STUDY OF COMPARATIVE BEHAVIOUR OF THREE SPECIES OF *SITOPHILUS* (=*CALANDRA*), *S. GRANARIUS* (L.), *S. ZEA-MAIS* MOTSCH. AND *S. ORYZAE* (L.) - (COLEOPTERA : CURCULIONIDAE)

Thesis submitted for the Degree of Doctor of Philosophy

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BY

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A B S T R A C T

The interest of the problem lies in the fact that Sitophilus zea-mais Motschulsky and Sitophilus oryzae (Linnaeus) are so closely related that they have only recently been separated as two distinct species. A third species Sitophilus granarius (Linnaeus) commonly found with them in the same habitats was also used in these experiments. A comparative study of the behaviour of the three species was carried out. The different behavioural aspects examined in the present work were the preference of the weevils for oviposition sites , some factors inducing flight, their climbing ability on glass, their reactions in different humidity gradients and in a temperature gradient, and finally their behaviour to a source of light. The behaviour of the fourth instar larvae in a horizontal beam of light and in a steep humidity gradient was also determined. The sensory organs involved in some of these mechanisms were located and described. The differences in the behaviour pattern of the three species substantiate their taxonomic separation.

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I. INTRODUCTION

The granary and the rice weevils have attracted the attention of many workers as they are extremely important from the economic point of view, and are severe pests of a number of stored cereals. The taxonomic position of the two species of the rice weevils namely of S. zea-mais Motsch. and of S. oryzae (L.), was a matter of dispute for several years until recently when Kuschel (1961) gave a satisfactory settlement and described two convincing morphological differences between the two species. Over a century ago , the description of Sitophilus zea-mais Motsch. (1855) raised the problem as to whether there were one or perhaps two species included within the S. oryzae complex. Various authors maintained different positions. Whilst some entomologists have held the opinion that the two forms are separate species, others considered the differences between them to be an expression of intra-specific variation within one and the same species. Genetical studies on mixed populations revealed that the two forms were inter-sterile (Richards 1944, and Birch 1944). Both authors found some biological and ecological differences between the two species, and differences in their body size and accordingly considered them as two

strains of the same species, a large one and a small one. The experimental observations were not considered by these authors to be sufficient for the recognition of two separate species since no certain morphological characters for their separation were discovered before the work of Kuschel. Slight differences, however, were described by Floyd and Newsom(1959).

The aim of the present work was to reveal the differences that may exist in the behaviour of the two species of the rice weevils in an attempt to support their taxonomic separation, and on the other hand to compare them with S. granarius, a closely related species which was frequently mentioned in the literature as occurring with the two species of the rice weevils in the same habitats.

The aspects of behaviour examined in this study dealt with :- 1) The preference of the female weevils for their oviposition sites on four cereals presented separately and as mixtures. 2) Some factors which induced flight in the two species of the rice weevils. 3) The climbing ability of the weevils on smooth glass surfaces.4) Their reactions in different humidity gradients. 5) The temperature preferendum of the adults. 6) Their reactions to light. 7) Few experiments on the behaviour of the fourth instar larvae in a steep humidity gradient, and a horizontal beam of light. 8) The role of the sensory organs involved in some of the above patterns of behaviour. The relevant review of literature on each subject is included in the corresponding sections.

II. REARING TECHNIQUE

Standard cultures were brought from the Imperial College Field Station, Berks. The insects were reared on English wheat of 14.2 % moisture content in equilibrium with 70 % R.H., in a constant temperature room held at 25° C., 70 % R.H., and in complete darkness.

The grain was first sterilised at 60°- 80 ° C. for two hours and then allowed to cool slowly, in a closed container, over night to avoid excessive condensation (Richards, 1947). This gave insect-free grain. This grain was conditioned by exposure in single layers over perforated zinc plate, in the constant temperature room for about two days, to reach equilibrium with the appropriate relative humidity.

Cultures were kept in 7- lb. jars, half-filled with English wheat, and the tops covered with muslin fitted with rubber bands. Small cultures were kept in 1- or 2-lb. jars.

III. FACTORS INVOLVED IN RECOGNITION OF THE OVIPOSITION SITES

A. INTRODUCTION AND REVIEW OF LITERATURE

Though much work has been done on the environmental factors which influence the rate of oviposition of Sitophilus weevils (Nakayama 1941, Eastham and McCully 1943, Birch 1945, Richards 1947, Reddy 1950,a , Segrove 1951, Howe 1952 , and Prevett 1960), there is very little reference to their oviposition sites in the different cereals. Maclagan and Dunn(1936) stated that there is a marked preference for laying eggs in the hairy end of the wheat grain in C.oryzae (S. oryzae), and that oviposition became indiscriminate only under conditions of crowding. The preference for this site was also observed in C..granaria (S. granarius) by Richards (1947). The work of Ewer (1945) and Richards(1947) clearly showed that C. granaria choose large wheat grains for oviposition rather than the small ones,whether in mass-c-ultures or when offered two at a time. The possibility of the role played by the size of the kernel on the prefere-ntial oviposition of the rice weevil was also mentioned by Reddy (1950,b). He concluded that in mixed cultures of sound and halved kernels, whether based on equal numbers, equal surface area or equal weight, more eggs were laid in sound than in halved kernels. Seshagiri (1953) stated that grain

size was the major factor concerned in the relative attractiveness to different varieties of rice by C. oryzae (heavier breeding occurred in big-grained varieties).

