowded	Male	16	43.2	16.601	2.70	0.1063		26	30	44	
		Female	19	39.7	17.691	2.71	0.1031	5	13	8	43	32
C	Isolated	Male	21	33.0	16.919	2.72	0.1179			5	86	10
		Female	18	36.0	20.285	2.73	0.1225			6	72	22
S_1	Isolated	Male	17	34.3	18.254	2.76	0.0834				71	30
		Female	12	31.9	13.633	2.74	0.0708			8	33	58
S_1	Isolated	Male	18	20.2	8.749	2.87	0.0960				56	44
		Female	20	22.8	13.139	2.80	0.0992				50	50

TABLE 4. — COMPARING THE PERCENTAGES OF TIME SPENT MARCHING FOR NYMPHS OF VARYING PARENTAGE AND UPBRINGING. BASED ON FIGURES IN TABLE 3.

	GROUPS COMPARED.		MALES.		FEMALES.	
			t	P	t	P
A	C parents	Crowded $\}$ Nymphs Isolated	6.76937	less 0.01	3.98223	less 0.01
B	S_1 parents	Crowded $\}$ Nymphs Isolated	0.26376	0.80-0.70	1.55684	0.20-0.10
C	S_3 parents	Crowded $\}$ Nymphs Isolated	5.14069	less 0.01	3.02820	less 0.01
D	Crowded nymphs	C $\}$ Parents S_3	2.21129	0.05-0.02	3.55830	less 0.01
E	Isolated nymphs	C $\}$ Parents S_3	2.88939	less 0.01	2.40772	0.02-0.01
F	Crowded nymphs	S_1 $\}$ Parents S_3	1.13994	0.20-0.30	0.41183	0.50-0.40
G	Crowded nymphs	S_1 $\}$ Parents C	3.66667	less 0.01	2.75736	less 0.01
H	Isolated nymhhs	S_1 $\}$ Parents C	0.22825	0.90-0.80	0.61645	0.60-0.50
I	Isolated nymphs	S_1 $\}$ Parents S_3	2.93960	less 0.01	1.83056	0.10-0.05

and as adults were kept in pairs of one male and one female per cage. S_3 parents came from a line that had been reared singly as nymphs and in pairs as adults for three generations. The great-great grand-
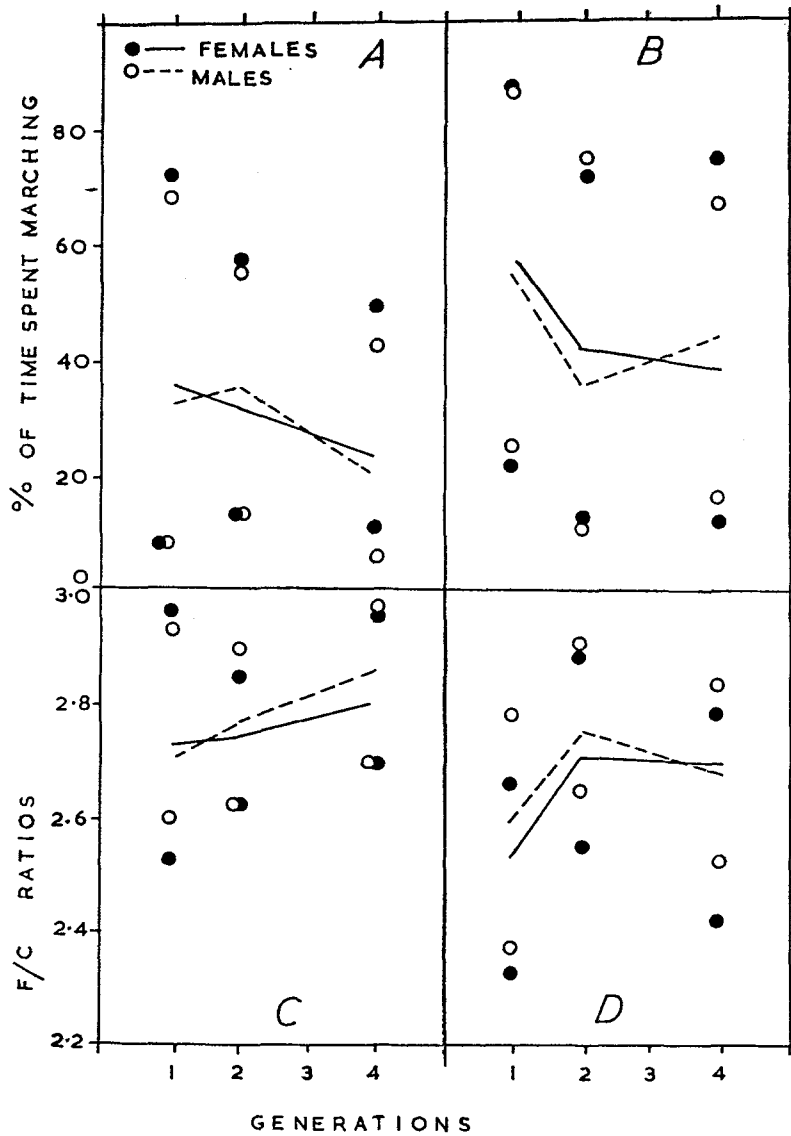
Fig. 1. — *The influence of parental rearing conditions on F/C ratios and marching of offspring.*

