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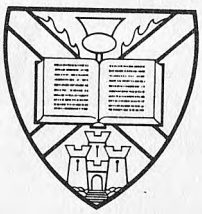

THE SOCIAL BEHAVIOUR OF IMMATURE ADULTS OF TWO SPECIES OF LOCUST, SCHISTOCERCA GREGARIA (FORSKÅL) AND LOCUSTA MIGRATORIA MIGRATORIOIDES (REICHE AND FAIRMAIRE).

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CONTENTS.

FIGURES.

INTRODUCTION.

Little experimental work has been carried out in the laboratory on the social behaviour of immature adult locusts. Ellis (1953, 1959, 1963a, 1963b, 1964a, 1964b) and Ellis and Pearce (1962) have carried out detailed work on the behaviour of hoppers of Schistocerca gregaria and Locusta migratoria migratorioides as well as on several other locust and grasshopper species. Norris (1954, 1963) and Loher (1959, 1960) have studied the effects of maturation on the mating and oviposition behaviour of older adult Schistocerca and Locusta. Haskell (1957) has investigated social influences during flight of Schistocerca.

This study was primarily concerned with quantitative differences in grouping in Schistocerca adults with respect to the phenomenon of phase and was restricted to density-dependent influences. Grouping was also studied in relation to aging and sexual maturation of the adults of Schistocerca and Locusta.

One of the difficulties of studying locust phase polymorphism is that of choosing a criterion of phase that is relevant, reliable and quantifiable. It is recognised that the ecological significance of the phase difference of locusts is in their behaviour. As Uvarov (1921) first showed in Locusta, great anatomical differences are possible in a species, these differences being a consequence of the environmental and social experience of the individuals. For some time these striking differences in shape and integument colour were considered the criteria for phase discrimination. Detailed systems of identification were erected based on morphological measurements (Dirsh 1953, Stower, Davies and Jones 1960)

and on classification of colour of hoppers (Gunn and Hunter-Jones 1952, Stower 1959). When Uvarov first defined this phase phenomenon he used a behavioural approach in determining the extreme forms "gregaria" and "solitaria" but in fact behavioural measurements were not used for classification and the terms "gregaria" and "solitaria" were applied as an explanation of the mechanisms involved in phase determination, not as a measure of the end product. This dichotomy of means and ends eventually resulted in a situation in which Key (1950) could write "it is clear that gregariousness can no longer be an invariable character of phase gregaria". Initially this confusion arose as a consequence of the assumption that the overt and easily quantifiable morphometric criteria exactly mirrored the underlying physiological and behavioural characteristics. Later the quantifiable morphometric criteria were emphasised because of their convenience. If the relationship between morphology and behaviour was exactly correlated, the assessment of phase condition would be relatively straightforward; as straightforward as any system can be when it attempts to break down a "contimuous spectrum" polymorphism (Kennedy 1961) into discrete quanta.

Several workers (Faure 1923, Ellis 1953, 1959, 1963a, 1963b; Gunn and Hunter-Jones 1952) have established that it is possible to reproduce the phase morphs of locusts in the laboratory by applying appropriate rearing conditions. Gregaria characteristics are shown by those locusts that experience conditions of crowding at high density while solitaria are produced by rearing locusts in visual and tactile isolation from the time of hatching. Intermediate transiens forms may be obtained by rearing the experimental locusts in low density crowds. Once determined, the phase morphs

are not necessarily static but may be reversed by changing the rearing conditions.

As well as colour and morphometrics, several other physiological factors are affected by rearing density in the laboratory. Gregaria females tend to have fewer ovarioles and to produce larger eggs than do solitaria females (Albrecht, Verdier & Blackith 1959, Papillon 1960); solitaria frequently pass through an extra instar and, as each instar gives rise to an eyestripe, solitaria adults often have an extra eyestripe (Roonwal 1947). Behavioural differences have also been observed (Ellis 1951, 1953, 1962), the most striking being the tendency to form groups and to "march".

From studies on laboratory populations, there is now experimental evidence to show that the different criteria of phase do not necessarily alter in parallel when the rearing conditions change. Ellis (1964a) has demonstrated that changes in colour occur more slowly than changes in behaviour, and morphometrics change even more slowly than colour does (Gunn & Hunter-Jones 1952). It must also be remembered that once an individual completes its final moult, changes in its physiological and behavioural state can no longer be registered in its gross body structure.

Another disadvantage of using criteria other than behavioural ones is that these criteria are often affected by factors besides locust density which was the principle influence under study here. Colour may be influenced by the rearing temperature, darker forms being produced at lower temperatures (Husain & Ahmad 1936); conditions of high humidity tend to produce the green hopper form typical of solitaria (Faure 1932); Locusta and Locustaria are also able to

adjust their cuticular colour to blend with the environment (Faure 1932).

In a similar fashion it has been shown that E/F ratio (elytron length to femur length) may be affected by temperature (Husain & Mather 1944, Gunn & Hunter-Jones 1952) and the latter authors have shown that humidity also affects E/F ratio. Haskell and Highnam (1964) found that daily flying accelerated the maturation of isolated and crowded Schistocerca as measured by growth of oocytes.

While it would be interesting to establish the effect on behaviour of these non-density-dependent environmental factors, it would be unwise to attempt to deduce the social history or present phase state of an individual solely from such evidence. This is particularly so in the field where locusts are subjected to widely varying environmental conditions. Several field observers have noted a discrepancy between the behaviour and morphological appearance of locusts. Lea in 1938 observed adults of Nomadacris septemfasciata with morphometrically solitaria characters which exhibited gregarious swarming behaviour, and Kennedy (1939) made a similar observation on Schistocerca.

For these reasons, little attention has been paid in this study to the classical phase characteristics of colour, morphometrics, instar numbers or ovariole number. The method of assessment of phase state is primarily a behavioural one, limited to the study of density-dependent effects. The technique used allows one to determine whether active grouping is occurring and also to make quantitative comparisons between different samples.

It was decided to limit this phase study to immature adults

and so investigate phase differences independent of the possible complicating effects of maturation. The main aim of this study was to measure the amount of social grouping exhibited by isolated and crowded laboratory adults, and to relate this to the biology of the locusts in the field.

It is not clear how solitaria adults meet to mate in the field. It is most likely that the effect of maturation in adults is to overcome the usual responses of repulsion between solitaria. Or it could be that the adult stage is one of aggregation while the hopper stage is one of dispersal in solitaria populations. Whichever is the mechanism of finding a mate, it is still very dependent on chance as locusts, unlike many solitary living grasshoppers, are not known to have a call song to attract mates over a distance and attraction is most likely to be visual. Any meetings must be dependent upon environmental features. It is more likely that adults would chance upon each other in a patchy vegetation than in a lush uniform environment. But it is the latter environment that the mating locusts are more likely to experience if their maturation is attuned to rainfall and the ensuing growth of vegetation.

Apart from direct comparison of effects on behaviour of different rearing treatments, the grouping behaviour was studied through several generations of isolation. Several phase characteristics are known to be altered in a cumulative fashion over several generations when the conditions of rearing are changed. Ellis (1959) was able to show that when rearing conditions were changed from crowding to isolation the colour of Locusta hoppers changed to the green solitaria colouring, in an additive fashion over several generations of isolation. In a similar way, the amount of time

spent marching declined, while the F/C ratio (femur length to head width) increased cumulatively with successive generations of isolation. Albrecht, Verdier and Blackith (1959) were also able to show that another phase criterion, ovariole number, was affected cumulatively by reversal of rearing density. Nomadacris females in a line which had been taken from isolation and crowded over four generations showed a steady reduction in ovariole number.

Two points emerged from the above studies. One was that the most marked differences occurred in the first generation subjected to the change in rearing conditions. In subsequent generations reared at the new rearing density there were small increments of change following the initial trend. The other point, which is in fact the corollary of the first, was that a return to the original rearing density did not result in an immediate and complete return to the initial value of the phase criterion, indicating a residual effect being carried over.

The other area of interest in this project was based on the observation made by several field workers (Kennedy 1939, Ellis & Ashall 1957) that there is a period of dispersal shortly after fledging in Schistocerca swarms. Rainey (1962) believes that this type of behaviour is determined by local climatic conditions: young adult locusts are likely to experience the disruptive effects of divergent winds while maturing adults are more likely to experience the concentrating effects of convergent winds.

It may be argued that as the principal mode of dispersal is flight it is meaningless to study this phenomenon under laboratory conditions which prohibit flight. It would be very difficult to

study the social aspects of flight in a laboratory. As the social behaviour of locusts is not restricted to flight it may be assumed that the distribution of locusts on the ground reflects a phase state that is common to ground and flight conditions.

MATERIALS.

The animals used in this study were all bred at the Anti-Locust Research Centre (A.L.R.C.), London, with the exception of those used for one experiment which were reared in the Zoology Department, Edinburgh University. The two principal species of locust used were the Desert Locust, Schistocerca gregaria (Forskål) and the African Migratory Locust Locusta migratoria migratorioides (Reiche & Fairmaire), both of which have been reared in this laboratory, although in different laboratory buildings, for more than 20 years. Other species tested were the Red Locust Nomadacris septemfasciata (Serville); the Australian Plague Locust Chortoicetes terminifera (Walker) and the non-swarming grasshopper Humbe tenuicornis (Schaum).

The rearing regime employed in the laboratory was that described by Hunter-Jones (1961). The locusts were reared in glass-fronted aluminium cages 15" x 15" x 16", in a constant temperature room maintained at 27°C. Additional light was provided for 7 hours a day, 5 days a week, by a 60 watt bulb in the back wall of each cage. This raised the air temperature in the centre of the cage to approximately 33°C, although a temperature gradient was created in the cage.

Fresh grass supplemented with dry bran was fed to the locusts 6 days a week, and in the winter when the quality of the grass was poor, green vegetables were also provided.

The feeding of moist grass necessarily resulted in fluctuations in the humidity in the cages throughout the day. Several hours after

feeding humidity was at its highest level of approximately 65%. This fell to approximately 20% overnight just prior to the next morning's feeding.

The density of the locusts in the cages was high, starting with about 900 hatchlings and being reduced, mainly by cannibalism, to approximately 200 adults per cage. Locusts reared in these conditions were referred to as "crowded". As the stock of Chortoicetes was newly established and still small, and the animals less then half the size of the other species, they were bred in cylindrical perspex cages 8" diameter, 14" deep. This ensured an amount of crowding comparable to that experienced by the larger species in the larger cages. The rearing density of Humbe does not affect its behaviour (Ellis, unpublished).

Experiments were also carried out on locusts that were reared individually. These, termed "isolated", were separated immediately after hatching and were then kept singly throughout their lives in 4 lb glass jars (capacity 1.5 litres). These jars were stacked, in specially constructed shelves, roundabouts, around two 60 watt bulbs which provided heat and light (See Plate 1).

In certain experiments the method of feeding varied and these differences will be described in the appropriate part of the text. For all the experiments that were not concerned with the method of feeding, the isolated locusts were fed individually 5 to 6 days a week with fresh grass. As with the crowded locusts the humidity fluctuated, but as ventilation in the jars was less efficient than in the larger cages, the range was from 80% R.H. after feeding to 40% R.H. the following morning.

PLATE 1

On several occasions hatchlings were initially kept in 1 lb jars and then transferred to the larger jars.

Under crowded conditions in the Anti-Locust Research Centre Laboratory, Schistocerca and Locusta take about 4 weeks to pass through the hopper stages and become adult, and a further 3 to 4 weeks to become mature. When isolated, Schistocerca shows great variability in its rate of development; hoppers may take as long as 8 weeks to become adult and this period often includes an extra (6th) instar. The maturation of the adults may also be delayed for several months. The effect of isolation on the maturation of Locusta adults is, however, the reverse. Maturation is accelerated and copulation may occur within 3 days of fledging.

There are several criteria used to assess the onset of sexual maturation of adult locusts: the first occurrence of copulation; the first oviposition by the female; and the associated change in body colour of both sexes, that have been described by Norris (1954) for Schistocerca.

Since for the most part this study was not concerned with the effects of maturation on behaviour, it was essential to eliminate the possible effects of reproductive behaviour on asexual social behaviour. For this reason the earliest estimate of maturation was chosen; i.e. copulation. This may be a stringent criterion for physiological pueposes, for in certain species oviposition may not occur for some time after copulatiom; for example several days for isolated Locusta, over several weeks for Chortoicetes (personal communication A. Antoniou); but it was essential that no copulatory pairs be formed during the experiment.

Assuming that the first copulation does not occur in crowded Locusta and Schistocerca before 2 to 3 weeks at the earliest, it was decided to test adults at 10 days of age. It was assumed that these adults were immature.

It was more difficult to set a precise testing age for immature, isolated Schistocerca. Because of the variability in their hopper and adult development, it was often impossible to obtain enough (10) adults of exactly the same age for testing. In some cases the range of age and testing was between 5 to 17 days after fledging. Because of the frequent delayed maturation of isolated Schistocerca, it was considered reasonable to assume that the 17 day old adults were immature.

Because of the very early onset of copulation behaviour of isolated Locusta, no effort was made to breed or test them.

APPARATUS.

The apparatus used to test adult Schistocerca, Locusta and Nomadacris in this study was a circular arena 75 cms in diameter and 20 cms deep, made out of cardboard that had been painted with a clear varnish to allow washing down between tests. The arena was covered with a sheet of glass and illuminated centrally from above by a light bulb. This, the only source of light in the experimental room, hung 90 cms above the floor of the arena and was surrounded by a shade of lower diameter 75 cms. For the experiments on activity and aggregation the floor of the arena was marked off radially into 10 equal segments and a circular inner wall of diameter 35 cms was added to prevent experimental animals congregating in the central area (Fig. 1). For the choice experiments another arena floor was marked off into 3 equal radial segments.

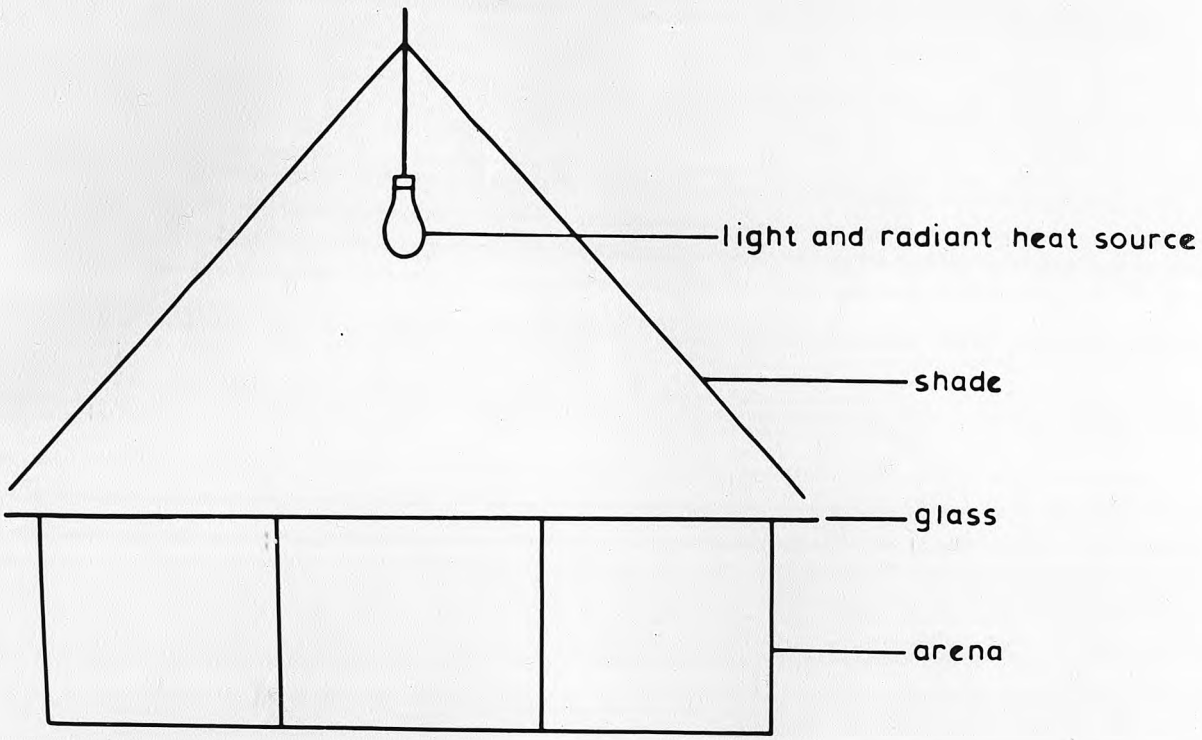
As adult Humbe and Chortoicetes are less than half the size of the adults of the above species, another arena was built to provide a comparable body size to arena ratio. This area was 50 cms in diameter and 10 cms deep, and had an inner wall 23 cms in diameter. It was used also to test 4th instar hoppers. Tests on 2nd instar hoppers were carried out in an even smaller arena, 20 cms in diameter and 2 cms deep, with an inner wall of 11 cms diameter.

Before all tests the overhead light was switched on for 15 to 30 minutes to allow the arena temperature to stabilise. With a 150 watt bulb the arena temperature was approximately $4^{\circ}C$ above the ambient room temperature of $32^{\circ}C$; a 100 watt bulb gave an increment of approximately $2^{\circ}C$ over the room temperature.

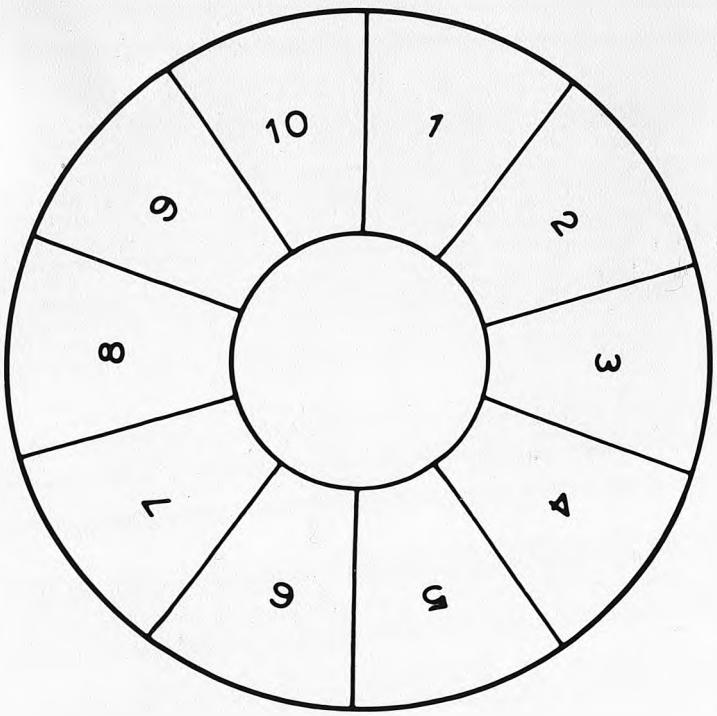
FIG. 1

APPARATUS – UNIFORM ENVIRONMENT ARENA FOR TESTING AGGREGATION

ELEVATION



AERIAL PLAN



ACTIVITY.

These experiments were carried out to determine the optimum conditions for aggregation on the assumption that, total immobility apart, the less active the locusts were, the more likely it was that large, stable groups would be formed.

Method.

Ten locusts were placed in the arena and every 2 minutes a note was taken of their distribution in relation to the floor segments of the arena. The mean number of 2 minute moves in ten minutes was plotted over two hours. Three two hour tests were made for each set of conditions. The mean and standard deviation were calculated for each condition and "t" test comparisons made.