Host selection by Sitophilus weevils was the subject of some previous work. The weevils were allowed to oviposit in a mixture of different cereals and the number of offspring was counted in each. Khabirova (1938) found that S. granarius attacked pearl barley more readily than other cereals. These were in the following decreasing order of attractiveness :- wheat, rice, maize and then barley. Laverkhin (1939) mentioned that C. oryzae and C.granaria showed a great preference for wheat and rye; barley was less infested by them and oats scarcely at all. C.granaria exhibited a decided preference for certain varieties of wheat. Sandner (1958) found that pearl barley was the most acceptable food to C. oryzae, and that the females oviposited in it in preference to wheat, rye, rice , barley and oats. The same author (1959) concluded that the adults of C.granaria and S. oryzae selected rye and wheat for breeding in preference to barley and only rarely laid in oats and rice. Floyd and Newsom (1959) found a clear preference exhibited by S. oryzae for sorghum followed by unpolished rice, wheat, rough rice and then maize, while S. sasakii preferred sorghum

to the following cereals in a decreasing order of preference wheat, unpolished rice, rough rice and maize. Both species produced no offspring in oats. Although the preferred oviposition media were determined in these experiments no indication of the actual number of eggs laid in each cereal was given. Richards (1947) mentioned that normally one larva of Calandra can develop in each grain and that if more than one egg is laid in the same grain it is eliminated by cannibalism.

In the present series of experiments the preferred oviposition sites of the three species of Sitophilus were located in four cereals, offered to the weevils separately and mixed in all possible combinations. These were wheat, rice, maize and sorghum, which all differed greatly in shape, size, texture and chemical constitution, and presumably in taste.

B. METHODS AND TECHNIQUE

The oviposition of Sitophilus was tested on four cereals previously sterilised and then conditioned at 25°C., 70 % R.H. for a few days (see rearing technique). The moisture content of each cereal was estimated by grinding a sample of the grain in a small hand-mill . A certain weight was dried in a ventilated electric oven for about 4 hours at 115°C. The dry material was allowed to cool for about 30 minutes in a desiccator and then reweighed. The percentage moisture was calculated from the loss of weight on drying of three samples of each cereal. The four cereals used were :-

1. English wheat var. Cappelle Desprez (14.2 % M.C.)
2. Argentine plate maize (13.14% M.C.)
3. American brown rice var. Blue Bonnet (13.04% M.C.)
4 Sorghum var. American Milo (13.06% M.C.)

The aim of the experiment was to determine the preferred oviposition sites on the cereals and to see whether they were the same in the three species of Sitophilus. The grain was presented to the weevils in four different positions, exposing half of the grain at a time. This was achieved by embedding half of the grain in a thin layer of paraffin wax (7-10 mm.) just before it solidified inside a Petri dish. When the grain

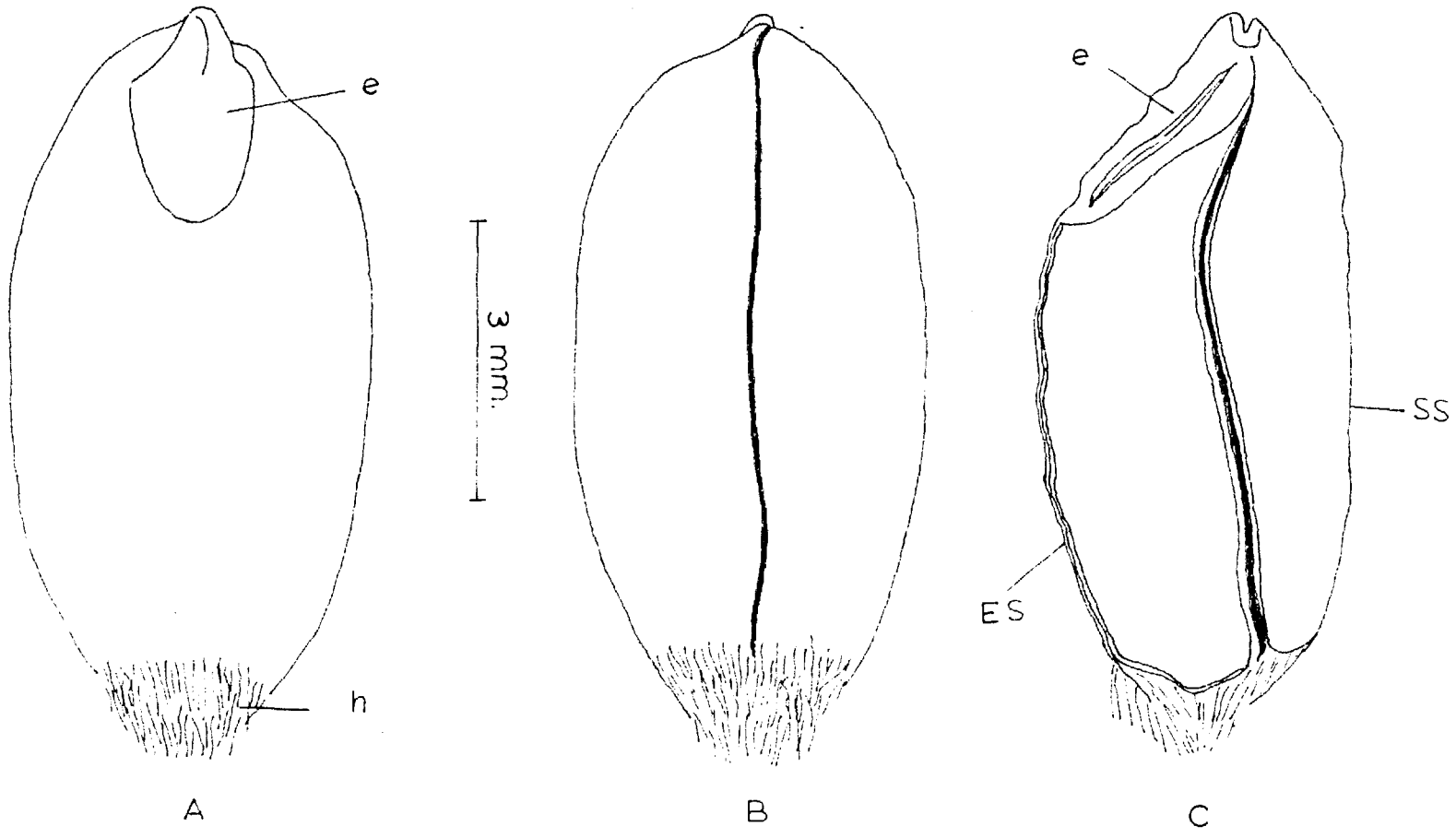


Fig. 1 : Outline of a wheat grain ; A, entire side ; B, sutured side ; C, sagittal half ; e, embryo ; h, hairy end ; ES, entire side ; SS, sutured side.