Starting with parents from a crowded line, parents were reared isolated for four generations. A and C, offspring reared isolated. B and D, offspring reared crowded. Circles show range of individual results, curves give average results.

parents were C adults. Pairing for this line was carried out so as to avoid close inbreeding.

All three types of parent were available at the same time and the experimental work occupied a period of four months.

On the whole, the offspring of isolated parents were paler at hatching

than those from crowded parents, but the different coloured hatchlings were not separated during these tests.

The average percentages of time spent marching, F/C ratios and colour classes are shown in table 3. For nymphs with C or S_3 parents, those reared crowded marched significantly more of the time than those reared isolated; averages were 55% and 33%, 43% and 20% for males; 58% and 36%, 40% and 23% for females (table 3 and table 4 A,C). The results for these eight groups of nymphs also show that those from C parents marched for more of the time than those from S_3 parents (table 4 D,E). That is, for these particular fourth instar nymphs, marching behaviour was determined both by the density at which they had themselves been reared and by the rearing density of the parental line.

The F/C ratios followed a similar pattern to the results for marching, remembering that the isolated nymphs have the higher ratios. Crowded nymphs from C parents gave averages of 2.59 for males and 2.53 for females. When reared in isolation the results were 2.72 for males and 2.73 for females. The corresponding values for nymphs with S_3 parents were 2.70, 2.71, 2.87, and 2.80 (table 5 A,C,D,E).

If we now turn to the results for the nymphs from S_1 parents we find that when reared crowded they behaved in a similar way and had similar F/C ratios to those reared isolated (table 3, table 4B, and table 5B). These results can be looked at in another way. When offspring were reared crowded, the nymphs from S_1 and S_3 parents were similar; marching averages were 36% and 43% for males, and 42% and 40% for females; F/C ratios averaged 2.75 and 2.70 for males, and 2.71 and 2.71 for females (table 4 F,G; table 5 F,G).

When the offspring were reared in isolation, nymphs from S_1 parents behaved in a similar way to those from C parents; percentages of time spent marching averaged 33 and 34 for males, 36 and 32 for females; F/C ratios averaged 2.72 and 2.76 for males, 2.73 and 2.74 for females (table 4 H,I; table 5 H,I).

Figure 1 shows a series of graphs, illustrating marching behaviour and F/C ratios for offspring reared in the same way. In the case of the isolated nymphs, the experiment concerned a line of individuals that were reared isolated for four generations, having originated from a stock that had been repeatedly crowded. The first nymphs to be placed in isolation showed a very large drop in marching activity (c.f. results for the first generation in figure 1A and IC). Continuing to rear this line of locusts in isolation resulted in further small reductions in marching activity with each generation (figure 1A). Turning to the F/C ratios (figure 1B), there was again a small shift towards the *solitaria* ratios with each generation spent in isolation. The range of results for each generation is of interest. The amount of variation for nymphs reared in isolation was less when the parents were S_1 or S_3 than when they were C parents (figure 1A and 1B; standard deviations in table 3). Further, some of the results for marching and F/C ratios for the nymphs from C parents

TABLE 5. — COMPARING F/C RATIOS FOR CROWDED OR ISOLATED NYMPHS OF VARYING PARENTAGE. FIGURES BASED ON TABLE 3.

