THE INFLUENCE OF CERTAIN FACTORS ON THE REPRODUCTION OF *SITOPHILUS ORYZAE* (L.) (COLEOPTERA : CURCULIONIDAE)

by

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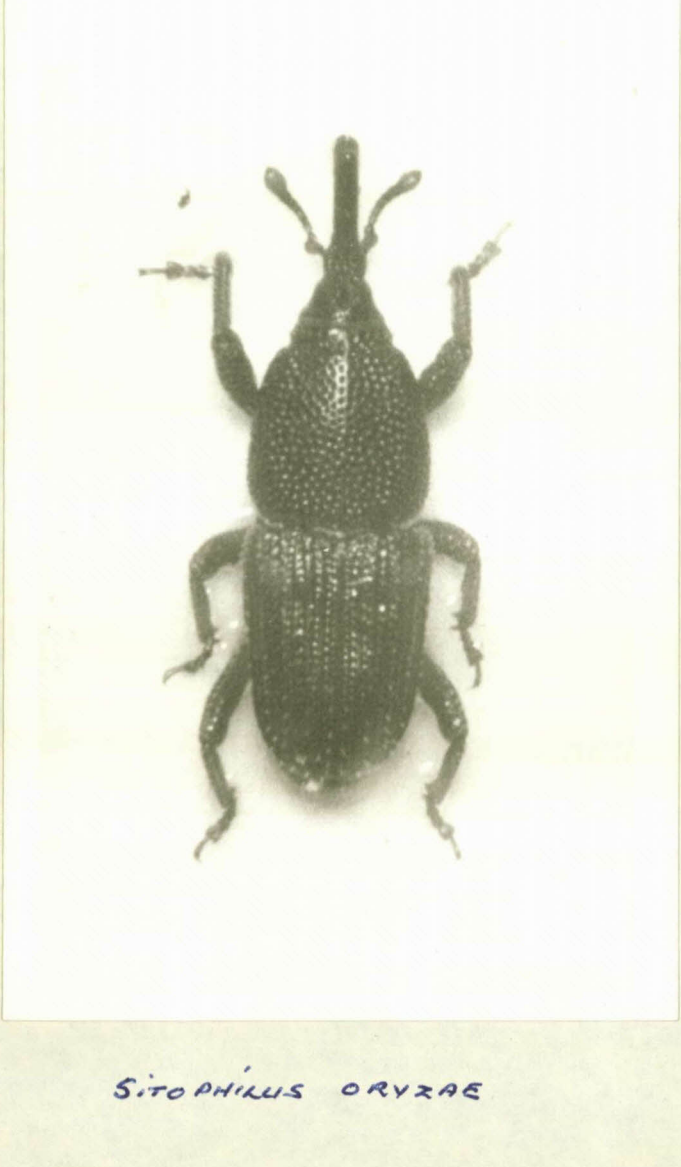

SITOPHILUS ORYZAE

I N T R O D U C T I O N

The rice weevil, Sitophilus oryzae (L), has been known as a serious pest of cereals and cereal products for many years. It occurs in most countries of the world (Reddy, 1950) and in South Africa it is regarded as one of the major pests of stored grain, causing great annual losses.

There are two species of the rice weevil, a large one and a small one. Floyd and Newsom (1959) stated that the name S. oryzae (L) is applicable to the large species and S. sasakii (Takahashi) to the small species. These two species were formerly regarded as two strains.

In the case of a pest of stored grain, the factors that influence the oviposition rate are of prime importance. According to Richards (1946) the factors which influence the fecundity of grain weevils are (i) the living conditions of the larvae, (ii) the genetic constitution of the population, (iii) bodyweight, (iv) conditions under which the weevil spends the first ten days of its life, (v) the external physical conditions of temperature, relative humidity and CO_2-concentration, (vi) age of

the weevil and the time since it was fertilized, (vii) the kind of grain in which it was reared and (viii) the crowding effect.

A study of the extensive literature on the influence of these factors on the rate of egg production reveals that much of the work that has been done is inappropriate. Reddy (1950) stated: "Previous work on oviposition has frequently fallen short of requirements for several reasons. Where full-scale experiments have been carried out, e.g. Kunike (1936) and Lavrekhin (1937), the control of environmental conditions has been too inadequate for the results to have any great value. Where a more rigid control has been attempted, short term experiments on rates of oviposition have usually been conducted, e.g. Maclagen and Dunn (1936), Crombie (1942) and Richards and his co-workers (1944 and 1946). Only in the case of the small strain (Birch, 1944) have full data been obtained under adequately controlled conditions."

Each country has its own climatic conditions and the weevils which occur under these conditions for many years might show marked differences even

though they exist in partly protected surroundings. A difference in reproduction as well as the factors influencing reproduction is therefore to be expected.

These different factors are of great importance in the case of grain weevils, because they have an influence on the rate of oviposition and, therefore, on the growth of the population. For this reason a knowledge of these factors is important.

Bearing this in mind, the effect of a number of these, and other, conditions on the reproduction of S. oryzae was studied in South Africa. These conditions were:

(a) The effect of temperature, moisture content and amount of food consumed on reproduction - Immature stages.

(b) The effect of temperature and moisture content on reproduction - Adult stages.

(c) Bodyweight.

(d) Duration of copulation.

(e) Frequency of copulation.

(f) Male/female ratio's.

CHAPTER 1

MATERIALS AND METHODS

A large sample of weevils was collected in a store room at the Glen Agricultural College. About six weeks prior to the commencement of the experiment approximately one hundred weevils per jar were placed in 10 two-pint preserve jars. "Boesman" maize kernels were supplied as food. The jars were kept in a controlled temperature and humidity room (see later). The weevils were removed after about three weeks and their progeny was collected daily as they emerged from the maize. Different random samples were drawn from these collections and these samples were used in all experiments. None of the adult individuals used in the experiments was older than 24 hours at the commencement of each experiment.

Some of the experiments were conducted in a constant temperature room at 27°C and a relative humidity of 70%, while others were conducted in desiccators stored in incubators set at different

constant temperatures. Potassium hydroxide was used to control the relative humidity in the desiccators and this was done according to a method given by Solomon (1951).

Where progeny counts had to be done, the parent weevils were transferred fortnightly to fresh maize. The maize from which they had been removed was then kept in the controlled temperature and humidity room for another 14 days. This was done to allow the immature stages to develop sufficiently to be easily seen when the maize was sectioned for progeny counts. The method used for counting the larvae was as follows: The maize was boiled in water for about five minutes and immediately thereafter placed into acid fuchsin (acid fuchsin - 0.5g.; HCl,10% - 250c.c.; distilled water - 300 c.c. See Kennedy, 1949) for about fifteen seconds.

The small holes bored by the ovipositing females stained much darker than the surrounding parts. Each hole did not always contain an egg. This was probably because the female sometimes deserted such a hole to oviposit somewhere else probably whenever she was disturbed. Therefore the kernels were

sectioned to count the immature stages inside. These counts were facilitated by the fact that the cavities inside the kernels were also stained darker than the surrounding tissue.

In the experiments carried out in the controlled temperature room, the weevils were transferred to fresh maize at fortnightly intervals. Before the weevils were allowed on to the maize, water was added to the kernels until a moisture content of 15% was attained. A Marconi-meter was used to determine the moisture content. The maize used in the experiment to determine the effect of temperature and moisture content of maize on reproduction was brought to a moisture content of 12% or 14%, as required.

In some of the experiments a difficulty encountered was to keep the moisture content of the maize at the same level throughout. In this connection Richards (1946) stated: "In grain as in a number of other substances, there is a fairly well defined relation (largely independent of temperature) between moisture content and the relative humidity of the air. The moisture content which is in equilibrium

with a particular relative humidity depends partly on the type of grain". For English wheat he gave the following figures:

40%	relative humidity of air	-	9.9%	moisture content of wheat
60%	"	-	12.6%	"
80%	"	-	18.8%	"

Similar determinations were done in the laboratory at 12% and 14% moisture content of "Boesman" maize. It was found that the relative humidity which was in equilibrium with these moisture contents was 50% and 62% respectively.

Most of the statistical analyses were calculated from data derived at from repeated measurements on the same individuals over a period of time. For this reason the usual statistical methods could not be employed and use was made of a method described by Danford, et al (1960). The assumption of equal variances and covariances was tested for the first experiment and found to be valid. In all other similar analyses, equal variances and covariances were assumed.

The weights were determined on a Mettler Multi-Purpose Balance.

The figures in brackets in Tables 6, 8, 10, 12, 15 and 18 represent the mean of the five replicates in each case.

The experiments continued until most of the weevils died.

CHAPTER 2

RESULTS

(a) The Effect of Temperature, Moisture Content and Amount of Food consumed on Reproduction - Immature stages

The aim of the experiment was to determine whether the adult weevils showed differences in rate of reproduction when their immature stages were exposed to different treatments of temperature and moisture content of maize. The temperatures used were 30°C, 26°C, 22°C and 18°C. These temperatures were each combined with 12% and 14% moisture content of maize. At the same time, the amount of food consumed by the larval stages at these different treatments was determined as given in Table 1. The influence of these different amounts of food consumed on the bodyweight of the adults was also determined and these results are given in Table 4.

Two desiccators were filled with maize kernels and brought to a moisture content of 12% and 14% respectively. To obtain eggs, about three hundred

adult weevils were transferred to each desiccator. The females deposited their eggs inside the kernels. After four days the adult weevils were removed and the egg-laden maize was weighed into 4 in. x 1 in. glass tubes (about 16 gram per tube). Five tubes per desiccator were exposed to each treatment. Each desiccator also contained one tube with maize which was at the same moisture content as the others in the desiccator, but without any eggs. These tubes with maize served as controls.

All the tubes in each treatment were examined twice daily and all the adults that had emerged were collected, counted and weighed on these occasions. The amount of food consumed was assumed to be the weight loss of the maize after the faeces of the larvae had been removed. This was done by carefully opening the maize kernels (from which the adults had emerged) with a scalpel and removing the powdery faeces with a soft brush. Care was taken not to lose fragments of the kernels in the process. The control was used to determine whether the maize lost or gained weight when confined in the desiccators under the conditions of the experiment.

(i) Weight of food consumed by larvae:-

The figures in each cell of Table 1 represent the mean weight of food consumed per larva per replicate. The number of larvae per tube varied from 3 to 5, so that the overall row means in Table 1 were based on 15 to 25 individuals in each case.

