Some studies on the population dynamics of the bread beetle stegobium paniceum (l) (coleoptera : anobiidae)

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SOME STUDIES ON THE POPULATION DYNAMICS OF THE BREAD BEETLE *STEGOBIUM PANICEUM* (L) (COLEOPTERA : ANOBIIDAE)

by

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ABSTRACT

Some aspects of the population dynamics of the bread beetle Stegobium paniceum were studied using a laboratory culture of the species. Initial density of adults was found to influence reproductive success, the number of progeny produced by S. paniceum females decreasing with increased adult density. Using densities ranging from 0.013 - 6.70 adult beetles/g, 0.66 beetles/g was found to be the density above which the number of progeny decreased markedly. Using different immature stages in densities from 0.33 to 40 per g, the egg stage showed the highest apparent mortality, although infertility of eggs was not taken into account. Mortality of the larval stages had little effect on the resulting adult numbers, although when larval density increased above 8.33 per g the mortality rate increased. One of the main factors limiting the population increase was decreased fecundity of females due to mutual interference with oviposition. The frequency of copulation decreased when a density of 12 pairs per dish was exceeded, fecundity of females also being reduced above this density.

The capacity for increase r_c under the experimental conditions was found to be 0.52/beetle/day with 94% of eggs being laid before the females were 8 days old and the mortality being greatest between days 10 and 16.

When females were provided with antennectomised males at comparatively low densities of 0.02 and 0.06 beetles/g, the progeny per female decreased by over 50% compared to that of females provided with normal males. Antennectomised males took longer to find females and to copulate than did control males. More than 90% of the control males copulated within 15 minutes whereas only 5% of antennectomised males copulated within this time.

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I. INTRODUCTION

Stegobium paniceum (L) (Coleoptera : Anobiidae) is a dark brown beetle 2-3 mm long, which commonly infests stored products. It is cosmopolitan but is more common in temperate than tropical latitudes. It has been recorded infesting stored grain, drugs, spices, tobacco, leather and books with a moisture content of 6% - 15% (Lefkovitch, 1967). Under conditions of 30$^{\pm}$ 1^{o}C and 75% r.h. the duration of life from birth to death is approximately 66 days for the male and 71.5 days for the female. The egg stage lasts for 7 days, followed by 5 larval instars lasting in all 28 days. The duration of the pupal stage is 4 days and the newly formed adults spend 4-5 days in the cocoon before emerging after about 42 days from oviposition. The cocoon is formed by the second instar larva and is increased in size by each stage until pupation (Lefkovitch, 1967). The adult stage is non-feeding, utilizing food reserves formed during the feeding larval stages.

A further relevant feature of the biology of this species is the presence of a sex pheromone communication system between the sexes. Females emit an attractant when they are sexually mature (3-5 days old). Males orientate towards the odour source by means of chemoreceptor sensillae on the three distal antennal segments, and on reaching the pheromone-emitting female they are excited to copulate.

The significance of such a communication system in terms of population dynamics may be as follows. At low density the chance of a male finding a female will be enhanced and population increase will be faster. Once numbers have increased and chance meetings are more frequent, the sex pheromone may become less important. At high densities there may even be an element of population limitation as a result of confusion of males in the presence of excessive amounts of the pheromone.

This hypothesis is somewhat speculative but it was hoped that the following study might provide some insight into the importance of the sex pheromone in the population dynamics of S. paniceum.

The aims of the work presented here were to investigate:

(i) the effect of increasing adult density on the resultant numbers of offspring.

(ii) the mechanisms involved in the regulation of the numbers of offspring, by determining the effect of density on the mortality of the larval and egg stages.

(iii) the effects of increasing density on oviposition rates and on the frequency of copulation.

(iv) the effect of antennectomised males on the numbers of progeny at low densities, and the effect of antennectomy on the success of copulation.

In order to control an insect pest, detailed information is required on the population dynamics of the species. For control measures to operate effectively they must be introduced at the correct stage of the life cycle, otherwise density dependent mechanisms may come into effect and nullify the control. It is hoped that this work will provide some insight into these control problems. Feasible control may be achieved by saturating the atmosphere with pheromone to confuse males, thus making location of females difficult.

II. GENERAL MATERIALS AND METHODS

The insects were reared in an insectory of dimensions 3.05 x 2.74 x 2.59m at 30 ± 1°C and 75 ± 2% r.h. in a 12h light : 12h dark photoperiod. The culture medium comprised wheat feed sterilized at 60°C for at least 2h. 150g of this medium was put into 2lb Kilner jars with 1 crumpled 'Kimwipe' to increase the surface area for the beetles. Jars such as these were used for stock cultures and experimental cultures for experiment 1. Black filter paper discs held in place by metal ring tops served as lids, allowing passage of air into the container. The dark background revealed any mites present. The jars were placed 8cm apart in a film of liquid paraffin to reduce the spread of mite infestations.

Jam jars (1lb capacity) containing 30g of wheat feed were used for experiment 2. Black filter paper discs held in place by rubber bands served as lids. This experiment was scaled down to reduce the numbers of immature individuals required. When individuals of known sex were required, the pupal cocoons were sieved from the cultures, the pupae carefully removed and the sex determined according to Halstead (1963). The sexes were kept apart in petri dishes, with a square of moistened filter paper attached to the lid to raise humidity and prevent the pupae desiccating. When the adults emerged 4-5 days later, they were considered to be one day old when the elytra had darkened to the same extent as the thorax. These were then transferred in groups of ten to 5 x 1 cm glass vials, with filter paper provided as a substrate and as a strip for the insects to climb on.

Petri dishes 9cm diameter were used in experiment 3.

Glass vials 5 x 1 cm were used in experiment 4.

Buckets of 9 l capacity (25cm x 24cm) containing 500g wheat feed, with 5 crumpled 'Kimwipes' to increase surface area were used in experiment 5. About 5cm from the lip of the buckets, vaseline was spread to prevent the insects escaping. The tops were covered with clear polythene held by

string, with holes in the polythene to allow passage of air into the container.

III. EXPERIMENT I.

The effect of adult density on the numbers of progeny.

Introduction

This experiment was performed to determine whether adult density affects the numbers of offspring produced per female.. Similar experiments have been done with the Azuki bean weevil Callosobruchus chinensis (L). Utida (1941) showed that there is an optimum density for reproduction, the numbers of progeny being reduced at very low and very high densities. With Tribolium confusum Duval and Oryzaephilus surinanmensis (L), however Crombie (1943) showed a decrease in numbers of progeny at increased adult densities.

Method

Pairs of newly emerged adults were taken from the stock culture and introduced to the medium at densities of 1, 3, 10, 50, 125, 200 and 500 in Kilner jars with replicates as shown in Table 1. For the three lower densities sexed individuals were used, for the four higher densities, a 1 : 1 sex ratio was assumed, and beetles were collected using an aspirator and counted; all insects were not more than 3 days old when introduced to the culture medium. The jars containing beetles at the four lower densities were checked each day (by eye) to assess mortality, this being particularly important in the low density cultures. Individuals dying within the first three days were replaced by others of the appropriate age and sex.

After about 42 days the new adult generation started to emerge. The beetles emerging were removed and counted by aspirator every three days. Before collection, the jars were placed at room temperature for about 30 minutes to slow the insects down, thus making them easier to handle. This procedure was continued until emergence was completed.

Results

The number of offspring emerging was expressed in terms of numbers produced per parent female. The adult density was expressed in terms of log number per g, (Table I : Figure I).

Table I : Mean number (± S.E.) of progeny emerging per female

No. of pairs	Log no. per g	No. of replicates (n)	Mean no. of progeny/♀ ± S.E.
1	0.0055	10	61.7 ± 5.1
3	0.0170	6	51.2 ± 4.5
10	0.0531	3	45.6 ± 3.0
50	0.2201	3	52.3 ± 2.8
125	0.4314	3	15.5 ± 2.4
200	0.5682	3	18.0 ± 3.8
500	0.8865	2	8.6

A regression analysis was performed on the results obtained, from which a line of best fit for Figure I was obtained using the equation

$$y = a + bx$$

where a = intercept on the y axis

b = slope of line

The correlation coefficient r was also calculated for the line and was found to be -0.9153. This shows that the number of progeny per female decreases significantly with increasing adult density, ($P<0.02$).

Student t-tests were also performed to test for significant differences between densities, using (n + n - 2) degrees of freedom, (Table II).

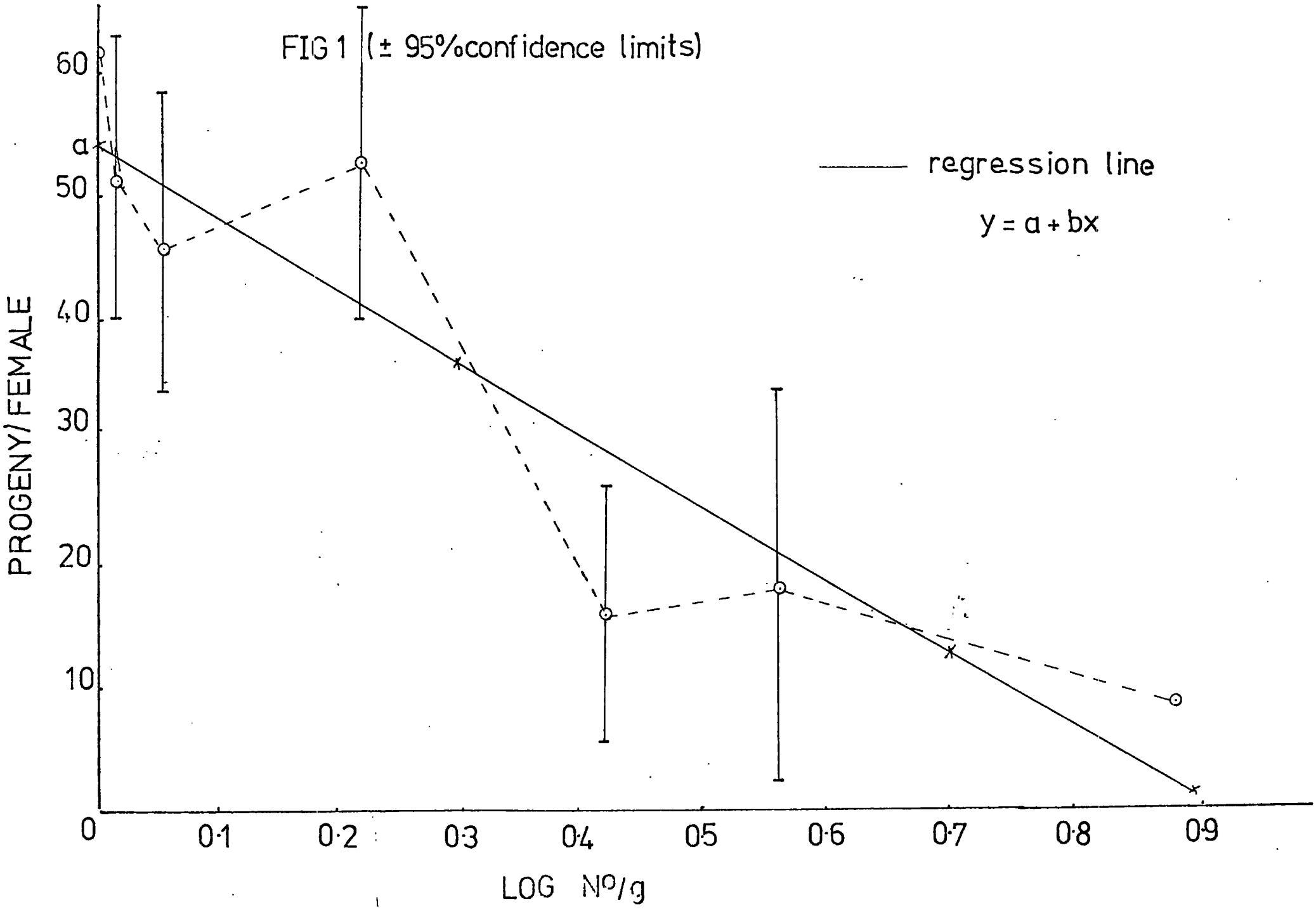


FIG 1 (± 95% confidence limits)
regression line
y = a + bx
PROGENY/FEMALE
60
a
50
40
30
20
10
0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
LOG Nº/g

Table II : Comparison of numbers of offspring emerging from different initial parent population densities.