	Groups compared.		Males.		Females.	
			t	P	t	P
A	C parents	Crowded / Isolated } Nymphs	4.20639	less 0.01	6.81437	less 0.01
B	S_1 parents	Crowded / Isolated } Nymphs	0.20424	0.80-0.90	0.69282	0.50-0.40
C	S_3 parents	Crowded / Isolated } Nymphs	4.88716	less 0.01	2.80829	less 0.01
D	Crowded nymphs	C / S_3 } Parents	3.15697	less 0.01	6.74990	less 0.01
E	Isolated nymphs	C / S_3 } Parents	3.93614	less 0.01	1.91562	0.10-0.05
F	Crowded nymphs	S_1 / S_3 } Parents	1.54286	0.20-0.10	0.14432	0.90-0.80
G	Crowded nymphs	S_1 / C } Parents	4.82324	less 0.01	6.71952	less 0.01
H	Isolated nymphs	S_1 / C } Parents	0.94362	0.40-0.30	0.23809	0.90-0.80
I	Isolated nymphs	S_1 / S_3 } Parents	3.62700	less 0.01	1.87254	0.10-0.05

are higher and some are lower than those for nymphs from S_1 parents. Thus, placing nymphs in a different social environment for the first time increased their morphological and behaviour variability at both ends of the range.

With the nymphs that were reared crowded the combination of the factors of isolation and crowding were more complicated. Parental rearing in isolation for only one generation made it impossible for the offspring, when reared crowded, to show the extreme gregarious marching, F/C ratios or nymphal colours (figure 1C and 1D and table 3, table 4 D,G and table 5 D,G). However, parental rearing in isolation for subsequent generations did not appreciably alter marching or F/C ratios further when the offspring were reared crowded (table 4F, table 5F). In this series, the amount of variation shown by the offspring of the various parents was similar (figure 1C and 1D; table 3).

The percentages of fourth instar nymphs per colour class (p. 23) are shown in table 3. When the offspring were reared crowded, there was a decrease in the percentage of gregariously coloured' nymphs with each parental generation that had been reared in isolation. The difference was particularly great between nymphs from C and S_1 parents. When the offspring were reared isolated there was a similar shift towards *solitaria* colours with each generation that the parental line had been reared isolated. In the case of female nymphs, isolated ones from S_1 and S_3 parents were similar. More will be said about this on pp. 35.

Correlations between phase characters.

The percentage of time spent marching and F/C ratios tended to be influenced in a similar way by the various combinations of parental and nymphal rearing density. The data for the six nymphal groups were combined and in both males and females there was a significant correla-

TABLE 6. — CORRELATIONS BETWEEN MARCHING AND F/C RATIOS..

FACTORS CORRELATED.	SEX.	No. NYMPHS.	CORRELATION COEFFICIENT.	REGRESSION EQUATIONS.	P
F/C ratios (Z) and marching (M)	Male	125	0.41 ± 0.08	Z = 2.71-0.0025 (M-39.6) M = 39.6-63.5 (Z-2.71)	less 0.001
F/C ratios (Z) and marching (M)	Female	115	0.54 ± 0.07	Z = 2.68-0.0034 (M-40.0) M = 40.0-86.9 (Z-2.68)	less 0.001

tion between F/C ratio and marching (table 6). This need not mean that correlations will exist under all conditions of varying rearing density. There also appeared to be a positive relationship between colour and F/C ratios, and colour and marching behaviour (table 7, table 8).

TABLE 7. — TABLE ILLUSTRATING THE RELATIONSHIP BETWEEN NYMPHAL COLOUR AND MARCHING. FIGURES ARE PERCENTAGES BASED ON 125 MALE AND 115 FEMALE NYMPHS.