Table 1.- Weight of food consumed per larva per replicate under the different treatments of temperature and moisture content.

Temperature (°C)	Moisture Content (%)	Replicates					Mean per replicate
		1	2	3	4	5	
30	12	28.2	27.6	21.7	22.4	25.0	25.0
	14	10.8	15.7	12.6	14.3	17.7	14.2
26	12	30.3	31.2	30.8	32.0	29.1	30.7
	14	23.9	21.9	22.4	22.3	23.6	22.8
22	12	40.7	37.2	45.4	42.2	41.8	41.5
	14	35.4	30.1	33.2	37.9	37.0	34.7
18	12	44.1	44.6	46.5	40.1	44.1	43.9
	14	49.0	46.3	37.9	44.6	40.2	43.6

The analysis of variance in Table 2 was calculated to determine whether the different weights of food consumed by the larvae under the different treatments could be ascribed to chance and also whether there was a significant interaction between the effects of temperature and moisture content.

Table 2.- Analysis of variance for the data given in Table 1.

Source of variation	D.F.	S.S.	M.S.	F
Temperature	3	3562.30	1187.43	100.801 **
Moisture content	1	410.88	410.88	34.880 **
Temperature x moisture content	3	146.78	48.93	4.154 **
Error	32	376.80	11.78	
Total	39	4496.76		

From the F. values in Table 2 it is evident that both treatment components had a significant effect and also that there was a significant inter-

action between temperature and moisture content.

Table 3.- Mean weight of food consumed per larva under the different treatments of temperature and moisture content.

Moisture content \ Temperature	30°C	26°C	22°C	18°C
12%	25.0	30.7	41.5	43.9
14%	14.2	22.8	34.7	43.6

The mean weights of food consumed by larvae under the different treatments are given in Table 3. Considering the means at a 12% moisture content of maize, it may be concluded that, on the average, food consumption increased as the temperature decreased. Duncan's New Multiple Range test was applied to compare significance among the means. All the means differed significantly at the 5% level, except in the case of the difference between 22°C and 18°C. As far as the weight of food consumed at 14% moisture content is concerned, the consumption also increased as the temperature decreased, but in this case all

the differences were significant at the 5% level. Thus, it may be seen, that in the case of 14% moisture content the trend at the lower temperatures differed from the trend at the lower temperatures at 12% moisture content. This probably accounts for the greater part of the interaction.

It is also evident that the larvae required more food to complete their development at 12% moisture content than at 14%. In this case all the differences among the means were significant at the 5% level, except in the case of 18°C. From this observation it follows that as the temperature decreased, the effect of moisture content on the weight of food consumed diminished progressively and at the lowest temperature the effect of moisture content was no longer significant at the 5% level.

(ii) Influence of food consumed by larvae on weight of adults. - A correlation table, as shown in Table 4, was drawn up to test whether there was a significant correlation between the weight of food consumed by the larvae and the bodyweight of the corresponding adults. For this purpose the mean

weight of food consumed by the larvae under the different treatments, described in the previous section, was correlated with the mean weight of the corresponding adults.

Table 4. - Correlation between food consumed by larvae and bodyweights of adults.

Temperature (°C)	Moisture contents (%)	Mean weight (mg) of food consumed by one larva	Mean weight (mg) of one adult
30	12	25.0	1.92
	14	14.2	1.88
26	12	30.7	2.10
	14	22.8	2.03
22	12	41.5	2.21
	14	34.7	2.17
18	12	43.9	2.35
	14	43.6	2.32

The value of r (0.9558) proved to be highly significant.

An analysis of variance, contained in Table 5, was calculated to test whether there were significant differences in the bodyweight of weevils of which the

larvae had been reared under the different treatments.

Table 5. - Analysis of variance of the bodyweights of adults.

Source of variation	D.F.	S.S.	M.S.	F.
Temperature	3	0.2051	0.0684	526.154 **
Moisture content	1	0.0041	0.0041	31.539 **
Error	3	0.0004	0.00013	
Total	7	0.2096		

The F-values in Table 5 indicate that both the temperature and the moisture content at which the larvae were reared had a highly significant effect on the bodyweights of the adults. Tests of t were done to establish whether the differences among the mean weights of the adults were significant at the 5% level. All the differences at the various combinations of temperature and moisture content were found to be significant.

The highly significant value of r indicates

that the larvae which consumed large amounts of food resulted in heavier adults. From the experimental results given in Tables 4 and 5, it may also be concluded that the effect of temperature and moisture content on the weight of food consumed by the larvae was still evident in the weights of the adults and it may be stated that the larvae reared at the lower temperatures and lower moisture content gave rise to heavier adults and vice versa.

(iii) Relation between larvae exposed to different treatments and the reproduction of their corresponding adults. - Immediately after emergence, the adults were separated into groups. Each group consisted of two males and two females. The males were distinguished from the females by their shorter and stouter rostrum (Halstead, 1963). The separation of the adults was carried out in such a way that five groups were drawn at random from each treatment. Each group was transferred to a 6 in. x 1 in. glass tube with maize at a moisture content of 15%. This moisture content was in equilibrium with the 70% relative humidity in the controlled temperature and humidity room in which this experiment had to be conducted.

The larval progeny of each group was counted every 14 days and Table 6 contains the results.

Table 6.- Larval progeny of two females per replicate, counted at 14-day intervals after their immature stages were exposed to the stated treatments.

	Treatments	Replicates	14-day Periods 1	2	3	4	5	6	7	Overall mean per two females
14% M.C.	18°C	1	48	62	91	58	53	52	46	415
		2	45	59	85	60	60	54	53	
		3	50	70	85	65	57	55	48	
		4	45	60	90	59	54	50	40	
		5	48	64	75	66	55	60	53	
			(47)	(63)	(85)	(62)	(56)	(54)	(48)	
	22°C	1	30	72	75	86	71	63	48	446
		2	32	69	78	80	79	67	54	
		3	33	70	76	84	70	60	50	
		4	31	67	71	76	70	65	51	
		5	34	65	76	83	78	58	52	
			(32)	(69)	(75)	(82)	(74)	(63)	(51)	
	26°C	1	22	57	72	68	63	52	37	374
		2	24	56	68	70	69	47	46	
		3	28	53	71	65	62	50	43	
		4	20	63	69	69	67	41	41	
		5	26	59	64	63	70	53	40	
			(24)	(58)	(69)	(67)	(66)	(49)	(41)	
	30°C	1	16	41	55	58	51	40	35	289
		2	20	40	41	51	49	43	33	
		3	18	39	50	51	53	45	34	
		4	16	43	51	50	50	47	30	
		5	20	46	53	49	48	45	31	
			(18)	(42)	(50)	(52)	(50)	(44)	(33)	
12% M.C.	18°C	1	46	81	87	76	65	52	51	443
		2	50	73	69	83	61	60	42	
		3	40	69	84	80	63	59	46	
		4	45	85	71	65	62	53	39	
		5	41	76	76	90	75	56	46	
			(44)	(77)	(77)	(79)	(65)	(56)	(45)	
	22°C	1	40	75	83	85	67	58	53	451
		2	34	68	80	76	70	66	50	
		3	34	70	75	75	63	59	46	
		4	43	69	79	87	68	62	44	
		5	39	76	81	95	71	64	43	
			(38)	(72)	(80)	(84)	(68)	(62)	(47)	
	26°C	1	35	63	72	75	78	51	46	419
		2	30	68	78	72	69	60	40	
		3	38	60	80	78	70	56	47	
		4	42	70	83	70	65	48	35	
		5	34	56	78	75	70	53	45	
			(36)	(63)	(78)	(74)	(71)	(54)	(43)	
	°C	1	23	47	61	75	68	53	36	
		2	25	49	67	77	67	50	40	

After a square root transformation was done on the data contained in Table 6, an analysis of variance (see Table 7) was calculated to test whether there were significant differences in the number of larval progeny of the adult weevils, of which the immature stages were exposed to the different treatments.

Table 7.- Analysis of variance of the data given in Table 6.

Source of variation	D.F.	S.S.	M.S.	F.
Temperature	3	53.851	17.950	193.011**
Moisture content	1	11.624	11.624	124.989**
Temperature x M.C.	3	6.863	2.288	24.602**
Error (a)	32	2.975	.093	
14-day periods	6	260.492	43.415	563.831**
14 days x temperature	18	19.848	1.103	14.325**
14 days x M.C.	6	3.372	.562	7.299**
14 days x M.C. x temperature	18	7.268	.404	5.247**
Error (b)	192	14.824	.077	
Total	279	381.117		

From the F-values in Table 7 it is obvious that both temperature and moisture content of maize, as well as the age of the adults, had a highly significant effect on the number of larval progeny produced by the weevils after their immature stages were subjected to the different treatments.

After Duncan's Multiple-range Test was carried out on the data, it was further concluded that when the immature stages were reared at 12%, instead of 14% moisture content of maize, the adults produced significantly more progeny. The differences among the numbers of progeny due to moisture content were significant at the 5% level in the case of all the 14-day periods, except the last one.

In the case of 14% moisture content, the number of progeny produced reached a maximum after 6 weeks in cases where the immature stages were reared at 20°C and 18°C and after 8 weeks in the case of the other two temperatures. Rearing the immature stages at a 12% moisture content of maize and 26°C resulted in a maximum production of progeny after 6 weeks. In the case of the other temperatures at this moisture content, a maximum was reached after 8 weeks (See figures 1 and 2).