Densities compared pairs*	$t\ (n_1 + n_2 - 2)$	P
1:200	8.3	<0.001
1:125	7.0	<0.001
1:10	2.8	<0.02
3:200	4.8	<0.001
3:125	6.9	<0.001
50:200	7.3	<0.001
50:125	10.2	<0.001

* Only pairs showing significant differences are shown ($P<0.05$).

The highest numbers of progeny occurred at the lowest density. The lowest numbers of progeny occurred at the highest adult densities of 1.70 beetles/g, 2.70 beetles/g and 6.70 beetles/g. At the three intermediate densities the numbers of progeny were less than at the lowest density, but differences were not significant (Figure I : Table II).

Although for the sake of uniformity the number of beetles/gram is used as an index of density, the adult insects do not move into the medium. They remain on the surface, on the tissue and sides of the jar and particularly on the underside of the lid.

Discussion

The results show that the number of offspring produced per female decreased with increasing density; the regression analysis performed gave a high degree of correlation between these two factors. Crombie (1943) working with T. confusum obtained the same effect; he found that females oviposited fewer eggs at higher densities due to interference with ovipositing females from other insects. In Figure I the 95% confidence limits show significant differences between the four lower and the three higher densities but the differences between the four lower densities are not significant. The reason for the fall in the number of offspring of S. paniceum at higher densities was investigated in the following experiments of this text.

IV. Experiment 2.

The effect of the density of certain immature stages of S. paniceum on the resulting adult numbers.

Introduction

The following experiment was conducted in order to determine whether the mortality of any one preimaginal stage had a significant effect upon the members of adults emerging. Three stages were used for this investigation; the egg stage, small larval instars (1st and 2nd) and larger larval instars (4th and 5th). The densities used were as near as practicable to those used in experiment 1, although the experiments were scaled down to reduce the numbers required, by decreasing the size of the jars and the amount of medium used.

Method

The following densities were used for all three stages:

10	individuals	per	30g,	giving	a density of	0.33 per g.
30	"	"	30g,	"	"	1.00 per g.
100	"	"	30g,	"	"	3.33 per g.
250	"	"	30g,	"	"	8.33 per g.
400	"	"	10g.	"	"	40.00 per g.

(10 grams of medium was used for the highest density to reduce numbers required).

The eggs were obtained by keeping approximately 100 adult insects in 1lb Kilner kars with 1cm squares of black filter paper for oviposition sites. After two days the filter paper was removed and examined under a X10 binocular microscope for eggs. The eggs were added to the medium on the paper in the appropriate densities.

The small larvae were sieved from the medium using a 0.5mm sieve. They fell through the sieve on to a petri dish which had lines 1cm apart drawn on it. The grid was scanned under the microscope, and the number of larvae per division counted. They were then added to the medium at the

above densities. The large larvae were sieved from the medium using a 2.00mm sieve, picked out with a small dental spoon, and added to the experimental jars at the correct densities.

An additional experiment was done to determine if the older larvae influenced the mortality of younger stages. An intermediate density (100 individuals per 30g) was chosen and 50 eggs were added to the medium as previously described. One week later another 50 eggs were added. The number of adults emerging per jar were collected and counted, using the method described in experiment 1.

Results

Adult emergence was expressed both as numbers and as percentages emerging (Table III and Figures 2 and 3).

Table III Mean number of adults emerging from each immature stage and percentage of adults emerging.

Initial density no./g	No. of replicates	Mean no. emerging			Mean % emerging		
		Egg ± SE	Small Larvae ± SE	Large Larvae ± SE	Egg	Small Larvae	Large Larvae
0.33	10	7.7 ± 0.3	8.7 ± 0.5	9.5 ± 0.2	77	87	95
1.0	5	22 ± 2.3	29 ± 1.0	29 ± 0.4	74	97	98
3.33	3	77 ± 1.7	86 ± 1.8	94 ± 2.1	77	86	84
3.33*	3	85 ± 1.7			85		
8.33	3	153 ± 6.7	108 ± 8.5	231 ± 3.2	61	83	92
40.0	3	208 ± 5.1	313 ± 47.1	354 ± 1.7	52	78	88

* 50 eggs + 50 eggs one week later

Student t-tests were performed to test for significant differences between the numbers emerging for different stages at equivalent densities.

Table IV : Statistical comparison between numbers of adults emerging from immature stages at the same initial densities.

Density and stage compared no./30g	$t_{(n_1 + n_2 - 2)}$	P
400e : 400S	2.2	<0.05
400e : 400L	27	<0.001
250e : 250S	3.4	<0.03
250e : 250L	10.5	<0.001
100e : 100S	3.4	<0.02
100e : 100L	6.3	<0.02
30e : 30L	2.0	<0.05
30e : 30L	3.0	<0.02
10e : 10S	1.75	N.S.
10e : 10S	5.2	<0.001

Key: e = egg
S = small larvae
L = large larvae
N.S = no signficant difference

Since mortality of early immature stages will be dependent upon the mortality at each later stage, corrected values for each stage were calculated as follows. The corrected value for the egg stage was found by subtracting the number dying in the small larval instar, at the same density from the number dying in the egg stage. The corrected number dying in the small larval stage was found by subtracting the number dying in the large larval stage from that in the small larval stage, the corrected percentage dying being found using the percentage values from Table III

Table V : Corrected values for the numbers dying in each stage, and for the percentage dying in each immature stage at varying densities.

Density nos./30g	Corrected no. dying			Corrected % dying		
	Egg	Small larvae	Large larvae	Egg	Small larvae	Large larvae
10	1.0 ± 0.3	0.8 ± 0.5	0.5 ± 0.2	10	8	5
30	7.0 ± 1.9	0.0	1.0 ± 0.6	23	1	2
100	9.0 ± 3.2	8.0 ± 2.2	6.0 ± 2.2	9	8	6
250	55.0 ± 6.8	23.0 ± 7.8	19.0 ± 3.2	22	9	8
400	105.0 ± 43.7	41.0 ± 22.8	46.0 ± 1.7	26	10	12

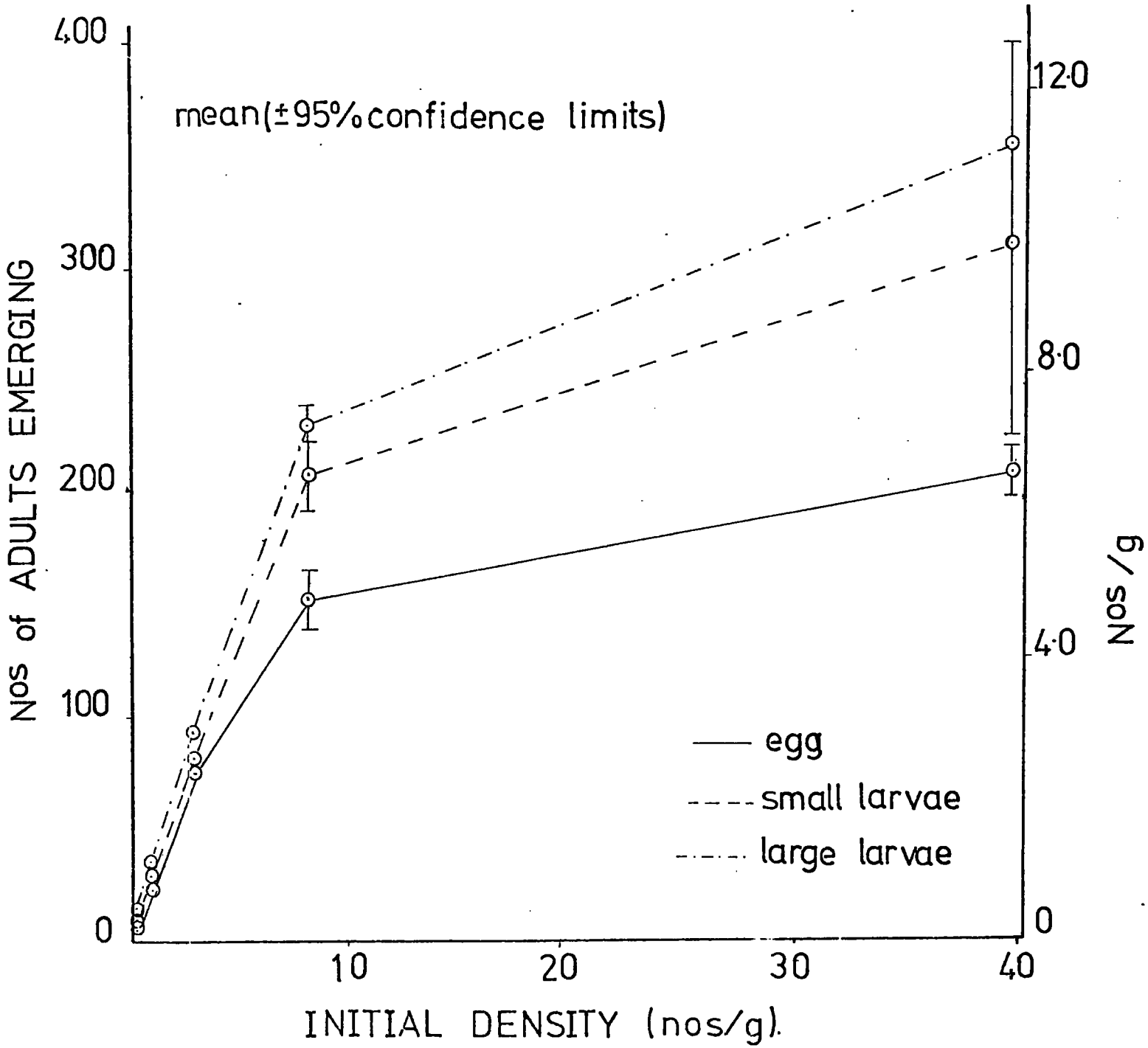
A student t-test was performed to test for significant differences between the correct numbers emerging at each density.

Table VI : Comparison of numbers of adults emerging from each stage at each density.