This was not an absolute measure of activity as it took no account of the distance moved by the locusts. The closer the activity approached zero, the more accurate became the assessment. This method of recording had the advantage that it measured activity under the conditions of apparatus and locust density that were later to be used in the grouping tests. The measure was therefore of greater relevance to the aggregation study than the more accurate method of individual study in an actograph.

If "marching" (Ellis 1951) occurred during activity or aggregation tests, the test was terminated as this very mobile behaviour pattern was not considered to be conducive to the formation of large, stable groups.

Experiments and results.

Two different conditions of both daytime and temperature were

studied. The tests were carried out on crowded Schistocerca and Locusta adults 10 ± 1 days after fledging.

A. The effect of daytime. In an arbitrarily chosen temperature condition of 32°C with illumination provided by a 150 watt light bulb, locusts were tested in the morning (between 10.30 am and 1.00 pm) and in the afternoon (between 2.30 pm and 5.00 pm) to determine if there were any differences in activity level in the two parts of the day. Standard deviations are quoted in all activity tables.

Table 1. Mean Activity, morning and afternoon, tested at 32°C.

	Morning	Afternoon	"t"	Significance 22 d.f.
Schistocerca	2.6 ± 0.6	3.1 ± 0.1	2.0833	$p < 0.05$
Locusta	3.0 ± 0.7	3.2 ± 0.5	0.2857	not sign.

From Fig. II and table 1, it can be seen that Schistocerca shows a borderline significant difference with daytime, being slightly more active in the afternoon, and that Locusta shows no significant difference of activity with daytime. Because of the difference found with Schistocerca was so small, and beacuse of the limited time available, it was decided to combine the results of morning and afternoon readings for both species in all subsequent activity experiments.

B. The effect of temperature. Tests were made under two regimes of ambient room temperature; 28°C with illumination and radiant heat provided by a 100 watt bulb, and 32°C with a 150 watt bulb.

FIG. II

EFFECT OF DAY-TIME ON ACTIVITY

Each test - 10 day old adults, 5♂♂+5♀♀, crowded (mean of three tests)
(standard deviation quoted)

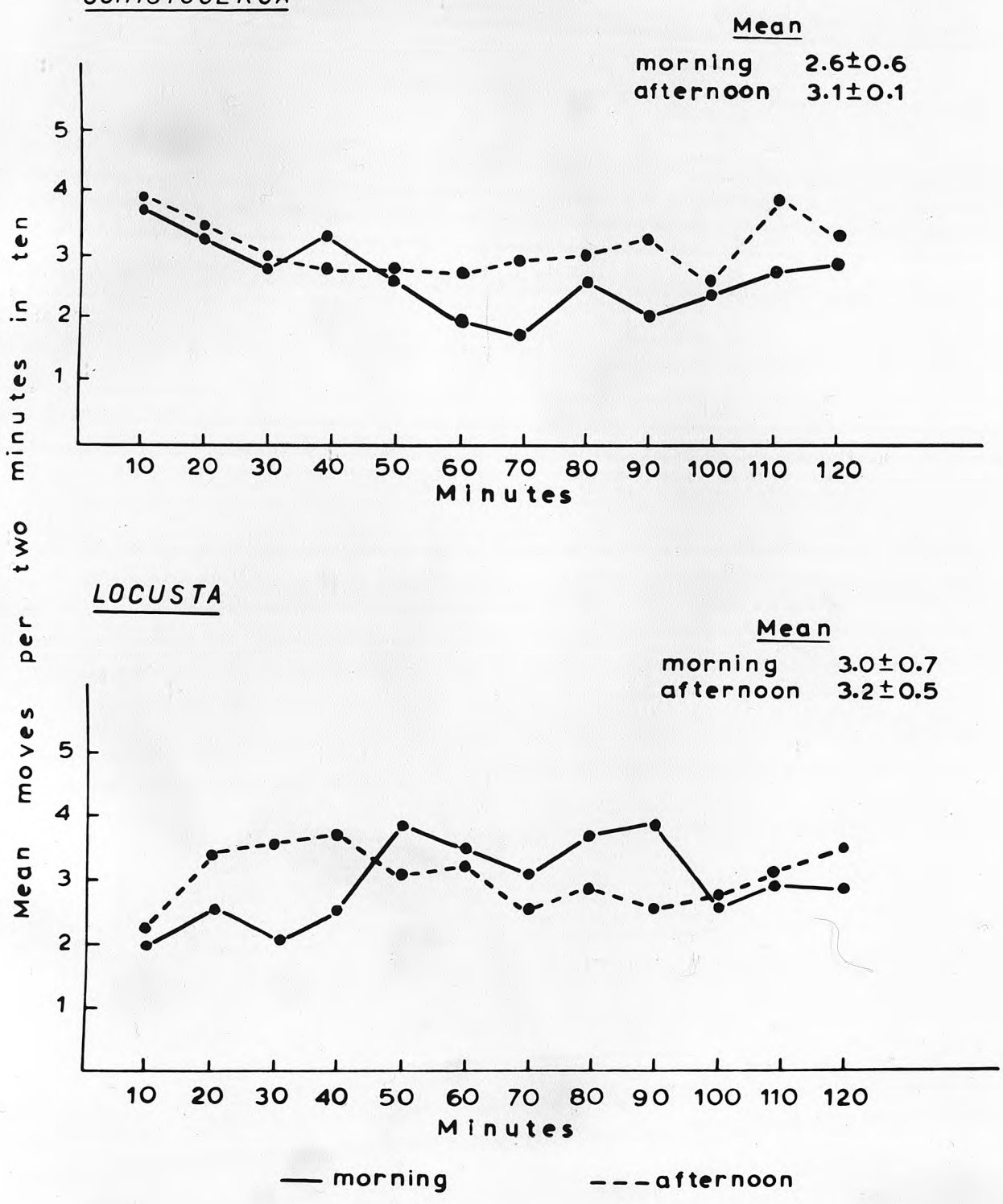


Table 2. Mean Activity at two temperatures.

	28°C	32°C	"t"	significance 22 d.f.
Schistocerca	3.8 ± 0.5	2.3 ± 0.6	6.6551	$p < 0.001$
Locusta	2.2 ± 0.4	3.9 ± 0.6	8.5000	$p < 0.001$

Fig. III and Table 2 show that Schistocerca are significantly less active at the higher temperature than at the lower, but that Locusta show the opposite response to temperature, being significantly more active at 32°C than at 28°C.

C. The effect of temperature associated with disturbance. These experiments were essentially the same as B, but the experimental animals were disturbed every half hour. The disturbance consisted of banging on the glass arena cover, or if necessary putting a hand in the arena and manually stirring the locusts. This experiment was carried out to determine how quickly after disturbance resettling occurs, and therefore how frequently readings could be taken during the aggregation experiments.

Table 3. Mean Activity at two temperatures, disturbed every half hour.

	28°C	32°C	"t"	significance 22 d.f.
Schistocerca	2.6 ± 0.6	2.3 ± 0.8	1.0391	not sign.
Locusta	1.9 ± 0.5	1.3 ± 0.5	2.8285	$p < 0.001$

FIG. III

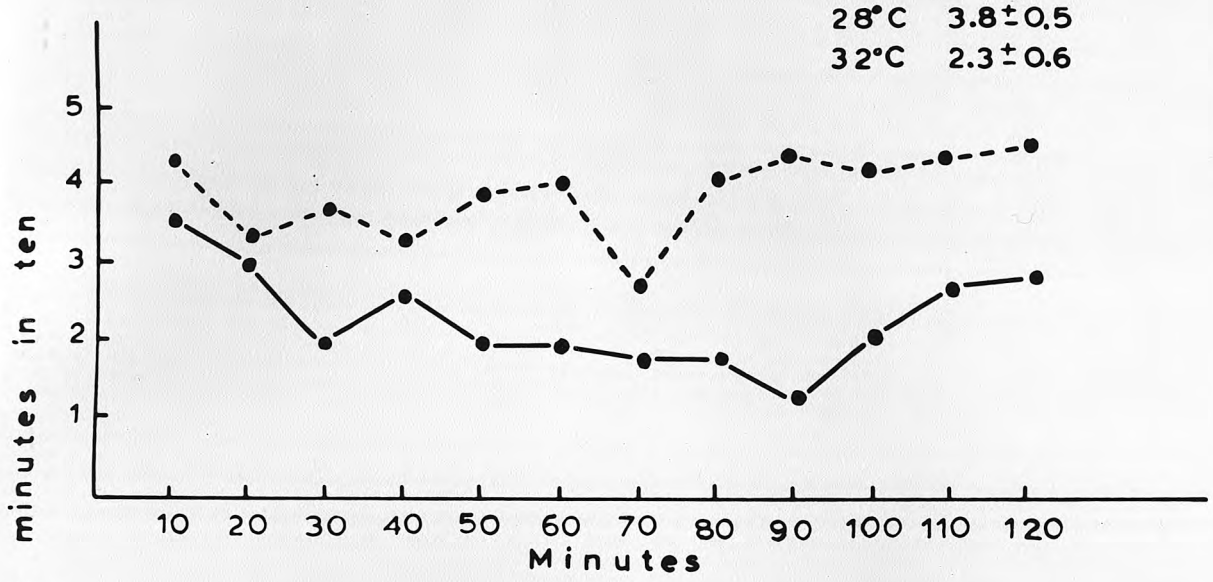
EFFECT OF TEMPERATURE ON ACTIVITY

Each test – 10 day old adults, 5♂♂ + 5♀♀, crowded (mean of three tests)
(standard deviation quoted)

Undisturbed

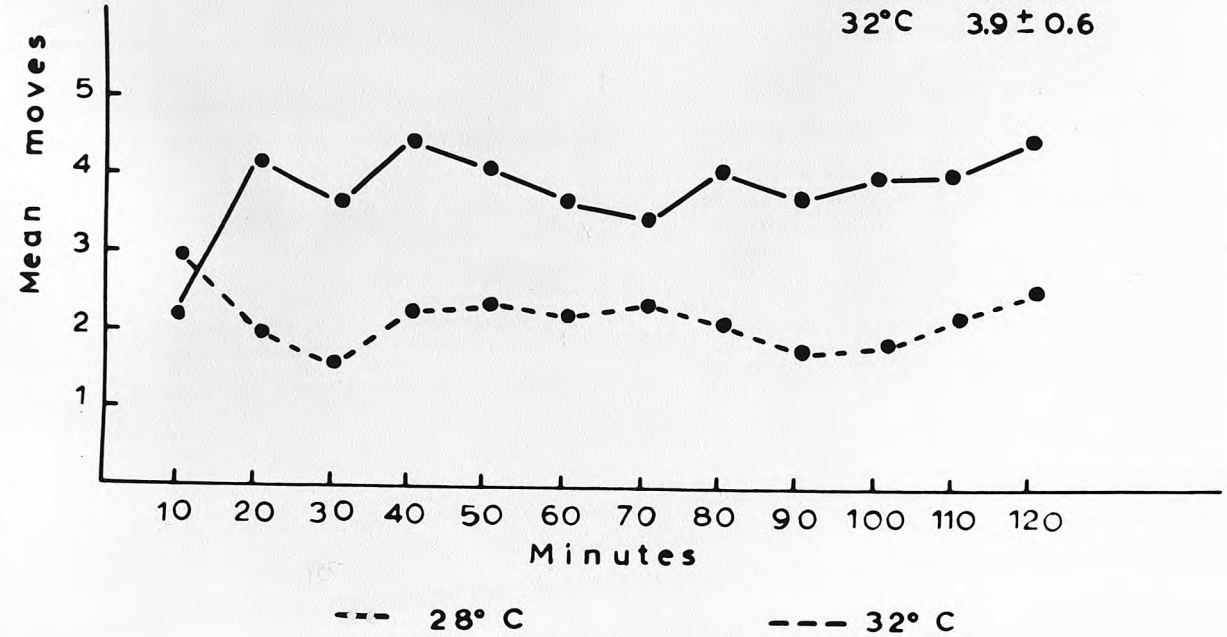
SCHISTOCERCA

Mean
28°C 3.8 ± 0.5
32°C 2.3 ± 0.6



LOCUSTA

Mean
28°C 2.2 ± 0.4
32°C 3.9 ± 0.6



--- 28° C — — — 32° C

FIG. IV

EFFECT OF TEMPERATURE ON ACTIVITY

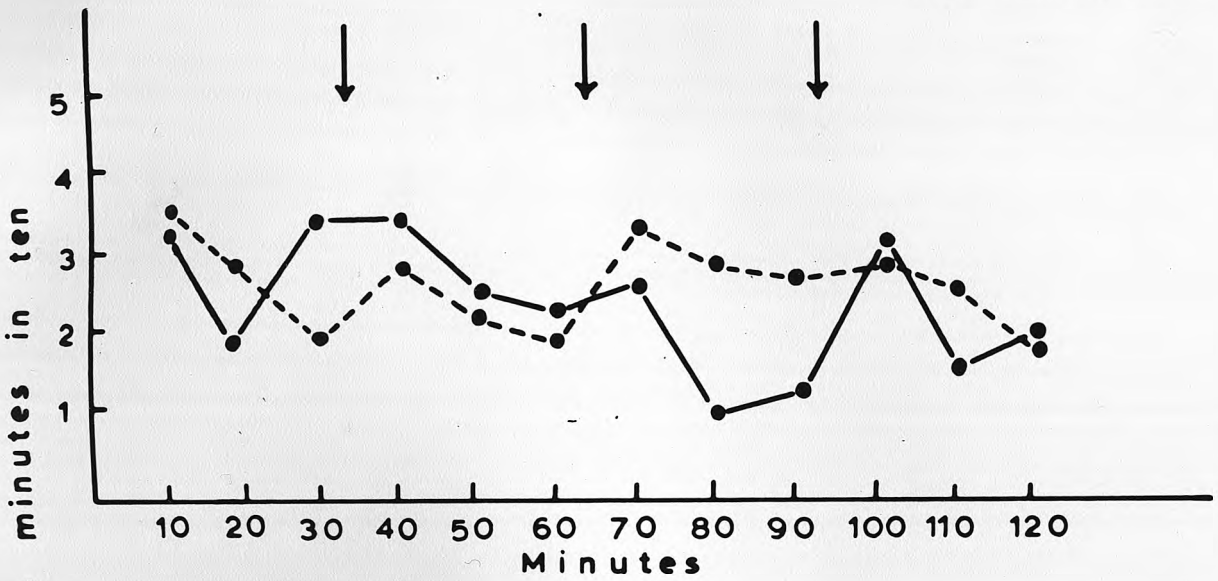
Each test – 10 day old adults, 50♂♂ + 50♀♀, crowded (mean of three tests)
(standard deviation quoted)

Disturbed

SCHISTOCERCA

Mean

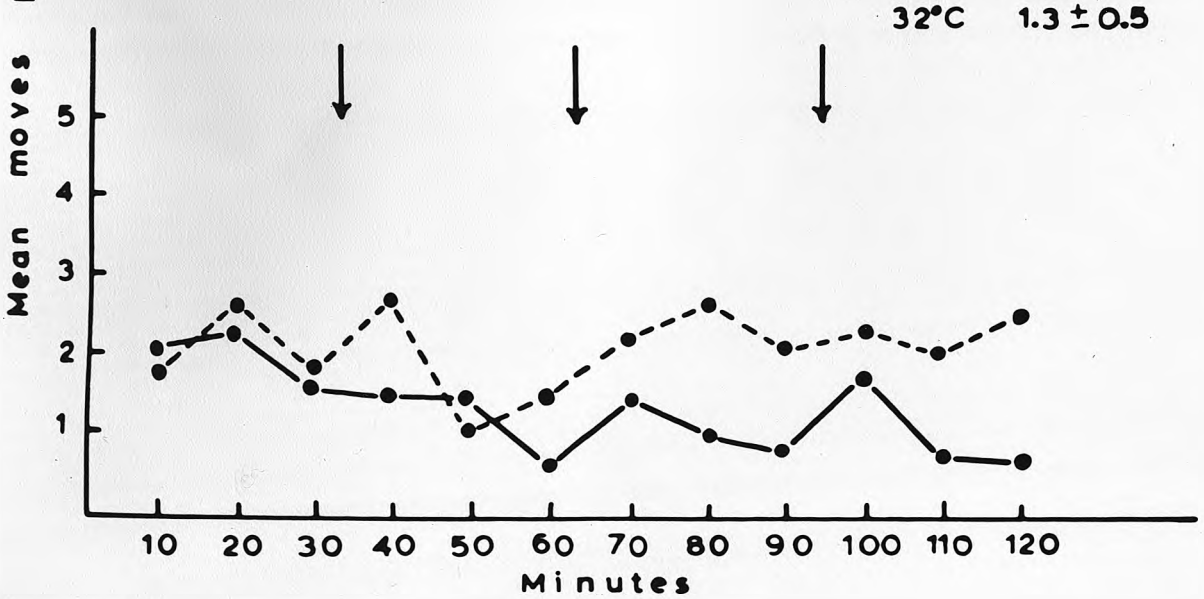
28°C 2.6 ± 0.6
32°C 2.3 ± 0.8



LOCUSTA

Mean

28°C 1.9 ± 0.5
32°C 1.3 ± 0.5



↓ disturbed — 28° C — 32° C

It would appear that, when disturbed, Schistocerca are still less active at the higher than the lower temperature, but not significantly so. When disturbed, Locusta are significantly less active at 32°C than at 28°C which is the reverse of their response to temperature when left undisturbed.

Fig. IV shows that while there was a consistent rise in activity in the ten minutes after disturbance, this was very small and did not persist. It was therefore decided that in the aggregation experiments readings might be taken more frequently than every half-hour, namely, every quarter-hour.

Table 4. Comparison of Mean Activity Level for undisturbed and disturbed conditions.

	Temp.	Undisturbed	Disturbed	"t"	significance 22 d.f.
Schistocerca	28°C	3.8 ± 0.5	2.6 ± 0.6	5.8824	$p < 0.001$
	32°C	2.3 ± 0.6	2.3 ± 0.8	0.0000	not sign.
Locusta	28°C	2.2 ± 0.4	1.9 ± 0.5	1.6225	not sign.
	32°C	3.9 ± 0.6	1.3 ± 0.5	11.5350	$p < 0.001$

When mean activity levels for undisturbed and disturbed conditions were compared (Table 4 above, Figs. V and VI), it was seen that there was a significant depression in the activity of both species, associated with disturbance. But this depression was manifest at different temperatures; the temperature at which activity was greater being 28°C for Schistocerca, 32°C for Locusta. Disturbance had no effect on activity when adults were less mobile.