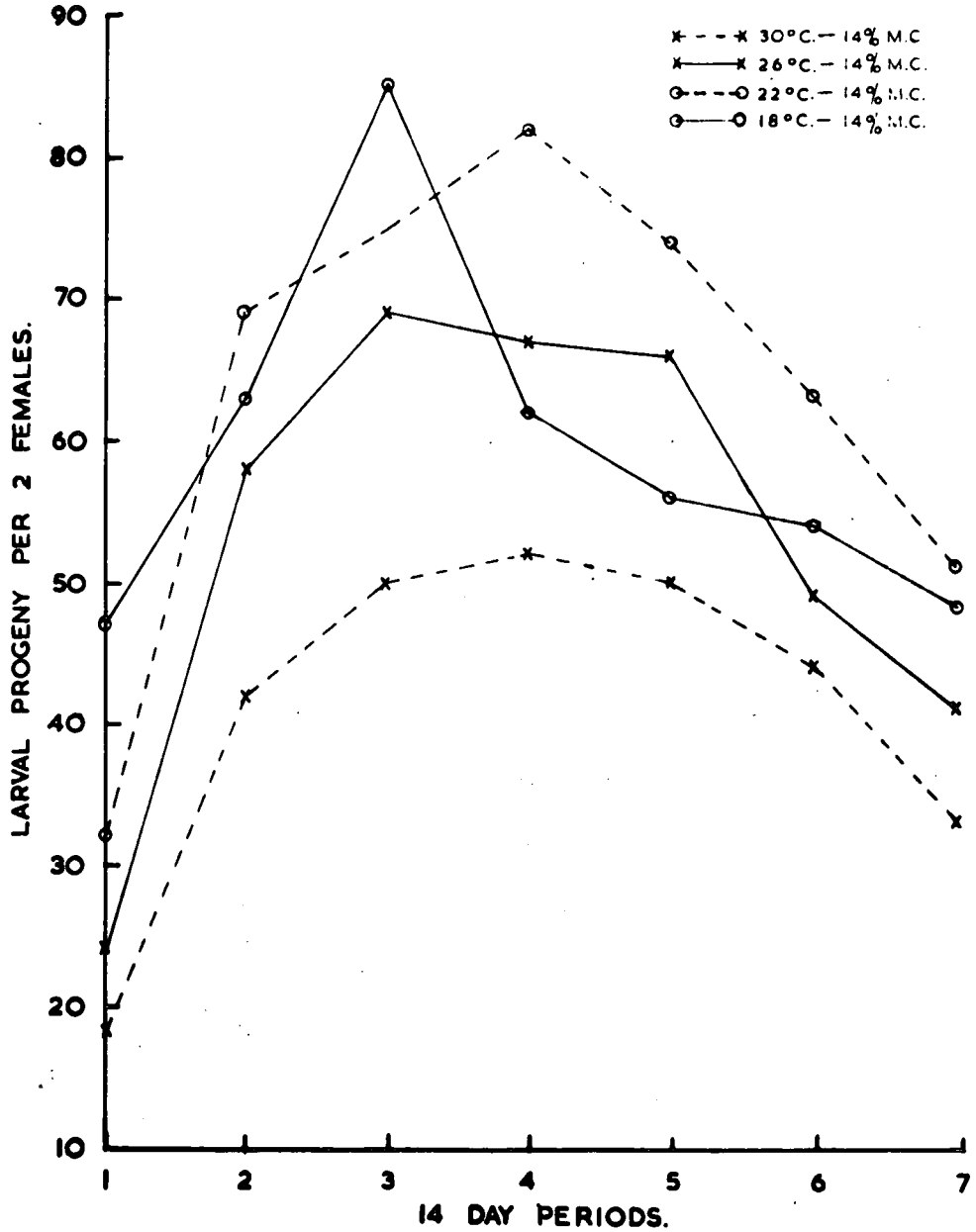

Fig.1 - Larval progeny of S. oryzae, counted at 14-day intervals, after their immature stages were exposed to different temperatures at a moisture content of 14%.

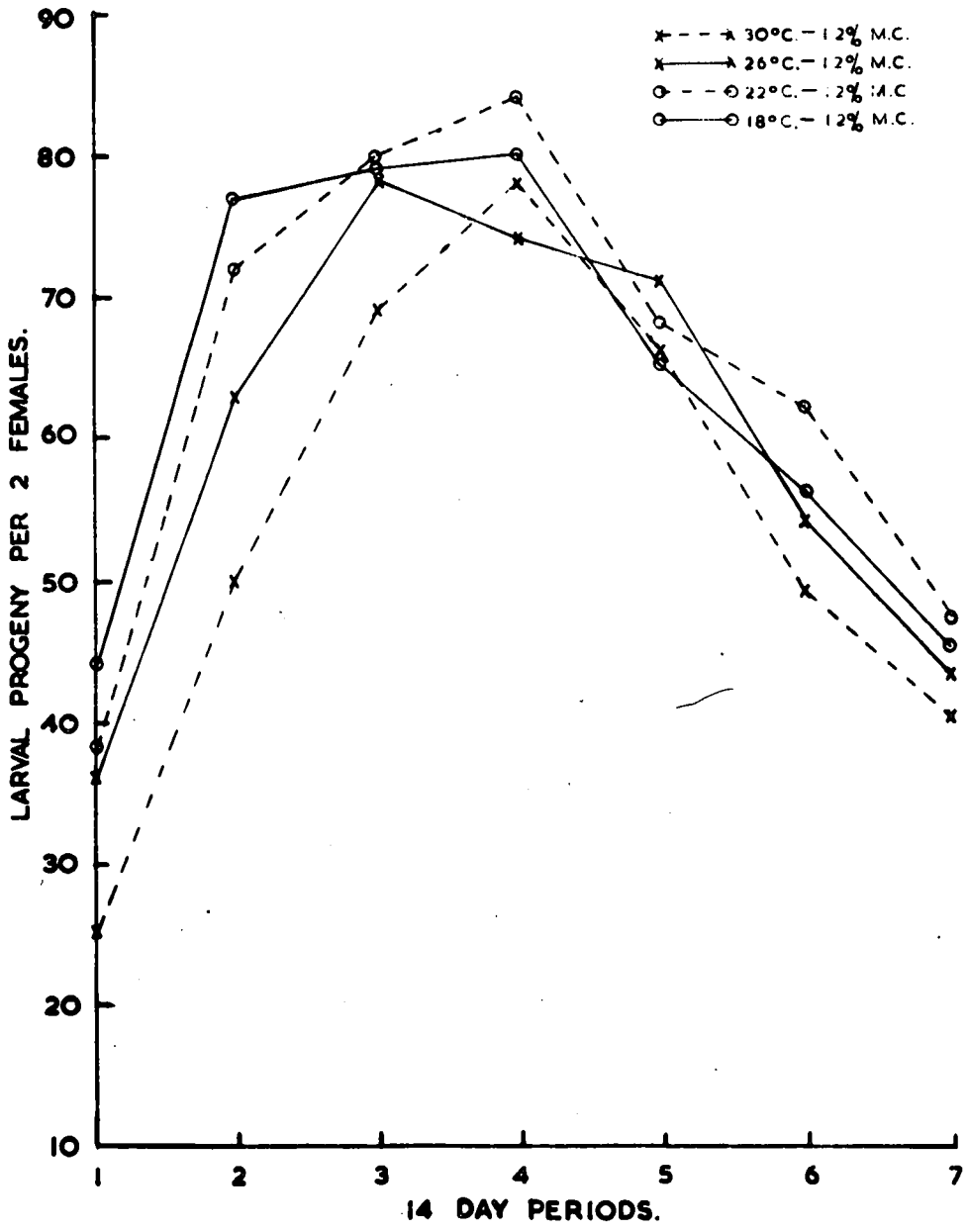

Fig.2 - Larval progeny of S. oryzae, counted at 14-day intervals, after their immature stages were exposed to different temperatures at a moisture content of 12%.

In the case of both moisture contents, most progeny were produced when the immature stages were reared at 22°C, although there was no significant difference at the 5% level between 18°C and 22°C in the case of 12% moisture content.

No significant difference due to moisture content was found to exist between the number of progeny produced by the adults, of which the immature stages were reared at 22°C, while the differences in the number of progeny due to the other temperatures, differed significantly at the 5% level.

Although the number of progeny produced in the case of both moisture contents responded approximately in the same way to temperature and time, the significant interactions indicate that the number of progeny was not equally affected by the different treatments at the various levels of the experiment.

(b) <u>The Effect of Temperature and Moisture Content of Maize on Reproduction - Adults</u>

In this experiment, adult weevils were subjected to the same conditions as described for the immature stages in the previous section. One pair of newly

emerged adults was transferred to each of a number of 4 in. x 1 in. glass tubes with maize. Five replicates were used in the case of each treatment. The same methods as described in the previous experiment were used to maintain the required moisture content and to keep the moisture content at the same level. The weevils were transferred to fresh maize at fortnightly intervals and their larval progeny was also counted fortnightly. The results are given in Table 8.

Table 8.- Larval progeny of one female per replicate counted at 14-day intervals under the stated conditions.

	Treatments	Replicates	14-day Periods							Overall mean per two females
			1	2	3	4	5	6	7	
14% M.C.	18°C	1	15	20	19	20	16	18	6	128
		2	21	25	23	26	19	15	13	
		3	19	25	21	20	14	11	10	
		4	17	23	20	21	20	17	9	
		5	16	21	24	27	18	13	11	
			(18)	(23)	(22)	(23)	(17)	(15)	(10)	
	22°C	1	24	32	37	33	23	18	14	174
		2	26	29	33	28	26	21	17	
		3	24	32	28	30	21	11	13	
		4	27	30	31	32	28	22	18	
		5	23	30	29	27	20	15	14	
			(25)	(31)	(32)	(30)	(24)	(17)	(15)	
	26°C	1	38	47	45	36	31	21	18	244
		2	40	46	46	40	30	25	20	
		3	41	54	50	43	33	23	17	
		4	34	50	45	43	28	24	21	
		5	36	51	48	34	25	22	15	
			(38)	(50)	(47)	(39)	(29)	(23)	(18)	
	30°C	1	31	44	45	35	26	22	13	225
		2	34	41	46	49	30	23	14	
		3	35	43	40	36	25	22	19	
		4	28	42	39	39	31	25	17	
		5	36	45	40	40	29	24	18	
			(33)	(43)	(42)	(40)	(28)	(23)	(16)	
12% M.C.	18°C	1	7	15	14	8	5	3	4	66
		2	11	17	11	11	9	5	6	
		3	6	12	16	10	8	6	3	
		4	8	15	12	9	9	8	7	
		5	6	13	12	17	12	6	8	
			(7)	(14)	(13)	(11)	(9)	(6)	(6)	
	22°C	1	16	24	29	12	10	8	10	106
		2	19	23	30	14	11	10	7	
		3	15	20	21	15	14	9	6	
		4	16	25	27	14	13	12	13	
		5	13	18	25	12	6	7	6	
			(16)	(22)	(26)	(14)	(11)	(9)	(8)	
	26°C	1	34	33	35	21	22	18	16	172
		2	26	34	34	24	22	19	14	
		3	30	31	30	19	20	17	18	
		4	29	37	38	20	19	15	17	
		5	31	35	40	21	18	16	12	
			(30)	(34)	(35)	(21)	(20)	(17)	(15)	
	30°C	1	31	36	26	18	18	12	11	155
		2	35	40	35	22	20	15	10	
		3	34	35	32	21	14	13	6	
		4	29	35	27	17	17	9	5	
		5								

To test whether there were significant differences in reproduction among the weevils exposed to the different treatments, a square root transformation was done on the data given in Table 8, and an analysis of variance was calculated as given in Table 9.