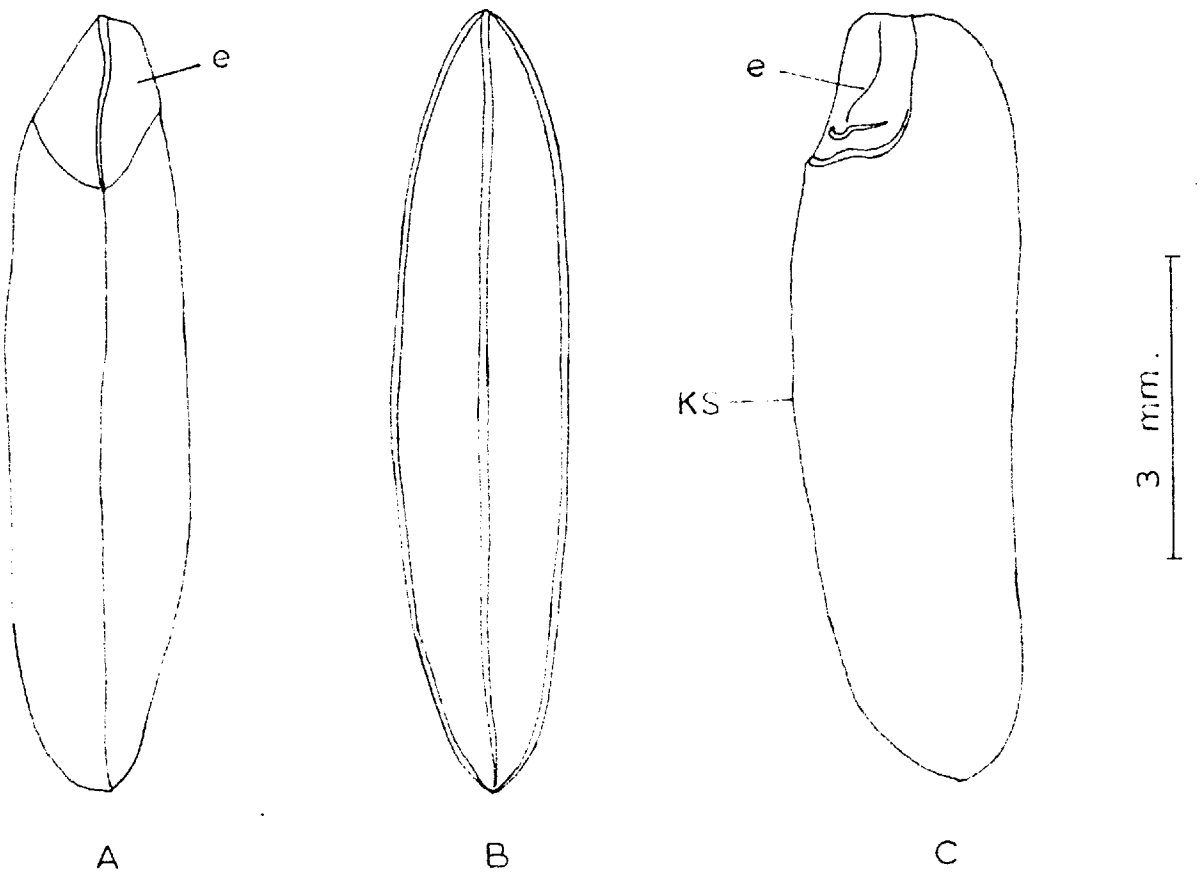


Fig. 2 : Outline of a rice seed ; A, keeled side ; B, sutured side ; C, sagittal half; e , embryo ; KS, keeled side.

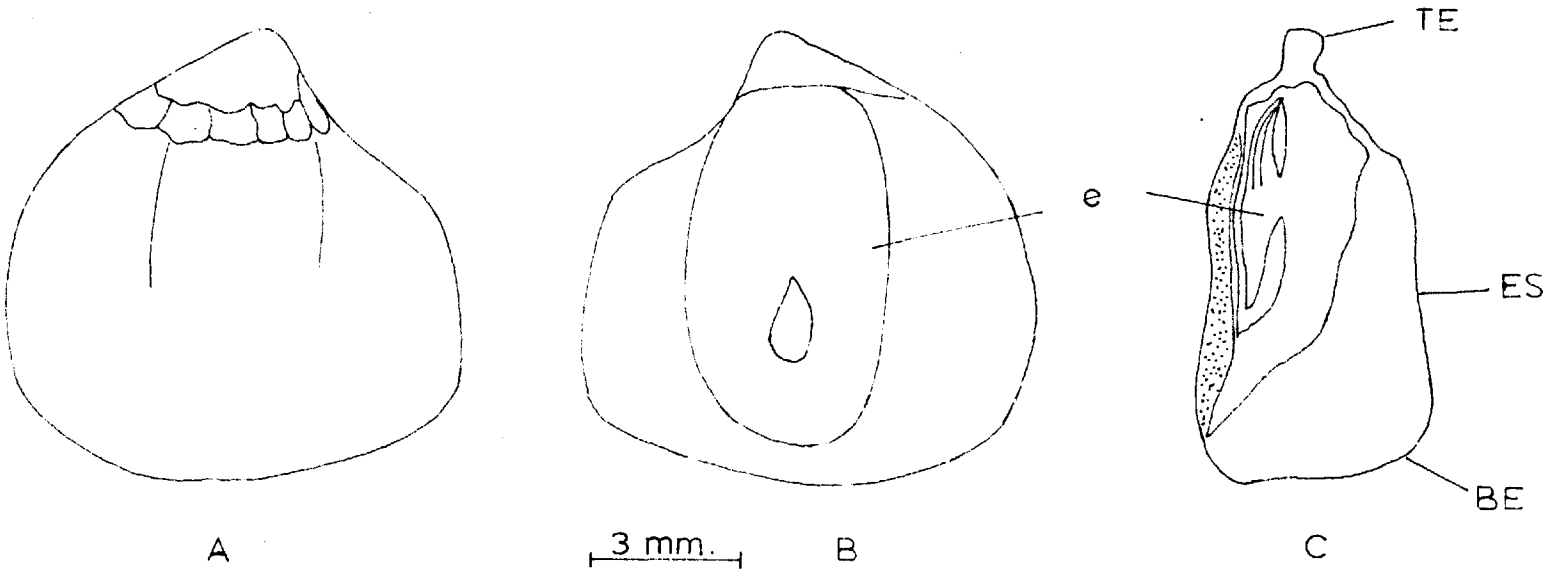


Fig. 3 : Outline of a maize seed; A, entire side; B, embryo side; C, sagittal half; e, embryo; TE, tapering end; ES, entire side; BE, broad end.