FIG. V

EFFECT OF DISTURBANCE ON ACTIVITY

Each test – 10 day old adults, 5♂♂+5♀♀, crowded (mean of three tests)
(standard deviation quoted)

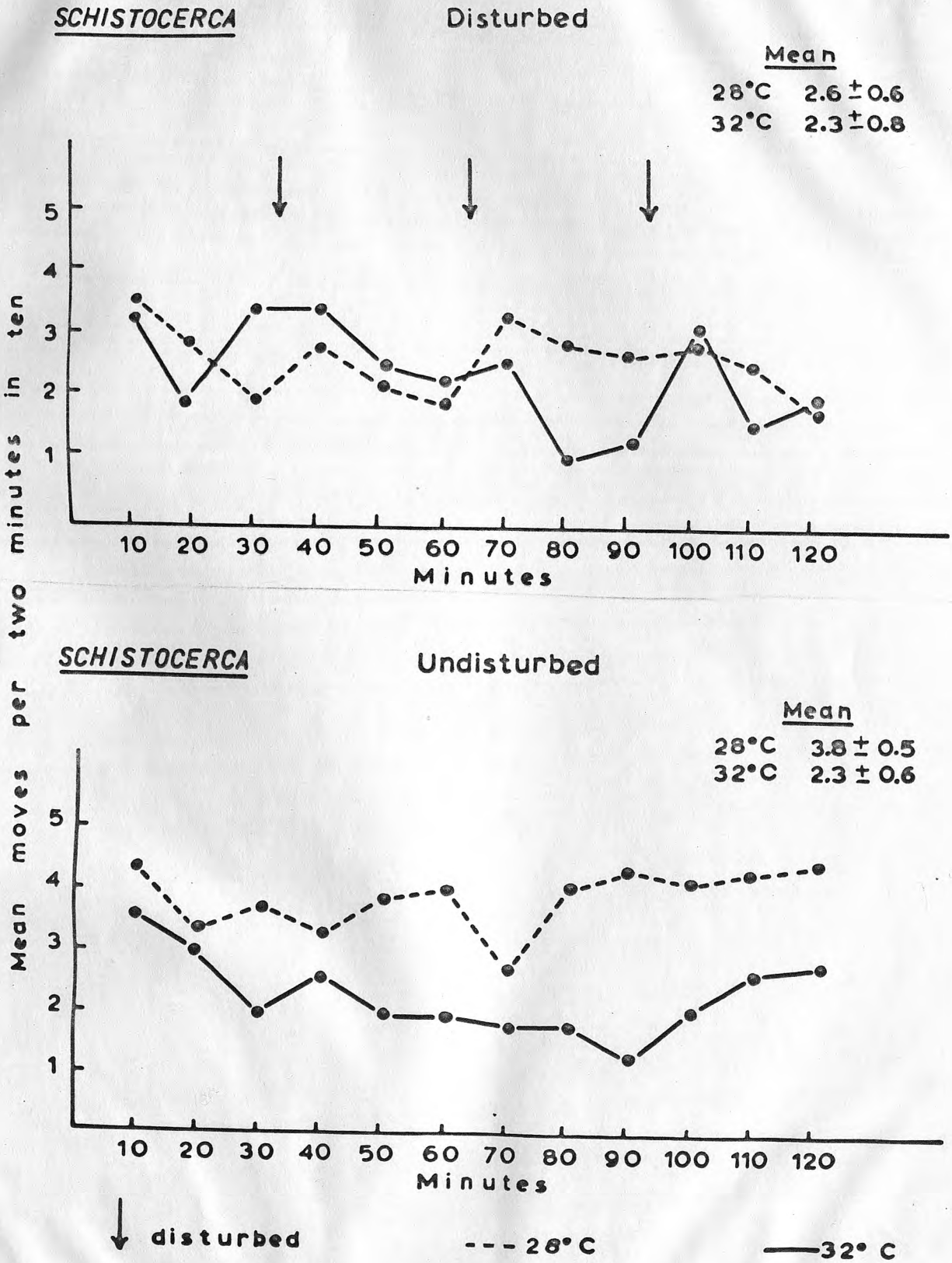
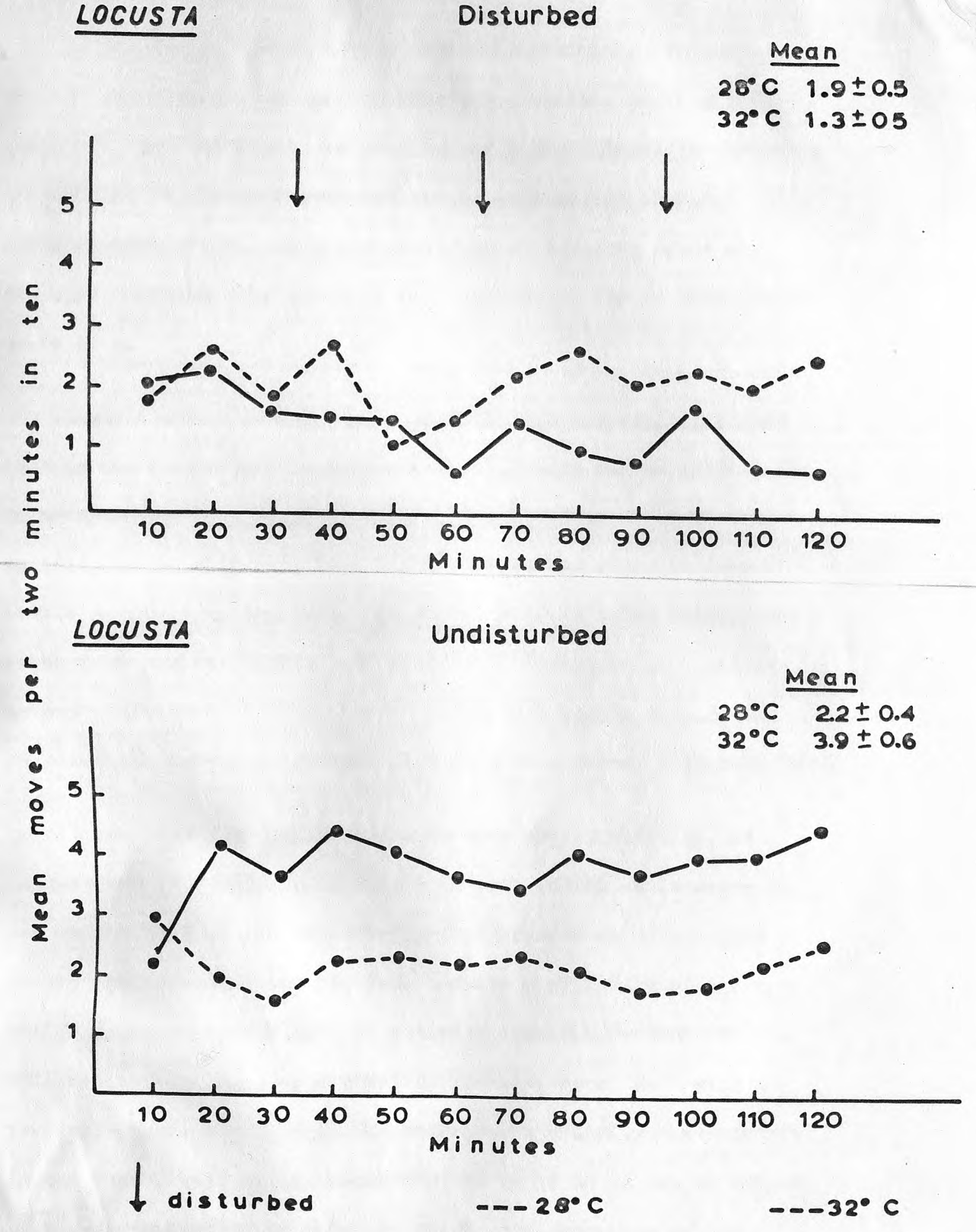


FIG. VI

EFFECT OF DISTURBANCE ON ACTIVITY

Each test – 10 day old adults, 5♂♂ + 5♀♀, crowded (mean of three tests)
(standard deviation quoted)



DISCUSSION.

A. Activity.

In the field, locust hopper and adult activities follow a well-defined diurnal pattern of roosting, feeding, basking and marching. This routine is related to the micro-climate (principally temperature and light-intensity) of the environment (Kennedy 1939, Ellis & Ashall 1957). In the restriction of breeding cages and the more constant conditions of the laboratory, the rhythms appear to be lost.

Edney (1937), working on Locusta hoppers and adults, showed that in the laboratory locomotor activity, measured on individuals in an actograph, is light-dependent. A high level of continuous activity is maintained during light periods and there is very little movement in the dark. Schistocerca adult males respond to light in a similar fashion and their light reaction is "instantaneous". Reversal of an alternate light-dark regime results in an immediate matching reversal of locomotor rhythms. (Odhiambo 1966)

Edney also found that over a 24 hour period activity, in hoppers and in adults up to 7 days of age, showed an increase in the second half of the recording period regardless of the time of day the recording was started. (Adults over 7 days of age showed an even distribution of activity over the 24 hour period.) This indicated a lack of diurnal periodicity associated with a particular part of the day. The increase in activity that occurred in the latter half of the recording was found to be due to hunger, as it was impossible to maintain fresh grass supplies in the experimental apparatus without disturbing the recording. There was also evidence of a 2 to $2\frac{1}{2}$ hour periodicity in activity in

some of the experimental animals which was considered to be a hunger rhythm.

In an attempt to reduce fluctuations in activity due to hunger, the animals used in these experiments were given sufficient grass in the morning so that it remained moist and palatable in the breeding cages at least during the day. No animals were tested until approximately an hour after feeding had commenced.

The nature of the experiments described here would mask any periodicity of as short a duration as 2 to $2\frac{1}{2}$ hours, for the tests only lasted 2 hours, they were not started at exactly the same time after feeding, and 10 animals were tested at a time without regard to individual activity.

Nevertheless, the results for the experiments on the effect of daytime on activity show that at 32°C Locusta activity does not vary significantly between the two halves of the day. Schistocerca shows a small significant difference, being slightly more active in the afternoon. Despite the difference in measuring technique this is in most part consistent with Edney's findings. It is not entirely surprising that locusts do not show any diurnal rhythm in activity in the relatively constant conditions of the laboratory. The cycle of field activities is associated with the physiological condition of the locust i.e. body temperature, which is in turn dependent on the climatic conditions throughout the day. There is no regular behaviour rhythm associated with daytime as shown by Periplaneta americana (Harker 1954). The laboratory locusts will still carry out the same activities as wild populations but instead of the activities of the majority of locusts being determined by daytime-dependent climatic conditions

they are related to the spatial gradient of conditions in the breeding cage, e.g. at all times of day there will be some locusts basking round the light bulb in the back wall of the cage and some pottering and feeding on the floor of the cage.

The results of the experiments on the effects of ambient temperature on activity show that Schistocerca are more active at the lower temperature than at the higher, while Locusta show the opposite response. This is in keeping with Ellis' (1963c) finding that it is easier to induce Locusta hoppers to march than Schistocerca hoppers by raising the temperature.

The experiments on resettling showed that the immediate effect of disturbance is slight in both species. There was a small consistent rise in activity after disturbance but this was short-lived (approx. 10 minutes) and resettling soon occurred, hence it was decided to take readings every 15 minutes rather than every 30 minutes in the later aggregation experiments. Hoppers are more excitable than adults and Ellis (1953) found that in order to disturb young hoppers it was sufficient to cast a shadow on them, that this disturbance increased the activity level three-fold, and that it took approximately 20 minutes to fall back to pre-disturbance level.

The effect of disturbance, however, reversed the response of Locusta to temperature. As under these conditions both Locusta and Schistocerca were less active at 32°C it was decided to carry out aggregation tests at this temperature.

A subjective impression was developed of the response of the different species to disturbance. Schistocerca were difficult

to disturb and required to be mixed manually; Locusta were more sensitive and would respond to the glass arena cover being banged. In the aggregation experiment where other species were tested, Nomadacris proved easy to disturb but their immediate, sharp response of jumping was short-lived as they remained immobile wherever they landed; Chortoicetes were again easy to disturb and were active for some time afterwards; Humbe were fairly unresponsive.

An unexpected finding did emerge from these tests on disturbance. A comparison of the overall level of activity (Table 4) between disturbed and undisturbed conditions shows that the effect of disturbance is to depress activity significantly at the temperature at which the locusts are most mobile, i.e. in the more active condition they are more sensitive to disturbance. It is easy to appreciate that mobile locusts are more alert than settled locusts and therefore need less stimulus to alter their behaviour. What is surprising is that the alteration of behaviour is in the opposite direction to what one would expect. Instead of an increase in activity there is in fact a depression of activity.

Kennedy and Moorhouse (unpublished) have found a similar unexpected reversal response to stimulation while testing the response to wind of locusts tested in a flat bed wind-tunnel. In this situation 5th instar Schistocerca hoppers that have been allowed to settle bask in the tunnel without wind and respond to applied wind by turning and moving downwind. But hoppers that have been highly stimulated, by being shaken and precipitated into the tunnel show an upwind response.

In the activity experiments and the wind-tunnel experiments

the difference in the initial "excitatory state" has resulted in a different response to a constant stimulus. It must be remembered that animals in the activity experiments have been removed from high density breeding cages (approx.150 to 200 adults per 59.0 litres) and placed in a relatively spacious arena (10 adults per 72.5 litres) thus reducing the amount of mutual stimulation between the individuals. It may be that at this low level of stimulation a more cryptic behaviour is exhibited, the response to external stimulation then being immobility which can be described as behaviour more typical of solitaria.

AGGREGATION.

The striking grouping behaviour of hoppers of both Schistocerca and Locusta has been demonstrated experimentally by Ellis (1953, 1959). The following experiments were carried out to measure some aspects of this behaviour in the adults of both species.

Two particular aspects of gregarious behaviour were studied. One was that of possible fluctuations in the amount of grouping associated with adult aging and sexual maturation; in the field a post-fledging dispersal followed by a regrouping for mating and egglaying has been observed (Kennedy 1939, Ellis & Ashall 1957). The other study was of the quantitative difference in grouping expected to be associated with different phase states; Ellis was able to rear in the laboratory hoppers which were similar to field solitaria and gregaria and to show differences in their grouping potential.

The method of measuring aggregation in this study was that used and described by Ellis (1953) for hoppers. A given number of experimental animals was placed in a uniform environment arena - in this case an annular arena (Fig. I). In this study three different arenas were used; a large one for adult Schistocerca, Locusta and Nomadacris septemfasciata as well as 5th instar Schistocerca and Locusta; a smaller one for 4th instar Schistocerca and Locusta and adult Humbe; and an even smaller one for 2nd instar Schistocerca. The exact measurements are given in the section on apparatus. No attempt was made to compute arena size in proportion to size of locusts being tested. A rough guide to arena size was that all experimental animals being tested at once could fit into one

segment of the arena and so give the highest score for grouping.

Grouping was measured in two ways. In one method a note was taken of the number of locusts per segment of the arena. The other method of assessing the amount of grouping was the more subjective one of estimating groups independent of the arena floor segments and judging animals that were within two body lengths of each other to be in a group. The latter method would tend to include locusts that were strung out in a long group over several segments whereas these groups would not be scored as whole groups by the area-dependent method. But this was balanced by the fact that the segment-dependent method could score locusts as being in a group when they were more than two body-lengths apart.

By examining data that will be presented later in the text it is possible to compare the two methods of assessment. As the number of locusts in the three different size groups (of 1, 2 or 3 and more) is interdependent (the more there are in one group the less there will be in the other two groups) in each test, it is more profitable to look at the assessment of the larger groups (3 or more locusts).

It appears from Table 5 (below, p.24) that there is no consistent tendency either to exaggerate or to diminish group size when the more subjective method (B) is compared with the area-dependent method (A); in 8 cases method B gave a larger assessment of group size, in 3 cases a smaller estimate and in one case the figures for the two methods were identical. This inconsistency made the method based on assessment of locusts within two body lengths unreliable for interspecific comparisons and therefore only data based on segments was used in analysis in this study.

Table 5. Two assessments of locust groups as number of locusts in groups of three or more. Method A - number of locusts per segment; Method B - number of locusts within two body lengths of another locust.

Species	Stage	Method A	Method B
Schistocerca	5th instar	253	204
	5-day-old adult	216	216
	10-day-old adult	193	219
	mature adult	241	298
Locusta	5th instar	203	272
	5-day-old adult	189	292
	10-day-old adult	194	220
	mature adult	189	302
Humbe tenuicornis	immature adult	140	121
Nomadacris septemfasciata	immature diapausing adults	147	125
Chortoicetes terminifera	immature adults	182	222

The distribution of locusts measured as the number of locusts per segment was compared, by means of a χ^2 test, with a random expected value based on the binomial expansion which relates the number of available segments to the number of experimental animals. Throughout this study 10 locusts were tested at a time in the ten-segment arena. Any significant deviation from the random distribution could be attributed to active attraction or repulsion between locusts while no significant difference

from the random indicated a lack of strong interaction between experimental animals.

The expansion of the binomial $(\frac{9}{10} + \frac{1}{10})^{10}$ for 10 animals in 10 segments gives the following expected distribution -

35%	segments with no locusts
39%	1
19%	2
6%	3
1%	4
0.1%	5

The last three values in this distribution are combined to avoid distorting the significance of the results. This gives an expected distribution of 7% of segments with locusts in groups of three or more. The total random expected values for experiments with different numbers of two-hour tests are shown in Appendix I along with the actual distributions obtained in each experiment.

Each experiment for any set of conditions consisted of seven 2-hour tests, unless otherwise stated. Readings were taken every 15 minutes and the locusts were disturbed between readings. This gave 8 readings per test and 560 readings per 7-test experiment.

Table 6 (pp. 26 - 28) gives the χ^2 value for each experiment when actual distribution is compared with random. Tables in the text will extract from Table 6 χ^2 values of immediate relevance to the experiment discussed and direct comparison between experiments will also be made in the text. Two methods of inter-experiment comparison were used. One was a direct comparison of total

Table 6. χ^2 comparison of actual distribution obtained during experiment with random obtained by expansion of the binomial $(\frac{9}{10} + \frac{1}{10})^{10}$. (Reared at A.L.R.C. unless otherwise indicated.)

* and + = same experiment.

Species	Stage	Rearing treatment	Testing conditions	No. of tests	No. of readings	χ^2	Significance at 3 d.f.
Schistocerca	adult	crowded	at 28°C	7	560	27.68	$p < 0.001$
			at 32°C	7	560	70.96+	$p < 0.001$
			in morning	7	560	66.24	$p < 0.001$
			in afternoon	7	560	55.30	$p < 0.001$
Locusta	adult	crowded	at 28°C	7	560	23.59	$p < 0.001$
			at 32°C	7	560	54.35*	$p < 0.001$
			in morning	7	560	9.64	$p < 0.05$
			in afternoon	7	560	32.16	$p < 0.001$
Schistocerca	adult	crowded	32°C	7	560	70.96	$p < 0.001$
		1st generation isolated	32°C	7	560	40.37	$p < 0.001$
		3rd generation isolated	32°C	7	560	38.85	$p < 0.001$
		5th generation isolated	32°C	6	480	28.48	$p < 0.001$

Table 6 continued.

Species	Stage	Rearing treatment	Testing conditions	No. of tests	No. of readings	χ^2	Significance at 3 d.f.
Schistocerca	5th instar	crowded	32°C	14	560	69.90	$p < 0.001$
	5 day adult	"	32°C	7	560	44.76	$p < 0.001$
	10 day adult	"	32°C	7	560	70.96+	$p < 0.001$
	mature adult	"	32°C	7	560	24.58	$p < 0.001$
Locusta	5th instar	"	32°C	14	560	31.39	$p < 0.001$
	5 day adult	"	32°C	7	560	17.43	$p < 0.001$
	10 day adult	"	32°C	7	560	54.35*	$p < 0.001$
	mature adult	"	32°C	7	560	13.49	$p < 0.001$
Nomadacris	adult diapause	crowded	32°C	7	560	1.71	not sign.
Humbe	adult	crowded	32°C	7	560	0.51	not sign
Chortoicetes	adult	crowded	32°C	7	560	13.99	$p < 0.001$

Table 6 continued.