Density and stage compared no./30g*	t $(n_1 + n_2 - 2)$	P
$e_{250} : S_{250}$	3.1	<0.05
$e_{30} : S_{30}$	3.68	<0.005
$e_{30} : L_{30}$	3.03	<0.01

* Only pairs showing significant differences are shown ($p<0.05$)

FIG 2


mean(±95% confidence limits)
Nos of ADULTS EMERGING
400
300
200
100
0
12·0
8·0
4·0
0
Nos /g
10
20
30
40
INITIAL DENSITY (nos/g)
egg
small larvae
large larvae

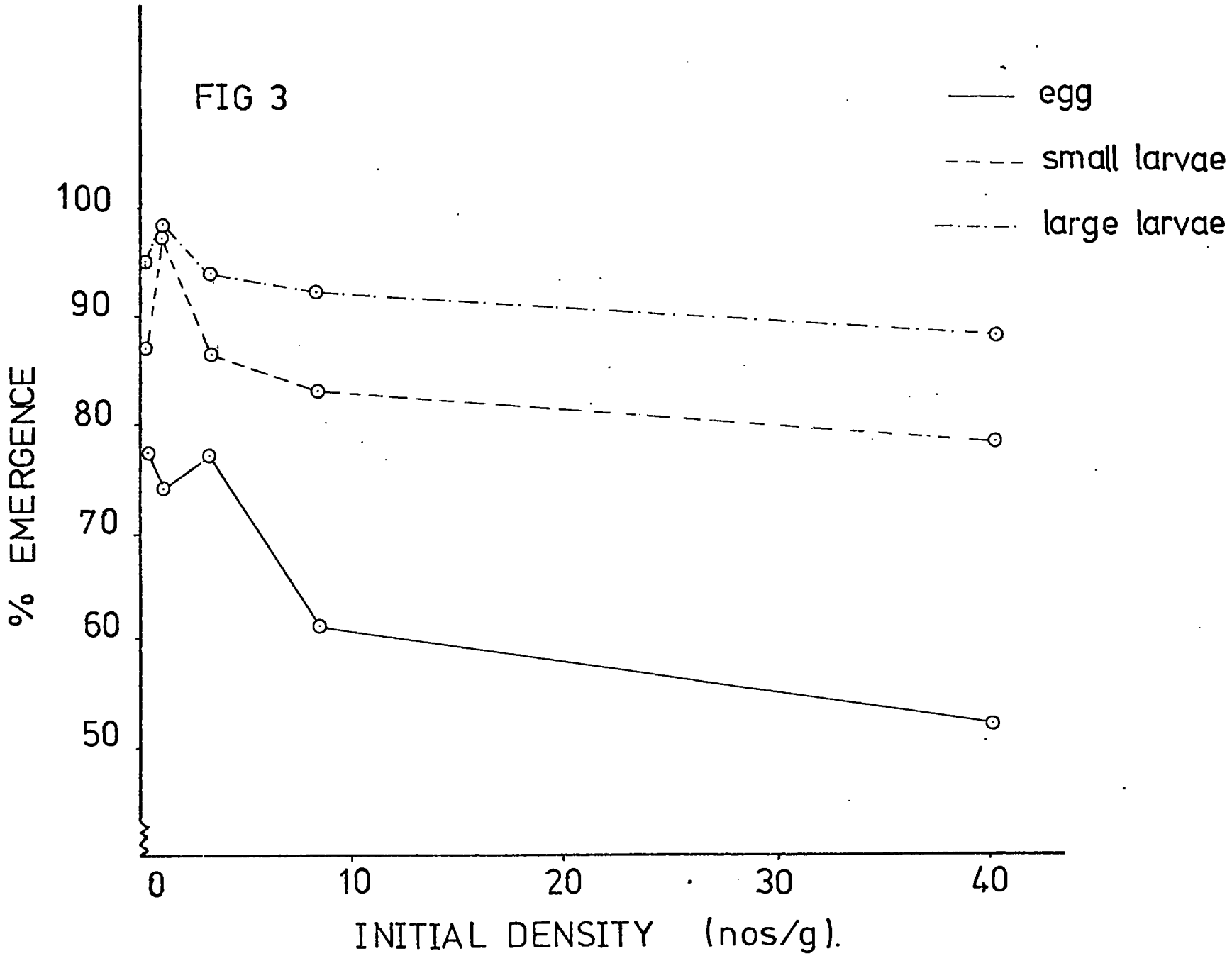


FIG 3
egg
small larvae
large larvae
100
90
80
70
60
50
% EMERGENCE
0
10
20
30
40
INITIAL DENSITY (nos/g).

Discussion

From experiment 1 it is evident that adult density affected the apparent female fecundity. In this experiment it has been shown that as the density of each immature stage is increased, the number of adults emerging per initial individual is decreased. From Table III it can be seen that the large larval stages contributed only 12% mortality, as opposed to 48% mortality from the egg stage at a density of 40 beetles/g. It therefore appears that mortality factors operate before the large larval stage is reached. The mortality during the early larval stages was 22% at the highest density.

Significant differences were found between the numbers emerging from the egg and large larval stages and also between the numbers emerging from the egg and small larval stages as can clearly be seen from Figure 2. No significant differences were found between the numbers of adults emerging from the two larval stages at each density.

At first sight it appears that mortality during the egg stage is greatest and that this stage largely determines the numbers of adults emerging. Infertility of eggs is usually 25-30% using densities of 1 or 2 per glass vial (Barrett, in preparation), and when this is taken into account, assuming that infertility is similar under these conditions, it accounts for the mortality in the three lower densities of the egg stage, leaving a 23% mortality at the high density of 40/g unexplained. When however the corrected values for the numbers dying are considered (Table V.) mortality of the egg stages at all densities is accounted for by egg infertility. Utida (1941) found that the fertility of C. chinensis eggs decreased with increasing density. This has not been examined here, but these results do tend to substantiate this trend.

The mortality of the two larval stages is fairly constant over the range of densities employed, being particularly low at 1.0 beetle/g, the percentage dying at higher densities being slightly greater than for low

densities (TableIV). This is probably due to competition between individuals for space to construct cocoons for pupation. The beetles start constructing cocoons during the second larval instar. These cocoons are enlarged as the larva grows and at high densities therefore, the chances of two individuals competing for space is increased. Mortality may occur due to damage of the larvae during handling or fighting between individuals for cocoon building material. Presumably, this also occurs with the large larval instars. They are removed from their cocoons for experimental purposes, and have to construct new cocoons when introduced to the new medium. This might influence the results, by increasing mortality in the large larval stage as more fighting may occur over cocoon building material. This experiment suggests that some competition for cocoon building material may occur, but more replicates would need to be done to elucidate these factors in detail.

The experiment in which eggs were added at two different times shows that emerged larvae probably do not feed on the eggs, or smaller stages. This suggests that cannibalism is not an important factor in the regulation of numbers; however only one density was tested in this way, and this would need further investigation.

From these results it appears that natural infertility of eggs probably accounts for most of the mortality in the egg stage of S. paniceum. Mortality in the larval stages is slightly greater at high densities than low densities and accounts for mortality due to factors other than egg infertility, such as fighting between larvae for cocoon material.

V. Experiment 3

The effect of adult density on frequency of copulation and fecundity of females.

Introduction

This experiment was designed to determine the effect of increasing density upon copulation success and fecundity of females. At high densities it might be assumed that the number of contacts between individuals by random activity increases, and that this might result in disturbance of mating pairs. At low densities there is presumably less chance of adults meeting and thus less chance of copulation occurring. Therefore one might expect an optimum density for copulation (Utida, 1941). Females were kept with males at varying densities, to investigate the effect of density on copulation success. This experiment was allowed to continue to enable oviposition to occur since incomplete or interrupted copulation may lead to reduced numbers of eggs being produced. Another experiment was performed using mated females with equal numbers of virgin females at the same densities as before. This was to eliminate the copulation factor and examine the effect of varying densities upon oviposition, and hence the effect of interference from other females with oviposition, on the number of eggs produced per female.

Method

The insects were sexed as previously described and when four days old were introduced to the arena, which consisted of a petri dish (9cm) inverted over a filter paper circle of larger diameter. A single layer of large wheat flakes was spread over the paper to provide oviposition sites. The densities used were 1, 3, 6, 12, 25 and 50 pairs per dish, and the insects were allowed five minutes to become accustomed to the experimental conditions. The number of pairs copulating per minute was noted for thirty minutes. During copulation the male mounts the female

and when genital contact is achieved they turn through 180° to assume a back-end to back-end position. This was considered to be the point when copulation takes effect.

The insects (males and females) were retained for oviposition to occur. After one week the filter paper and wheat flakes were removed for examination for eggs, being replaced by new paper and flakes. The paper was examined under a X10 microscope for eggs. Most of the eggs were attached to the filter paper under large flakes, but a few were found loose in the medium. This procedure was repeated one week later to ensure that the majority of eggs had been collected and the experiment was then terminated.

Another experiment was conducted in conjunction with that above. Four day old males and females were mated in a 5 x 1cm glass vial (one pair per tube) inverted on a filter paper circle, and left together for 24 hours. The mated females (being slightly larger than the males) were removed and put into the culture dish, as previously described. Equal numbers of virgin females were added to make up the required densities equivalent to those in the previous experiment. The eggs were collected and counted as before.

Results

Under crowded conditions copulating pairs were often broken up before the back-end to back-end position was adopted, and frequently two males attempted to mount one female. The number of eggs obtained per female was very low compared to the average number of about 60 under these conditions. It was thought that the four day old males may not have been fully mature and that a high percentage of their sperm may have been infertile and so reduced the number of eggs produced per female.

The results are presented both as the mean percentage in copula per five minutes, and the mean percentage in copula over thirty minutes for each density, see Table VII and Figures 4 and 5.

Table VII : Mean percentage of insects in copula per five minutes and thirty minutes at different densities.

Initial density nos.pairs	No. of replicates	Mean % in copula per 5 mins					Mean % in copula per 30 mins
		5-10	10-15	15-20	20-25	25-30	
1	8	16.7	25.0	47.5	52.5	47.5	39.6
3	6	22.7	34.4	43.3	46.7	40.0	36.0
6	4	32.5	35.8	38.3	35.8	38.3	36.1
12	4	32.0	40.4	35.8	30.0	25.8	32.4
25	3	15.2	24.3	23.5	25.9	17.3	20.4
50	3	24.9	29.5	28.6	14.7	14.1	21.7

Significant differences between the numbers copulating at different densities were tested for using a probability matrix Table VIII.

This matrix was constructed as follows:

In each case 2 densities are compared, a mean line is drawn between the values for the 2 densities. In this case there are five values at each density, therefore the chances of all the values for one density being below the mean line is 2^5 i.e. 1 in 32 chance.

This is equivalent to a p value of 0.03, which is a significant result.

e.g. Compare densities 25 : 3

All values for d = 25 are below those of d = 3

$\therefore$ p = 0.03

So it can be said there is a significant difference in numbers copulating at these 2 densities.

Table VIII: Probability matrix, showing the values of p for comparison between the various densities.

	1	3	6	12	25	50
1	-					
3	0.125	-				
6	0.125	0.125				
12	0.125	0.125	0.125			
25	0.03	0.03	0.03	0.03	-	
50	0.125	0.08	0.03	0.03	0.03	-

Figure 5 shows certain trends in the numbers of pairs copulating over the five minute periods in the arena. At densities of 50, 25 and 12 pairs the numbers copulating are high in the first fifteen minutes and then decrease. At the lower densities (1 and 3 pairs) the number copulating increased with time to twenty minutes and then decreased slightly over the last five minute period. With 6 pairs there was little variation over the whole time period. The probability matrix Table 8 shows significant differences for the number in copula between 25 pairs and all other densities. It also shows differences between 50 pairs and 6, and 12 pairs but not between 50 and 1 and 3 pairs.