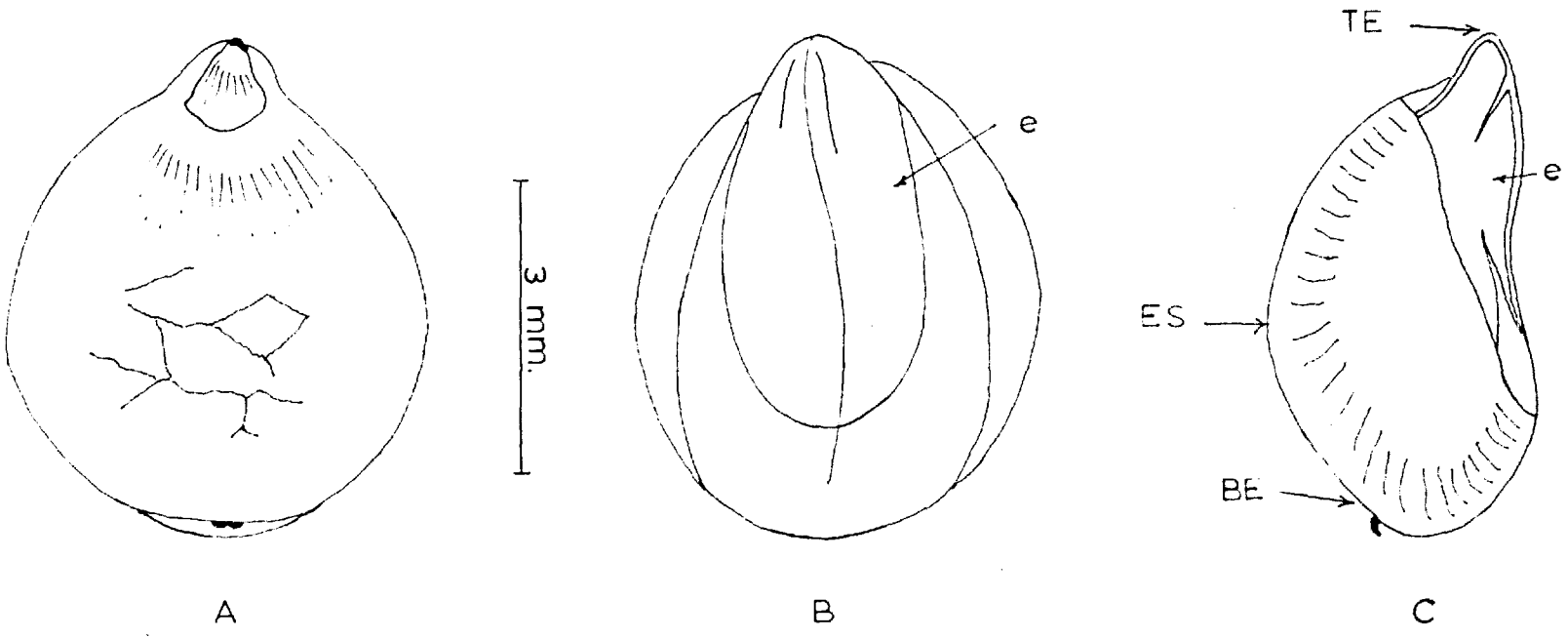


Fig. 4 : Outline of a sorghum seed ; A, entire side ; B, embryo side ; C, sagittal half ; e, embryo ; TE, tapering end ; ES, entire side ; BE, broad end.

was embedded horizontally or vertically, two positions were obtained in each case. The nomenclature of these positions was related to the position of the embryo , which was located by examining a sagittal half of the grain which was cut by means of a razor blade (see Figs. 1 - 4). When the grain was placed horizontally, the exposed halves were called " sides ", and when embedded vertically they were called " ends ". Thus in case of wheat there was the entire side (ENT), s-utured side (STD), embryo end(EMB), and the hairy end (HAR)(Fig.1). In rice there were the keeled (KLD) and sutured(STD) sides, and the embryo (EMB) and tapering (TAP) ends (Fig. 2). In maize there were the entire and embryo sides, and the tapering and broad (BRD) ends (Fig. 3). In sorghum there were the entire and the embryo sides, and the tapering and broad ends (Fig. 4). That the fixed grain provides a more favourable conditions for oviposition than when it is loose has been shown by Coombs (1957) in his experiments on C. granaria. Exposing halved kernels to the weevils seemed to have no inhibiting effect on the oviposition rate of the rice weevils as has been mentioned by Reddy (1950,b).

The large grains of wheat, rice and sorghum, and the smallest of maize seeds, were chosen for these experiments. 10 females (3-6 weeks old) were placed inside

each dish, covered with a perforated plastic dish (9.5 c m. in diameter and 7 mm. high). The number of the fixed grains was such that each female was offered equal numbers of each position in all the possible combinations. In case of wheat, rice and sorghum the following combinations were made :-

	Number of dishes	Number of grains in each dish	Number of positions
	4	40	1
	12	40	2
	16	30	3
	4	40	4
Total	36	1280	

As maize grains are large, only half the number of seeds was placed in each dish. The experiments were carried out in a constant temperature room kept at 25°C., 70 % R.H. and in complete darkness. The females were allowed to oviposit for 48 hours, except in wheat, in the case of which the experiments were conducted for 96 hours. The experiments with wheat were the first ones but later it was found that 48 hours sufficed to obtain an appreciable number of eggs.