Species	Stage	Rearing treatment	Testing conditions	No. of tests	No. of readings	χ^2	Significance at 3 d.f.
Schistocerca	2nd instar	crowded	28°C	14	560	202.26	$p < 0.001$
	"	isolated	28°C	14	560	89.92	$p < 0.001$
	4th instar	crowded	28°C	14	560	29.91	$p < 0.001$
	"	isolated	28°C	10	400	34.81	$p < 0.001$
Schistocerca	2nd instar	isolated undisturbed	28°C	10	400	31.78	$p < 0.001$
	"	isolated + polythene	28°C	10	400	76.68	$p < 0.001$
Schistocerca	2nd instar	Edinburgh isolated	28°C	6	240	5.88	not sign.
Schistocerca	adult	Edinburgh isolated	32°C	7	560	8.80	$p < 0.05$
	"	"	retested at A.L.R.C.	5	400	4.33	not sign.

distribution by means of a χ^2 contingency test. The other method compared the mean number of locusts in groups of three or more by means of a Student's "t" test. This mean number was obtained from the number of locusts in groups of three or more in each test. While χ^2 analysis could only be carried out on data where groups of 3 to 10 animals were amalgamated into one class, the actual records from experiments allow one to compute exactly how many locusts comprised these groups of three or more. The χ^2 analysis is based on the number of groups of a given size, the comparison of means is made on the number of locusts making up these groups.

Experiments.

Two preliminary experiments were carried out to determine the effects of testing at different times of day and at two different temperatures.

1) Time of day. As Schistocerca showed a small significant difference in their activity levels at different times of day, it was decided to test if this difference was sufficient to affect grouping. Aggregation tests were therefore carried out in the morning and afternoon on Schistocerca and Locusta at an arbitrarily chosen temperature of 32°C using 10-day old adults; 5 males and 5 females were tested at a time.

The χ^2 value obtained by comparing the actual distributions with random shows that active aggregation was occurring in both morning and afternoon tests (Table 6). Table 7 shows the direct comparison of distributions for the two species using the χ^2 contingency analysis and the "t" test comparison of the mean number of locusts in groups of three or more.

Table 7. Comparison of distribution of Schistocerca and Locusta immature adults in morning and afternoon tests, by means of "t" test and χ^2 contingency test.

Species	Mean number of locusts in 3+ groups (s.e. quoted)		"t" (10 d.f.)	χ^2 contingency (3 d.f.)
	morning	afternoon		
Schistocerca	36.6 ± 3.6	30.3 ± 4.2	1.1435 (not sign)	7.86 ($p < 0.05$)
Locusta	24.4 ± 2.6	27.3 ± 3.9	0.6135 (not sign)	3.47 (not sign.)

Locusta did not show any significant difference in the amount of grouping which occurred in the two parts of the day. Schistocerca showed a significant difference in aggregation as measured by the contingency analysis, with more larger groups formed in the morning than in the afternoon (see distribution, Appendix I). No difference was apparent when the mean number of locusts in groups of three or more (3+) was compared. Since very significant grouping was occurring at both times of the day, and since only one of the two methods of analysis showed any significant difference resulting from time of day, it was decided to eliminate the difference by maintaining a balance of tests carried out in the morning and afternoon in each experiment.

2) Temperature. Aggregation tests were carried out to ascertain if the significant differences in the level of activity related to the temperature at which the tests were carried out (see section

on Activity) were in fact great enough to affect the extent of aggregation at these temperatures.

Tests were carried out on 10-day-old adults, 5 males and 5 females at a time. Morning and afternoon test results were combined. The total distributions compared with random are shown in Table 6 and the inter-experiment comparisons by the two forms of analysis in Table 8.

Table 8. Comparison of distribution of Schistocerca and Locusta immature adults tested at two temperatures, by means of "t" test and χ^2 contingency test.

Species	Mean number of locusts in 3+ groups (s.e. quoted)		"t" (10 d.f.)	χ^2 contingency (3 d.f.)
	28°C	32°C		
Schistocerca	27.6 ± 3.2	35.7 ± 4.1	1.5253 (not sign)	7.07 (not sign.)
Locusta	27.7 ± 2.3	32.6 ± 2.6	1.3951 (not sign)	0.38 (not sign.)

At both temperatures, both species show very significant aggregation (Table 6). No significant difference in the amount of grouping occurring at 28°C and 32°C can be shown for either species by either method of analysis.

As both species showed a greater (although insignificantly so) amount of grouping at the higher temperature, it was decided to carry out all subsequent tests on adults at 32°C.

Study of the amount of grouping at different ages in relation to fledging.

Aggregation experiments were carried out on 5th instar hoppers and adults of Schistocerca and Locusta at various times after fledging to determine if laboratory populations show fluctuations in grouping behaviour after fledging as has been reported to occur in some field populations.

Tests were made on adults 5 ± 1 and 10 ± 1 days after the final moult, and also when mature at approximately 4 to 6 weeks after fledging. These tests were carried out at 32°C and no animals were retested; there was no follow-up of a particular sample through its adult life but different animals were used for each stage. The results were compared with those obtained from testing 5th instar hoppers at 28°C. Seven two-hour tests were made on each adult stage, and 14 two-hour tests on 5th instar hoppers to give 560 animal readings per stage.

The χ^2 value for the comparison of the actual with the random distributions is given in Table 6. All stages were aggregating significantly in both species.

The mean number of locusts in groups of 3 or more are shown in Figs. VII and VIII and in Table 9 (p. 33).

As fluctuations in grouping rather than a consistent trend were being investigated, a "t" test analysis was carried out between each stage rather than a regression analysis over all stages.

In both species there was a fall in the amount of grouping

FIG. VII

FLUCTUATION IN GROUPING WITH AGE AFTER FLEDGING

(Each point mean of 7 tests)

SCHISTOCERCA G.

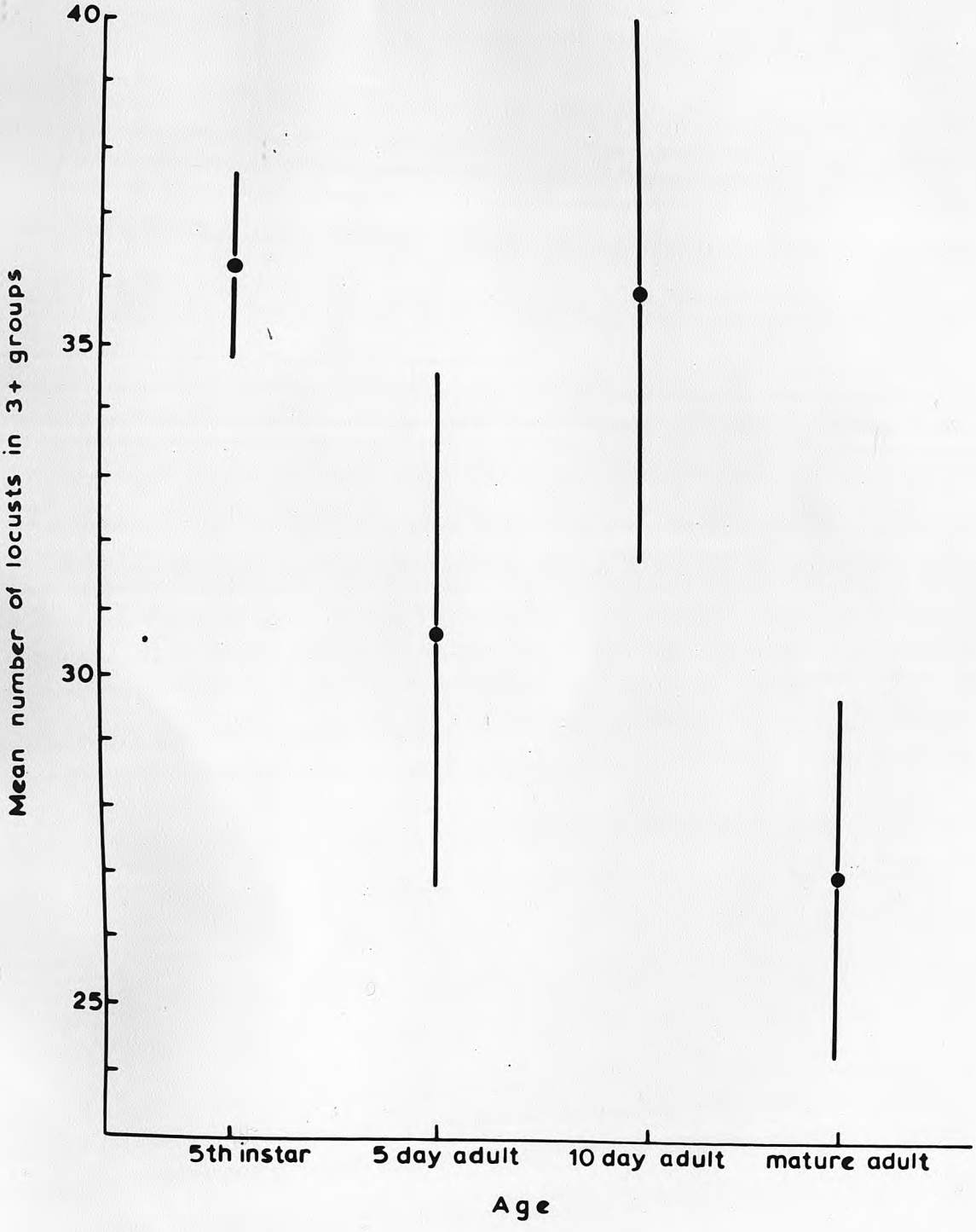
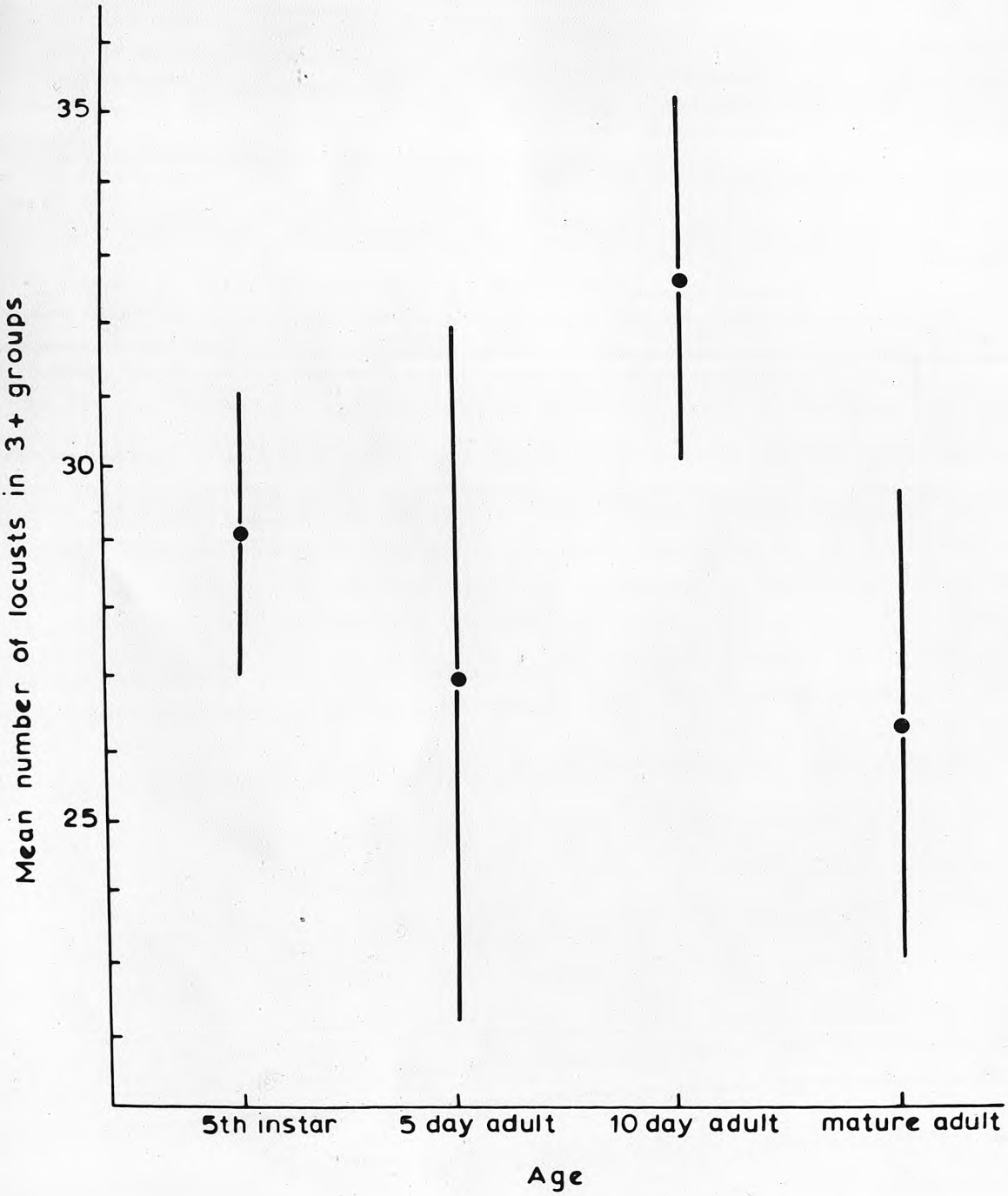


FIG. VIII

FLUCTUATION IN GROUPING WITH AGE AFTER FLEDGING

(Each point mean of 7 tests)

LOCUSTA M. M.



after fledging and again at maturation, but these variations were not significant.

Table 9. Mean number of locusts in groups of 3 or more for Schistocerca and Locusta at different ages in relation to fledging.

Species	Stage	Mean no. of locusts in 3+ groups. (s.e. quoted)	"t" (12 d.f.)
Schistocerca	5th instar	36.1 ± 1.3	1.4103 - not sign.
	5-day adult	30.6 ± 3.9	0.9444 - not sign.
	10-day adult	35.7 ± 4.1	1.8723 - not sign.
	mature adult	26.9 ± 2.7	
Locusta	5th instar	29.0 ± 1.9	0.4225 - not sign.
	5-day adult	27.0 ± 2.6	1.1429 - not sign.
	10-day adult	32.6 ± 2.6	1.5897 - not sign.
	mature adult	26.4 ± 3.3	

What is shown, particularly in Figures VII and VIII, is the smaller degree of variation in grouping of hoppers compared with that of adults. A comparison of this variation about the mean was made by means of a Variance Ratio shown in Table 10.

Table 10. Variance Ratio obtained by comparing variance for hopper stage with each of three adult stages for Schistocerca and Locusta.

Species	Stage	F (for 6 & 6 d.f.)	
Schistocerca	5-day adult	8.0457	($p < 0.02$)
	10-day adult	9.5948	($p < 0.01$)
	mature adult	3.7328	(not sign.)
Locusta	5-day adult	5.9727	($p < 0.02$)
	10-day adult	1.8032	(not sign.)
	mature adult	3.0109	(not sign.)

The analysis in Table 10 shows that in half of the cases the variation about the mean is significantly greater for adults than for hoppers.

A comparison of grouping was also made between the two species for each stage, Table 11.

Table 11. Comparison of mean number of locusts in groups of three or more between Schistocerca and Locusta for four different ages in relation to fledging.

Stage	"t" for 12 d.f.	
5th instar	3.0206	$p < 0.02$
5-day adults	0.6303	not sign.
10-day adults	0.6264	not sign.
mature adults	0.1003	not sign.

There is a significant difference between the two species in the amount of grouping in 5th instar hoppers but not in adults. More Schistocerca hoppers are found in groups of three or more than are Locusta hoppers.

The effect of rearing conditions on social behaviour.

An attempt was made to reproduce the field solitaria and gregaria phase morphs by rearing locusts, from hatching, in isolated and crowded conditions respectively.

1. Aggregation experiments.

Aggregation experiments were carried out at 32°C on immature Schistocerca adults of three different generations of an isolated line. The results of these experiments were compared with those obtained previously from 10 day old, crowded Schistocerca tested at the same temperature; these showed significant grouping behaviour and may be considered gregarious. The results of tests on Humbe tenuicornis which is a non-swarming grasshopper are also quoted. Crowding does not affect the behaviour of Humbe (Ellis, pers.comm.), which may be considered equivalent to the solitarious phase in swarming locusts. Because Humbe was tested in the intermediate size arena, direct comparison was not made between Humbe and Schistocerca. Instead, two other criteria of the solitaria extreme of behaviour were adopted; the actual results obtained from tests on diapausing Nomadacris adults which showed a random distribution and the hypothetical case calculated from the binomial expansion. The latter gave 6 segments with three or more locusts (see Appendix I), which gives a minimum of 18 locusts in groups of three or more per test.

The results of these experiments and the comparative analysis of the data obtained are shown in Tables 12 - 14.

Table 12. χ^2 value obtained from comparison of distribution of animals subjected to different rearing conditions of Schistocerca adults and Humbe adults with random distribution.

Species	Condition	No. of tests	χ^2	Significance at 3 d.f.
Schistocerca	crowded	7	70.96	$p < 0.001$
Schistocerca	1st generation isolated	7	40.37	$p < 0.001$
Schistocerca	3rd generation isolated	7	36.85	$p < 0.001$
Schistocerca	5th generation isolated	6	28.48	$p < 0.001$
Humbe	crowded	7	0.51	not sign.
Nomadacris	crowded	7	1.71	not sign.

Very significant grouping occurred in all experiments on Schistocerca irrespective of the rearing conditions experienced by the locusts. Humbe and Nomadacris had a total distribution very similar to random and did not therefore actively aggregate.

The comparisons of the different treatments of isolated Schistocerca with the gregaria morph, i.e. Schistocerca crowded condition, was made in two ways; a direct comparison of total distribution by means of a χ^2 contingency test and "t" test comparison of mean number of locusts in groups of 3 or more. (Table 13, p. 38)

Table 13. "t" test and χ^2 contingency comparison of distribution of animals subjected to different rearing conditions, 3 different isolated generations of Schistocerca adults compared with crowded Schistocerca adults.

Rearing condition	Mean no. of locusts in groups of 3+	"t" compared with crowded	χ^2 contingency comparison with crowded (3 d.f.)
crowded	35.7 ± 4.1	-	-
1st generation isolated	31.6 ± 3.5	0.7455 (not sign.) for 12 d.f.)	2.53 (not sign.)
3rd generation isolated	31.1 ± 2.4	0.9312 (not sign. for 12 d.f.)	3.38 (not sign.)
5th generation isolated	28.7 ± 1.9	1.4109 (not sign. for 11 d.f.)	4.82 (not sign.)

Using both these methods of comparison, no significant difference was found between the gregarious, crowded Schistocerca and any of the isolated Schistocerca.

The comparison of the different Schistocerca rearing treatments was made with the equivalents of phase solitaria by comparison of the mean number of locusts in groups of three or more (Table 14, p. 39).

Not only are the crowded Schistocerca behaving significantly differently from the solitaria condition, but so are the three treatments of isolated Schistocerca. Both rearing conditions produced gregariously acting adults.

Table 14. "t" test comparison of the mean number of locusts in groups of 3 or more - 3 different isolated generations of Schistocerca adults and crowded Schistocerca adults compared with Nomadacris adults and the hypothetical random.

	Nomadacris 20.1 ± 2.2 locusts in 3+ groups		Hypothetical random 18.0 ± 0.0 locusts in 3+ groups	
crowded	3.2133	$p < 0.01$	4.1121	$p < 0.01$
1st generation isolated	2.7515	$p < 0.02$	3.8655	$p < 0.01$
3rd generation isolated	3.3996	$p < 0.01$	5.5817	$p < 0.01$
5th generation isolated	2.8667	$p < 0.02$	6.1378	$p < 0.01$
Hypothetical	0.9656	not sign.	-	-

A regression analysis was carried out to ascertain if there was any cumulative effect of isolation acting to reduce the amount of grouping occurring in successive generations. The number of locusts in groups of three or more in each test was regressed on the number of generations of isolation. The correlation coefficient so obtained is -0.1720, although there is a negative trend, i.e. reduction in the number of locusts found in groups of three or more, it is not significant at 18 degrees of freedom.