FIG 4

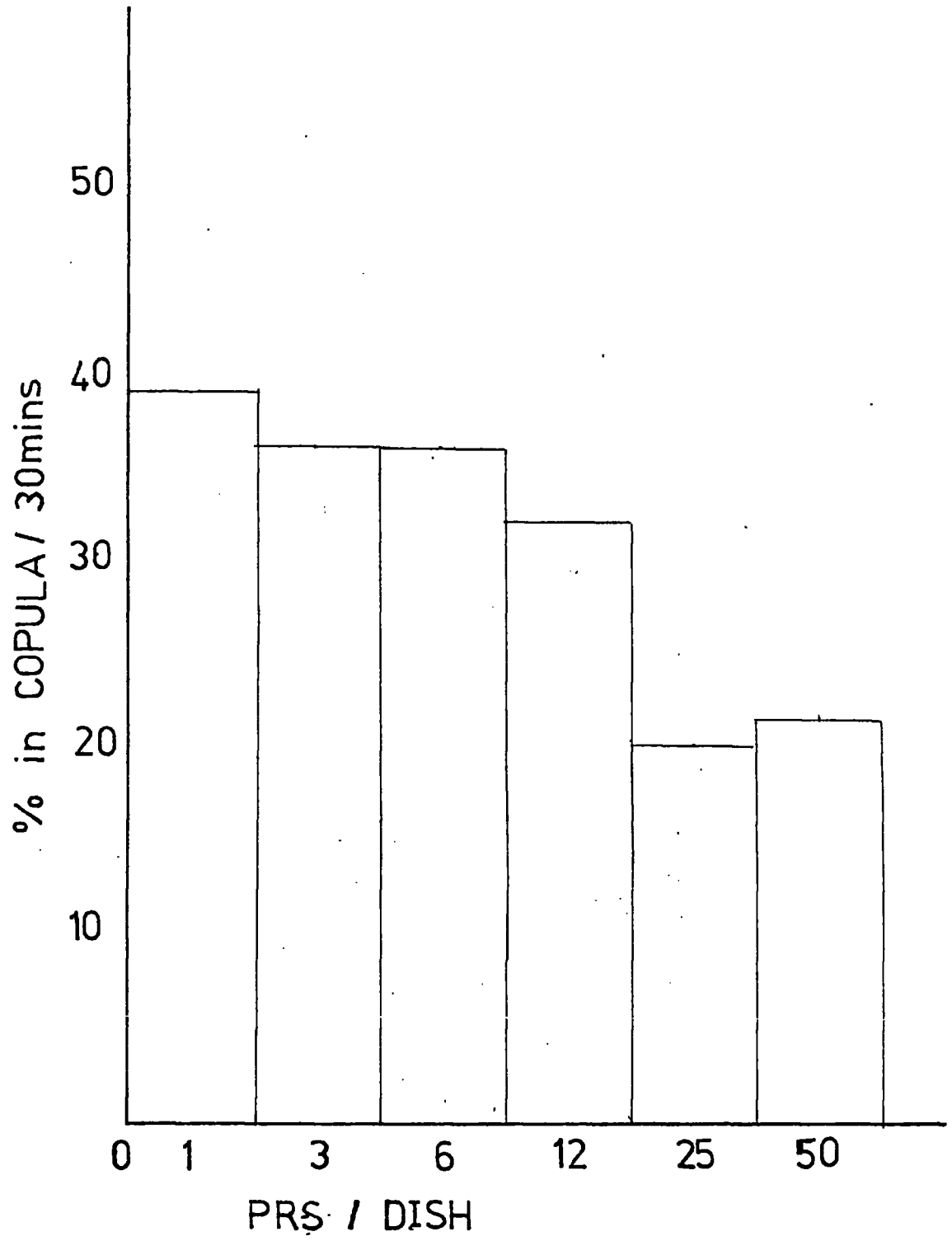
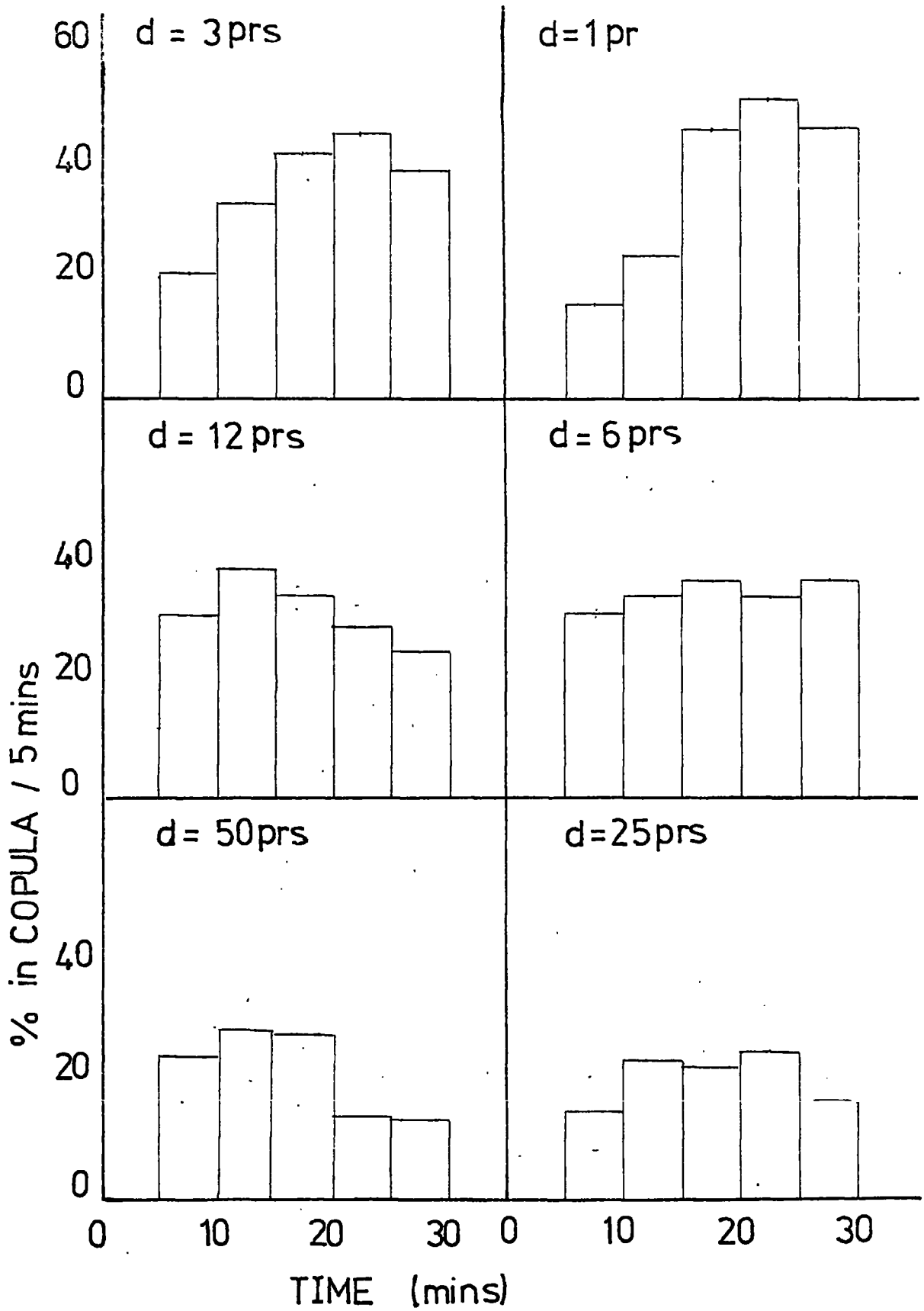


FIG5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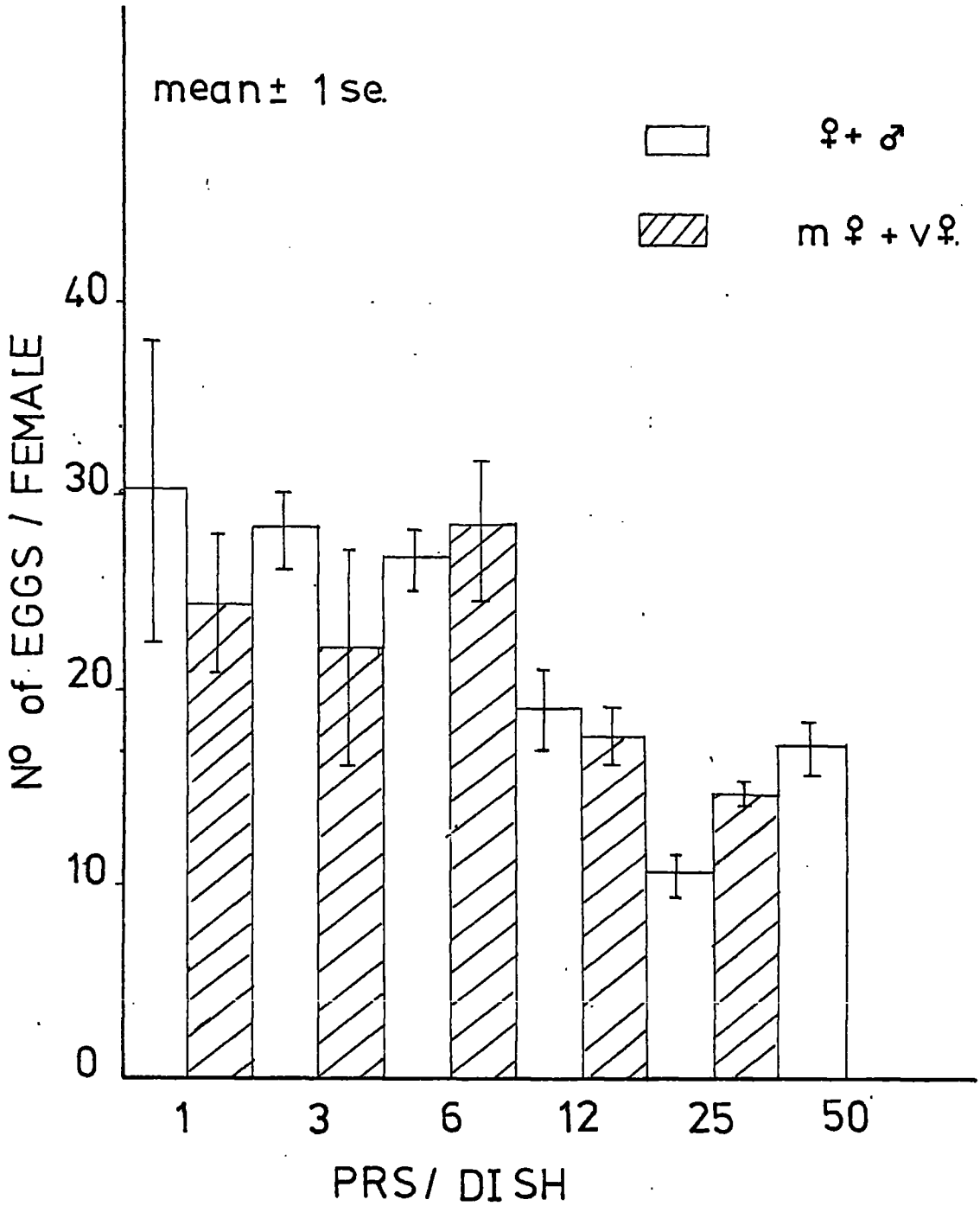
d=1pr
d = 12prs
d = 6prs
d= 50prs
d=25prs
60
40
20
0
40
20
0
40
20
0
% in COPULA / 5mins
0
10
20
30
0
10
20
30
TIME (mins)

FIG 6



The fecundities of females at different densities are given in Table IX and Figure 6, which show the mean numbers of eggs produced at each density by females associated with males and by mated females associated with virgin females.

Table IX: The mean number of eggs produced per female at various densities.

Initial density no. of pairs	No. of replicates (n)	Mean no. of eggs/♀ assoc. with ♂ ± S.E.	Mean no. of eggs/m ♀ assoc. with v ♀ ± S.E.
1	8	30.3 ± 7.6	24.5 ± 3.9
3	6	28.3 ± 2.0	22.2 ± 5.8
6	4	26.6 ± 1.5	28.1 ± 3.6
12	4	19.0 ± 2.1	17.7 ± 1.7
25	3	10.8 ± 1.3	14.9 ± 0.24
50	3	17.0 ± 1.4	-

The means were compared using student t-distribution in order to show significant differences between the numbers of eggs laid at different densities. Only significant differences are shown in Table X.

Table X : Comparison of numbers of eggs at different densities for ♀ associated with ♂.

Densities compared for ♀ with ♂	$t_{(n + n - 2)}$	P
1 : 50	4.4	<0.001
1 : 25	6.6	<0.001
1 : 12	3.6	<0.002
3 : 50	6.2	<0.001
3 : 25	9.7	<0.001
3 : 12	4.6	<0.001
6 : 50	5.7	<0.001
6 : 25	9.5	<0.001
6 : 12	4.0	<0.002
12 : 25	4.5	<0.002
25 : 50	3.8	<0.01

Table XI : Comparison of numbers of eggs at different densities for ♀ associated with virgin (v) ♀

Densities compared m ♀ v ♀	$t_{(n_1 + n_2 - 2)}$	P
1 : 25	4.7	0.001
1 : 12	2.9	0.02
3 : 25	3.0	0.001
6 : 25	6.8	0.001
6 : 12	4.5	0.003

The results show significant differences between the numbers of eggs laid at densities of 1, 3 and 6 pairs and 12, 25 and 50 pairs. The number of eggs produced by 12 pairs of females associated with males differed significantly from the number produced by 25 and 50 pairs per dish (Table X).