PERCENTAGE OF TIME SPENT MARCHING.	COLOUR CLASSES.									
	Males.					Females.				
	1	2	3	4	5	1	2	3	4	5
0.1-30.0	2.4	2.4	6.4	20.0	49.6	2.6	0.9	0.9	21.7	10.4
30.1-60.0	12.8	6.4	5.6	16.0	2.4	9.6	3.5	4.3	18.5	10.4
60.1-90.0	8.0	2.4	2.4	3.2	0.0	9.6	2.6	1.7	1.7	1.7

TABLE 8. — TABLE ILLUSTRATING THE RELATIONSHIP BETWEEN NYMPHAL COLOUR AND F/C RATIOS. FIGURES ARE PERCENTAGES BASED ON 125 RESULTS FOR MALES AND 115 FOR FEMALES.

F/C RATIOS.	COLOUR CLASSES.									
	Males.					Females.				
	1	2	3	4	5	1	2	3	4	5
2.21-2.50	8.0	0.0	0.0	1.8	0.0	8.7	0.9	0.0	0.9	0.0
2.51-2.80	14.4	10.4	10.4	25.6	6.4	15.7	5.2	2.6	29.6	17.4
2.81-3.10	0.0	0.8	3.2	13.7	5.6	0.0	0.9	1.7	10.4	6.1

Differences in marching, F/C ratios and colour related to sex.

Although Key (1936) reported some differences in locust activity related to
sex, on the whole there appears to be little reason for separating males and
females when behaviour patterns like marching are considered (Ellis,
1951). The results discussed above (page 31) give further information
on this point. If the percentages of time spent marching for males and
females are compared, nymphs with the same parentage and rearing
density behaved in the same way regardless of sex (table 9). On the
whole, the ranges of results for the sexes were also similar (figure 1A
and 1C).

TABLE 9. — COMPARING MARCHING AND F/C RATIOS FOR MALE AND FEMALE NYMPHS.
DATA FROM TABLE 3.

PARENTS.	NYMPH REARING.	% TIME MARCHING.		F/C RATIO.	
		t	P	t	P
C	Crowded	0.57668	0.6-0.5	2.19824	0.05-0.02
S_1	Crowded	0.90784	0.4-0.3	1.14118	0.2-0.1
S_3	Crowded	0.60573	0.6-0.5	0.28194	0.8-0.7
C	Isolated	0.50641	0.7-0.6	0.12961	0.9-0.8
S_1	Isolated	0.38787	0.7-0.6	0.66531	0.5-0.6
S_3	Isolated	0.70647	0.5-0.4	2.16491	0.05-0.02

The F/C ratios present an interesting picture. In the two extreme
groups, crowded nymphs from C parents and isolated nymphs from S_3
parents, the males gave a significantly higher ratio than the females
(table 9). This is also usual in adults from the two extreme types of field
population (Dirsh, 1951). In all the other groups, however, male and
female fourth instar nymphs were similar (table 9). Taking the nymphs
reared isolated (figure 1B), males and females from C parents had similar
F/C ratios, but the differences in the ratios of the sexes became steadily
larger with each successive generation reared in isolation. Higher
F/C ratios in any one sex go with greater shift towards *solitaria*, so that

these results suggest that the female nymphs acquired *solitaria* ratios more rapidly than the males. For the offspring reared crowded the picture is more complicated (figure 1 D), but a tendency for the females to retain *solitaria* characteristics more readily than the males would explain the differences between the sexes in the various generations.

Table 3 shows that in crowded nymphs from C parents female nymphs gave the higher proportion of extreme *gregaria* colours. In all the other groups the male nymphs were more like *gregaria* (or less like *solitaria*) in colour than the females. This, as in the case of the F/C ratios, suggests that females respond more rapidly to rearing in isolation. Isolated females from S_1 and S_3 parents were rather similar in colour, suggesting that perhaps the females of this line were by the last generation as far towards *solitaria* as it was possible for them to be. The males may well have produced a further approach to the *solitaria* colours if they had been reared in isolation for a fifth generation. The work of Joly (1951) and Nickerson (1954, 1956) has shown that the nymphal colours are hormone controlled, so sex differences in rates of change would not be unexpected.

Discussion.

Active marching is characteristic of swarming populations and of laboratory locusts reared in crowds. It is clear that the maximum amount of marching shown by a particular nymph under optimal conditions of temperature, lighting etc., is governed by the internal condition, or state, of the nymph concerned.