It may be that the gregarious behaviour exhibited here by isolated locusts is sufficient to mask the possible effect of several generations of isolation.

Choice experiments.

Another assessment of social behaviour was made by placing individual immature Schistocerca adults in a choice situation. The whole experimental arena was made available to the locust under observation and the arena floor was marked out radially into three equal segments. One segment was left empty, one segment had 3 dead immature Schistocerca adults placed centrally in the segment, and the last segment had 3 live immature Schistocerca adults tethered centrally in the segment. The live decoys were tethered in such a fashion that their legs and antennae were free, and a little movement of the animals was possible.

Each test lasted two hours, readings were made every 15 minutes, and the experimental animal was disturbed between readings. For each reading a note was taken of which segment the animal was in, and if it was in a segment with decoys a note was also taken of whether it was within two body lengths of the decoys. 12 males and 12 females of both 1st generation isolated and crowded rearing conditions of Schistocerca were tested. The results are expressed in Tables 15 and 18.

A. Ignoring within segment distribution.

Table 15. Choice experiment testing male and female immature Schistocerca adults reared isolated and crowded, ignoring the distribution within segments.

Segment / Sex & Rearing	Empty	3 dead decoys	3 live decoys
Crowded male	17	35	44
Crowded female	16	45	35
Isolated male	27	36	33
Isolated female	37	30	29

To determine if there was any significant difference between the sexes in these tests, a contingency χ^2 analysis was applied to the distributions of males and females for isolated and crowded rearings.

Table 16. χ^2 contingency comparison of male and female distributions for isolated and crowded rearings.

Comparison	χ^2	Significance at 2 d.f.
Isolated adults male vs. female	2.37	not significant
Crowded adults male vs. female	2.31	not significant

As no significant difference was shown between the sexes, comparison using isolated and crowded distributions were made on combined male and female data.

In Table 17, the actual distribution of crowded and isolated conditions is compared with the average distribution expected of 64 readings per segment, i.e. 32 males and 32 females.

Table 17. Comparison of actual distribution of locusts from isolated and crowded rearings with average value by means of χ^2 test.

Rearing	χ^2 for 2 d.f.	Significance
Crowded (males + females)	35.17	$p < 0.001$
Isolated (males + females)	0.13	not sign.

The distribution of the crowded locusts was very significantly different from random. Inspection of the actual distribution (Table 15) shows that these locusts were in the empty segment very much less frequently than in either of the segments with decoys. There appeared to be no difference in the attractiveness of the segments with dead and live locusts; compare 80 times found in with dead decoys against 79 times in with live decoys.

In the isolated condition the distribution of experimental locusts was random. The decoys appeared to be neither attractive nor repulsive.

A contingency χ^2 comparison of the isolated and crowded distributions showed that there was a significant difference between the two ($\chi^2 = 13.30$, for 2 d.f., $p < 0.01$).

B. Considering within segment distribution.

Table 18 shows, in more detail, the distribution of locusts in those segments which had decoys; those locusts which were found within two body lengths of the decoys are compared for different rearing conditions, by means of an analysis of variance.

Table 18. The distribution of experimental locusts within the segments which had decoys.

Rearing \ Segment	Dead decoys		Live decoys	
	Outwith two body lengths	within two body lengths	outwith two body lengths	within two body lengths
Crowded	21	59 (73.8%)	19	60 (75.9%)
Isolated	27	39 (59.1%)	25	37 (59.7%)

When the data for those locusts within two body lengths of the decoys is compared by means of analysis of variance, it appears that dead and live decoys are equally attractive irrespective of rearing condition of experimental locusts ($F=0.11$, 1+1 d.f.). But there is a significant difference in the number of locusts that settle next to the decoys. Fewer isolated locusts than crowded ones stay within two body lengths of the decoys ($F = 205.44$, $p < 0.05$ for 1 + 1 d.f.).

DISCUSSION

B. Aggregation.

When it became apparent that it was not possible to demonstrate solitaria-type behaviour in aggregation tests on isolated immature adults reared and tested at A.L.R.C., several factors possibly responsible for this were investigated; firstly that the method of assessing aggregation prohibited the expression of solitarious behaviour; secondly that at the start of the test the adults were solitarious but rapidly changed to gregaria; or lastly that conditions of visual and tactile isolation were not sufficient to rear solitaria locusts in the A.L.R.C. laboratory. Should all of these considerations be eliminated, there was the possibility that the adult phase is one of aggregation irrespective of rearing conditions, age or maturation.

A. Method of assessing aggregation.

With the same technique as was used in the present aggregation tests, Ellis (1953, 1962) was able to show that hoppers reared isolated did not aggregate significantly. It was therefore thought likely that the possible difference in the technique of measuring aggregation was not one of pure design but of arena proportions. Below a certain proportional size of arena, any animal will be so restricted that no form of solitarious behaviour could be demonstrated by this method. No attempt was made in these experiments to compute the arena size in relation to size of adults to be tested. Not enough is known of this situation to enable one to equate external conditions, such as ratio of volume of arena to density of experimental animals, in young hoppers and in adults. It is not therefore

possible to ascertain the optimum or critical arena size for a given size of animal.

Tests on young, diapausing adults of the Red Locust, Nomadacris septemfasciata showed that these locusts formed no more groups than would be expected in a random distribution (χ^2 = 1.71 for 3 d.f.). Adult Nomadacris are the same size as Schistocerca adults, which eliminates the possibility that the grouping of isolated Schistocerca was solely a result of a quirk in the ratio of locust body size to arena size.

B. Rapid habituation during the test.

To investigate the possibility of very rapid gregarising in the isolated adults during tests, a more detailed analysis was made of each test performed on each of the isolated conditions. Regression analysis was carried out on the "within test" readings to check any change during the test. "Between test" variance analysis was also carried out to assess differences between different batches of locusts tested. This would show if a few tests were biassing the experiments. The results for the three different generations isolated are shown in Tables 19 and 20.

Table 19. Relationship between time during tests and distribution for 3 conditions of isolated immature adult Schistocerca.

Treatment	Coefficient of correlation	
1st generation isolated	0.140	not sign. for 54 d.f.
3rd generation isolated	-0.059	not sign. for 54 d.f.
5th generation isolated	0.102	not sign. for 46 d.f.

Table 20. Variance ratio for between test comparison of distribution for 3 conditions of isolation of immature, adult Schistocerca.

Treatment	Variance Ratio		
1st generation isolated	0.7269	(6, 42 d.f.)	not sign.
3rd generation isolated	0.4472	(6, 42 d.f.)	not sign.
5th generation isolated	0.8794	(5, 35 d.f.)	not sign.

There was no linear trend of distribution with time in the tests on any of the three different generations isolated: the animals were not gregarising during the tests. Similarly, there was no marked difference in distribution between tests: the population tested was homogeneous. If no demonstrable change was occurring during the tests, it must be assumed that the experimental animals were already behaving gregariously at the start of the test.

C. Conditions of isolation.

Ellis (1959) showed that the strongest influences which induced phase gregaria characters in laboratory locusts were tactile and visual stimulation. But as the precautions taken to eliminate these two influences were not sufficient to prevent the development of gregarious behaviour, airborne (auditory and olfactory) stimuli were also considered. An auditory influence was not thought likely to play a major part in determining the physiological state of isolated locusts. Sound is not known to be important in the behaviour of Schistocerca. Although Haskell (1957)

has shown that sounds emitted by adult Schistocerca during flight can be heard by other adults and Loher (1959) has demonstrated stridulation in mature males of this species, it was considered more likely that an olfactory stimulus would affect behaviour. Schistocerca produce several chemical substances, pheromones, which are involved in intraspecific communication. Mature male Schistocerca produce a pheromone which accelerates and synchronises maturation of other young adults (Norris 1954, 1964); ovipositing female Schistocerca secrete a pheromone which serves to concentrate egg-laying (Norris 1963), and there appears to be a hopper pheromone which also acts as a concentrating device (Ellis, unpublished). These last two pheromones do not act as attractants over a distance but serve to hold locusts within an area and the maturation pheromone works most effectively at short range.

In the present case if the stimulus that causes isolated Schistocerca to act in a gregarious manner is a pheromone, it must be one that acts over a distance of some feet at least in order to influence the locusts isolated in jars stacked on the roundabouts (see section on Materials). In 1963 Nolte was able to demonstrate, in similar circumstances, that such a pheromone affected pigmentation; isolated Schistocerca hoppers subjected to this factor developed the pigmentation typical of gregarious hoppers.

Two circumstantial factors were considered when proposing this hypothesis; that previous A.L.R.C. laboratories in which locust behaviour had been studied had a smaller background stock of crowded locusts and that Norris has observed a gradual reduction

in the maturation time of adult Schistocerca in three different A.L.R.C. laboratories over the last 20 years (unpublished). This would indicate that a build-up of pheromone could occur within a laboratory and so affect successive generations. This consideration would be very relevant in the case of the present A.L.R.C. laboratory which maintains very large stocks of locusts and where the laboratory air is recirculated and not completely flushed. Within the scope of tactile stimulation, there was a further possible stimulus that might induce gregarious behaviour; that the disturbance involved in daily feeding was acting as a tactile stimulus. Ellis (1959) has demonstrated that it is possible to shift the behavioural characteristics of hoppers from solitarious to gregarious by treating isolated hoppers to periods of stimulation by fine wires, thus mimicking the tactile stimulation experienced by crowded locusts. The stimulus of the fine, dry grass was not considered to be a very strong influence, or Ellis would never have been able to produce behavioural solitaries previously.

Three different experiments were set up to test these different hypotheses:- 1. Differential responses in adults and hoppers; 2. Olfactory influence from laboratory acting on adults and hoppers; and 3. the tactile stimulation experienced during feeding affecting behaviour.

1. In A.L.R.C. aggregation tests were carried out on 2nd and 4th instar crowded and isolated Schistocerca hoppers. While detailed comparisons between adults and hoppers were not attempted, the comparison with a random distribution was used as a mutual reference point to determine phase state.

2. To test the hypothesis of contamination in the A.L.R.C.

laboratory, a culture of isolated Schistocerca was set up in an otherwise locust-free laboratory in a new building of the Zoology Department, Edinburgh University. The conditions of rearing such as light regime, temperature, etc., were the same as in the A.L.R.C. laboratory, and identical conditions of visual and tactile isolation were established. The only difference in conditions, apart from the principal consideration of background stock of crowded locusts was that local grasses were used for feeding. It was not considered that this dietary difference would affect behaviour. The locust roundabouts were housed in a room of 10,000 litres cubic capacity with a ventilation system that gave approximately 8 air-changes per hour.

3. Complete elimination of external disturbance due to feeding was impossible in the 1.5 l. jars, particularly with older hoppers because of their large food requirements. For this reason it was decided to test 2nd instar Schistocerca hoppers as these could be successfully reared on growing wheat or grass, in isolation jars. It was found that only one change of grass in the 10 days of growth to mid-2nd instar hopper was necessary. To prolong the life of the growing turf or wheat, the clod of earth and roots was wrapped in a polythene bag to reduce evaporation. If this was not done, mortality of hoppers was high as the moisture required to maintain the grass alive resulted in too high a humidity for healthy growth of the hoppers. Comparisons were made of these undisturbed hoppers with 2nd instar isolated hoppers fed daily in the usual routine. A control experiment to eliminate possible effects of the polythene was carried out by placing a polythene bag in the bottom of jars in which normal daily feeding routines were observed.

Experiments.

1. On hoppers in A.L.R.C. laboratory.

Crowded and isolated Schistocerca hoppers were tested in the 2nd and 4th instar. Tests were made on 10 hoppers at a time at least 24 hours after moulting from the previous instar. No hoppers were tested more than once. As hoppers are more excitable than adults (see section on activity) 4 readings only were made in each 2 hour test, thus allowing $\frac{1}{2}$ hour for resettlement between readings. Hopper tests were carried out at 28°C as Ellis (1963a) used this temperature on Schistocerca and Locusta hoppers. In order that the number of readings should be comparable to the number of adult readings per experiment, twice as many tests were carried out on hoppers as on adults. Throughout this study no comparisons were made directly between different aged locusts, only between different rearing treatments within an instar.

Comparison of distribution was made by χ^2 contingency test and "t" test analysis as with the adults (see Table 21). The χ^2 value of distribution compared with random is shown in Table 6.

Table 21. Comparison of amount of grouping shown by 2nd and 4th instar Schistocerca subjected to isolated and crowded rearing conditions, tested at 28°C, standard error quoted.

Instar	treatment	no. of 2 hr. tests	χ^2 contingency for 3 d.f.	mean number in 3+ groups	"t"
2nd	crowded	14	13.72	49.4 ± 3.3	2.7922
	isolated	14	$p < 0.01$	35.6 ± 2.7	$p < 0.02$ (26 d.f.)
4th	crowded	14	1.45	30.0 ± 4.5	0.9579
	isolated	10	not sign.	34.2 ± 1.7	not sign. (22 d.f.)

It can be seen that, while isolated 2nd instar did aggregate significantly when compared with random (Table 6), it is possible to show a significant difference between the crowded and isolated treatments because of the very high grouping of the crowded hoppers.

Fourth instar hoppers also aggregated significantly irrespective of the rearing conditions experienced (Table 6); the difference between the two treatments was not significant. The 4th instar results were similar to those obtained by comparing isolated and crowded treatments in adults both in the magnitude of grouping and the lack of difference between treatments (Table 22). But the difference between 2nd and 4th instar was the amount of grouping shown by the crowded hoppers. There was a fall in grouping.

Table 22. Measure of differences in grouping between isolated and crowded Schistocerca at three different ages.

	Measure of difference			
Age	χ^2 contingency (3 d.f.)		"t" value	
2nd instar	13.72	$p < 0.01$	2.7922	$p < 0.02$ for 12 d.f.
4th instar	1.45	not sign.	0.9579	not sign. for 10 d.f.
immature adult	2.53	not sign.	0.7455	not sign. for 12 d.f.

2. On isolated adult and 2nd instar hoppers reared and tested at Edinburgh.

As it was essential to avoid contamination of isolated locust stocks at Edinburgh by any pheromone present, no crowded locusts were reared there. For this reason the A.L.R.C. crowded stock were used for comparison. Both Edinburgh and A.L.R.C. isolates were then compared with the same control.

Tests were carried out on hoppers as described in above section (A). Seventy isolated adult Schistocerca and 60 isolated 2nd instar Schistocerca hoppers were reared and tested at Edinburgh.

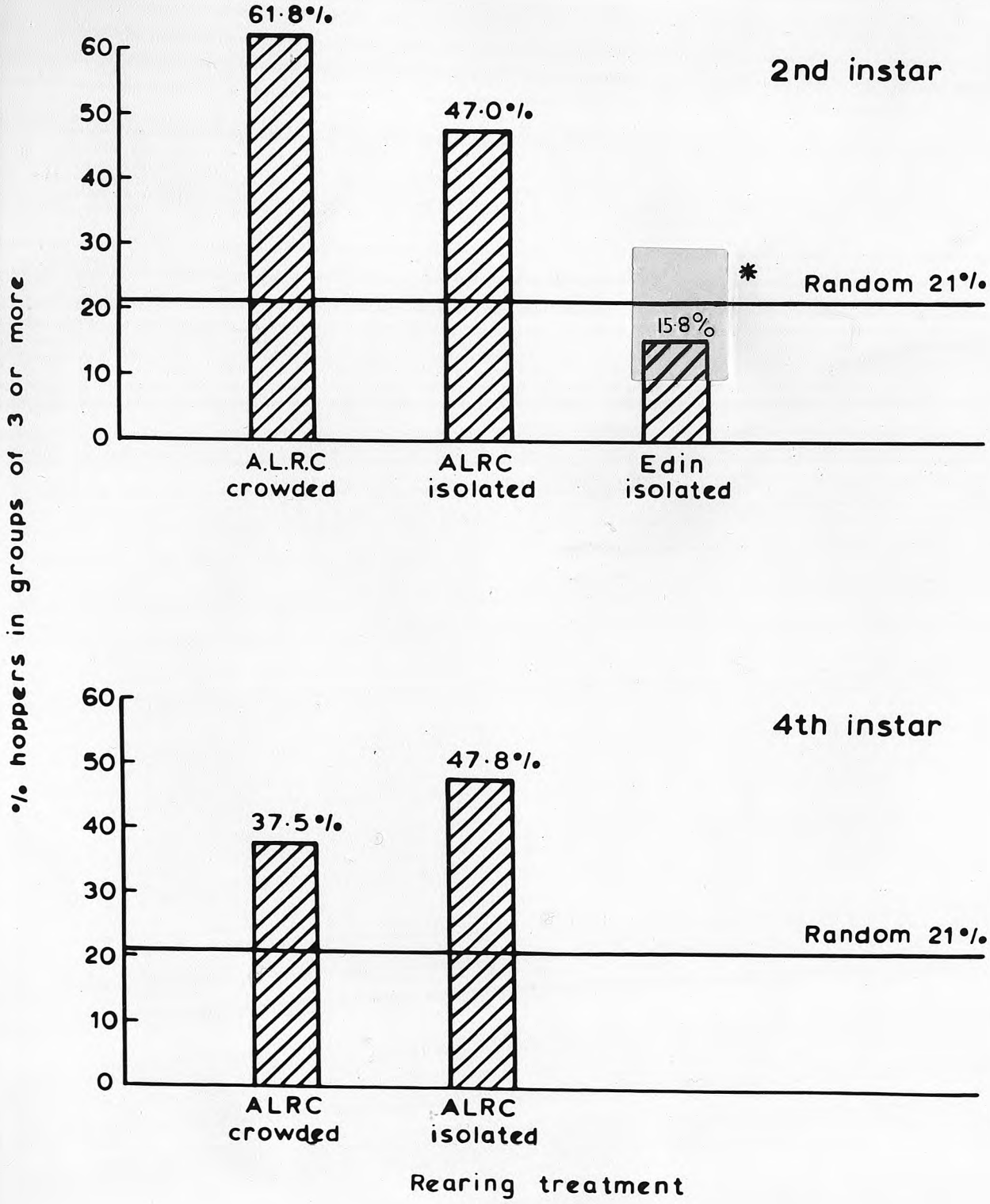
The results of this experiment are shown in Table 23 and Figs. IX and X a & b. To facilitate comparison the A.L.R.C. crowded and isolated Schistocerca results and Humbe results are also shown.

Statistical comparisons, using both methods of analysis, have been arranged in block diagrams.