Table XI shows significant differences between the numbers of eggs laid by mated females associated with virgin females at densities of 1 and 6 and at 25 and 12 pairs. Also those produced by 3 pairs differed significantly from the numbers produced at 25 pairs per dish.

No significant differences were found between the numbers of eggs produced by females kept with males and those kept with virgin females at the same density.

Discussion

The results show the trend that as density of adults increases the numbers copulating decrease, and fecundity of females is reduced. Bearing in mind that a sex pheromone system is in operation at a low density it is possible that males rely on this to find a female so, as shown at the lowest density, copulation does not occur at once, but numbers copulating increase with time. At the high densities males probably locate females quickly by chance contact, as well as utilizing the pheromone. As time progresses the concentration of pheromone will build up in the arena and may lead to confusion of the males. Also at high densities single males were often seen to break up copulating pairs, and several cases were observed where one female was being courted by two males. Therefore as time advanced the number copulating at the high densities decreased due to confusion of, and competition between, males. From Figure 5 it is seen that the skew of the histograms develops from a negative skew at high densities to a positive skew at low densities.

The fecundity of females associated with males fell with increasing density, numbers of eggs produced at low densities being significantly higher than numbers produced at high densities.

These results may be explained in several ways:

(i) At high densities interference with oviposition will be increased.

(ii) Breaking up of copulating pairs before complete copulation has occurred.

(iii) A delay in copulation will lead to reduction in numbers as older females produce fewer eggs, (Azab, 1943).

(iv) Confusion of males due to high concentration of pheromone may decrease their ability to locate females.

The fecundity of mated females associated with virgin females also decreased with increasing density.

Possible explanations of this effect are:

(i) Interruption of oviposition at high density.

(ii) Competition for oviposition sites.

Utida (1941) found with C. chinensis that there was an optimum density for copulation frequency, as at low densities the insects had less chance of meeting and at high densities interference from other insects broke up pairs. With S. paniceum no optimum density was found for copulation frequency, possibly because the containers used were small and males and females found each other within a short time. McLagan and Dunn (1935) working with T. confusum found that at low densities, frequency of copulation increased with increasing density up to a density of 0.4 insects per grain, above which it decreased, so that an optimum density was again found.

The fecundity of females associated with males decreased with increasing density. Utida (1941) also found this with C. chinensis and reasoned that, as the density increased and frequency of copulation decreased that the number of unfertilized females increased, producing fewer eggs. For virgin S. paniceum about 1.5 infertile eggs are produced per female (Barratt, 1975). It appears that if pairs do not copulate in the back-end to back-end position for at least one minute the spermatophore may not be transferred from the male resulting in the production of very few fertile eggs, (Barratt, 1975). This may occur at high densities due to interruption of copulating pairs.

Interference with ovipositing females will increase from both males and females at high densities. Crombie (1943) working with T. confusum and Utida (1941) with C. chinensis both found this effect, thereby decreasing the numbers of eggs oviposited. At high densities males may take longer to start copulation, due to saturation of the atmosphere by the pheromone. Older females produce fewer eggs and this may therefore contribute to the decrease in fecundity.

With the mated females associated with virgin females, none of these copulation problems arise. As previously stated workers have found that interference with oviposition and competition for oviposition sites leads to reduced numbers of eggs being produced. In this case when the density

exceeds 12 insects per dish the numbers of eggs produced are significantly reduced. No significant differences were found in the numbers of eggs produced in these experiments at comparable densities. This suggests that interference with oviposition and competition for oviposition sites are the main depressors of fecundity at high densities. It is possible therefore that under these conditions the effect of density on copulation frequency has little effect on the fecundity of the females, or that the range of densities was not great enough (particularly at the low end) to display this effect.

VI. Experiment 4

A life table and calculation of the capacity for increase of *S. paniceum*.

Introduction

Life tables are vital tools in the understanding of population dynamics as they provide information on expectation of further life and on survival or mortality rates. In the following experiment an age-specific life table was constructed, based on the fate of a real cohort of individuals all belonging to a single generation (Southwood, 1966). Time specific life tables are also commonly used, but these are based on individuals from different generations and therefore are not applicable in this one generation situation. In this case only an adult life table was constructed, the pre-imaginal stages being excluded.

Where a pest species is concerned it is important to determine the rate at which the population can multiply under specified conditions. To determine the capacity for increase or the intrinsic rate of natural increase a fecundity table was drawn up from data on the number of female eggs produced per female.

Lokta (1925) devised the following formula for determination of the intrinsic rate of natural increase for the human population, and his equation was later used by workers for insect populations.

$$\frac{dn}{dt} = rN$$

or

$$N_t = N_o e^{rt} \qquad \text{(i)}$$

where N_t = number of individuals at time, t,

N_o = number of individuals at time, o,

r = growth rate of population,

e = base of the natural logs.

'r' is the population growth rate in an unlimited environment with a stable age distribution, which corresponds to the intrinsic rate of

natural increase, r_m, (Birch, 1948; Andrewartha and Birch, 1954).

The situation described below is however equivalent to a pioneering population of S. paniceum invading a vacant environment. Laughlin (1965) used the statistic, r_c, the capacity for increase, to apply to such a population with no overlapping generations. This statistic is derived from the survival rates and reproductive capacity of a cohort of females, the equation being:

$$r_c = \frac{\log_e R_o}{T_c} \qquad \text{(ii)}$$

Where R_o = net reproductive rate, or the number of times a population multiplies per generation,

T_c = cohort generation time or the mean age of mothers in the cohort at the time of production of female offspring.

R_o is determined from the fecundity table, which shows the numbers of female eggs produced per female during each time interval.

$$R_o = \Sigma\, l_x\, m_x \qquad \text{(iii)}$$

where l_x = number of survivors at start of age interval x.

m_x = fecundity rate corresponding to the number of female eggs per female per age interval x.

$$T_c = \frac{\Sigma\, l_x\, m_x\, x}{\Sigma\, l_x\, m_x} \qquad \text{(iv)}$$

Female oviposition is extended over a period of time although it may be considered to be concentrated at one point of time, successive generations being spaced T_c units apart. The product of $l_x\, m_x$ in the last column of Table XIII is a frequency distribution with the individual items concentrated at the mid-point of each age group. The mean of this distribution is the approximate value of T_c.

Method

The sex of the insects was determined during the pupal stage as described earlier. When one day old, 2 males and 2 females were each

placed in a 5 x 1cm glass vial containing a few coarse flakes of wheat to provide oviposition material. A strip of filter paper was provided for the insects to climb on. The wheat and filter paper were checked daily under a X10 microscope for eggs, and the presence of dead females noted. If a male died it was replaced by one of a similar age. This experiment was performed using 50 pairs of beetles and was continued until the last female died.

Results

A fecundity table (Table XII) was drawn up from the data obtained, namely number of eggs produced per female and day of female death. As a 1 : 1 sex ratio was again assumed the number of female eggs produced was taken to be 50% of the total number produced. Since the egg laying period was fairly short, single daily age classes were used. These results were plotted in Figure 7, which shows the number of female eggs produced per female. The curve is negatively skewed, with a peak at 4 days followed by a gradual decline until day 12. The majority of eggs (94%) was laid in the first 8 days.

Table XII : Fecundity table for female S. paniceum calculated from a cohort of 50 adult pairs.

Age X days	No. surviving at start of age class lx	No. of ♀ eggs/♀/day, mx ± S.E.	Vx lx mx
0	1.0	0	0
1	1.0	0	0
2	1.0	0	0
3	0.98	1.85 ± 0.8	1.813
4	0.98	4.75 ± 1.4	4.655
5	0.98	3.45 ± 0.8	3.280
6	0.98	2.65 ± 0.3	2.597
7	0.96	2.75 ± 0.5	2.640
8	0.94	2.05 ± 0.5	1.930
9	0.94	0.53 ± 0.05	0.498
10	0.90	0.43 ± 0.04	0.397
11	0.78	0.15	0.119