Table 9.- Analysis of variance for the data given in Table 8.

Source of variation	D.F.	S.S.	M.S.	F.
Temperature	3	130.955	43.652	223.856**
Moisture content	1	77.496	77.496	397.415**
Temperature x M.C.	3	0.611	0.204	1.046 N.S.
Error (a)	32	6.253	0.195	
14 day periods	6	157.775	26.296	337.128**
14 days x temperature	18	13.097	0.728	9.333**
14 days x M.C.	6	6.287	1.048	13.436**
14 days x M.C. x temperature	18	4.982	0.277	3.551**
Error (b)	192	15.021	0.078	
Total	279	412.477		

It is evident from the F. values in Table 9 that both moisture content and temperature, as well as the age of the weevils, had a highly significant effect on the number of larval progeny when the adult weevils were exposed to the different treatments.

Duncan's test indicated that most progeny were produced when the adult weevils were kept at 26°C, although there were no significant differences at the 5% level between 26°C and 30°C in the case of 14% moisture content of maize. All the other differences due to temperature were significant.

When the adults were kept at 14%, instead of 12% moisture content, they produced significantly more progeny. The differences among the numbers of progeny due to moisture content were significant at the 5% level in the case of all the 14-day periods.

In the case of 14% moisture content of maize the number of progeny produced reached a maximum after four weeks when the adults were kept at 30°C, 26°C and 18°C and after six weeks at 22°C. Subjecting the adults to a 12% moisture content, resulted in a maximum production of progeny after four weeks in the case of 30°C and 18°C. In the case of

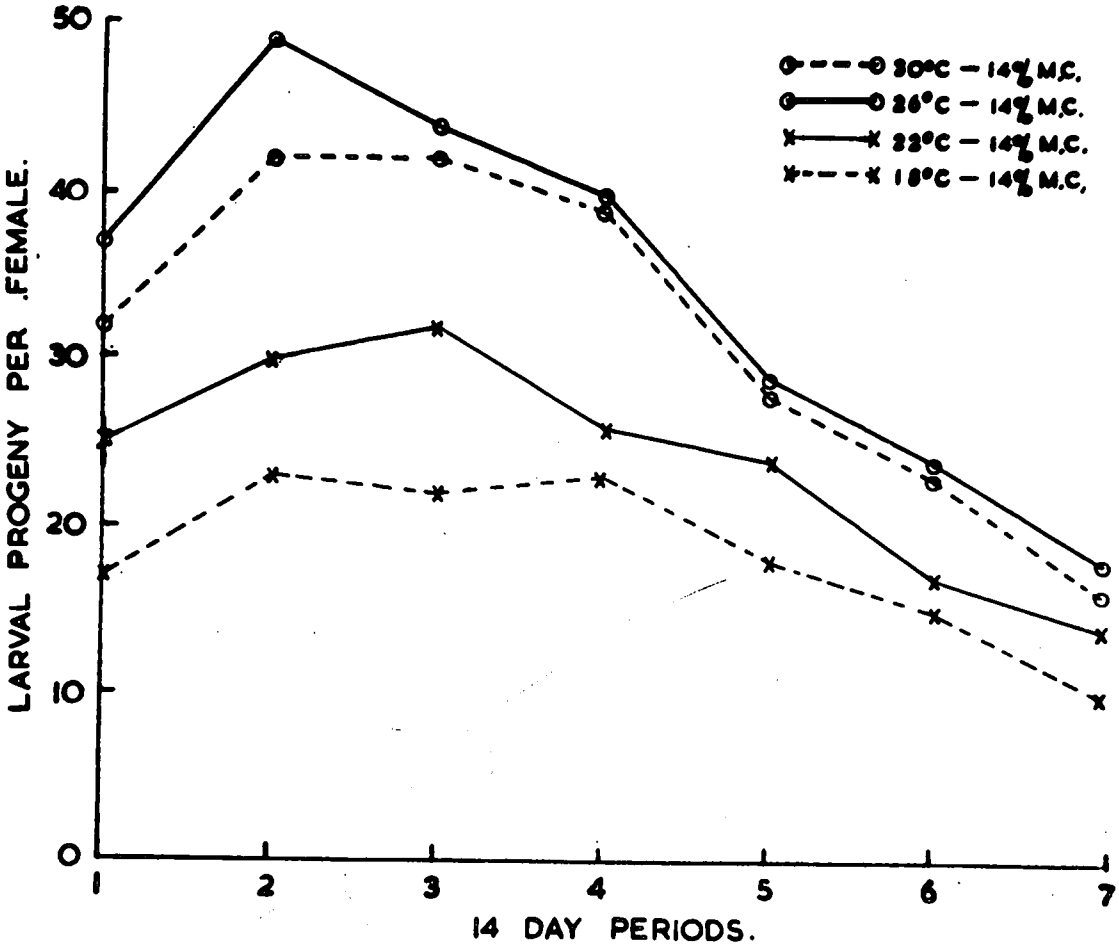

Fig.3 - The influence of different temperatures, at a moisture content of 14%, on the larval progeny of S. oryzae.

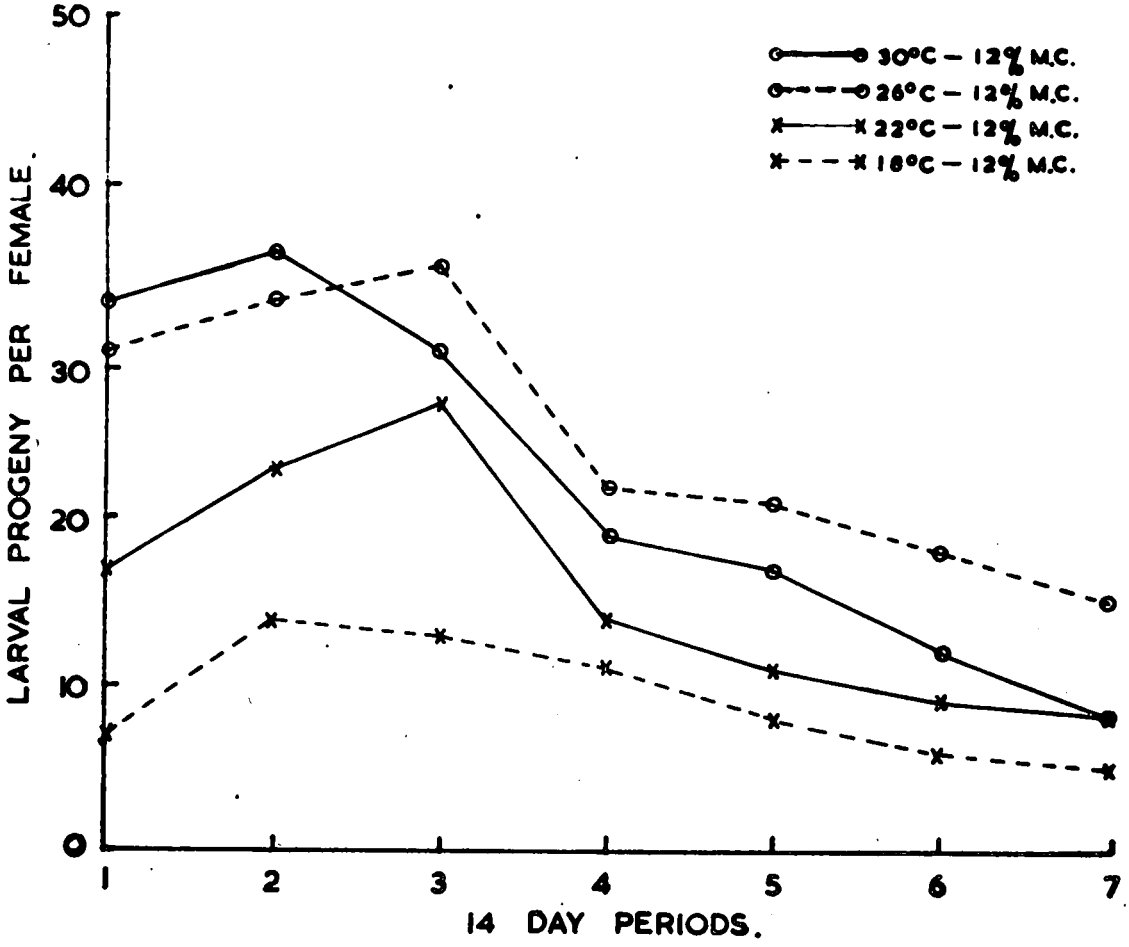

Fig.4 – The influence of different temperatures, at a moisture content of 12%, on the larval progeny of S. oryzae.

the other temperatures at this moisture content a maximum was reached after six weeks. (Figures 3 & 4).

Although the number of progeny produced in the case of different 14-day periods responded in approximately the same way to temperature and moisture content, the significant interactions between time and temperature, and time and moisture content, indicate that the progeny produced during the different 14-day periods was not equally affected by temperature and moisture content. There was no significant interaction between temperature and moisture content.

(c) The Effect of Different Bodyweights on Reproduction

According to Richards (1946) there is little doubt that the size of a weevil is one of the chief factors determining the oviposition rate and that size itself is extremely sensitive to both environmental and genetic influences. He found in the case of S. granarius that when the female weevils were kept for periods of 7 to 14 days, until their ovaries contained many eggs, dissection showed that the ovarial score (total number of eggs in ovary) was

closely related to the size of the weevil. Once a female was fertilized and began to lay eggs, there was a tendency towards a balance between the oviposition rate and the rate of production of new eggs in the ovaries.

To determine whether S. oryzae exhibited the same trend, the following experiment was conducted: A random sample of female weevils was drawn and separated into three weight-classes, namely mean weights of 1.77 mg., 2.19 mg. and 2.54 mg. The differences in weight were assumed to be mainly due to genetic factors since the females were drawn from the same culture in the controlled temperature and humidity room. A series of groups, consisting of two females, together with two males, were placed in 6 in. x 1 in. glass tubes (one group per tube) with maize. Five replicates were randomly drawn from each weight class.