FIG. IX

% SCHISTOCERCA HOPPERS IN GROUPS OF 3 OR MORE FOR DIFFERENT REARING TREATMENTS

* Distribution not significantly different from random



% ADULT *SCHISTOCERCA* IN GROUPS OF 3 OR MORE FOR DIFFERENT REARING TREATMENTS

(*Humbe tenuicornis* included for comparison)

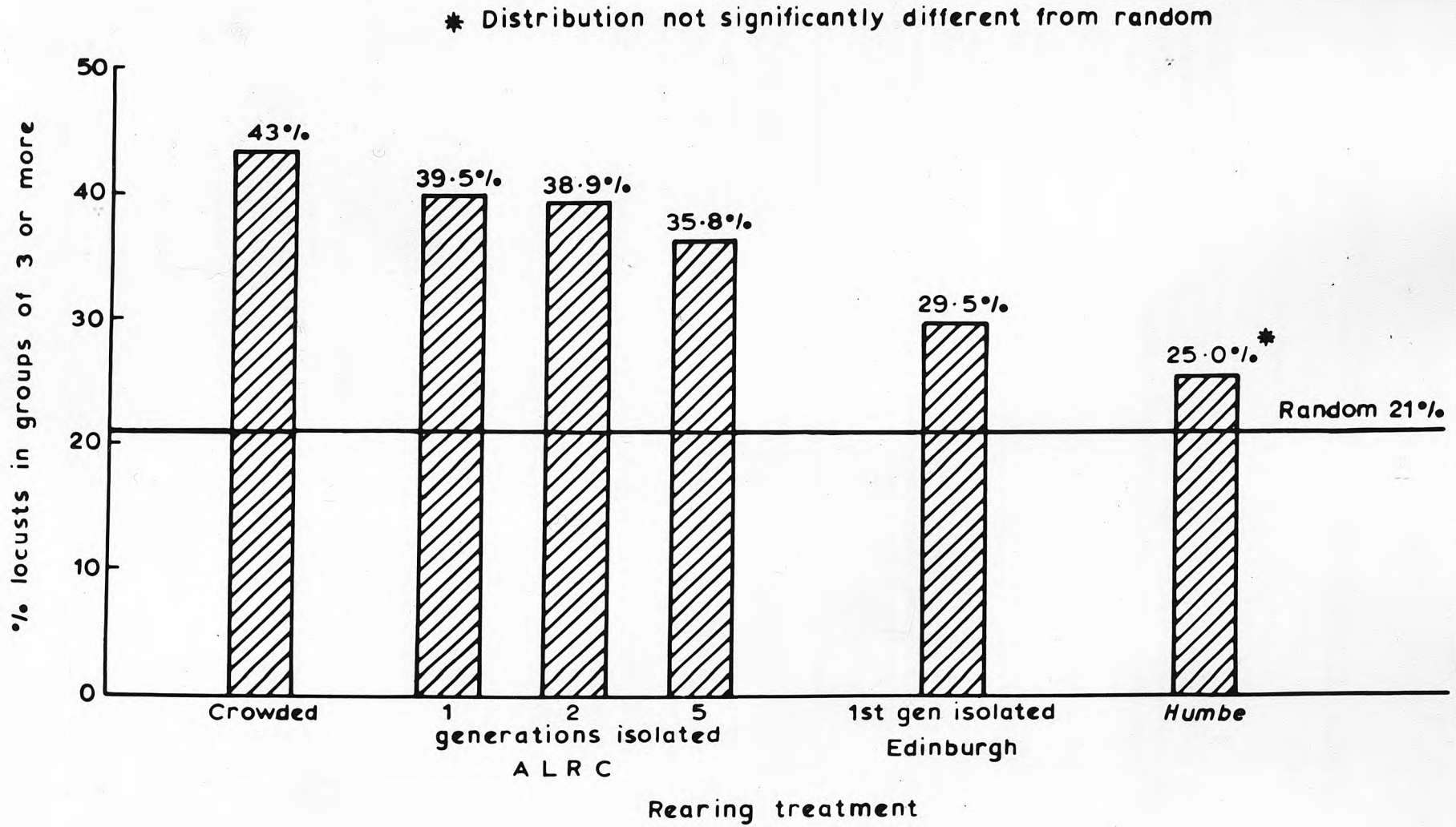


FIG. X a

MEAN NUMBER OF LOCUSTS IN GROUPS OF 3 OR MORE FOR DIFFERENT REARING CONDITIONS OF *SCHISTOCERCA* AND FOR CROWDED *HUMBE*; STANDARD ERROR QUOTED

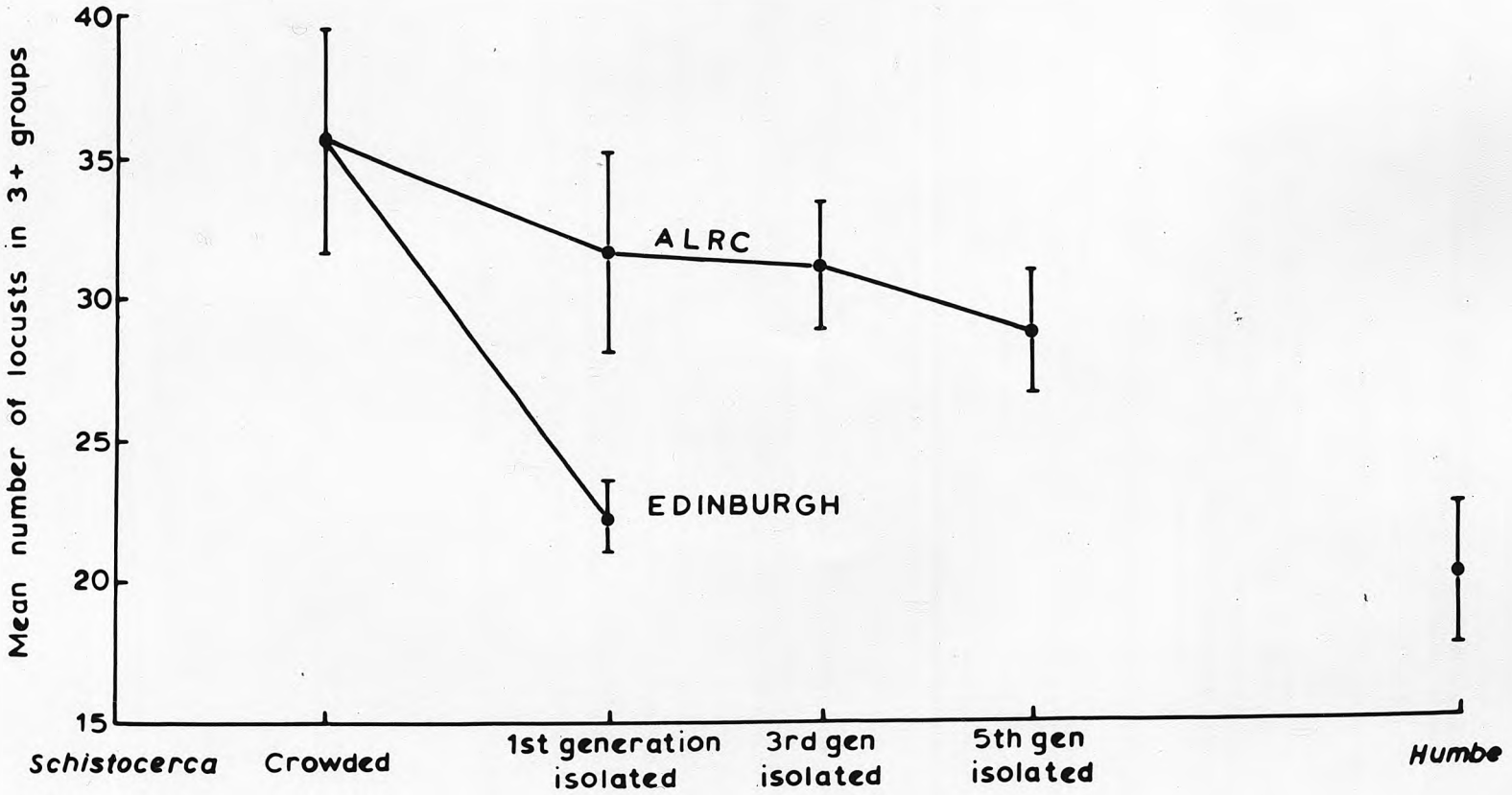


FIG. X b

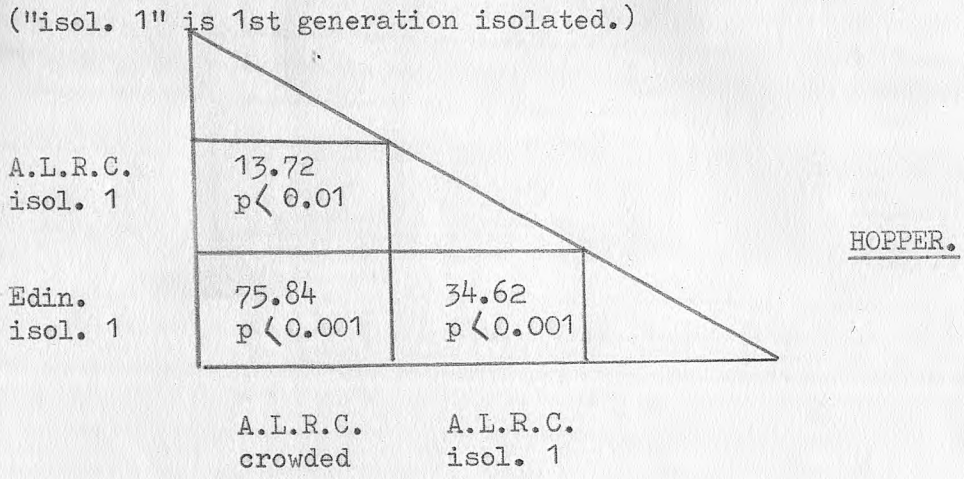
Table 23. Results of aggregation tests on isolated 2nd instar hoppers and immature adult Schistocerca reared and tested at Edinburgh University, given as χ^2 comparison of distribution with random distribution and mean number of locusts in groups of 3 or more.

Rearing treatment	No. of tests	χ^2 with random (3 d.f.)	Mean no. of locusts in 3+ groups
ADULTS			
Schistocerca			
Edinburgh 1st gen. isolated	7	8.80 $p < 0.05$	23.6 ± 1.3
A.L.R.C. crowded	7	70.96 $p < 0.001$	35.7 ± 4.1
A.L.R.C. 1st gen. isolated	7	40.37 $p < 0.001$	31.6 ± 3.5
Humbe			
crowded	7	0.51 not sign.	20.0 ± 2.6
2nd Instar			
Schistocerca			
Edinburgh isolated	6	5.88 not sign.	12.7 ± 7.8
A.L.R.C. crowded	14	202.26 $p < 0.001$	49.4 ± 3.3
A.L.R.C. isolated	14	89.92 $p < 0.001$	37.6 ± 2.7

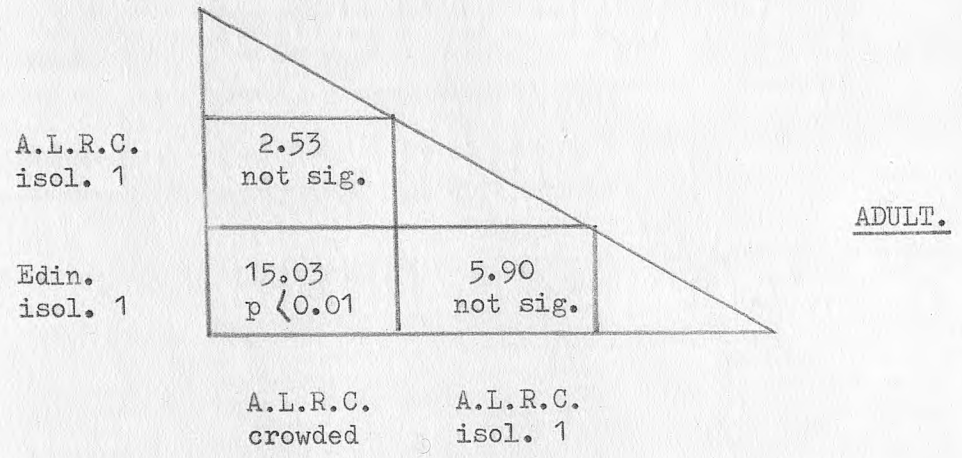
Block diagrams to show comparison between different rearing treatments.

1. Contingency χ^2 comparison of total distributions. (3 d.f.)

("isol. 1" is 1st generation isolated.)

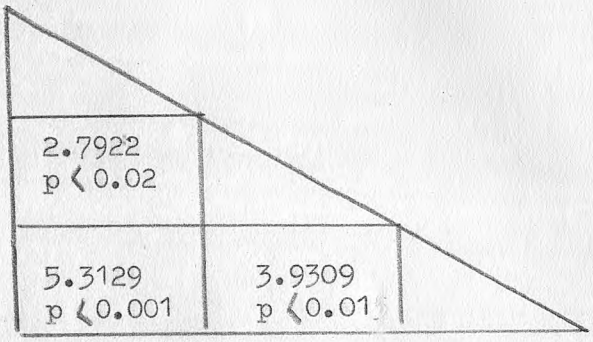


HOPPER.



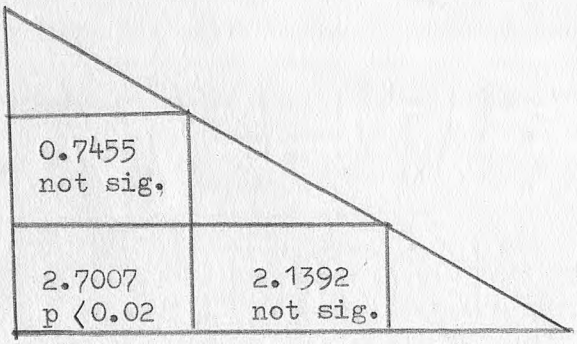
ADULT.

2. "t" test comparison of mean number of locusts in groups of three or more.



HOPPER.

(for degrees of freedom, see table)



ADULT.

(12 degrees of freedom.)

As was mentioned previously, it is possible to show a significant difference in grouping between 2nd instar hoppers reared under different density conditions at A.L.R.C., in spite of a significant degree of aggregation shown by the isolated hoppers. When comparison is made between isolated and crowded hoppers from A.L.R.C. and isolated hoppers from Edinburgh, it is seen that the Edinburgh stock is much nearer the solitaria condition. The χ^2 value of 5.88 for isolated 2nd instar Edinburgh hoppers shows that their distribution was not significantly different from

random while contingency test comparison and "t" test analysis shows that Edinburgh isolated hoppers are significantly different from A.L.R.C. isolated hoppers: the difference between the Edinburgh isolated and A.L.R.C. crowded conditions is even greater than the difference between A.L.R.C. isolated and crowded conditions.

A similar comparison of the adult conditions tested also showed a difference between the locusts reared in the two laboratories, although it was not as marked as in the 2nd instar tests. Direct comparison of isolated adult stock in the two laboratories does not show a significant difference by either form of statistical analysis. However, some differences between the two stocks do exist; while A.L.R.C. isolated and crowded adults are not significantly different, isolated Edinburgh adults are significantly different from crowded A.L.R.C. adults.

The comparison of the grouping of Edinburgh isolated adults with that of the solitarious Nomadacris and with the hypothetical solitaria (see p. 36) is made in Table 24. (see p. 57)

While the Edinburgh isolates are significantly different from the extreme hypothetical solitaria, they are not significantly different from the Nomadacris adults that have been demonstrated as exhibiting solitarious behaviour, see Table 6. Both adult and 2nd instar locusts reared isolated in the locust-free environment at Edinburgh behave in a more solitary manner than did isolated locusts at A.L.R.C..

Table 24. "t" test comparison of the mean number of locusts in groups of three or more for Schistocerca adults reared isolated at Edinburgh with that of the two equivalents of the solitaria morph.

	Nomadacris 20.1 ± 2.2	Hypothetical 18.0 ± 0.0
Edinburgh isolated adult Schistocerca 23.6 ± 1.3	1.3361 not sign.	4.3244 $p < 0.001$

Ten of the Edinburgh adults were taken to A.L.R.C. and retested there. These were the last of the Edinburgh culture to become adult; seven out of the ten had passed through an extra instar. They were retested for 2 hours, once a day, for 4 consecutive days. By the end of these tests, the adults had experienced 10 hours social experience in low density conditions (i.e. 10 locusts in 72.5 litres). Between tests the adults were isolated in 1.5 litre jars and kept in the A.L.R.C. constant temperature laboratories.

As a more detailed investigation was required of the effects of social experience over the test periods and of the effect of exposure to a possible pheromone in the A.L.R.C. laboratory, analysis was made on each test individually as well as on the summed distribution for the tests.

The results from each test shown in Table 25 demonstrate the consistency of the behaviour over this period.

Table 25. Readings from retest experiments carried out at A.L.R.C. on isolated adult Schistocerca reared and first tested at Edinburgh.

No. of animals per segment	No. of segments with 0, 1, 2 or 3+ animals over two hours.						Total
	Random	Edinburgh 1st test	A.L.R.C. retest 1	2	3	4	
0	28	27	26	29	28	38	148
1	31	34	39	32	30	25	160
2	15	13	8	12	18	8	59
3+	6	6	7	7	4	9	33

Table 26. χ^2 values for each test individually compared with random value as shown above.

No. of test	χ^2	Significance for 3 d.f.
Edinburgh	0.59	-
A.L.R.C. 1	5.64	-
A.L.R.C. 2	0.83	-
A.L.R.C. 3	1.30	-
A.L.R.C. 4	9.50	$p < 0.05$

Distributions in all of the tests were very similar except for the last one, which gave a distribution just significantly different from random.

When the distributions of the 5 tests are summed and then compared with the random distribution (the routine analysis employed in all previous experiments) the total distribution is not significantly different from random (χ^2 = 4.33 for 3 d.f.) even though one of the tests, the last, showed significant grouping.

While there was no consistent trend in grouping over the five tests, it is interesting that significant grouping was occurring during the final test. This could conceivably be due to the 10 hours social contact experienced by the experimental adults, to the exposure to some olfactory contaminant in the A.L.R.C. laboratories, or to both influences.

Non-behavioural measurements of phase.

In the course of the Edinburgh experiment, several other phase parameters were measured, on isolated and crowded adults at A.L.R.C. and isolated adults at Edinburgh. The adult morphometric characters of elytron length (E), femur length (F) and head width (C) were measured and the number of eye-stripes noted. As it was not possible to make any observations on the colour of the hoppers reared at Edinburgh, no colour comparisons were made between laboratories. Because of the long delay involved in the maturation of isolated Schistocerca females, no comparison was made of ovariole numbers with A.L.R.C. females reared isolated and crowded.

The morphometric measurements are quoted in Appendix II. A Generalised Distance Diagram (Stower, Davies & Jones 1960) was used to compare the morphometrics of the two laboratory cultures with each other and with a reference field population; in this case

the cool population from the Red Sea Coast (Fig. XI).

As can be seen from the diagram, both laboratories produced locusts intermediate between the solitaria and gregaria forms of the field population. The laboratory crowded and isolated were transiens. But within this range there is some difference between the different rearing conditions. The Edinburgh isolated adults were nearer the solitaria pole than were the A.L.R.C. isolates. There was very little difference in morphometrics between A.L.R.C. isolated and crowded conditions particularly in the females.

Twenty-five of the 69 Edinburgh isolated adults (36%) had the 7th eyestripe characteristic of the solitaria phase. All 36 of the A.L.R.C. isolated adults measured for this character had only 6 eyestripes as did all 37 of the crowded adults examined.