One of the most important factors contributing to the internal state of a nymph is undoubtedly its own rearing conditions. Only if it has been crowded with others does maximum marching develop. The mechanism by which this in brought about is unknown, but, since nymphs that have been reared isolated are capable of some marching under suitable conditions, it would appear that crowding alters behaviour in a quantitative rather than a qualitative way. Perhaps the mechanism is one of facilitation. As a result of continuous proximity to other locusts, the individual is more easily able to respond to the others, for active marching has been shown to depend to a large extent on optical and tactile inter-actions between nymphs (Ellis, 1953a).

Secondly, the colour of the nymphs at hatching appears to be related during the early instars to marching activity, dark hatchlings marching better than pale ones. Again the mechanisms behind this difference are unknown. Perhaps there are some differences in the optical systems of the two types of locust nymph, since marching partly depends on an opto-motor reaction (Uvarov, 1928; Ellis, 1953a). Alternatively, colour may be related to a fundamental difference in the activity of these two types of nymph. Whatever the reasons, the difference is only a transitory

one, for the nymphs own rearing conditions rapidly become the more important factor.

Thirdly, there is the influence of parental rearing conditions. Put in simple terms, the changes brought about by isolating the parents are handed on to the offspring, so that in the present experiments there was an accumulation of *solitaria* characteristics from generation to generation. This effect can be seen in offspring that are themselves either reared isolated or crowded, when allowance has been made for the fact that the nymph's own rearing conditions are always a very powerful factor. It would be interesting to know if the effects of crowding are also accumulated from generation to generation, starting with a line that has been isolated for many generations and then rearing them crowded. A further very interesting point is the relatively large response shown by the isolated nymphs from C parents, that is the first nymphs of the crowded line to be placed in isolation.

How is this effect of parental crowding handed on? Some form of non-genic inheritance would appear to be the simplest explanation and as far as marching is concerned, an inherited difference in spontaneous activity may be the crux of the problem (see Hunter-Jones, 1958). It might be argued that the two types of laboratory habitat (isolation or crowding) selected different genotypes. However, it is difficult to see how this could be brought about. A record kept of the deaths amongst nymphs reared in isolation shows that deaths were low and similar for the three groups with different parents (table 10). In crowded cages most of the deaths resulted from cannibalism at moulting time.

TABLE 10. — THE PERCENTAGE OF DEATHS IN NYMPHS REARED IN ISOLATION FROM BIRTH TO THE 4TH INSTAR.

PARENTAGE.	NUMBER OF NYMPHS.	% DEATHS.
Crowded	49	20.4
Solitary 1	38	23.7
Solitary 3	47	19.2

Finally, the accumulation of the *solitaria* characters (and presumably also those of *gregaria*) from generation to generation must be considered in relation to population dynamics and locust outbreaks. The behaviour potentialities will be different at the beginning of an outbreak than they will be at the end. At the beginning the nymphs will have *solitaria* characteristics so that the most severe crowding (which is presumably

forced on them under natural conditions by a patchy physical environment) will not immediately produce the maximum marching of which the species is capable. Similarly at the end of an outbreak, the nymphs will be strongly gregarious and several generations in isolation will be required before full *solitaria* behaviour is shown. During the course of an outbreak of *Locusta*, therefore, the development of the maximum swarming behaviour requires several consecutive generations at high density.

Although parental rearing density appears to influence marching behaviour independently of the factors related to hatchling colour, the two will tend to reinforce one another. Isolated parents produce far more pale hatchlings than crowded ones, so that their progeny will not only begin with reduced potentialities for marching due directly to the rearing conditions of the parents, but also due to those correlated with paleness in colour.

Summary.

1. When *Locusta* nymphs are reared crowded they generally show a number of characteristics that are typical of swarm populations in the field, i.e. they march well, have low F/C ratios and are generally black and orange in colour in the later instars. Nymphs reared in isolation, on the other hand, show low marching activity, high F/C ratios and are generally green or fawn in colour. Thus, the nymphs' own rearing conditions profoundly affect these characters.

2. Newly hatched nymphs vary in colour from jet black to fawn. During the first and second instars, nymphs that were pale at hatching marched less than those that were dark. However, the nymphs' own rearing conditions rapidly became the more important factor, so that by the third instar, nymphs that were pale at hatching showed similar marching behaviour to those that were dark at hatching.