The experiment was conducted in the controlled temperature room and the larval progeny was counted fortnightly. The results are given in Table 10.

Table 10.- Larval progeny of two females per replicate, counted at 14-day intervals.

Weight classes	Replicates	14-day periods							Overall mean per two females
		1	2	3	4	5	6	7	
1.77 mg.	1	21	51	63	39	33	20	20	250
	2	20	56	67	38	35	24	12	
	3	22	50	65	35	31	19	19	
	4	25	58	70	34	36	23	16	
	5	26	54	62	40	33	21	15	
		(23)	(54)	(65)	(37)	(34)	(21)	(16)	
2.19 mg.	1	38	61	69	43	49	34	23	324
	2	34	67	73	44	40	37	25	
	3	40	72	78	45	49	31	27	
	4	35	63	72	50	47	33	20	
	5	40	69	76	49	44	30	25	
		(35)	(66)	(74)	(46)	(46)	(33)	(24)	
2.54 mg.	1	53	82	87	63	59	43	36	408
	2	50	83	81	56	60	40	31	
	3	51	84	89	59	54	45	33	
	4	48	84	85	60	56	41	28	
	5	52	79	88	64	49	41	29	
		(51)	(82)	(86)	(60)	(56)	(42)	(31)	

To test whether there were significant differences in the number of progeny produced by the

females in the different weight classes, a square root transformation of the data was done and an analysis of variance, given in Table 11 was calculated.

Table 11.- Analysis of variance for the data given in Table 10.

Source of variation	D.F.	S.S.	M.S.	F.
Weight	2	51.819	25.909	411.255**
Error (a)	12	.761	.063	
14-day periods	6	167.122	27.854	506.435**
Weight x 14 days	12	2.221	.185	3.364**
Error (b)	72	3.969	.055	
Total	104	225.892		

From the F values in Table 11 it is obvious that both weight and age of the weevils, had a highly significant effect on the number of larval progeny.

The maximum number of larval progeny produced by the females in each weight class was reached after six weeks (see figure 5).

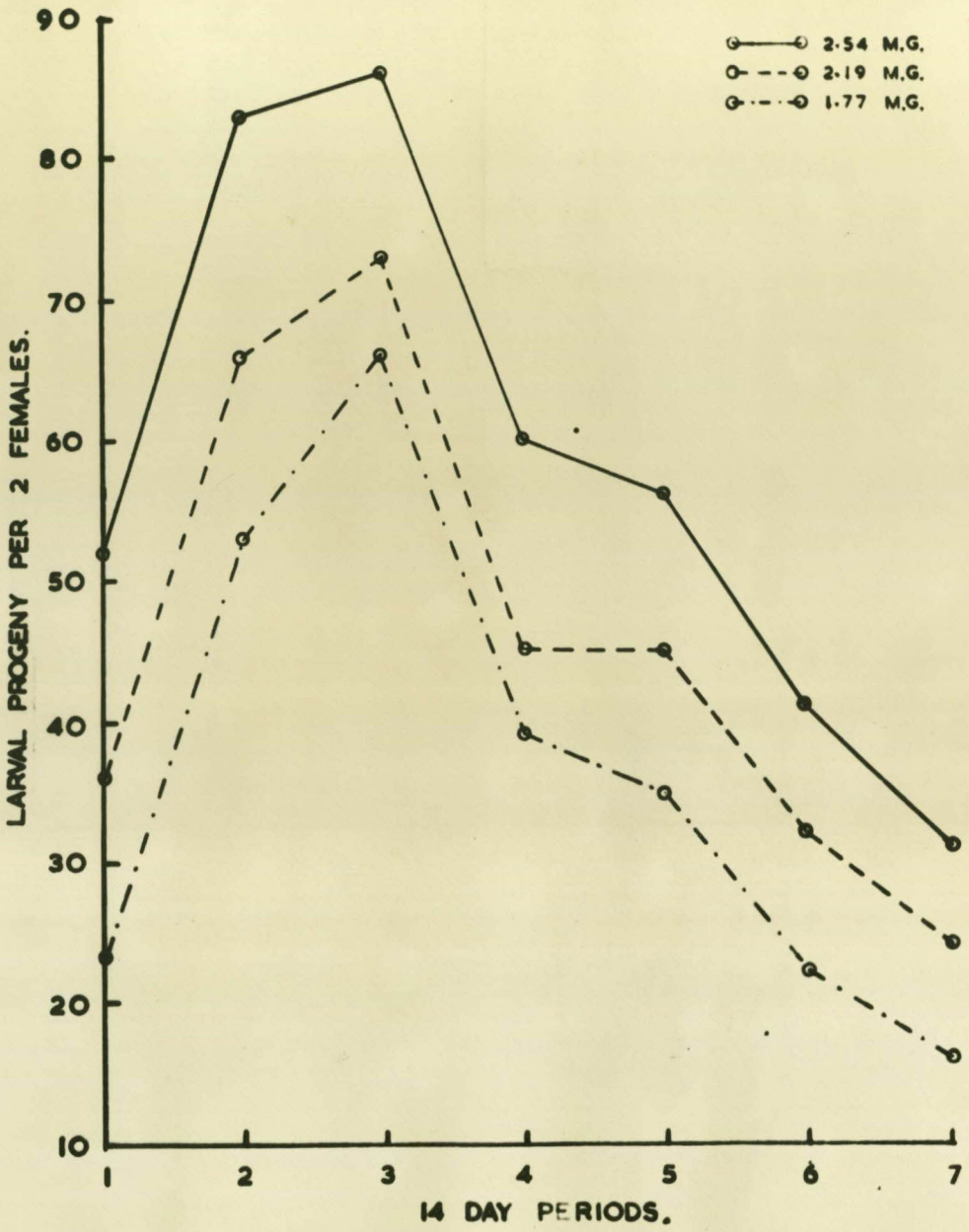

Fig.5 - The influence of bodyweight on the larval progeny of S. oryzae.

Duncan's test showed that all the differences in the number of larval progeny, produced by the females in the different weight classes, differed significantly at the 5% level. It may further be concluded that the heavier females produced most progeny.

There was a highly significant interaction between the weight of the females and the 14-day periods.

(d) The Effect of the Duration of Copulation on Reproduction

An experiment was carried out to determine whether the duration of copulation had an effect on reproduction. Soon after the emergence of the adults from the kernels the males and females were collected and kept separate for one week. This was done to allow the females to become sexually mature and to ensure that copulation would take place when the males and females were again brought together. After this period one male and one female were transferred to a small glass tube (2 in. x $\frac{3}{8}$ in.). Copulation took place almost immediately the copulating weevils were separated

at random into five groups. One group was allowed to copulate for 15 minutes, and the others for 30 minutes, 60 minutes, 120 minutes and 180 minutes respectively. After these different periods the sexes were again separated and each female was placed in a 4 in. x 1 in. glass tube with maize at a moisture content of 15%. From each group five replicates were drawn randomly. The progeny was counted fortnightly and the results are contained in Table 12.

Table 12.- Larval progeny of one female per replicate, counted at 14-day periods after the different durations of copulation.

Duration of copulation	Replicates	14-day Periods							Overall mean per female
		1	2	3	4	5	6	7	
15 minutes	1	43	57	50	25	19	19	-	224
	2	43	63	43	36	20	25	-	
	3	38	56	46	30	26	14	-	
	4	48	60	64	37	25	18	-	
	5	46	59	45	27	18	15	-	
		(44)	(59)	(50)	(31)	(22)	(18)	-	
30 minutes	1	54	69	50	41	20	17	-	246
	2	56	62	54	34	24	19	-	
	3	42	63	53	30	25	20	-	
	4	50	67	59	28	19	16	-	
	5	46	70	55	36	28	23	-	
		(50)	(66)	(54)	(34)	(23)	(19)	-	
60 minutes	1	48	60	59	40	24	21	-	262
	2	52	57	58	38	30	29	-	
	3	54	63	63	49	27	20	-	
	4	50	59	61	43	23	18	-	
	5	49	55	58	41	29	26	-	
		(51)	(59)	(60)	(42)	(27)	(23)	-	
120 minutes	1	50	58	59	53	38	28	-	302
	2	55	65	63	50	40	30	-	
	3	61	60	60	57	45	34	-	
	4	61	56	61	55	36	33	-	
	5	59	62	65	59	35	31	-	
		(57)	(60)	(62)	(55)	(39)	(29)	-	
0 minutes	1	61	71	53	53	44	40	-	310
	2	63	63	60	49	41	37	-	
	3	57	68	66	50	40	34	-	
	4	54	67	58	56	40	33	-	
	5	56	60	56	46	[illegible]	[illegible]		

To determine whether there were significant differences in larval progeny among the different groups, an analysis of variance, contained in Table 13, was calculated after a square root transformation of the data was done.

Table 13.- Analysis of variance for the data given in Table 12.

Source of variation	D.F.	S.S.	M.S.	F.
Duration of copulation	4	30.669	7.667	43.811 **
Error (a)	20	3.502	0.175	
14-day periods	5	173.375	34.675	381.044 **
Duration x 14-day periods	20	12.536	0.627	6.890 **
Error (b)	100	9.094	0.091	
Total	149			

The F. values in Table 13 indicate that both duration of copulation and 14-day periods had a highly significant effect on the number of larval progeny.

Duncan's test showed that there were no

significant differences among the number of larval progeny of females that copulated for 180 and 120 minutes and females which were allowed to copulate for 30 and 60 minutes. All the other differences in number of larval progeny due to different durations of copulations were significant at the 5% level. Further it may be concluded that females which copulated for long periods produced more larval progeny than females which were allowed to copulate for short periods. In this experiment the females which copulated for 15 minutes, produced significantly the least larval progeny.

In the case of females which were allowed to copulate for 180-, 30- and 15-minute periods a maximum number of larval progeny was reached after four weeks, while those which were allowed to copulate for 120- and 60--minute periods, reached a maximum after six weeks (See figure 6).

The significant interaction indicates that the number of larval progeny produced during the different 14-day periods was not equally affected by the different periods of copulation.