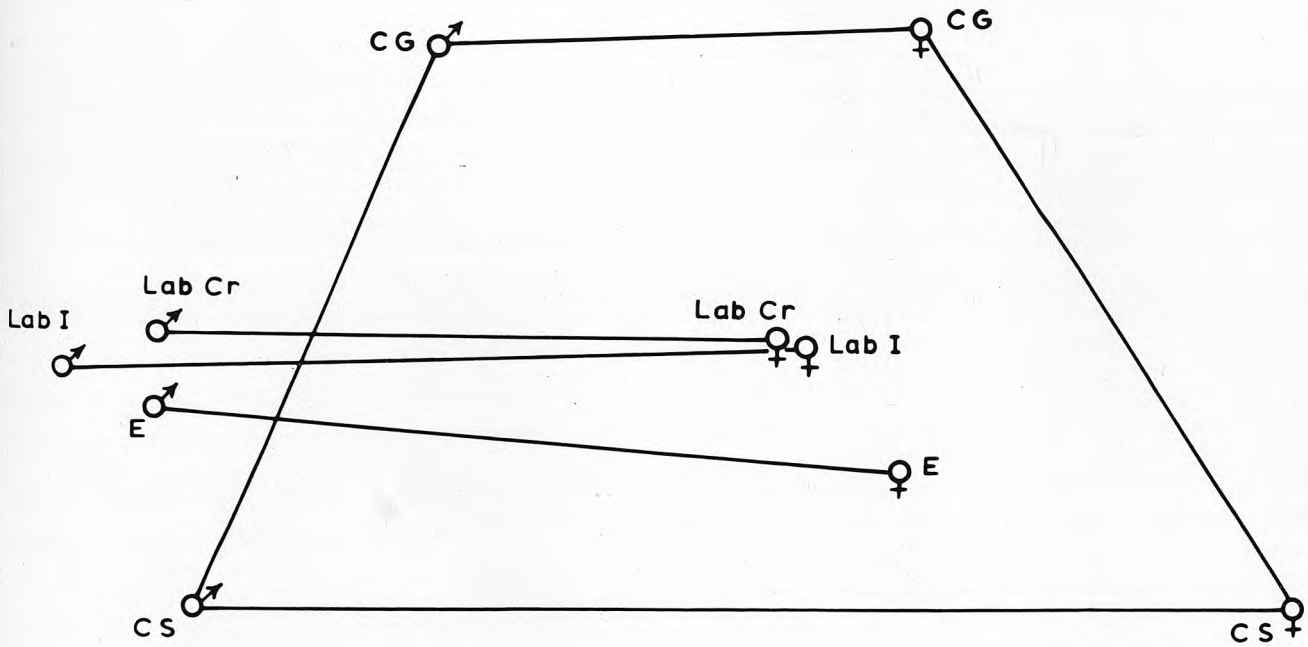
It appears that both behavioural and anatomical parameters of phase are affected by the different conditions in the Edinburgh laboratory.

3. On possible effect of disturbance during feeding.

This experiment was carried out at A.L.R.C. on 2nd instar Schistocerca hoppers reared isolated, and fed on growing grass, the roots of which were tied up in a polythene bag. This avoided the daily disturbance caused by the usual method of feeding with cut grass; only one change of grass was then necessary during the rearing period. It is known (Slama & Williams 1956) that certain chemicals present in some wood pulps and paper can affect the physiology of insects and it is conceivable that behaviour could be affected by the presence of the polythene. To estimate the

FIG. XI

GENERALISED DISTANCE DIAGRAM COMPARING THREE LABORATORY CULTURES WITH A FIELD POPULATION BY MEANS OF MORPHOMETRIC ANALYSIS



C Field population bred on Red Sea Coast in cool temperature conditions

S Solitarious

G Gregarious

Lab Cr ALRC crowded

Lab I ALRC isolated

E Edinburgh isolated

influence of this potential contaminant, another experiment was carried out in which 2nd instar hoppers were tested after being isolated and fed in a normal fashion but with a polythene bag left in the jar.

Comparison of grouping was made with the isolated A.L.R.C. 2nd instar hoppers tested previously in Section 1 above, Table 23. The χ^2 comparison with random is shown in Table 6.

Table 27. Amount of grouping by isolated 2nd instar hoppers, and isolated undisturbed 2nd instar hoppers.

Rearing condition	Mean no. of locusts in groups of 3 or more
Isolated normal feeding	37.6 ± 2.7
Isolated undisturbed	33.6 ± 5.6
Isolated normal feeding and polythene bag	42.6 ± 5.8

A "t" test comparison of mean number of locusts in groups of three or more between polythene combined with daily feeding and polythene combined with the original undisturbed condition does not show any significant difference in the amount of grouping ("t" = 0.7030, 10 d.f.).

Similarly, comparison of total distribution by means of a χ^2 contingency test showed no difference between these three rearing treatments (Table 28).

Table 28. χ^2 contingency comparison of distribution of 2nd instar hoppers subjected to three different feeding treatments.

	χ^2 contingency	Significance at 3 d.f.
Isolated normal feeding vs. isolated undisturbed	3.5203	not sign.
Isolated undisturbed vs. isolated normal and polythene	5.1116	not sign.
Isolated normal feeding vs. isolated normal and polythene	3.2550	not sign.

Relationship between two criteria of phase.

During the course of the experiments on isolated hoppers the relationship between the colour of the hoppers and the numbers of hoppers aggregating was investigated.

The colours of these hoppers ranged from the solitarious pale beige or pale green with no black pigment to the full yellow and black pigmentation typical of the gregarious phase. For these experiments no attempt was made to classify the hopper colours in the detail of the scheme established by Stower (1959). Hoppers that were totally green and intermediate forms that had a green background to the black pigmentation were classified as green.

This rough division may be compared with the colour scheme erected by Ellis (1959) for 2nd instar Schistocerca hoppers. Her "a" and "b" classes are equivalent to 'black' here, and her "c" and "d" classes to "green".

The number of "green" hoppers in each test of 10 hoppers was noted and this was correlated with the number of locusts found in groups of three or more. Data were obtained from tests on both isolated and crowded hoppers. The results are shown in Table 29 and the regressions plotted in Figs. XII and XIII.

Table 29. Relationship between the number of "green" hoppers per test and number of locusts found in groups of three or more Schistocerca hoppers.

Age	Correlation coeff.	Regression coeff.
2nd instar	-0.4460 $p < 0.05$ for 23 d.f.	-0.9349
4th instar	0.0695 not sign. for 22 d.f.	0.1451

Second instar hoppers show a small significant negative correlation between colour of experimental animals and the size of groups they form; the more green hoppers per test the fewer are the groups of three or more formed. This relationship is not shown by 4th instar hoppers.

FIG. XII

REGRESSION OF NUMBER OF HOPPERS IN 3+ GROUPS ON NUMBER OF GREEN HOPPERS PER TEST

2nd INSTAR *SCHISTOCERCA G.*

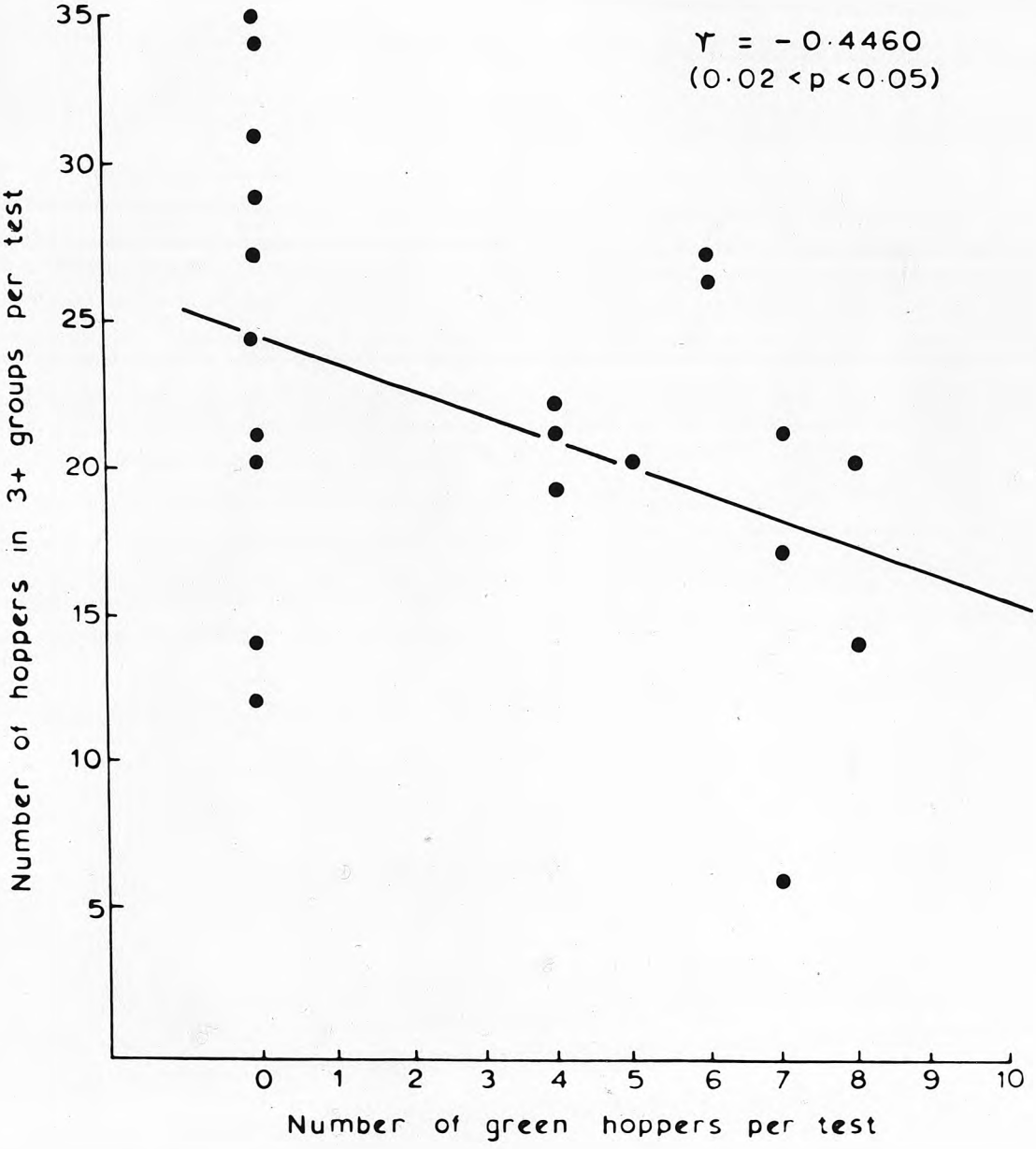
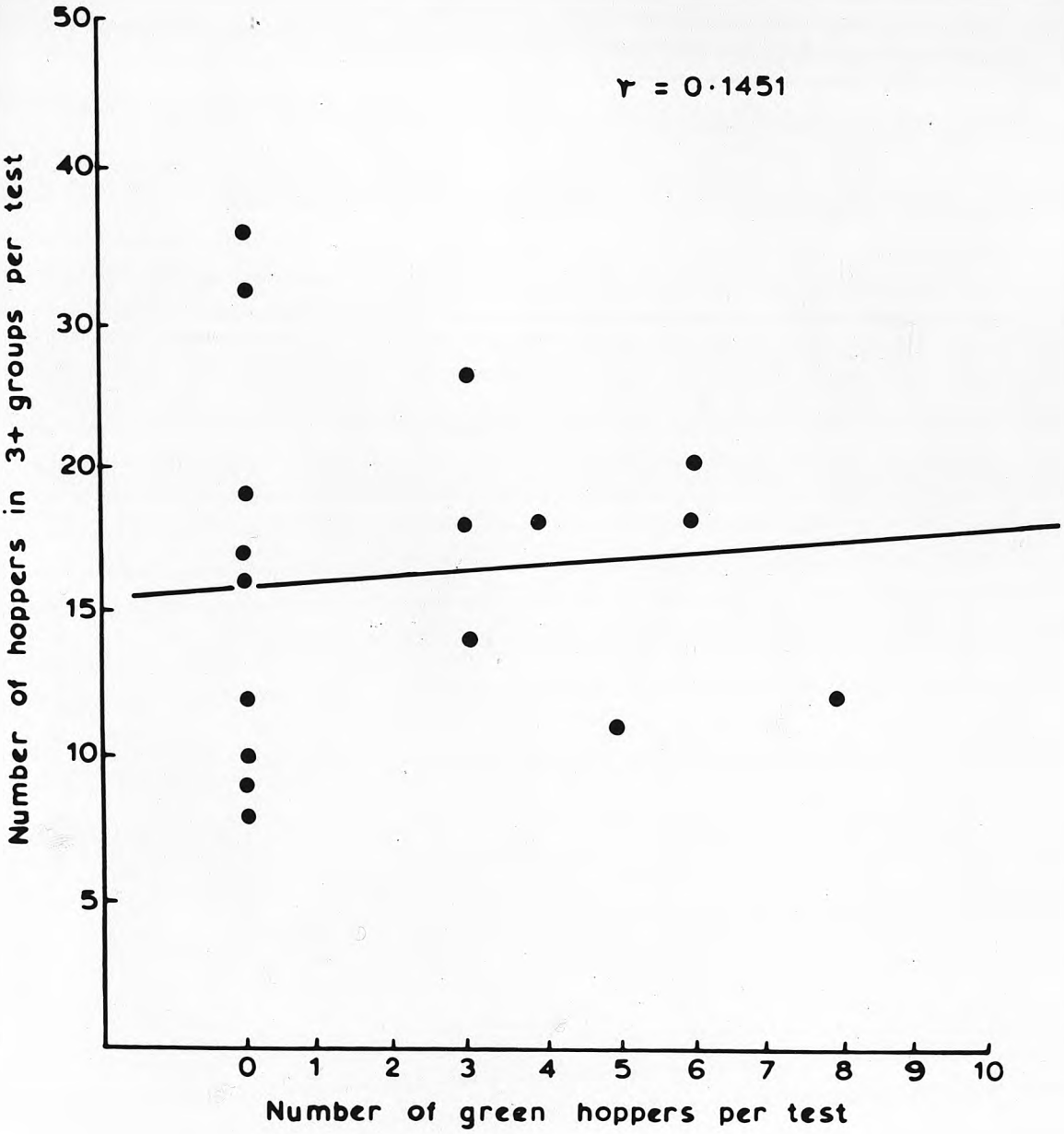


FIG. XIII

REGRESSION OF NUMBER OF HOPPERS IN 3+ GROUPS ON NUMBER OF GREEN HOPPERS PER TEST

4th INSTAR *SCHISTOCERCA G.*



DISCUSSION.

C. Aggregation.

The amount of aggregation that can be expected, in the form of stable groups, is necessarily dependent on the level of activity of the experimental locusts. Schistocerca do not show any significant difference in activity at the two temperatures 28°C and 32°C under disturbed conditions, nor is there any significant difference in the amount of grouping at these two temperatures. Locusta, however, appear to be more sensitive to the temperature difference although what constitutes a significant difference in activity is very small; at 28°C activity is 1.9 ± 0.5 s.d. units and at 32°C 1.3 ± 0.5 s.d. units. The means differ by 0.6 unit, only 6% of the 10 units maximum possible difference. This difference is insufficient to affect noticeably the amount of grouping although there is a consistent trend for both species in that lower activity and higher grouping occur at the higher temperature.

Schistocerca show a small significant difference in activity between morning and afternoon testing times (5% of 10 activity units). A difference in behaviour is shown also by one of the two methods of assessing grouping. In the afternoon, when activity was higher, grouping was significantly reduced.

Because this difference was small and could only be shown by one of the analytical methods, and because very significant aggregation was occurring in both the morning and afternoon, it was decided to combine the results from morning and afternoon tests. A balance of the two was maintained in each experiment. This allowed a good deal more work to be completed than would have been possible by restricting tests to mornings or afternoons.

If laboratory locusts do not show a diurnal rhythm independent of environmental conditions (see Activity section), it is difficult to explain the small significant difference in grouping shown by Schistocerca tested morning and afternoon. It is conceivable that morning-tested Schistocerca were better fed, having recently eaten fresh grass, but the grass was still available to afternoon-tested locusts which were by no means starved. It may be that the morning-tested locusts had all eaten synchronously but that by the afternoon the $2\frac{1}{2}$ hour hunger cycles were out of phase. Thus some of the locusts were more hungry than others despite the available grass. It would be interesting to synchronise afternoon feeding by removing food for a few hours, then replacing the food and testing the locusts an hour after feeding commenced. This regime is effectively what morning-tested locusts experience, as little food is left overnight prior to the morning feeding. If this eliminated the difference between morning and afternoon activity and grouping, it would establish that leaving fresh food in the cage does not necessarily mean that all the Schistocerca are sufficiently well-fed for behavioural tests. If this is the explanation, Locusta appears to be less sensitive to hunger. Ellis (1951) found that marching activity in Locusta hoppers is directly related to the time of starvation. Phipps (1963) found that for Schistocerca 1st instar hoppers there was no consistent relationship between morning activity (after 12 hours starvation) and afternoon activity (5 hours starvation), but his tests were carried out right through the instar and were influenced by the nearness of the moult as afternoon activity was higher than morning activity in the middle of the moult but the reverse was the case near the end of the instar.

Neither for crowded Schistocerca nor for Locusta was it possible to show any significant fluctuation in grouping with age from the 5th instar to adult maturation. It may be that the expected dispersal behaviour occurs immediately after fledging; testing this is complicated by the disruption of behaviour, such as a drop in activity, which is known to occur around the time of moulting due to physiological changes which occur, particularly in the final moult (Edney 1937, Ellis 1951, Phipps 1963). It may of course be that the dispersal behaviour observed in the field is associated with the final moult (although activity is reduced around the time of moult) or that the stimulus and/or means of dispersal are the local climatic conditions as suggested by Rainey (1962). It is not possible to determine this from the experiments carried out in this study. The field dispersal is unlikely to be innate and this is in keeping with the flexibility of locust behaviour and the lack of marked circadian rhythms in the laboratory.

It would be interesting to extend the experiments on mature adults of both species which in these experiments showed the lowest level of grouping. From the work of Norris (1963) it is known that ovipositing Schistocerca females show a high level of grouping behaviour. In the present apparatus oviposition is prohibited and this would probably result in increased activity and reduced grouping as females searched for laying sites. An attempt was made to test mature Schistocerca females, alone without males, but 5 out of the 8 tests (62.5%) were abandined because marching occurred. This may be compared with 10 tests abandoned out of 111 tests (9%) of all other tests on 5th instar and adults of both species. This high proportion of marching may have been induced by a few females in each test being ready to lay, searching for oviposition sites

and communicating their restlessness to the other females. Perhaps in the mixed-sex tests on mature adults, the males act to dampen the activity of the females. This might easily occur if the males were less sensitive to the activity of the few very active females and so the initial marching behaviour did not "snowball" in the characteristic manner of locust swarming behaviour.

Comparison of the variance of the mean number of locusts in groups of three or more showed that in half the experiments adult locusts were more variable than 5th instar hoppers. A comparison of the variances from different hopper instars (shown in Table 30) taken from different grouping experiments on Schistocerca showed that 2nd instar hoppers exhibit a variability that was significantly larger (at the 5% level) than that of the 5th instar hoppers.

Table 30. Variance of amount of grouping of different instars of crowded Schistocerca hoppers compared with 5th instar hoppers.

Instar	Variance	Variance Ratio compared with 5th instar (6 & 6 d.f.)	
2nd	63.4	5.47	$p < 0.05$
4th	11.0	0.95	not sign.
5th	11.6	-	-

It appears that there is no consistent trend in variability throughout the instars although the 4th and 5th instars show more repeatable behaviour than 2nd instar or adults. It would be desirable to test 1st and 3rd instar also for this variability.

It is difficult to assess the validity of the above comparisons. Care has been taken in this study to avoid making detailed comparisons between instars tested in different size arenas. It could be that the ratio of animal to arena size affects not only the degree of grouping but also the range or variability of that grouping. The ratio of body size to available space might affect the balance, in the crowded locusts, of the tendency to move about the arena with the tendency to form groups.