The eggs laid in each position were counted by dissecting the grains, which had been soaked over night in

50 % alcohol to soften them, and which were stained with acid fuchsin (Frankenfeld,1948) for a few minutes. The egg plugs which take up the stain were used as guides to the presence of the eggs but only those actually revealed by dissection were counted.

A second set of experiments was carried out to determine the preference of each species for oviposition on different sorts of cereals. All possible combinations of the four cereals were offered to the weevils. The grains were embedded in wax exposing the preferred site of each cereal which had previously been determined in the first set of experiments. Five females in each dish were offered five grains of each cereal, and the eggs were counted after 48 hours. In the experiments when the grains of four cereals were tested together, the data represent the number of eggs laid by 20 females in 80 grains of the mixture in each set of experiments. When three cereals were tested, the data are of the eggs laid by 20 females in 60 grains of the mixture in each set. When two cereals were tested together, the data represent the eggs laid by 10 females in 40 grains of the mixture in each set. The weevils were reared on English wheat of 14.2 % moisture content, in equilibrium with 70% R.H. at 25°C. The original cultures have been kept under these conditions for several years. Before testing the oviposition

preferences of the weevils, groups of 200 females were confined for two days in 2 lb. jars, half filled with the grain to be tested. In the experiments with mixtures of different cereals, equal volumes of the grain to be used were well mixed up and the female weevils were kept in that mixture for two days. This preconditioning seemed to play an appreciable role in maintaining high rates of oviposition in the new environment.

In the hope of identifying some of the sense organs involved in the oviposition behaviour, whole mounts of the ovipositor, labial and maxillary palps of the weevils, were bleached in diaphanol, cleared in methyl cellosolve and mounted in Euparal. Microscopic examination was at 1140 X magnification (oil immersion).

Sections through the stylus of the ovipositor were made according to the following procedure (Mercer and Birbeck,1961) :-

1. Whole insects were precooled at 0°C. for half an hour before fixation.

2. The ovipositor was dissected out and immersed into a 1 % solution of osmium tetroxide/sodium veronal buffer (p.H. 7.4), and left at 0°-4°C. for 1½ hours.

3. The material was transferred to distilled water for 5 minutes at 0°-4°C., and then dehydrated at that temperature in 25 % and then 50 % alcohol (for 15 minutes each), 75 %

alcohol (30 minutes) and then in 95 % alcohol (30 min.) which was warmed up to room temperature followed by 3 changes of absolute alcohol (30 min. each).

4. The material was embedded in methacrylate monomer (a mixture of methyl methacrylate and butyl methacrylate in the ratio 4 : 1), 25 %, 50 % and 75 % of methacrylate monomer in absolute alcohol for 30 minutes each, then 100% monomer for another 30 minutes.

5. The material was placed inside a small groove prepared in a small block of polymerized methacrylate inside a gelatinous capsule (supplied by Parke Davis Ltd.). The capsule was then filled with prepolymerized methacrylate and left to polymerize overnight at 60°C.

6. The hardened block was trimmed down to the embedded material and cut on a Porter-Blum microtome with a glass knife. The thickness of the sections was 0.5 u. The sections were examined under a phase contrast microscope at 1140 X magnification (oil immersion) .

C. RESULTS

PART 1 : One Cereal Offered to the Weevils

(For detailed data see Appendix:Tables 70-81)

1. Wheat

a) S. granarius : The total numbers of eggs laid by 360 females in 1280 grains in 96 hours were in the decreasing order of 1308 , 1204, 1061 and 902 eggs in the entire, hairy, sutured and embryo halves (Table 1). The selection of the different oviposition sites was highly significant ($P<0.001$). More eggs were laid in the entire side than in the sutured side (both were horizontal), but in both the preference for the hairy end instead of the embryo end was highly significant ($P<0.001$). The weevils showed no significant difference in their ability to choose the hairy end of the grain of the two horizontal positions i.e. of the entire and of the sutured side. When comparing the two vertical positions, it was found that more eggs were laid in the hairy end than in the embryo end. In both ends there was a significant preference for the sutured side of the grain. This preference was not significantly different in the hairy and the embryo ends.

TABLE 1

Preferred Oviposition Sites of S. granarius on Wheat

Total number of eggs laid by 360 females in 1280 grains in 96 hours							
Entire Side		Sutured Side		Hairy End		Embryo End	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
1066	242	878	183	484	720	372	530
1308		1061		1204		902	

Significance of Preference (X^2 Test)

Position	Order of preference	Significance
Entire side	HAR > EMB	$P < 0.001$
Sutured side	HAR > EMB	$P < 0.001$
Hairy end	STD > ENT	$P < 0.001$
Embryo end	STD > ENT	$P < 0.001$
Compared positions		
Four positions	ENT > HAR > STD > EMB	$P < 0.001$
Entire & Sutured	HAR > EMB	not significant
Hairy & Embryo	STD > ENT	not significant

b) S. zea-mais : In laying their eggs the weevils exhibited a decided ability to select between the four positions of the grain. The total numbers of eggs deposited by 360 females in 1280 grains in 96 hours were in the decreasing order of 1184, 998, 661 and 633 eggs in the entire side , hairy end, sutured side and the embryo end, (TABLE 2). The preference was highly significant between the four positions ($P < 0.001$). A highly significant preference was also found in the two horizontal positions namely the entire and the sutured sides in favour of the hairy end ($P < 0.001$). In the vertical positions the preference for oviposition in the sutured side to the entire side was highly significant in the embryo end ($P < 0.001$), but not in the hairy end. When the two horizontal positions were compared, the preference for laying the eggs in the hairy end rather than in the embryo end, differed highly significantly in the sutured side from the entire side.

c) S. oryzae : The weevils did not lay their eggs at random, and a clear preference for certain sites was determined by statistical analysis. The total numbers of eggs laid in the four positions of the wheat grain were in the decreasing order of 917, 738, 708 a nd 624 eggs in the entire side, sutured side, hairy end and in the embryo end (TABLE 3). The significance of preference was high ($P < 0.001$). The females showed a significant preference