The interaction is analized in Table 14 where

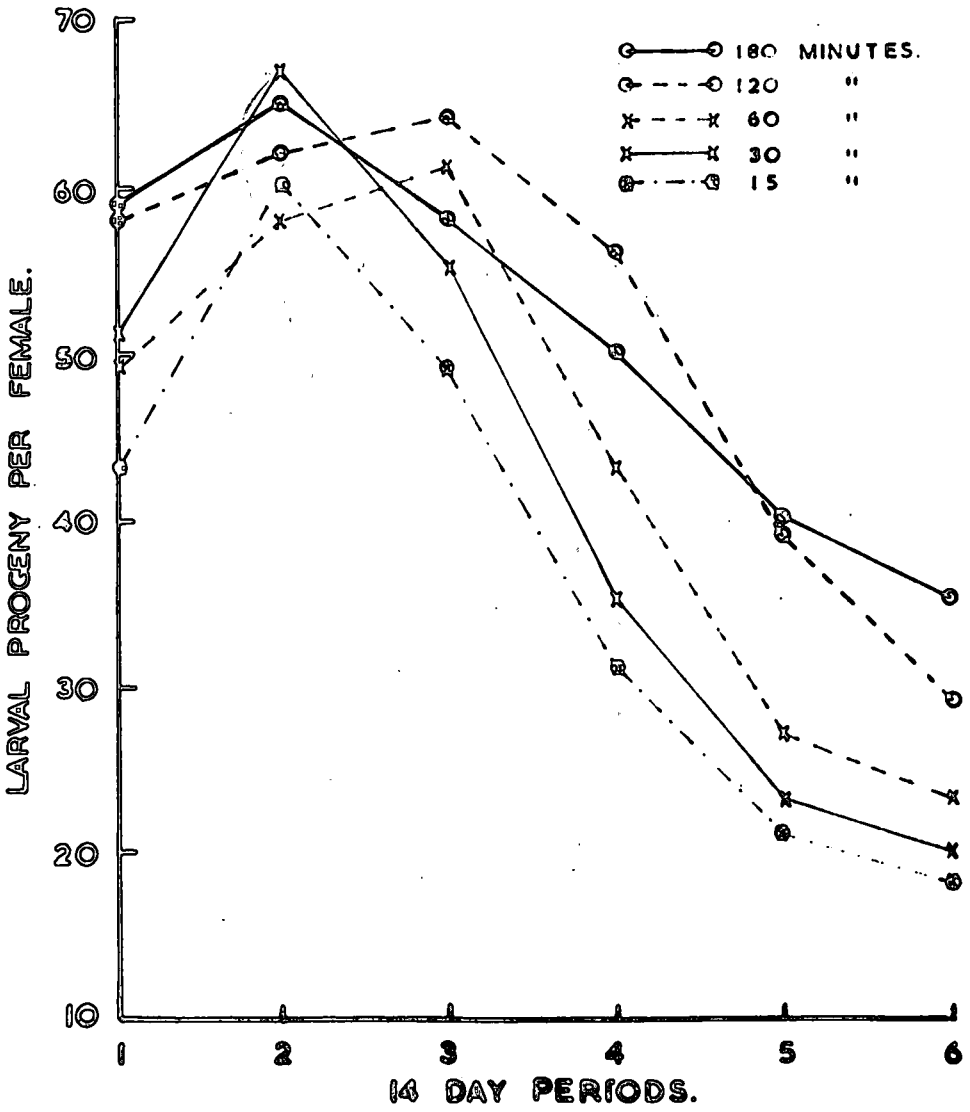

Fig.6 - Larval progeny of S. oryzae, counted at 14-day intervals, after different durations of copulation.

the periods of copulation during each 14-day period are arranged in descending order from the group of which the females produced most progeny to the group of which the females produced least. Non-significant differences in the number of progeny produced by two adjacent durations are underlined, e.g. during the first 14 days there were non-significant differences in larval progeny between 180- and 120 minutes, 180- and 60 minutes, 120- and 60 minutes and 60- and 30 minutes.

Table 14.- Differences in larval progeny between the different durations of copulation for each 14-day period. (For further explanation see test).

14-day periods	Different duration of copulation (minutes)				
1	180	120	60	30	15
2	30	180	120	15	60
3	120	60	180	30	15
4	120	180	60	30	15
5	180	120	60	30	15
6	180	120	60	30	15

(e) The Effect of Frequency of Copulation on Reproduction

Richards (1946) reported that under natural conditions, copulation probably takes place more than once, although a single mating may be sufficient for a long period of normal oviposition.

To investigate this phenomenon, the following experiment was carried out: The males and females were separated within two hours after their emergence from the kernels. After one week single pairs of males and females were transferred to 2 in. x $\frac{3}{8}$ in. glass tubes. One pair was placed in each tube. Copulation took place and each pair was allowed to copulate for three hours. The males were now removed and kept on maize until the next copulation. The females were randomly separated into four groups. One group was allowed to copulate once every fortnight, the second group once every month, the third group once every two months, while the fourth group copulated only once during their lifetime. The weevils were allowed to copulate for a period of three hours in each case. From each group five replicates were drawn randomly.

This experiment was conducted in the controlled temperature room and the maize on which the weevils were kept was at a moisture content of 15%. The progeny was counted fortnightly and the results are given in Table 15.

Table 15.- Larval progeny of one female per replicate, counted at fortnightly intervals after different frequencies of copulation.

Frequency of copulation	Replicates	14-day periods 1	2	3	4	5	6	7	Overall mean per female
Once / 14 days	1	31	48	50	54	35	21	23	247
	2	33	43	57	47	24	18	19	
	3	33	45	49	40	32	29	15	
	4	21	52	53	45	35	25	17	
	5	24	49	58	50	26	24	20	
		(28)	(47)	(53)	(47)	(30)	(23)	(19)	
Once / month	1	34	59	80	59	56	37	29	343
	2	30	58	69	54	49	33	31	
	3	35	61	71	53	57	45	33	
	4	33	65	70	49	56	34	34	
	5	32	50	73	50	54	40	36	
		(33)	(59)	(73)	(53)	(54)	(35)	(33)	
Once / 2 months	1	30	54	74	40	39	21	28	287
	2	32	51	68	46	43	24	23	
	3	31	49	70	36	45	25	24	
	4	32	53	77	33	41	22	20	
	5	30	53	74	39	50	28	25	
		(31)	(52)	(73)	(39)	(44)	(24)	(24)	
Once / lifetime	1	31	52	75	38	31	12	11	258
	2	30	56	69	35	21	16	12	
	3	35	54	74	45	25	11	14	
	4	32	61	71	39	36	10	10	
	5	31	55	76	43	30	17	19	
		(32)	(56)	(73)	(40)	(29)	(13)	(15)	

To test whether there were significant differences in the larval progeny among the different groups, an analysis of variance, given in Table 16, was calculated after a square root transformation of the data, contained in Table 15, was done.

Table 16.- Analysis of variance for the data given in Table 15.

Source of variation	D.F.	S.S.	M.S.	F.
Frequence of copulation	3	27.011	9.004	69.262 **
Error (a)	16	2,082	.130	
14-day periods	6	199.582	33.264	305.174 **
Frequency x 14 days	18	23.639	1.313	12.046 **
Error (b)	96	10.457	.109	
Total	139	262.771		

The F. values in Table 16 indicate that both the frequency of copulation and the age of the weevils had a highly significant effect on the number of larval progeny.

A multiple range test indicated that there were no significant differences between the number of larval progeny of females that copulated once every 14 days and those that copulated once per lifetime. All the other differences in number of larval progeny due to different frequencies of copulation were significant at the 5% level. Females that copulated once per month produced significantly the most larval progeny.

In the case of all the females, irrespective of copulation frequency, the maximum number of larval progeny was produced after six weeks. In the case of the females that copulated once every two months, the number of larval progeny showed a second increase after their second copulation (see figure 7). This was not true for the other females.

The highly significant interaction indicates that the number of larval progeny produced during the different 14-day periods was not equally affected by the different frequencies of copulation.

The copulation frequency in Table 17 is arranged in descending order, i.e. from the group of which the females produced most progeny to the group of

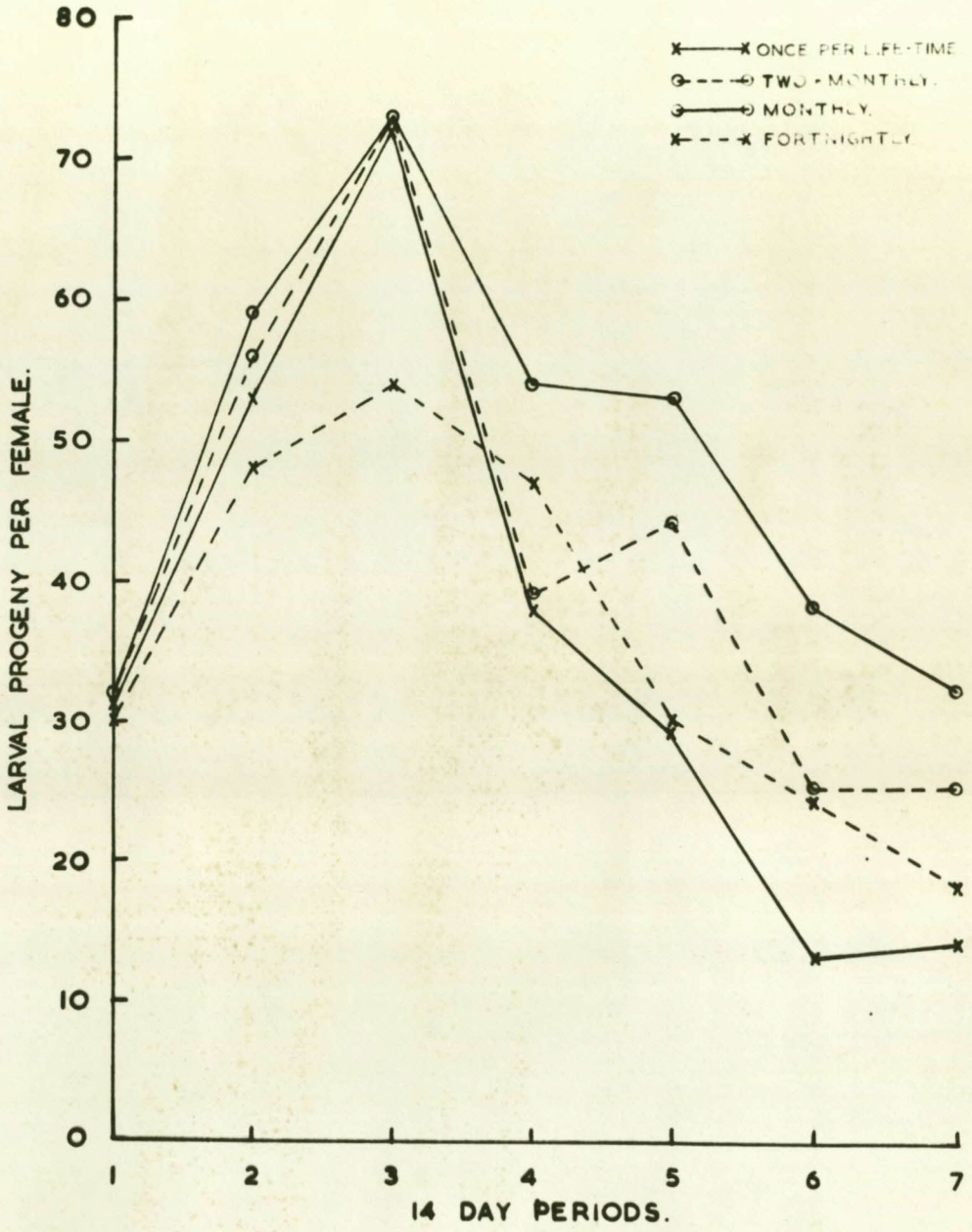

Fig.7 - Larval progeny of S. oryzae, counted at 14-day intervals, after different copulation frequencies.

which the females produced least. Non-significant differences between two adjacent frequencies are underlined.