The choice experiments carried out on adult Schistocerca do distinguish to some degree between the behaviour of the isolated and crowded locusts. Isolated locusts behaved in a random fashion in this situation, but not in the aggregation tests. The experimental conditions were not, however, very dissimilar in both situations; approximately the same space was available (72.5 litres) and approximately the same number of decoys (9 in the aggregation tests, 6 in the choice tests). Presumably the choice situation is more sensitive in testing for behavioural phase polymorphism. It is possible for the single experimental animal to stay in the empty segment but this is more difficult to achieve in the aggregation experiment when the 10 animals are mobile, even though there is sufficient space.

In these choice experiments neither crowded nor isolated locusts distinguished between live and dead locust decoys. Norris (1963) found that crowded ovipositing females show a preference for live decoys when given the two alternatives.

It would have been interesting to test some of the more solitary Edinburgh culture in the choice situation to observe

whether their distribution was random or whether they were found in the empty segment more often than were the A.L.R.C. isolated locusts. Solitary hoppers are known to be attracted to some degree towards live hoppers and artificial decoys, but unlike gregarious hoppers move away in response to contact by other locusts (Ellis & Pearce 1962), so it is possible that adult isolates may not show totally asocial behaviour.

The greatest apparent difference between the isolated cultures at Edinburgh and A.L.R.C. was in their background stock of locusts. For this reason it was considered that the gregarious behaviour of isolated A.L.R.C. adults and hoppers was most probably due to some contaminant from the very high density of crowded stocks of several species of locust at A.L.R.C.. This postulated olfactory contaminant, or pheromone, is thought to act as a "primer" rather than a "releaser" pheromone (Wilson & Bossert 1963), since it changes the physiological state of the animal rather than releasing a particular behaviour pattern. Nolte (1963) has found that an olfactory agent in a locust laboratory affects the melanisation of isolated locust stocks, and results in laying-down of the heavy black pigmentation associated with phase gregaria.

There are certain circumstantial factors that support this hypothesis of a "gregarising pheromone". Several pheromones are established in locust biology. One acts to accelerate maturation (Norris 1954); another as a releaser to concentrate oviposition sites of laying females (Norris 1963); and another acts over a short distance to hold hoppers in groups (Ellis unpubl.). Olfactory cues are also important in food-searching behaviour (Haskell, Paskin

& Moorhouse 1962) and in sexual behaviour (Loher 1960). The locust is well endowed with olfactory receptors, both on the antennae and on the rest of the body. It is not inconceivable that an olfactory stimulus should change locusts' behavioural state as well as their physiological state.

Analysing this trend towards gregarious behaviour by isolated hoppers is difficult because at the same time there is a fall in the amount of grouping shown by the older crowded hoppers and adults as compared with the 2nd instar (Table 31).

Table 31. The amount of grouping shown by crowded Schistocerca hoppers and adults.

Stage	Mean no. of locusts in groups of 3+	No. of locusts in groups of 6+ (out of 560)
2nd instar	49.4 ± 3.3	108
4th instar	30.0 ± 3.5	32
5th instar	36.1 ± 1.4	32
10-day adult	35.7 ± 4.1	38

No attempt is made to quantify this trend as the experiments were carried out in different sized arenas and hopper size in relation to arena size could bias the results. It appears, however, that the crowded 2nd instar hoppers group more than subsequent instars as indicated by the mean number of locusts in groups of three or more and the number of locusts found in large groups (6 or more). It

would be interesting to establish whether grouping of gregarious locusts is affected by available space. Presumably gregarious locusts will group independent of arena size (as long as they are within visual range of one another), whereas solitary locusts will spread out to occupy all the available space.

Kennedy and Crawley (1967) have observed that one species of aphid, Drepanosiphum platanoides, does not show the usual tight aggregations of other aphid species. This species exhibits "spaced-out gregariousness" as each individual within the group preserves an "envelope" of space around it. This phenomenon is related to the production of the more agile winged form and the consequent reduction in predation. It is possible that such "spaced-out" grouping is responsible for the drop in grouping shown by the crowded adults. A disturbed adult would need more space in which to fly away than a disturbed hopper would need to walk away. Two observations make this explanation unlikely; that there is also a fall in grouping of 4th and 5th instar crowded compared with the grouping shown by 2nd instar crowded hoppers, and that adults can be seen in very dense groups in the laboratory cages and in the field.

There are two further possible explanations for this reduced grouping on the part of crowded adults. Phipps (1963) found that later instars of Schistocerca spent more time in locomotion than did earlier ones. The more active the locusts are, the less likely they are to maintain large, stable group formations; this could presumably explain the low grouping. Phipps, unfortunately, did not test adult activity and it is not very profitable to attempt to compare results of Phipps with those of Ellis (1953), who used different methods of activity measurement on different hopper

species, or to compare Ellis' results with those of the present study, using the same method of study but different locust species and ages. Comparison of locomotor activity and amount of group formation through the life of both species would be interesting.

The other consideration is that the conditions in the crowded cages are different at different stages in the life of the locusts. Not only does the bio-volume of animals in a standard size of cage change, but also the amount of stimulation received changes. Assuming an adult measures roughly 7 cms x 1 cm^2 (legs excluded) and a 2nd instar hopper 1.5 cm x 0.2 cms^2 (legs excluded), the bio-volume changes from approximately 54 cms^3 locust (900, 2nd instar) to 1400 cms^3 locust (200, adults). But the 2nd instar hoppers will afford each other more social intercourse because of their larger numbers than will the adults (the greater activity and reactivity of the younger hoppers has already been discussed) and may by this approach be experiencing more gregarious conditions than the adults and older hoppers.

It is difficult to assess the difference in the degree of solitary behaviour shown by Edinburgh adults and 2nd instar isolates. Once again only the most general comparisons can be made between different stages because of differences in arena size. Despite this handicap there appears to be a genuine difference in the aggregation behaviour of the 2nds and adults. Table 32 shows the amount of grouping shown by different stages of isolated Schistocerca in the two laboratories.

Table 32. The amount of grouping shown by isolated Schistocerca hoppers and adults in A.L.R.C. and Edinburgh laboratories.

Stage	Mean no. of locusts in groups of 3+	No. of locusts in groups of 6+
2nd A.L.R.C.	35.6 ± 2.7	12 out of 560
4th A.L.R.C.	34.2 ± 1.7	14 400
adult A.L.R.C.	31.6 ± 3.5	0 560
2nd Edinburgh	12.7 ± 7.8	0 240
adult Edinburgh	23.6 ± 1.3	6 560

From the table it can be seen that the amount of grouping shown (as measured by mean number of locusts in 3+ groups) is roughly similar for 2nds, 4ths and adult isolated locusts at A.L.R.C.. But Edinburgh adults show 50% higher grouping compared with Edinburgh 2nd instar. It may be remembered that this trend is the reverse of that shown by the crowded A.L.R.C. stock (see Table 30), where the adults form approximately 25% less groups than do the 2nd instar.

The adults show the behavioural extremes of phase ploymorphism less clearly than do the 2nd instar. Possibly the adult isolated in Edinburgh are susceptible to the accumulation of their own pheromone in the jars in which they are kept. This could easily be tested by changing the isolation jars daily.

Comparison of Table 31 and Table 32 also shows up differences

between the isolated and crowded rearings at A.L.R.C. in respect of the numbers of animals forming large groups (6 or more). In Table 33 a χ^2 contingency comparison is made of the distribution of locusts in groups of less than and more than 6 between isolated and crowded A.L.R.C. locusts.

Table 33. χ^2 contingency comparison of the distribution of locusts in groups of less than 6 and groups of more than 6 between isolated and crowded rearings at A.L.R.C..

Stage	χ^2 contingency	Significance (1 d.f.)
2nd instar	86.02	$p < 0.001$
4th instar	2.51	not sign.
adults	39.33	$p < 0.001$

Both 2nd instar and adult stages show a significant difference in the proportion of locusts in groups larger than 6+. Inspection of the raw data in Table 31 and Table 32 shows that in both cases crowded locusts formed more of these larger groups than did isolated locusts. The difference in the number of locusts found in the large groups was not significant for isolated and crowded 4th instar. This was because the isolated locusts were forming as many large groups as the crowded ones.

There is no significant difference in the mean number of locusts in 3+ groups for isolated and crowded adults at A.L.R.C.

(see Table 14), yet there is a difference in the number of locusts in groups of 6+. It must be that isolated A.L.R.C. adults form more groups of intermediate size (3 to 6) and so make the total number of locusts grouping comparable to that of crowded locusts which tend to form the larger groups.

The comparative analysis of the two phase characteristics, behaviour and colour, shows that colour is not a reliable criterion of the behavioural phase state of hoppers even in the relatively constant conditions of the laboratory. In the 2nd instar there is a small significant correlation between green colour and small-sized groups, but this correlation is lost by the time of the 4th instar. Ellis (1964) has shown that colour changes associated with changes in social experience do occur but that these are slower than the accompanying behavioural changes. This is substantiated in the present study, where no difference can be shown between the grouping behaviour of isolated and crowded 4th instar hoppers at A.L.R.C. but the colour of the isolates is not fully gregarious. From these experiments behaviour appears to be more sensitive to the olfactory stimulus than colour. (This is in contrast to the maturation pheromone which can cause very rapid colour changes.) It is in keeping with Ellis' findings that to induce full gregarious colouring in isolated hoppers the hoppers must be exposed to the full range of stimuli, tactile and visual. Similarly Chauvin (1941) found that full gregarious colour was only obtainable when hoppers were reared crowded with their own species.

Unfortunately it was not possible to carry out further tests on the Edinburgh isolated culture. With this material it would have

been possible to investigate the time and density of crowding necessary to induce gregarious behaviour and this might have been compared with the known habituation time of young Schistocerca hoppers (Ellis 1963a). By leaving the isolated Edinburgh 2nd instar hoppers and adults in the A.L.R.C. constant temperature rooms, one might have determined also if they were more or less sensitive to the pheromone than were A.L.R.C. isolated. From the retests of Edinburgh adults that were carried out, it appears that 10 hours low density social crowding combined with 5 days exposure to the pheromone resulted in some gregarious behaviour.

Maturation and oviposition pheromones differ from the "gregarising" pheromone in that they are more effective over short distances. The "gregarising" pheromone affects the behaviour over a distance of some feet as the locusts were isolated in jars on roundabouts, although it may be even more effective over a shorter distance. This could not be tested easily by using contact methods as the visual and tactile influences could not be eliminated. In a locust-free laboratory the effect of close contact of the pheromone alone could best be tested by taking rubbings or extracts from the cuticle of crowded locusts.

By this means it might also be established whether the olfactory stimulus that affects behaviour is the same as that which accelerates maturation and influences oviposition in adults, or is derived from hoppers. Hoppers are known to produce some factor which inhibits maturation (Norris 1964).

The fact that this pheromone acts over some distance implies that it is probably a side-effect of some other biological process.

In the field, locusts are not static for long periods. A pheromone which depends for its effect on a build-up in an enclosed space is thus unlikely to play an important part in locust biology. Any such substance would most probably be dispersed during hopper movements; hence visual and tactile stimuli are probably of more consequence in causing changes in solitaria phase to gregaria, and in maintaining the cohesion of the swarm.

SUMMARY.

Experiments were carried out to determine if the social behaviour of immature Schistocerca gregaria adults, like that of hoppers, was affected by the conditions of population density under which they had been reared since hatching. The conditions of rearing employed were the two extremes of visual and tactile isolation and heavy crowding. By testing the experimental locusts in a uniform environment arena, it was not possible to show any significant difference in the distribution of the isolated and crowded adults. The isolated locusts were forming as many groups as were the crowded locusts.

The unexpectedly large amount of group formation by the isolated locusts was considered to be a consequence of the conditions of the present Anti-Locust Research Centre laboratories, where a very high locust population has been reared in a restricted space for several years. The most likely factor involved was thought to be an olfactory stimulus. To avoid the action of this possible contaminant, a culture of isolated locusts was reared and tested in an otherwise locust-free laboratory at Edinburgh University Zoology Department. Some of these locusts were tested at 2nd instar and others when adult. They were found to be aggregating less than isolated 2nd instar and adult locusts reared and tested at A.L.R.C.. The most striking difference was found with 2nd instar hoppers. It is believed that some olfactory influence, a pheromone, is acting on these isolated locusts at A.L.R.C. in such a way that they exhibit aggregating behaviour without having had any previous social experience.

Experiments were carried out on Schistocerca gregaria and Locusta migratoria migratorioides to investigate the field report that there is a period of dispersal after fledging. The aggregation was measured of 5th instar hoppers, 5 day old adults, 10 day old adults and mature adults. There was a drop in aggregation after fledging and again at maturation, but these fluctuations were not significant. This laboratory study indicates that the dispersal observed in the field is probably not inherent to locusts. It is more likely to be a result of climatic conditions.

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APPENDIX I.

Experimental distribution of animals in arena. (Locusts crowded unless otherwise stated).

Experiment	Number of segments with 0 - 10 animals											Total
	0	1	2	3	4	5	6	7	8	9	10	
A.L.R.C. Schistocerca												
Adults tested at 28°C	241	165	101	31	14	7				1		560
adults tested at 32°C	263	151	84	26	25	5	4	2				560
adults tested in morning	261	161	71	32	24	4	5	2				560
adults tested in afternoon	261	141	102	27	20	4	4	1				560
adults 1st generation isolated	242	169	85	43	13	8						560
adults 3rd generation isolated	238	174	84	43	16	5						560
adults 5th generation isolated	206	140	84	33	12	5						480
adults 5 days old	245	158	93	46	14	2	2					560
adults mature	238	169	100	32	15	2	4					560
5th instar	261	153	77	43	13	8	3	2				560
2nd instar	317	106	54	39	19	9	8	5	2	1		560

2nd instar isolated	269	139	79	43	18	10	2				560
4th instar	240	174	88	37	13	3	4		1		560
4th instar isolated	178	119	55	30	13	3	1		1		400
2nd instar isolated undisturbed	181	120	55	24	13	3	2	1		1	400
2nd instar isolated + polythene	203	104	41	24	11	9	3	5			400

Edinburgh Schistocerca

2nd instar isolated	83	88	57	10	2						240
adult isolated	221	189	102	31	14	2	1				560

A.L.R.C. Locusta

adults tested at 28°C	234	174	95	40	11	6					560
adults tested at 32°C	249	160	83	46	15	6	1				560
adults tested in morning	221	191	98	34	11	3	2				560
adults tested in afternoon	242	164	97	35	15	5	2				560
5th instar	242	165	96	35	15	5	1	1			560
adults 5 days old	233	181	95	24	21	4	1	1			560
adults mature	224	188	95	30	20	3					560

	0	1	2	3	4	5	6	7	8	9	10	Total
Humbe tenuicornis	204	214	103	24	9	4	2					560
Nomadacris septemfasciata	205	209	102	32	10	1	1					560
Chortoicetes terminifera	228	186	96	31	11	4	3	1				560

Random distribution for:	0	1	2	3+
560 readings	196	218	106	40
480 readings	168	187	91	34
400 readings	140	155	75	30
240 readings	84	94	44	18
80 readings	28	31	15	6

APPENDIX II. Morphometric measurements on Schistocerca.

(Elytron length E, Femur length F, Head width C; measured in mms.)

A.L.R.C. crowded

	E	F	C		E	F	C
Females	55.1	27.2	7.5	Males	50.4	24.0	6.8
	57.9	26.8	7.6		50.3	23.1	6.9
	53.4	25.9	7.8		52.0	25.3	7.2
	57.4	27.6	7.7		49.0	23.0	7.0
	55.3	26.4	7.6		50.4	24.6	7.0
	54.5	26.3	7.4		49.1	24.0	6.9
	55.0	26.2	7.3		49.5	24.0	6.9
	51.4	24.1	7.2		49.4	24.7	6.8
	57.0	27.3	7.7		48.6	24.4	7.5
	56.9	27.6	7.3		49.3	23.5	6.8
	54.3	26.0	7.5		49.3	24.7	6.0
	52.0	27.2	7.4		49.5	24.0	7.0
	56.2	26.9	7.4		48.6	24.2	6.8
	56.5	27.5	7.8		48.5	24.3	6.7
	57.8	27.1	7.6		49.3	23.6	7.2
	54.2	26.9	7.6		47.9	23.2	6.7
	56.2	28.0	7.7		46.8	23.8	6.4
	57.6	27.3	7.8		47.9	22.7	6.5
	57.5	24.6	7.8		49.7	24.4	7.1
	56.9	25.8	7.5		48.7	23.0	6.8
Mean	55.7	26.6	7.6		49.2	23.9	6.9

A.L.R.C. isolated

	E	F	C		E	F	C
Females	55.7	26.8	7.6	Males	48.2	23.7	6.8
	58.2	28.2	7.5		48.0	22.3	6.6
	58.2	27.9	7.9		50.0	24.4	6.8
	55.6	26.9	7.3		48.7	23.1	6.5
	55.3	26.3	7.5		48.8	23.9	6.7
	55.5	26.1	7.4		47.3	23.6	6.7
	55.4	26.8	7.1		48.1	22.8	6.4
	55.4	25.9	7.3		50.1	25.7	6.7
	60.0	28.2	7.8		47.4	22.6	6.3
	57.9	26.5	7.6		49.4	25.1	6.8
	58.5	27.3	7.5		45.4	22.5	6.2
	55.7	27.0	7.4		45.0	22.2	6.6
	56.3	26.7	7.1		48.2	23.0	6.6
	53.8	25.5	7.3		48.6	22.3	6.7
	58.0	22.3	7.8		48.0	23.7	6.8
	58.2	27.4	7.9		48.7	23.1	6.7
	56.4	26.8	7.2				
	53.9	25.5	7.4				
	53.0	24.7	7.2				
	54.3	25.8	7.3				
	59.2	27.4	7.6				
	51.0	26.9	7.4				
Mean	56.2	26.5	7.5		48.1	23.4	6.6

Edinburgh isolated

	E	F	C		E	F	C
Females	56.3	27.2	7.6	Males	49.0	24.1	6.7
	56.6	27.1	7.3		48.0	23.4	6.8
	55.4	26.7	7.8		49.2	24.3	7.0
	54.3	27.2	7.4		47.3	23.0	6.6
	54.8	26.2	7.3		49.6	24.6	6.7
	56.4	28.5	7.8		49.6	24.7	6.8
	57.1	26.7	7.5		49.3	24.2	6.7
	54.8	27.1	7.2		45.4	23.0	6.3
	56.3	27.3	7.4		49.2	24.4	6.8
	57.1	27.8	7.7		49.1	24.3	6.4
	57.5	28.0	7.7		50.6	23.7	6.7
	57.6	27.3	7.4		47.9	23.2	6.8
	56.2	26.9	7.7		48.0	23.3	6.6
	56.9	28.3	7.6		49.1	24.7	6.9
	55.8	27.6	7.5		50.0	24.4	6.8
	55.4	27.5	7.3		49.0	25.1	6.8
	54.5	27.0	7.4		49.6	25.1	6.7
	57.1	26.8	7.8		51.2	24.5	6.6
	56.4	25.6	6.3		50.9	25.0	6.7
	59.4	28.2	8.1		49.3	23.5	6.8
	55.5	28.4	7.4		51.0	25.0	7.0
	60.6	31.3	8.0				
	62.2	30.6	7.9				
	59.9	29.7	7.8				
	58.9	27.8	7.5				
	56.2	28.7	7.7				
Mean	56.9	27.8	7.5		49.2	24.2	6.7