TABLE 2

Preferred Oviposition Sites of S. zea-mais on Wheat

Total numbers of eggs laid by 360 females in 1280 grains in 96 hours							
Entire Side		Sutured Side		Hairy End		Embryo End	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
745	439	482	179	498	500	253	380
1184		661		998		633	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	HAR > EMB	P< 0.001
Sutured Side	HAR > EMB	P< 0.001
Ha iry End	STD > ENT	not significant
Embryo End	STD > ENT	P< 0.001
Compared positions		
The four positions	ENT>HAR>STD>EMB	P< 0.001
Entire & Sutured	HAR > EMB	P< 0.001
Hairy and Embryo	STD > ENT	P< 0.001

for the hairy end when the grains were fixed in the two horizontal positions ($P < 0.001$), but this tendency was more pronounced in the sutured side than in the entire side ($P < 0.001$). Similarly there was a significant preference for laying the eggs in the sutured side rather than in the entire side when the grains were fixed in a vertical position with the hairy end exposed ($P < 0.001$), but no significant choice was made when the embryo end was exposed. The difference between these two preferences was significant ($0.02 > P > 0.01$).

d) Comparison of preferences for oviposition sites exhibited by the three species

The female weevils of the three species exhibited different tendencies in choosing their oviposition sites on wheat grains. The pattern of distribution of S. granarius eggs differed from that of S. zea-mais highly significantly ($P < 0.001$) inspite of choosing the same order of preference (see TABLE 4). Similarly the preference for the oviposition sites differed highly significantly in S. zea-mais and in S. oryzae ($P < 0.001$). On the other hand this pattern of behaviour in S. granarius and S. oryzae seemed to be similar.

TABLE 3

Preferred Oviposition Sites of S.oryzae on Wheat

Total numbers of eggs laid by 360 females in 1280 grains in 96 hours							
Entire Side		Sutured Side		Hairy End		Embryo End	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
510	407	540	198	272	436	290	334
917		738		708		624	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	HAR > EMB	$P < 0.001$
Sutured Side	HAR > EMB	$P < 0.001$
Hairy End	STD > ENT	$P < 0.001$
Embryo End	STD > ENT	not significant

Compared Positions		
The Four Positions	ENT > STD > HAR > EMB	$P < 0.001$
Entire & Sutured	HAR > EMB	$P < 0.001$
Hairy & Embryo	STD > ENT	$0.02 > P > 0.01$

TABLE 4

Significance of the preference for oviposition sites of the three species on wheat grain (Distribution of the eggs in the four positions). (X^2 Test)

Species Compared.		Significance
S. granarius	and S. zea-mais	$P < 0.001$
S. granarius	and S. oryzae	not significant
S. zea-mais	and S. oryzae	$P < 0.001$

2. RICE

a) S. granarius :- The total numbers of eggs laid by 360 females in 1280 grains in 48 hours were in the decreasing order of 528, 499, 425 and 355 eggs in the embryo end, keeled side, tapering end and in the sutured side (TABLE 5). This difference in egg numbers is highly significant ($P<0.001$). When the grains were embedded horizontally, the weevils preferred the embryo end to the tapering end on the keeled side ($P<0.001$), but on the sutured side this preference was not significant. In case of the vertically fixed grains , there was a preference for the keeled side of the embryo end ($0.01>P>0.001$), but no preference was shown for either side of the tapering end.

b) S. zea-mais :- The distribution of the eggs in the four parts of the grain differed highly significantly ($P<0.001$). The total numbers of eggs laid in the keeled side, embryo end, sutured side and the tapering end were in the decreasing order of 526, 299, 285 and 210 eggs respectively (TABLE 6). In both horizontal positions namely when the keeled or the sutured sides were exposed, the weevils showed a clear preference for laying in the embryo end ; the significance in both sets was high($P<.001$).

TABLE 5

Preferred Oviposition Sites of S.granarius on Rice

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Keeled Side		Sutured Side		Embryo End		Tapering End	
EMB	TAP	EMB	TAP	KLD	STD	KLD	STD
290	209	170	185	299	229	220	205
499		355		528		425	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Keeled Side	EMB > TAP	$P < 0.001$
Sutured Side	TAP > EMB	not significant
Embryo End	KLD > STD	$0.01 > P > 0.001$
Tapering End	KLD > STD	not significant

Compared Positions

The four positions	EMB > KLD > TAP > STD	$P < 0.001$
Keeled & Sutured	EMB & TAP	$0.01 > P > 0.001$
Embryo & tapering	KLD > STD	not significant

However, the tendency for choosing the embryo end was greater on the keeled side than on the sutured side ($0.01 > P > 0.001$). When the grains were vertically embedded, the weevils preferred the keeled side to the sutured side almost to the same extent in the embryo and in the tapering ends.

c) S. oryzae :- The preferred sites for oviposition were in the following decreasing order : the keeled side, sutured side, embryo end and the tapering end. The corresponding numbers of eggs laid in these positions were 511, 373, 367 and 312 eggs per 360 females per 1280 grains per 48 hours (TABLE 7).

The significance of the preference for the different parts of the grain was high ($P < 0.001$). In the horizontally embedded grains (keeled and sutured upper most), a greater tendency for choosing the embryo end existed. When the grains were fixed vertically the weevils preferred to oviposit on the keeled side.