Table 17.- Differences in larval progeny between frequencies of copulation for each 14-day period. (For further explanation see test).

14-day periods	Frequencies of copulation			
1	Once/ month	Once/ lifetime	Once/2 2 months	Once/ 14 days
2	Once/ month	Once/ lifetime	Once/ 2 months	Once/ 14 days
3	Once/ lifetime	Once/ 2 months	Once/ month	Once/ 14 days
4	Once/ month	Once/ 14 days	Once/ lifetime	Once/ 2 months
5	Once/ month	Once/ 2 months	Once/ 14 days	Once/ lifetime
6	Once/ month	Once/ 2 months	Once/ 14 days	Once/ lifetime
7	Once/ month	Once/ 2 months	Once/ 14 days	Once/ lifetime

(f) The Effect of Different Male/Female Ratios on Reproduction

In natural populations the males and females are present in a 50-50 ratio (Maclagen and Dunn, 1936). To determine the effect of different male/female ratios on reproduction, the following experiment was conducted: The adult weevils were collected soon after their emergence from the maize kernels and separated into 7 groups. Each group consisted of 5 females and 10, 8, 6, 5, 4, 2 and 1 male respectively. Five randomly drawn replicates were used in the case of each group. Each replicate was placed in a 6 in. x 1 in. glass tube. The experiment was conducted in the controlled temperature room and the larval progeny was counted fortnightly. The results are given in Table 18.

To test whether there were significant differences in the larval progeny among the different male/female ratios, the data was transformed to square roots and an analysis of variance, as given in Table 19, was calculated.

Table 18.- Larval progeny of 5 females per replicate and different male ratios.

Male/ Female ratios	Replicates	14-day periods							Overall mean per 5 females
		1	2	3	4	5	6	7	
5 females/ 1 male	1	74	84	121	107	100	90	45	648
	2	69	97	119	120	105	93	54	
	3	78	103	108	110	110	83	50	
	4	75	107	115	126	109	86	51	
	5	65	105	112	104	116	91	49	
		(72)	(99)	(115)	(115)	(108)	(89)	(50)	
5 females/ 2 males	1	90	170	136	108	86	70	40	699
	2	86	163	131	114	90	74	49	
	3	84	160	128	110	93	67	41	
	4	83	166	129	116	92	71	43	
	5	78	159	130	112	97	74	53	
		(84)	(164)	(131)	(112)	(92)	(71)	(45)	
5 females/ 4 males	1	33	141	111	82	68	51	46	547
	2	30	150	104	83	78	63	41	
	3	28	130	106	90	80	56	38	
	4	38	135	112	87	73	61	45	
	5	35	140	115	91	83	60	40	
		(35)	(139)	(110)	(87)	(76)	(58)	(42)	
5 females/ 5 males	1	37	123	90	78	48	42	39	455
	2	40	128	87	77	55	41	30	
	3	39	126	94	76	49	46	42	
	4	36	127	95	80	63	36	31	
	5	34	120	91	85	50	40	35	
		(31)	(125)	(91)	(79)	(53)	(41)	(35)	
5 females/ 6 males	1	54	103	65	61	40	37	27	401
	2	46	108	78	60	45	40	30	
	3	50	109	70	64	46	39	29	
	4	57	111	73	59	47	41	21	
	5	49	114	76	56	39	43	23	
		(51)	(109)	(72)	(60)	(43)	(40)	(26)	
5 females/ 8 males	1	48	95	52	59	40	34	26	337
	2	54	92	50	45	37	31	21	
	3	50	90	48	50	36	28	19	
	4	52	94	52	53	43	30	20	
	5	53	92	56	48	41	31	15	
		(51)	(93)	(52)	(51)	(39)	(31)	(20)	
5 females/ 10 males	1	28	54	47	51	29	22	20	254
	2	35	59	50	47	30	18	18	
	3	30	60	44	50	35	21	14	
	4	29	63	41	48	38	17	12	
	5	25	56	58	53	41	25	19	
		(29)	(58)	(48)	(46)	(35)	(21)	(17)	

Table 19.- Analysis of variance for the data given in Table 18.

Source of variation	D.F.	S.S.	M.S.	F.
Male/female ratios	6	425.528	70.921	770.880**
Error (a)	28	2.562	.092	
14-day periods	6	558.895	93.149	1095.871**
Male/female ratio x 14 days	36	99.195	2.755	32.412**
Error (b)	168	14.265	.085	
Total	224	1100.449		

It is obvious from the F. values in Table 19 that both ratios and time had a highly significant effect on the number of larval progeny. There was a highly significant interaction between the male/female ratios and the 14-day periods, which indicates that the different male/female ratios had a proportionately different effect at the different 14-day periods.

Duncan's Multiple-range Test was done to est establish whether the differences in number of larval progeny due to the different male/female ratios were

significant at the 5% level. All the differences were significant and 5 females together with 2 males produced most larval progeny.

In the case of 5 females, mated with 10, 8, 6, 5, 4 and 2 males respectively, the maximum number of larval progeny was produced after four weeks. In the case of 5 females and one male the maximum was reached after eight weeks (see figure 8).

In Table 20 the ratios for each 14-day period are arranged in descending order from the ratio that produced most progeny to the one that produced least. Non significant differences between two adjacent ratios are underlined.

Table 20.- Differences in larval progeny between the ratios for each 14-day period. (See test for further explanation.

14-day periods	Different male/female ratios						
1	5♀- 2♂	5♀-1♂	5♀- 8♂	5♀ - 6♂	5♀- 5♂	5♀- 4♂	5♀- 10♂
2	5♀- 2♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 1♂	5♀- 8♂	5♀- 10♂
3	5♀- 2♂	5♀- 1♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 8♂	5♀- 10♂
4	5♀- 1♂	5♀- 2♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 8♂	5♀- 10♂
5	5♀- 1♂	5♀- 2♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 8♂	5♀- 10♂
6	5♀- 1♂	5♀- 2♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 8♂	5♀- 10♂
7	5♀- 1♂	5♀- 2♂	5♀- 4♂	5♀- 5♂	5♀- 6♂	5♀- 8♂	5♀- 10♂

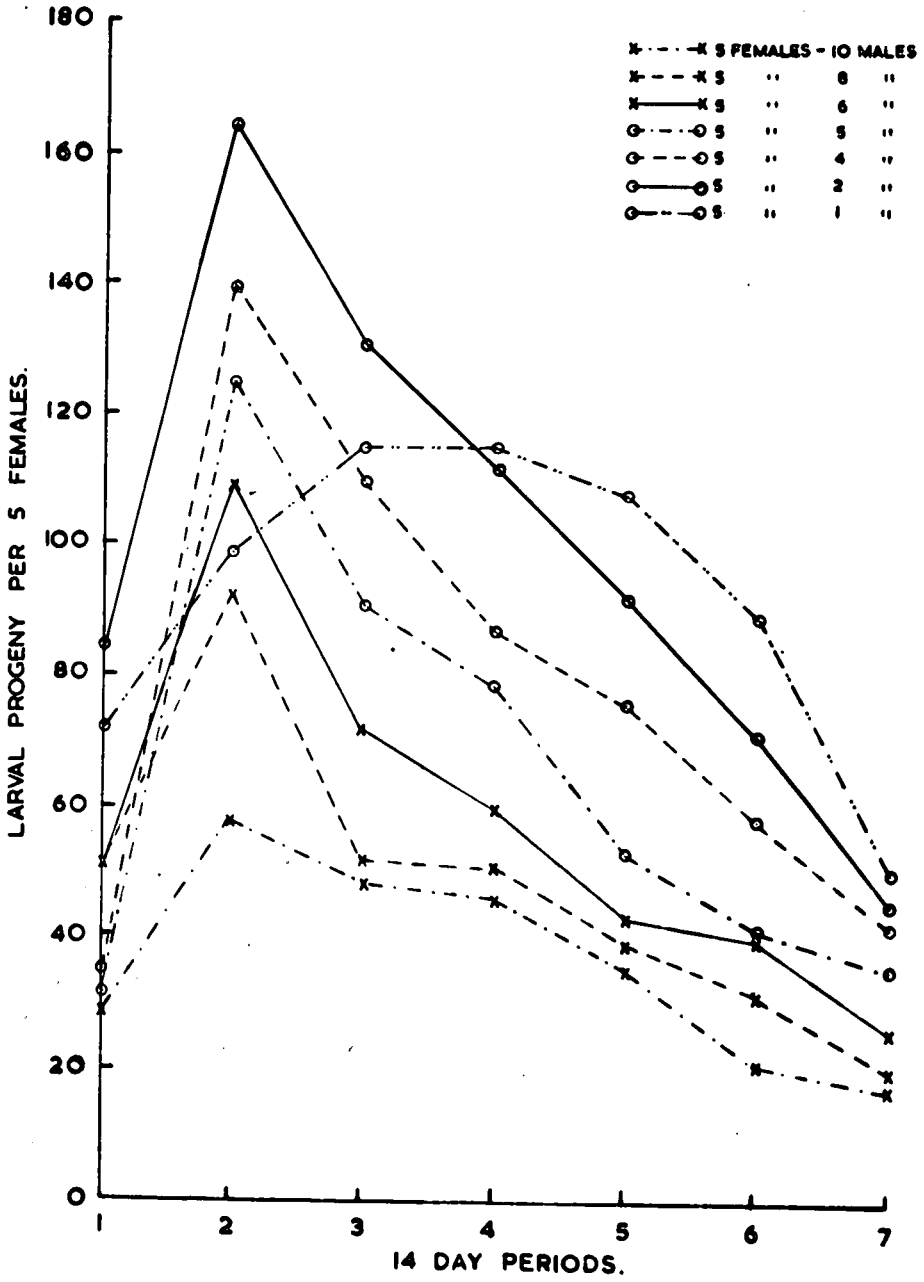

Fig.8 - The influence of different male/female ratios on the larval progeny of S. oryzae.