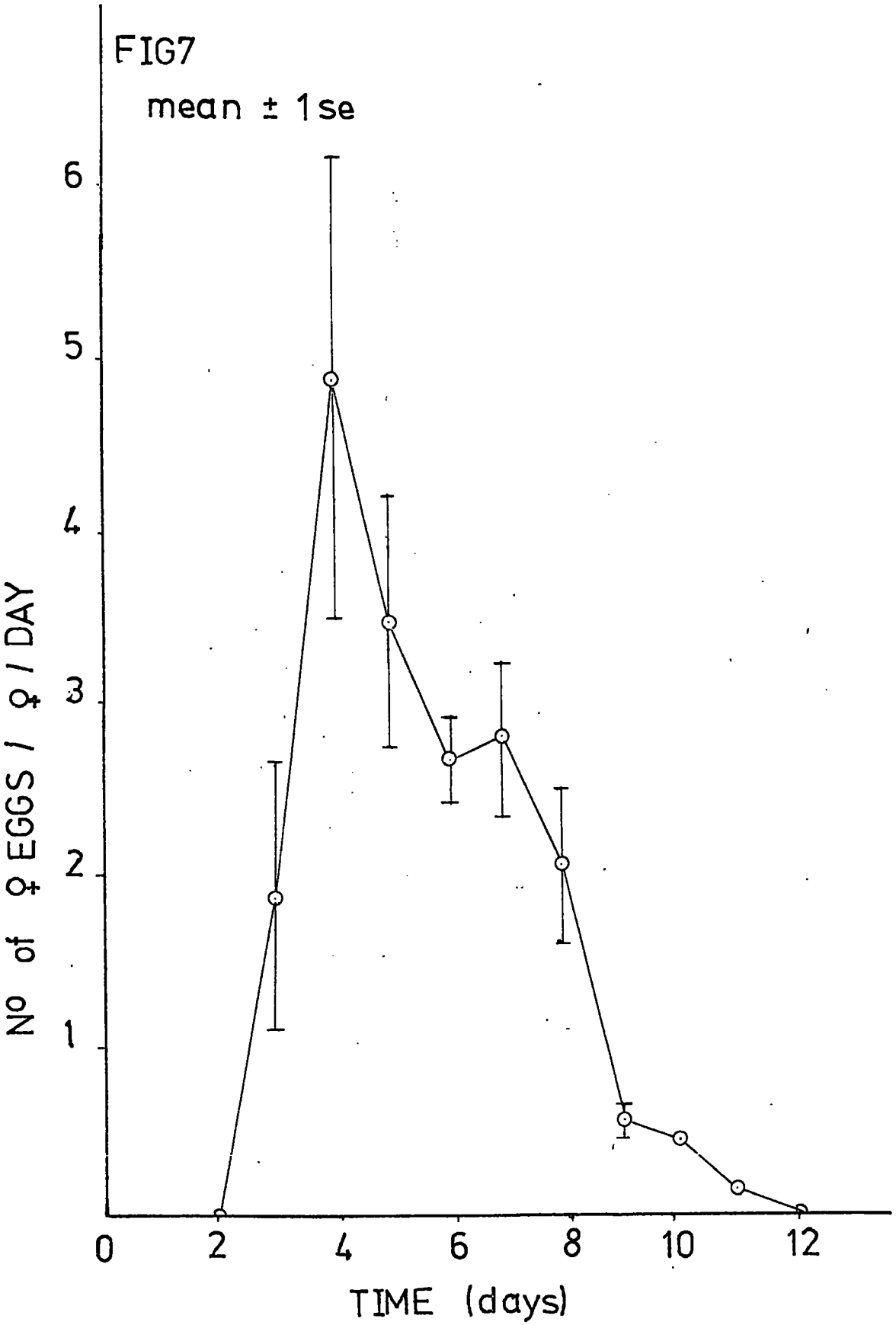
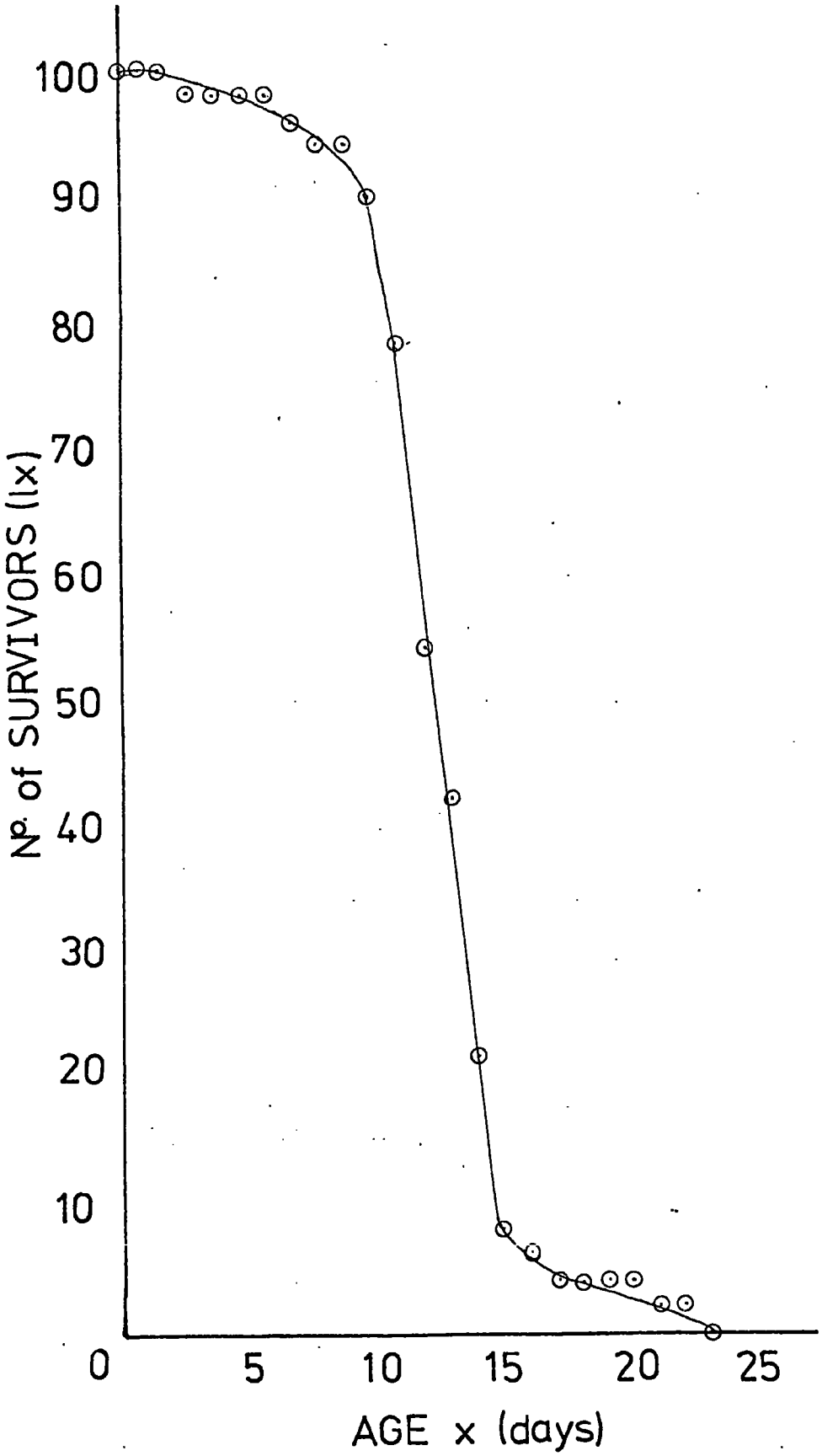


FIG7
mean ± 1se
6
5
4
3
2
1
Nº of ♀ EGGS / ♀ / DAY
0
2
4
6
8
10
12
TIME (days)

FIG8


100
90
80
70
60
50
40
30
20
10
0
5
10
15
20
25
Nº. of SURVIVORS (lx)
AGE x (days)

The capacity for increase was calculated from the fecundity table as follows:

$$R_o = \Sigma\, l_x m_x$$

$$R_o = 17.93$$

$$T_c = \frac{\Sigma\, l_x m_x x}{\Sigma\, l_x m_x}$$

$$T_c = 5.56$$

$$r_c = \frac{\log_e}{T_c}$$

$$r_c = 0.52/\text{beetle/day}$$

A life table (Table XIII) was constructed from the number of females dying per day. The rate of mortality, q_x and mean expectation of further life, e_x were calculated as shown for adult female beetles only.

The expectation of further life was calculated as follows:

Numbers of animals alive between age x and x + 1 = L_x

$$L_x = \int_x^{x+1} l_x\, d_x \qquad \text{(v)}$$

or $$L_x = \frac{l_x + l\,(x+1)}{2} \text{ since age intervals are small}$$

The total number of animals at x age units beyond the age x, is given by:

$$T_x = L_x + L(_x + 1) + L(_x + 2) \ldots\ldots L_w \qquad \text{(vi)}$$

In practice this is found by summing the L_x column from the bottom upwards.

Theoretically the expectation of further life is:

$$\theta_x = \frac{\int_x^W l_x\, d_x}{l_x} \qquad \text{(vii)}$$

The rate of mortality 1000 q_x was obtained from the formula

$$1000\, q_x = 1000\, \frac{d_x}{l_x} \qquad \text{(viii)}$$

Table XIII Adult life table for female S. paniceum calculated from a cohort of 50 females.

Pivotal age	No. surviving at start of age class l_x	No. dying d_x	Rate of mortality $1000q_x$	Mean expectation of further life e_x
0	1.00	0.00	0.00	12.47
1	1.00	0.00	0.00	11.47
2	1.00	0.02	20.00	10.47
3	0.98	0.00	0.00	9.66
4	0.98	0.00	0.00	8.66
5	0.98	0.00	0.00	7.66
6	0.98	0.02	20.40	6.66
7	0.96	0.02	20.83	5.79
8	0.94	0.00	0.00	4.90
9	0.94	0.04	42.55	3.90
10	0.90	0.12	113.30	3.05
11	0.78	0.24	307.69	2.45
12	0.54	0.12	222.20	2.31
13	0.42	0.20	476.20	1.83
14	0.22	0.14	636.40	2.05
15	0.08	0.02	250.00	3.75
16	0.06	0.02	333.00	3.83
17	0.04	0.00	0.00	4.50
18	0.04	0.00	0.00	3.50
19	0.04	0.00	0.00	2.50
20	0.04	0.02	500.00	1.50
21	0.02	0.00	0.00	1.50
22	0.02	0.02	1000.00	0.50
23	0.00	0.00	0.00	0.00

A survivorship curve was constructed, (Figure 8) by plotting the number of survivors lx against age x. From this it can be seen that the maximum mortality occurs in the period from 10-16 days, which is after the time of maximum egg production (day 4-8) see (TableXIII and Figure 7).

The mean expectation of life decreases for most of the adult life span (TableXIII). The average length of life was 12.5 days and 78% of females had died by day 14. At this point the mean expectation of further life increased to day 17 and then declined. The oldest female lived to 23 days, suggesting it may have copulated very late in its life span since on day 17, 18 eggs were produced. Another female lived for 20 days. This occurrence was not included in the calculation for the rate of increase, however r_c was calculated using these results and was found to be 0.501/beetle/day as opposed to 0.52/beetle/day using the rest of the population

Discussion

The life and fecundity tables were prepared to allow the capacity for increase, r_c, to be calculated, using the formula cited in the introduction of this chapter. The parameter r_c refers to a population with no overlapping generations which was the case here. If several generations had been included, and had overlapped to produce a stable age distribution the parameter r_m, (the innate capacity of natural increase) should have been calculated (Laughlin, 1965). With a population from a cohort all the same age, successive generations overlap more and more until individuals of all ages are present. Initially the slope of the log curve of equation (i).

$$\log_e N_t = r_t + \log_e N_o \qquad \text{(ix)}$$

is r_c, then as overlapping of generations increases the slope reaches the value r_m (Laughlin, 1965). The present experiment determines r_c, which is described by the initial slope of the curve so obtained. The ratio of $r_m : r_c$ depends upon the length of the reproductive period, and the net reproductive rate; as either of these increase r_m also increases with respect to r_c.

There are many problems associated with calculating rates of increase for a population as pointed out by Lefkovitch (1963). He agrees with Slobodkin that population growth can be expressed approximately by the equation:

$$N_t = N_o e^{rt}$$

Lefkovitch continues to argue that, although a constant, 'r' is not the innate capacity for increase since N_o is the number of adults at time o (therefore they are all the same age) and N_t refers to numbers in a mixed stage population. Therefore only when the population structure is constant over a period of time can one expect the rate of increase to be constant. As r_c was calculated in this experiment the adults were all the same age and this problem does not arise. The capacity for increase r_c, which was calculated above is therefore a good approximation for S. paniceum under these conditions.

Most of the eggs obtained were laid within the first 8 days of the female's life span, therefore in a population the young mothers contribute more to the rate of increase than older mothers. As S. paniceum adults are non-feeding, their food reserves are used up as they age, so that young females will have greater food reserves and will consequently have a higher fecundity than older females. As they age the food reserves will be depleted and the fecundity will decrease (Azab, 1943). It is thus an obvious advantage for 94% of eggs to be laid before day 8, or as early as possible.

Slobodkin (1965) showed four basic types of survivorship curve (Figure A).

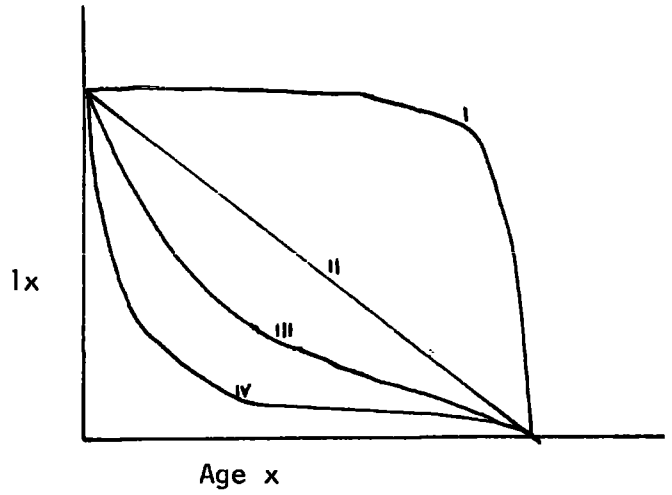


Figure A. Types of survivorship curves (after Slobodkin, 1965)

Type I. Mortality acts mainly on the older stages

Type II (lx scale arithmetic) constant number die per unit time

Type III (lx scale logarithmic gives a straight line) mortality rate is constant

Type IV mortality acts heavily on the younger individuals

If curves are plotted for all the stages of the life cycle a series of distinct steps is shown (Itô, 1961). In this case however only the adult stage is considered so this effect is not shown. The curve for S. paniceum adults corresponds mostly to Type I, with most mortality occurring in the later part of the adult life span. This curve is similar to ones obtained for Lactaodectus mactans the black widow spider (Deevy and Deevy, 1945) and for Tribolium confusum (Pearl, Park and Miner, 1941).

VII. Experiment 5

The effect on the progeny population of providing female S. paniceum with antennectomised males at low density, and a comparison of copulatory success between antennectomised and control males.