TABLE 6

Preferred Oviposition Sites of S.zea-mais on Rice

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Keeled Side		Sutured Side		Embryo End		Tapering End	
EMB	TAP	EMB	TAP	KLD	STD	KLD	STD
405	121	183	102	191	108	132	78
526		285		299		210	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Keeled Side	EMB > TAP	$P < 0.001$
Sutured Side	EMB > TAP	$P < 0.001$
Embryo End	KLD > STD	$P < 0.001$
Tapering End	KLD > STD	$P < 0.001$

Compared Positions		
The Four Positions	KLD > EMB > STD > TAP	$P < 0.001$
Keeled & Sutured	EMB > TAP	$0.01 > P > 0.001$
Embryo & Tapering	KLD > STD	Not significant

TABLE 7

Preferred Oviposition Sites of S.oryzae on Rice

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Keeled Side		Sutured Side		Embryo End		Tapering End	
EMB	TAP	EMB	TAP	KLD	STD	KLD	STD
330	181	217	156	219	148	175	137
511		373		367		312	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Keeled Side	EMB > TAP	$P < 0.001$
Sutured Side	EMB > TAP	$0.01 > P > 0.001$
Embryo End	KLD > STD	$P < 0.001$
Tapering End	KLD > STD	$0.05 > P > 0.02$
Compared Positions		
The four positions	KLD > STD > EMB > TAP	$P < 0.001$
Keeled & Sutured	EMB > TAP	Not significant
Embryo & Tapering	KLD > STD	Not significant

d) Comparison of Preference for Oviposition Sites on Rice Exhibited by the Three Species :-

The three species differed significantly from each other in their choice of oviposition sites in rice grains. S. granarius preferred the different parts of the grain in the following order : the embryo end to the keeled side, followed by the tapering end and lastly by the sutured side. S. zea-mais preferred the keeled side to the embryo end, followed by the sutured side and lastly by the tapering end. S. oryzae preferred the keeled side, sutured side, embryo end and the tapering end in this order. The order of preference differed highly significantly in the three species (TABLE 8).

TABLE 8

Significance of the preference for oviposition sites of the three species on rice grain. (Distribution of the eggs in the four positions. X^2 test).

Species Compared			Significance
S. granarius	and	S. zea-mais	$P < 0.001$
S. granarius	and	S. oryzae	$P < 0.001$
S. zea- mais	and	S. oryzae	$0.02 > P > 0.01$

3. M A I Z E

a) S. granarius :- The females exhibited a clear preference for laying their eggs in the tapering end of the maize seed, and the following positions were selected in the decreasing order of preference : the embryo side, the entire side and the broad end. The total numbers of eggs laid by 360 females in 640 seeds in 48 hours were 434, 223, 199 and 50 eggs in the four parts of the grain mentioned above (TABLE 9). The significance of the difference in the distribution of the eggs was high ($P < 0.001$). When the seeds were embedded horizontally i.e. the entire and the embryo sides were exposed, a highly significant preference for the tapering end of the seeds was observed, in both positions of the grain ($P < 0.001$). No significant difference existed between the behaviour of the weevils when the two horizontal sides were offered. When the seeds were embedded vertically, the females laid many more eggs in the tapering end than in the broad end of the seed, but no significant preference for the embryo side on either end was observed.

TABLE 9

Preferred Oviposition Sites of S. granarius on Maize

Total Numbers of Eggs Laid by 3 60 Females in 640 seeds in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
191	8	210	13	166	268	14	36
199		223		434		50	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	$P < 0.001$
Embryo Side	TAP > BRD	$P < 0.001$
Tapering End	EMB > ENT	$P < 0.001$
Broad End	EMB > ENT	$0.01 > P > 0.001$
Compared Positions		
The four positions	TAP > EMB > ENT > BRD	$P < 0.001$
Entire & Embryo	TAP > BRD	Not Signif.
Tapering & Broad	EMB > ENT	Not Signif.

b) S. zea-mais :- The total numbers of eggs laid by 360 females in 640 seeds in 48 hours were 320, 206, 185 and 100 eggs in the tapering end, the embryo side, the entire side and in the broad end of the seeds (TABLE 10). The preference for certain oviposition sites was highly significant ($P < 0.001$). In the horizontally embedded seeds the weevils laid very few eggs in the broad end compared with the numbers in the tapering end. A significant difference, however, existed between the two horizontal positions in that more eggs were laid in the broad end of the embryo side than in that of the entire side (the probability of significance was $0.01 > P > 0.001$). In the vertically embedded seeds, the numbers of eggs laid in the tapering end by far exceeded those laid in the broad end, and the preference for either the entire or the embryo side differed significantly in the two ends ($P < 0.001$).

c) S. oryzae :- The distribution of the eggs in the four positions of the maize seed was far from random ($P < 0.001$). The total numbers of eggs laid by 360 females in 640 seeds in 48 hours were in a decreasing order of 292, 169, 114 and 44 eggs in the tapering end, the embryo side, the entire side and in

TABLE 10

Preferred Oviposition Sites of S. zea-mais on Maize

Total numbers of eggs laid by 360 females in 640 seeds in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
180	5	181	25	171	149	17	83
185		206		320		100	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	P < 0.001
Embryo Side	TAP > BRD	P < 0.001
Tapering End	ENT > EMB	Not significant
Broad End	EMB > ENT	P < 0.001
Compared Positions		
The Four Positions	TAP > EMB > ENT > BRD	P < 0.001
Entire & Embryo	TAP > BRD	0.01 > P > 0.001
Tapering & Broad	ENT or Emb	P < 0.001

the broad end (TABLE 11). The weevils showed a significant preference for the tapering end of the horizontally fixed seeds ($P < 0.001$), but more eggs were laid near the broad end of the embryo side than in that of the entire side ($0.01 > P > 0.001$). A significant difference was also found between the choice of the embryo side of the tapering and of the broad ends of the vertically embedded seeds ($0.01 > P > 0.001$). While the choice between the embryo side and the entire side of the tapering end was not significant, a clear and significant preference for the embryo side was seen in the broad end of the seed ($P < 0.001$).

d) Comparison of preferences for the oviposition sites in maize exhibited by the three species.