CHAPTER 3

D I S C U S S I O N

Six complex experiments were done in which the influence of various environmental, and other, factors on the reproduction of S. oryzae were determined. The number of larval progeny over a period of time was regarded as a measure of the rate of reproduction. It was found that the temperature and the moisture content of maize kernels on which the larvae were reared had a highly significant effect on the number of larval progeny produced by the resulting adults. It was also established that the larvae consumed significantly more food at relatively low temperatures (18° and $22^{\circ}C$) and a low moisture content of maize (12%) than at higher temperatures (26° and $30^{\circ}C$) and a higher moisture content (14%). The reason for this is probably that the larvae take longer to complete their development at the lower temperatures and moisture contents. A highly significant positive correlation was found to exist between the weight of food consumed by the larvae and the weight of the corresponding adults. It was also determined

that heavier adults tended to produce significantly more larval progeny than lighter adults. This may explain the tendency of the adults resulting from larvae reared at relatively low temperatures and a relatively low moisture content, to produce more progeny. Dendy and Elkington (1921) stated that at ordinary room temperatures nearly all adults of S. oryzae were killed off during the winter, but large numbers of larvae survived in the interior of the grains. It is evident from the first experiment that weevils resulting from these larvae had a relatively high rate of reproduction. From the evidence in this paper it may be inferred that summer larvae might give rise to adults of which the rate of reproduction might be relatively low.

The number of larval progeny was counted at fortnightly intervals. The number of progeny reached a maximum when the adults were from four to six weeks old, irrespective of the treatment to which the larvae had been exposed. As may be seen from the different figures, reproduction in time exhibited approximately the same trends throughout, although the elevations of the curves differed

significantly in most cases.

Significant interactions were demonstrated among temperature, moisture content and time. This may be taken to indicate that the reproduction of the adults in time did not respond in the same way to different levels of temperature and moisture content. to which the immature stages were exposed. In some cases, the number of larval progeny "added" or "subtracted" by one temperature and/or moisture content of maize during a certain 14-day period was different from the number "added" or "subtracted" by another temperature and/or moisture content during the same 14-day period. This may indicate that different temperatures and moisture contents might have brought about important physiological changes in the weevils.

When adult weevils were subjected to the differemt conditions of temperature and moisture content of maize, the rate of reproduction differed significantly under the different treatments. At a moisture content of 14%, significantly more progeny was produced than at a moisture content of 12%. From the literature on the subject it may be inferred that the rate of reproduction increases up to a certain

point as the moisture content of grain increases, but beyond this point a further increase in moisture content results in a drop in the rate of reproduction. Birch (1944) stated that in the case of the "small strain" of S. oryzae, the number of eggs laid in grain at a 20% moisture content is slightly greater than the number laid in grain at a 14% moisture content. Other workers also reported a high egg output at high relative humidities with a sharp decrease below 60% (e.g. Howe, 1952).

The same trend was observed in the case of a rising temperature. From the results reported in section (b), it is evident that between 18°C and 26°C, reproduction increased as the temperature increased, but when the temperature increased to 30°C, the reproduction decreased. In the case of a 12% moisture content of maize (50% relative humidity), significantly more larvae were produced at 26°C than at 30°C. This was also true in the case of a 14% moisture content (62% relative humidity), although the differences in the number of larval progeny between 26°C and 30°C were not significant. This may be taken to show that the temperature at which most larvae were produced at a 14% moisture content of

maize is probably between 26°C and 30°C. Birch (1944) reported that in the case of the "small strain" of the rice weevil, more eggs were produced at 25.5°C than at 29.1°C at a moisture content of 14%. Reddy (1950), however, found that most eggs were laid and the largest percentage hatched at 30°C at a relative humidity of 84%. According to this author the optimum temperature zone for oviposition is between 28°C and 32°C.

Thus, it is obvious that the data given by the different authors is of a conflicting nature. As indicated by Reddy (1950), short term experiments were done in most cases. These experiments did little to elucidate the general pattern of oviposition and could seldom be regarded as a reliable index of the total fertility of the females.

As may be seen from figures 3 and 4, the number of larval progeny of adult weevils, kept at 22°C, 26°C and 30°C, (in the case of a 12% moisture content), rose rapidly to a peak which was reached between four and six weeks after the emergence of the adults. The number of progeny then gradually declined. The same trend was observed in the case of a 14% moisture

content at 20°C and 30°C. In the case of 12% moisture content at 18°C and 14% moisture content at 18°C and 22°C, the number of larvae rose gradually to a peak and then very gradually declined.

In general it may be stated that the adults reared from larvae exposed to what may be regarded as "unfavourable" conditions for development (low temperatures and a low moisture content), produced a large number of progeny, while adults which were kept at more or less the same "unfavourable" conditions, produced a small number of progeny. On the other hand, adults kept at favourable conditions (relatively high temperatures and a high moisture content) exhibited a high rate of reproduction.

As far as mating is concerned, it was found that females which copulated for long periods produced significantly more progeny than females which copulated for shorter periods. This was probably due to the fact that more sperms were transferred to the spermatheca during long periods of copulation than during short periods. Females that copulated for only 15 minutes, 30 minutes and to a certain extent for 60 minutes, did not produce any more

progeny after three months. This might have been due to the exhaustion of the sperms in the spermatheca. There was no significant difference in number of larval progeny produced by females that copulated once per lifetime and those that copulated every fortnight. Females that were allowed to copulate once per month produced significantly the most progeny.

Richards (1946) found that the presence of males had a depressing effect on the oviposition rate of the females. This was presumably because the males interfered with the ovipositing females, not only in the process of feeding, but also by trying to copulate. Approximately the same observation was made in the experiment where the effect of different male/female ratios on reproduction was determined. Five females, together with 10 males, produced significantly the least progeny, while 5 females, together with 2 males, produced significantly the most progeny. Segrove (1951) did the following experiment on S. oryzae: Twenty replicates of pairs of weevils were set up at 25°C and 70% relative humidity and supplied fortnightly with 20 fresh grains

of wheat. At the end of the first fortnight, the males were removed from 10 of the replicates, so that from then onwards the females in these replicates were in isolation. In the case of the isolated females, the rate of oviposition rose steeply to a high peak somewhere between the fourth and sixth weeks of oviposition, then rapidly fell away.

The average length of life of the adult weevils used in the different experiments was $3\frac{1}{2}$ months. After this period most of the weevils died and few progeny were produced. Other workers, e.g. Birch (1944) stated that the "small strain" lived for 3 months, while Okuni (1924) indicated that S. oryzae ("large strain") lived for about five months. Back and Cotton (1924) found that the normal life of the rice weevil was greatly prolonged in winter. The usual average lifetime during summer was $3\frac{1}{2}$ months, while it was 18 months during winter. Lavrekhin (1937) showed in Russia that the females died at an age of $3\frac{1}{2}$ to 4 months. Thus, it is obvious that the length of life differed from country to country. This is to be expected because of the different climatic conditions.

CHAPTER 4

S U M M A R Y

1. S. oryzae is a serious pest of cereals and cereal products throughout the world.

2. A study was undertaken in South Africa to determine the influence of various factors on the reproduction of this weevil.

3. The weevils were collected at the Glen Agricultural College and reared on maize in a controlled temperature and humidity room (27°C and 70% relative humidity). The progeny of these weevils were used in the different experiments after random sampling.

4. Some of the experiments were conducted in the above mentioned constant temperature and humidity room, while others were conducted in desiccators stored in incubators set at different constant temperatures. Potassium hydroxide was used to control the relative humidity in the desiccators.

5. The parent weevils used in the different experiments were transferred fortnightly to fresh

maize. The maize from which they had been removed was then kept in the controlled temperature and humidity room for another fourteen days and then sectioned for progeny counts.

6. (i) It was found that food consumption of the larvae increased as the temperature decreased. Larvae also required more food to complete their development at 12% than at 14% moisture content of maize. There was a highly significant positive correlation between the weight of food consumed by the larvae and the body weights of the corresponding adults. Larvae which consumed large amounts of food resulted in heavier adults. Thus it was concluded that the effect of temperature and moisture content of maize on the weight of food consumed by the larvae, was evident in the weights of the adults and it may be stated that larvae reared at lower temperatures and a lower moisture content, gave rise to heavier adults and vice versa.

(ii) When the immature stages were reared at 12%, instead of 14% moisture content of maize, the resulting adults produced significantly more progeny. In the case of both moisture contents, most progeny

was produced when the immature stages were reared at 22°C.

7. When the adults were exposed to the different treatments of temperature and moisture content, most progeny were produced at 26°C. Adults which were kept at a moisture content of 14% produced significantly more progeny than adults which were kept at a 12% moisture content.

8. Females which copulated for long periods produced significantly more progeny than females which copulated for short periods.

9. Females that copulated once per month produced significantly more larval progeny than females which were allowed to copulate every fourteen days, every two months and once per lifetime. There was no significant difference in the number of larval progeny produced by females which copulated once per lifetime and females which copulated fortnightly.

10. More progeny was produced by heavier females.

11. The "best" male/female ratio for reproduction was 5 females and 2 males. The presence of too many males had a depressing effect on the oviposition

rate of the females. It was found that 5 females, together with 10 males, produced significantly the least progeny of the different ratios.

12. The number of larval progeny in each experiment was counted at fortnightly intervals. The number of progeny reached a maximum when the adults were from 4 to 6 weeks old, irrespective of the different treatments, and then gradually fell away.

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