Introduction

This experiment was designed in order to investigate the importance of the female sex pheromone in attracting the male for mating. There are several ways of removing or significantly reducing the influence of the sex pheromone on the male, one of which is to remove the chemosensory receptors of the males. It has been shown that these receptors are located on the three distal segments of the antennae (Barratt, 1975 unpublished). Removal of these leads to failure by the males to respond to the presence of females. The major disadvantage of this technique is the possibility of affecting the insects in some way other than purely removing sensitivity to the pheromone. These effects might include interference with humidity responses or changes in behavioural characteristics.

A further experiment was performed to compare copulatory success of antennectomised and normal males. This was measured in terms of time taken for antennectomised males and control males to find females and copulate. This is directly relevant to the major part of this experiment as it could be a factor influencing the results obtained.

Method

The method of operation on males was as follows. They were held under a strip of filter paper with their heads projecting and the three distal segments of the antennae removed by a small scalpel. Males were antennectomised in this way when three days old, as younger insects did not recover well. They were allowed three days to recover, being kept in 5 x 1cm glass vials in groups of 10. When six days old they appeared comparable with control males in terms of activity and general appearance,

and were then introduced with females into the culture medium in densities as shown in Table XIV. The time taken for the first adult offspring to emerge was noted and the number of progeny counted every three days, until all the insects had emerged.

In the second part of this experiment males were antennectomised as before and kept until six days old before experimentation. The copulation arena was a 9cm diameter petri dish inverted on a circle of filter paper of larger diameter. From preliminary experiments, it was decided that two males and two females per dish gave consistent results. The insects were introduced to the arena and the number copulating within fifteen minutes noted. This time span was chosen as the majority of control males had copulated within this period. Clean dishes and fresh filter paper were used for each test to avoid a build up of pheromone on the surfaces which might have led to confusion of control and experimental insects.

The technique used for antennectomy was preferred to anaesthetising males or chilling them because they often withdraw their antennae under these conditions which made removal of the apical segments difficult.

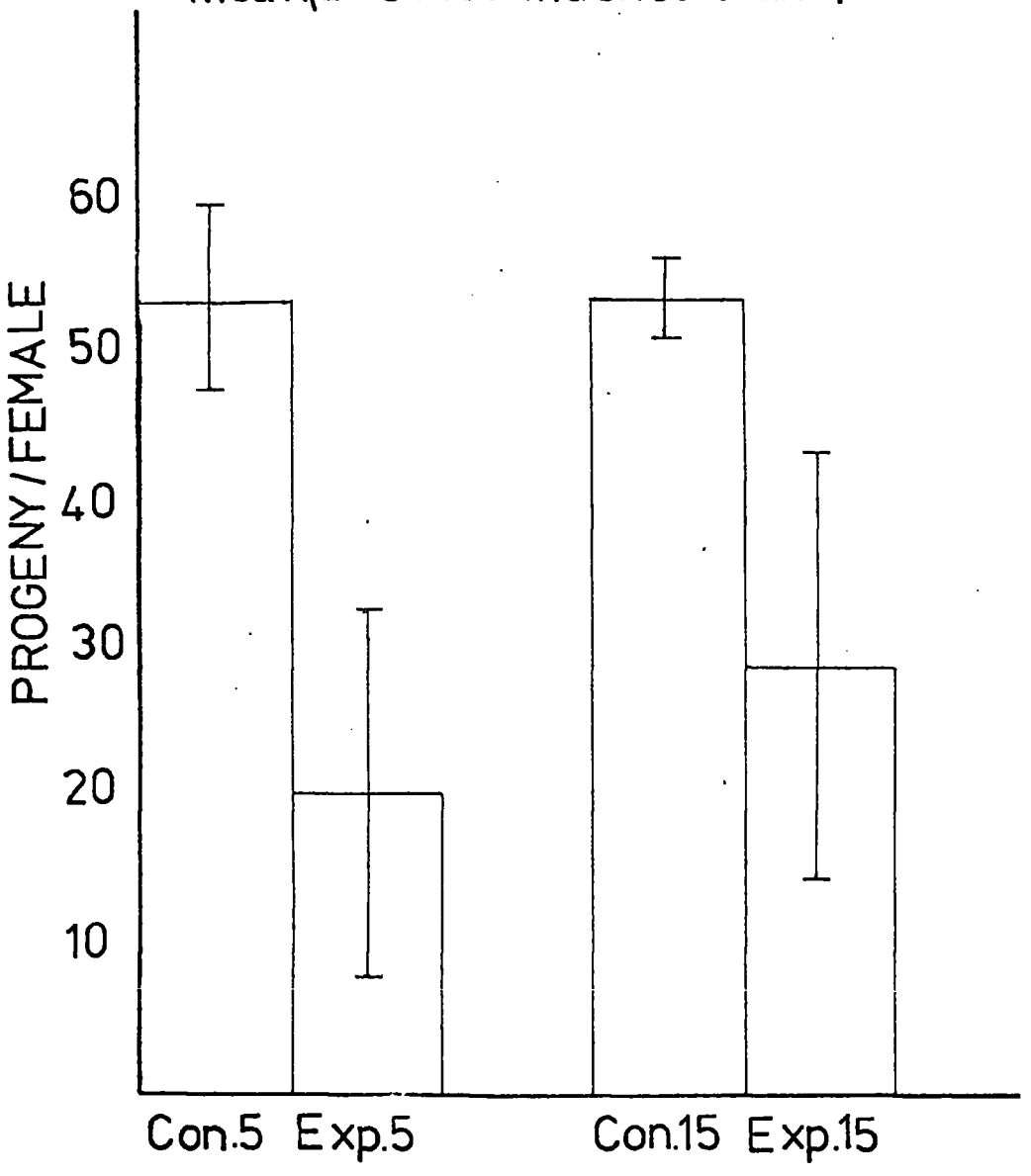
Results

The following results show the mean number of progeny emerging per female, and the number of days to emergence. The results were statistically compared using a student t-test to show significant differences in numbers of progeny per female at each density, (Table XIV, Figure 9).

Table XIV. Mean number of progeny per female and the mean number of days to adult emergence of the offspring from females kept with antennectomised and control males at two low densities.

Initial density	Treatment	No. of replicates	Mean No. of days to emergence ± SE	Mean no. of progeny per ♀ + SE	P
5	Control	8	42.8 ± 0.6	53.4 ± 2.8	<0.001
5	Experimental	8	45.6 ± 1.1	20.4 ± 6.2	
15	Control	4	42.5 ± 1.1	53.7 ± 1.7	<0.001
15	Experimental	4	45.3 ± 1.7	28.8 ± 7.1	

FIG9


mean(± 95%confidence limits)
PROGENY/FEMALE
60
50
40
30
20
10
Con.5
Exp.5
Con.15
Exp.15

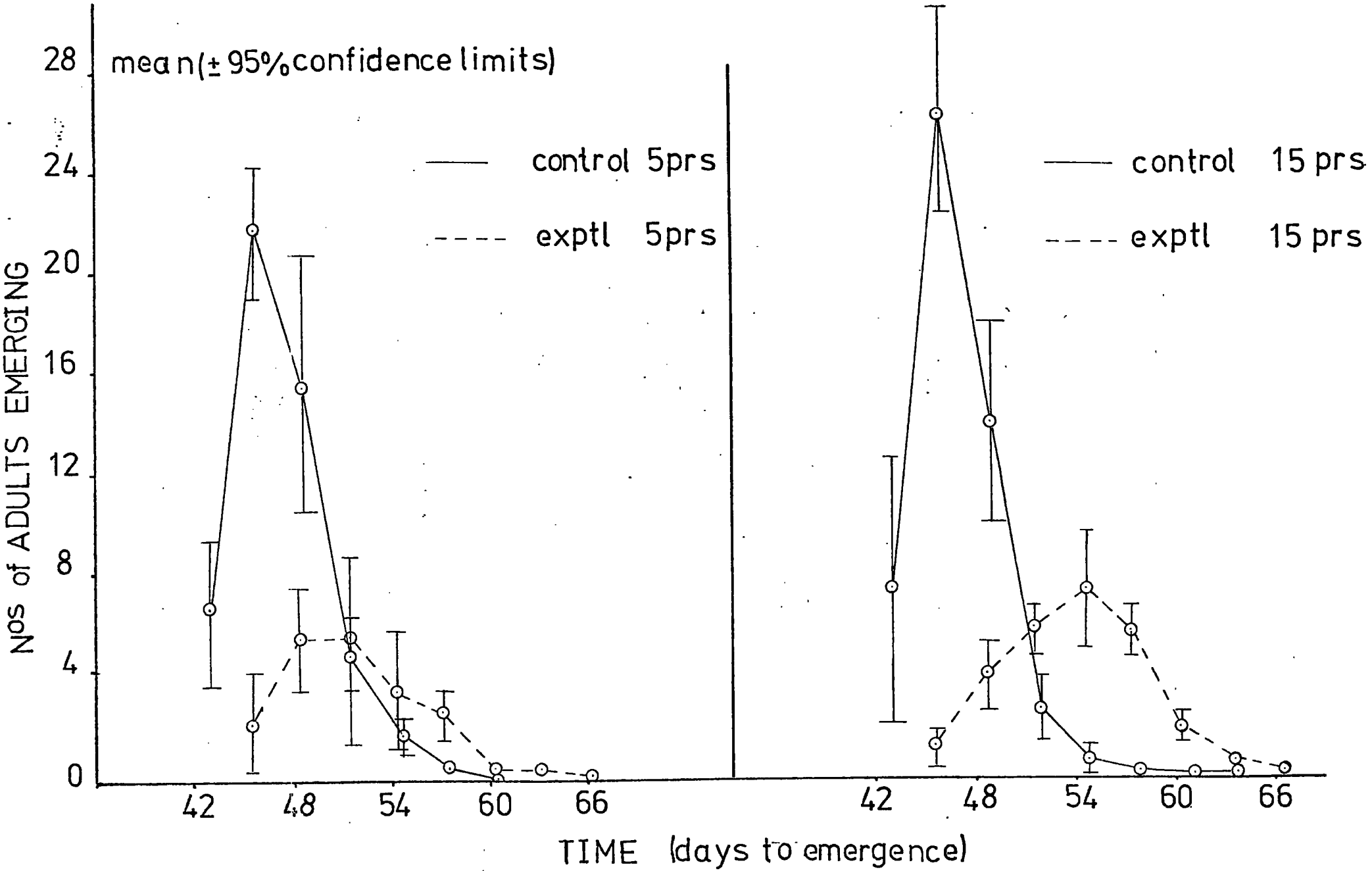

mean(± 95% confidence limits)
control 5prs
exptl 5prs
control 15 prs
exptl 15 prs
Nos of ADULTS EMERGING
0
4
8
12
16
20
24
28
42
48
54
60
66
TIME (days to emergence)

FIG 10

Table XV . Mean number of progeny per female per 3 days ± standard error.

No. of days from start of experiment.	Mean no. of progeny/♀/3 days ± SE			
	Con. 5	Con. 15	Expt. 5	Expt. 15
42	7.1 ± 1.5	7.7 ± 2.6	-	-
45	22.8 ± 1.3	26.9 ± 2.0	2.4 ± 1.1	1.5 ± 0.5
48	15.9 ± 2.5	14.4 ± 1.9	5.6 ± 1.1	4.2 ± 0.7
51	5.1 ± 0.8	3.0 ± 0.6	5.9 ± 2.4	6.2 ± 0.6
54	2.0 ± 0.3	0.9 ± 0.1	3.9 ± 1.2	7.6 ± 1.2
57	0.5 ± 0.1	0.4 ± 0.2	1.8 ± 0.5	6.1 ± 0.4
60	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	2.1 ± 0.3
63	0.2 ± 0.1	0.2 ± 0.03	0.4 ± 0.1	0.7 ± 0.2
66			0.1 ± 0.05	0.4 ± 0.1

For the second part of the experiment the number of pairs of a possible 40, copulating within fifteen minutes were recorded, together with the time at which copulation occurred.