3. The experiments have shown that the rearing conditions of the parents and grandparents etc. also influence the expression of phase characters in the offspring and that in a line of locusts reared continuously in isolation there was an accumulation of the *solitaria* characters from generation to generation.

4. The various phase characters appear to be related in a general way, but F/C ratios show a more steady cumulative effect from generation to generation than marching or colour.

5. As regards both F/C ratios and colour, the results suggested that during isolation females vary towards *solitaria* more easily than males, while under conditions of crowding they retained *solitaria* morphometrics and colour longer than the males.

Résumé.

1. Les larves de *Locusta* élevées en groupe possèdent habituellement plusieurs caractères qui sont typiques des populations grégaires dans la nature : elles marchent bien, les rapports F/C sont petits, et aux derniers stades, elles sont de couleur noire et orange. Par contre, les larves élevées en isolement marchent peu, les rapports F/C sont grands, et elles sont vertes ou beiges. Ainsi, les conditions d'élevage modifient profondément ces caractères.

2. La coloration des larves qui viennent d'éclore varie entre beige et noir-velouté. Les larves pâles à l'éclosion se déplacent moins aux stades I et II que celles de couleur noire. Mais les conditions d'élevage interviennent rapidement et, au troisième stade, les larves nées pâles marchent autant que les larves nées noires.

3. Les expériences ont montré aussi que la densité d'élevage des parents et des grands-parents a un effet sur les caractères phasaires des descendants ; dans une série de générations élevées continuellement en isolement, il y a une accumulation progressive des caractères de la phase *solitaria* d'une génération à l'autre.

4. Les caractères divers des phases semblent être liés de façon générale, mais le rapport F/C montre, de génération en génération, un effet cumulatif plus stable que l'activité ou que la couleur.

5. Les expériences relatives aux indices F/C et à la couleur indiquent que les femelles isolées deviennent *solitaria* plus facilement que les mâles ; cependant, les femelles en groupes retiennent leurs caractères morphométriques et la couleur de la phase *solitaria* plus longtemps que les mâles.

Zusammenfassung.

1. In einer Gruppe aufgezogene Larven von *Locusta* haben, im allgemeinen, eine Anzahl von Merkmalen, welche typisch für Schwarmpopulationen im Freiland sind : die Larven marschieren gut, haben ein niederes F/C Verhältnis und sind gewöhnlich während der letzten Häutungsstadien schwarz und orange. Isoliert aufgezogene Larven zeigen dagegen eine geringe Marschaktivität, ein hohes F/C Verhältnis und sind gewöhnlich grün oder hellbraun. Die Aufzuchtbedingungen beeinflussen also nachhaltig diese Larvenmerkmale.

2. Frischgeschlüpfte Larven variieren in der Farbe von schwarz bis hellbraun. Während des 1. und 2. Stadiums marschierten ursprünglich hellfarbige Larven weniger als solche, die nach dem Schlüpfen dunkel waren. Bald jedoch wurden die spezifischen Aufzuchtbedingungen maßgebend und vom 3. Larvenstadium an zeigten beide ursprüngliche Farbvarietäten unter gleichen Bedingungen ein ähnliches Marschverhalten.

3. Experimente haben gezeigt, daß die Aufzuchtbedingungen vorher-

gehender Generationen ebenfalls einen Einfluß auf die Ausbildung von Phasenmerkmalen der Larven ausüben. Ein mehrere Generationen lang isoliert aufgezogener Stamm zeigte von Generation zu Generation eine Ansammlung von *solitaria*-Kennzeichen.

4. Die verschiedenen Phasenmerkmale scheinen miteinander in Beziehung zu stehen, jedoch hat das F/C Verhältnis eine nachhaltigere Wirkung im Laufe der Generationen als das Marschverhalten oder die Färbung.

5. Isolierte Weibchen variieren im F/C Verhältnis und in der Färbung mehr gegen die *solitaria*-Phase¦ zu als die Männchen, während sie unter Bedingungen der Gruppenaufzucht die morphometrischen und Färbungsmerkmale der solitären Phase länger beibehalten als die Männchen.

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