Table XVI . Numbers of insect pairs copulating within fifteen minutes and mean time taken for copulation to begin.

	Number copulating within 15 mins.	Mean time before copulation (mins) ± SE
Control	38	6.0 ± 0.7
Experimental	2	12 mins 14 mins

From these results it appears that progeny from females kept with antennectomised males start to emerge three days later than the progeny of control insects. The total number of progeny from the experimental insects was significantly lower than that of the control insects. The number of offspring produced by experimental insects was 40% of that produced by the control parents.

In the second part of the experiment it was found that the time taken for copulation by experimental animals was much longer than for the control animals. Of the controls 94% copulated within fifteen minutes, whereas only 5% of the experimental insects did so.

Discussion

These experiments demonstrate that removal of male sensitivity to the sex pheromone of female Stegobium paniceum effectively reduces the female fecundity. This is presumably because, at the low densities used here, the male insects depend largely upon the guidance of the female sex pheromone to locate the females for copulation. At low density the meeting of a male and female insect due to chance encounter is reduced. This is reflected in the fact that at the higher of the two densities used here, the degree of difference between the numbers of progeny for the control and experimental situations was slightly reduced although this was not a significant difference.

The experimental animals took an average of 3 days longer to emerge than the control animals. This was probably a result of the experimental males taking longer to find females so that copulation consequently occurred later than with control animals.

When the numbers of offspring were compared every 3 days, those from the experimental populations were consistently lower than from the control population. The time taken for successful copulation by the experimental animals was also longer than for the control animals. These results therefore confirm the importance of the female sex pheromone in the location of the female by the male for mating. The reduction in number of offspring may be due to several effects; some females may never have mated, since several insects were found to be alive after 25 days in the experimental situation, but none were found amongst the controls. As virgins are known to live longer (21.5 ± 0.4 days as opposed to 15.3 ± 0.5 for mated females) (Barratt, unpublished), this suggests that these insects were probably virgins, which only lay a few infertile eggs. This would clearly reduce the total number of progeny. Another possible cause of apparently reduced female fecundity is the difficulty experienced by operated males in finding females, so that copulation may occur later in the female adult life span. As previously mentioned the fecundity of the

females is reduced with age which would also lead to a decrease in numbers of offspring. Operated males may be less viable than intact males and this could explain the reduced female fecundity. Antennectomised males were allowed 3 days to recover from the operation after which they appeared as active and healthy as control males. However a change in behaviour was observed, namely that males often rose on their hind legs and moved in a circular fashion with their wings outstretched. This happened almost exclusively with antennectomised males and might be the result of the removal of hygroreceptors as well as the chemoreceptors. This may lead to insects spending more time testing the atmospheric humidity, instead of searching for females for copulation, hence increasing the time taken to locate females and copulate. However it is thought that this is unlikely and that the pheromone effect can be held responsible for the results obtained.

The levels of general activity of the antennectomised males might have been reduced but this was not obvious. The activity of the operated males appeared to be normal, however it is known that operated males live longer than controls due to decreased metabolic rate.

VIII. GENERAL DISCUSSION

All animal populations are subject to inherent constraints upon their population growth, such as a limited reproductive capacity, limited capacity for food and a limited range of movement. All these factors vary from species to species and depend on environmental conditions. Competition within and between species for food, oviposition sites, interference from other individuals and cannibalism all limit the size of the population, and interact to produce a unique result for each species.

This study has been primarily concerned with the demonstration of any effects which density might have on reproductive and copulatory success of S. paniceum and on survival of its immature stages.

The effects of density were to decrease apparent female fecundity as adult density increased, with densities ranging from 0.013 - 6.7 adults/g of food medium resulting in a progeny population range from 0.4 - 0.054 young/g, corresponding to 61 progeny/female and 8progeny/female respectively. The regression analysis in Experiment 1 proved this to be a fairly strong relationship, the correlation coefficient 'r' being -0.915 ($P<0.02$). Crombie (1943) found a similar relationship with T. confusum, although this insect has a much longer life span than S. paniceum females living 447 days and males living 634 days on average.

Utida (1941) undertook a similar series of experiments with C. chinensis which is a pest of leguminous seeds in storage. The total duration of its life is 4.5 weeks. The adults live for 10 days and oviposition occurs within the first week, under experimental conditions (30°C, 70% r.h.) The adult life span of C. chinensis is about half that of S. paniceum and the average number of offspring from one pair of weevils was about 65 and egg fertility was 91%. Therefore C. chinensis has a shorter generation time than S. paniceum but the reproductive capacity is about the same. Utida used densities ranging from 0.2 - 76 insects/g of food medium, a

maximum number of progeny were produced at the intermediate density, therefore he found an optimum density for reproduction of C. chinensis. He suggested that this effect was due to there being a density where the weevils utilize the environment to best advantage, and this density was the optimum for the population but not the individual.

The largest effect on the resultant number of adults emerging from varying densities of immature stages is produced by the egg stage, with up to 25% of eggs not producing adults. The larval instar mortality apparently has little effect on the resulting population, although at higher densities the mortality rate does increase up to a maximum of 12%.

The fecundity of S. paniceum decreased with increasing density; above a density of 12 pairs/dish the number of eggs produced decreased by 40 - 50%. MacLagan and Dunn (1935) with Calandra oryzae found that egg production was reduced by approximately 92% at high densities as compared to numbers produced at low density. Utida with C. chinensis found a decrease in egg production of 95% at high densities. This reduction in egg productivity is much larger than found for S. paniceum and may be due to the much wider range of densities used for C. oryzae and C. chinensis.

Other workers have shown that egg infertility increases with increasing density. Utida found 96% egg mortality at high densities, and also that preimaginal mortality reached a peak at the density where the maximum number of viable eggs was produced, so that the more larvae that hatch the greater the number of individuals dying. The highest larval mortality of C. chinensis was 61% at a density of 12.8 weevils/g. Mortality rates of this size were not obtained for S. paniceum, suggesting that more (particularly higher) densities should be investigated or that mortality in the larval stages is not an important factor, but that egg infertility and mortality may be.

MacLagan and Dunn suggested that egg and larval mortality were the major control factors in their population of C. oryzae. Utida explained

his density effect by saying that a reduction in fecundity is more important than egg infertility and larval mortality at high densities, and egg mortality was the important check at low densities. From the results presented here for S. paniceum, it appears that reduced fecundity is important in population control at high densities, and that egg infertility (at least 20% under uncrowded conditions - Barratt, in prep.) accounts for most mortality at low densities. The reduced fecundity may be due to interference with ovipositing females by other insects, competition for oviposition sites or a decrease in the number of eggs produced in the ovaries due to overcrowding. The number of eggs laid by a species is associated with the number of ovarioles per ovary. Both quality and quantity of food influences total egg production and nutrition in the larval stages also influences fecundity of the resulting adults. Environmental factors such as temperature, humidity, and photoperiod affect the number of eggs produced, there being an optimum for these conditions (Engelmann, 1970). It has also been shown that population density effects on egg maturation and rate of oviposition are different in different species. Under crowded conditions total egg production is reduced in most species. The female's activities, such as resting, feeding, pairing and grooming are interfered with under crowded conditions, thereby reducing total egg production (Engelmann, 1970).

It was shown that, for S. paniceum the majority of eggs (94%) are oviposited before the females are 8 days old. In insects with non-feeding adult stages it is common to find most reproductive effort concentrated at the start of adult life, when food reserves built up in the larval stages are available. Tribolium confusum which has a feeding adult stage lays on average 971 eggs throughout its life span of about 500 days. With S. paniceum, if the eggs were laid at a steady rate throughout the life span, few eggs would be produced as the food reserves would be used for purposes other than egg production, such as metabolic processes. By laying most of the eggs at the start of the adult life span, the food

reserves are concentrated into producing eggs and not used solely for other purposes. Virgin females live longer than mated females because food reserves are not used up with egg production and therefore the food reserves supply the virgins for a longer period. Species with non-feeding adult stages usually have very short adult lives, compared to species with feeding adult stages.

The construction of life and fecundity tables is vital to the description and understanding of the population dynamics of a species, Deevy (1947) was the first to focus attention on the approach, which was long used by actuaries for determining the expectation of life of insurance clients. An age specific life table was constructed for S. paniceum to enable the capacity for increase r_c to be calculated with the help of a fecundity table; which was also formulated. Life tables have been constructed for several species of insects e.g. the garden chafer Phyllopertha horticola (L) (Laughlin, 1965) in which the immature stages were included. There are adult life tables for the black widow spider Lactrodectus mactans (Deevy and Deevy, 1945) and for T. confusum (Pearl, Park and Miner, 1941). The shape of the survivorship curves for these latter two species is similar to that obtained for S. paniceum.

With an insect species it is very important to know the rate at which the population can increase. The intrinsic rate of increase r_m may be calculated if the population has a stable age distribution (Birch, 1945). However with S. paniceum the stages of the life history were synchronised, therefore the capacity for increase r_c was calculated (Laughlin, 1965). This parameter has also been calculated for P. horticola (Laughlin, 1965). The innate capacity for increase has been calculated for several species e.g. C. oryzae (Birch, 1948) r_m = 0.57/head/week, compared to r_c = 0.52/ head/day for S. paniceum. This shows that the short lived S. paniceum have a faster rate of increase than the comparatively long lived C. oryzae whose adult life is 84 days.

Experiments performed with Protozoa, Insecta and Daphnia have shown

that either the rate at which young are produced or the duration of reproductive life is reduced as the density of the experimental population decreases (Andrewartha and Birch, 1954). There is a minimum density below which population increase will not occur. If individuals of a population are sparsely dispersed the chances of individuals meeting is greatly reduced and mating may not occur. In such a situation the use of a sex pheromone system may be beneficial, as males will be able to detect the pheromone and hence locate a female. This effect was investigated using the antennectomised males in low density situations, the number of progeny per female was reduced by approximately 50% compared to control populations. It was also shown that operated males took longer to find females and copulate. These results suggest that the pheromone is very important to male insects in the location of females. Many pests of stored products have pheromone systems which might have evolved as a result of their habits. These insects colonize new areas by flying, crawling or probably most commonly by being transported to them. The densities may be very low in the pioneering situation and hence the pheromone helps in the location of females by males.

Utida,(1941) studied the size and weight of individuals of C. chinensis and found that stunted underweight individuals were found at the optimum density for the population but not for the individuals. The weight of S. paniceum at different densities was looked at briefly, but no differences were found. However these observations were not statistically valid and so little importance can be placed on them. If this effect was studied in detail it may be found that larval crowding affects the weight of adults produced.

These results indicate that egg mortality (probably due to infertility) and decreased fecundity of females are the main controls in the S. paniceum population at high densities. Control of this pest would probably be best applied through manipulation of the pheromone system of this species. This work has shown that the detection of the pheromone by the males is vital to ensure successful copulation and interference with this system leads to

decrease in reproductive success. Since antennectomy on a large scale is obviously not practicable, similar control may be implemented by saturation of the atmosphere with pheromone to confuse the males, or by having areas of concentrated pheromone to attract males and hence they could be collected and killed.

Further work suggested by these results would include the effects of density on egg fertility. Using a wide range of densities the number of eggs reaching the first larval stage should be determined for each density. The effects of density on the rate of maturation of oocytes and on the egg producing capacity of females could be investigated. The intrinsic rate of natural increase r_m over several generations could be determined and the life table for the complete life cycle constructed giving the expectation of further life values for each stage. Competition for food and space between larvae at different densities and also competition for oviposition sites could be looked at. Repetition of some of the experiments performed in this study, over more densities (especially high ones) and with more replicates would be useful in clarifying the results obtained.

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