From TABLES 9, 10 and 11, it can be seen that the three species showed the same preference for laying eggs in the tapering end of the maize seeds when these were embedded vertically. The preference for that end was also remarkable when the seeds were fixed horizontally. The three species agreed in their choice of the oviposition sites but not always to the same extent. The behaviour of S. zea-mais differed significantly from that of S. granarius ($P < 0.001$) and from that of S. oryzae ($0.02 > P > 0.01$). The difference may be attributed to the greater proportion of eggs being laid

TABLE 11

Preferred Oviposition Sites of *S. oryzae* on Maize

Total numbers of eggs laid by 360 females in 640 seeds in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
113	1	148	21	133	159	6	38
114		169		292		44	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	$P < 0.001$
Embryo Side	TAP > BRD	$P < 0.001$
Tapering End	EMB > ENT	Not signif.
Broad End	EMB > ENT	$P < 0.001$
Compared Positions		
The four positions	TAP > EMB > ENT > BRD	$P < 0.001$
Entire & Embryo	TAP > BRD	$0.01 > P > 0.001$
Tapering & Broad	EMB > ENT	$0.01 > P > 0.001$

by S. zea-mais in the broad end. S. granarius and S. oryzae , on the other hand, did not vary significantly from each other (TABLE 12).

TABLE 12

Significance of the preference for oviposition sites of the three species on maize seeds. (Distribution of the eggs in the four parts of the grain.)(X^2 Test)

Species Compared	Significance
S. granarius and S. zea-mais	$P < 0.001$
S. granarius and S. oryzae	Not signif.
S. zea-mais and S. oryzae	$0.02 > P > 0.01$

4. SORGHUM

a) S. granarius :- The total numbers of eggs laid by 360 females in 1280 grains in 48 hours were 436, 397, 339 and 230 eggs in the entire and the embryo sides, and the tapering and in the broad ends in this order (TABLE 13). The significance of the preference for the different sites was high ($P < 0.001$). In the grains embedded horizontally the weevils showed a significant preference for the tapering end of both the entire and the embryo sides ($P < 0.001$). This tendency was significantly higher on the embryo side than on the entire side ($P < 0.001$). In the vertically fixed grains, the weevils preferred the entire side of both ends, but the significance of this behaviour was high in the tapering end, and not clear in the broad end.

b) S. zea-mais :- The weevils showed a marked preference for the horizontally embedded grains. The total numbers of eggs laid by 360 females in 1280 grains in 48 hours were 520, 418, 250 and 178 eggs in the embryo and the entire sides and in the tapering and the broad ends respectively (TABLE 14). The oviposition sites were not selected at random ($P < 0.001$). A highly significant preference for the tapering end of the two horizontal positions namely of the entire and the embryo

TABLE 13

Preferred Oviposition Sites of *S. granarius* on Sorghum

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
288	148	379	18	199	140	123	107
436		397		339		230	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	$P < 0.001$
Embryo Side	TAP > BRD	$P < 0.001$
Tapering End	ENT > EMB	$0.01 > P > 0.001$
Broad End	ENT > EMB	Not significant
Compared Positions		
The Four Positions	ENT > EMB > TAP > BRD	$P < 0.001$
Entire & Embryo	TAP > BRD	$P < 0.001$
Tapering & Broad	ENT > EMB	Not significant

TABLE 14

Preferred Oviposition Sites of S. zea-mais on Sorghum

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
279	139	450	70	143	107	111	67
418		520		250		178	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	P < 0.001
Embryo Side	TAP > BRD	P < 0.001
Tapering End	ENT > EMB	0.05 > P > 0.02
Broad End	ENT > EMB	P < 0.001
Compared Positions		
The Four Positions	EMB > ENT > TAP > BRD	P < 0.001
Entire & Embryo	TAP > BRD	P < 0.001
Tapering and Broad	ENT > EMB	Not signif.

sides also existed ($P<0.001$). This behaviour, however, was much more pronounced on the embryo side than on the entire side($P<0.001$). In the vertically fixed grains i.e. the tapering and the broad ends uppermost, the weevils laid significantly more eggs in the entire side than in the embryo side ; the difference between the behaviour of the weevils on the two ends did not vary significantly.

c) S. oryzae :- The female weevils selected their oviposition sites in the following order of preference : the embryo side, the entire side, the tapering end and the broad end. The corresponding total numbers of eggs laid in each part of the grain, by 360 females in 1280 grains in 48 hours , were 393, 381, 343 and 217 (TABLE 15). The significance of this choice of oviposition sites was high ($P<0.001$). In the horizontally fixed grains a clear preference for ovipositing in the tapering end in both the entire and the embryo sides was exhibited ($P<0.001$). No significant difference existed between the numbers of eggs in both the entire and the embryo sides of the vertically embedded grains namely in the tapering and in the broad end.

TABLE 15

Preferred Oviposition Sites of S. oryzae on Sorghum

Total numbers of eggs laid by 360 females in 1280 grains in 48 hours							
Entire Side		Embryo Side		Tapering End		Broad End	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
262	119	376	17	189	154	115	102
381		393		343		217	

Significance of Preference (X^2 Test)

Position	Order of Preference	Significance
Entire Side	TAP > BRD	$P < 0.001$
Embryo Side	TAP > BRD	$P < 0.001$
Tapering End	ENT > EMB	Not signif.
Broad End	ENT > EMB	Not signif.
Compared Positions		
The four Positions	EMB > ENT > TAP > BRD	$P < 0.001$
Entire & Embryo	TAP > BRD	$P < 0.001$
Tapering & Broad	ENT > EMB	Not signif.

d) Comparison between the three species in their choice of the oviposition sites in sorghum :-

The distribution of the eggs of S. zea-mais in the (in the) four positions of the grain differed highly significantly from that of S. granarius and of S. oryzae ($P < 0.001$). S. granarius and S. oryzae, on the other hand, did not differ significantly in their preference for oviposition sites (TABLE 16).

TABLE 16

Significance of the preference for oviposition sites of the three species on sorghum grain (Distribution of the eggs in the four parts of the grain) (X^2 Test)

Species Compared	Significance
S. granarius and S. zea-mais	$P < 0.001$
S. granarius and S. oryzae	Not significant
S. zea-mais and S. oryzae	$P < 0.001$

PART 2 : More than One Cereal Offered to the Weevils

a) S. granarius

In TABLE 17, the total numbers of eggs laid by the females in all the possible combinations of the four cereals are included. The numbers of eggs laid by 20 females in 80 grains of the four cereals were in the following decreasing order : 82, 8, 6 and 0 in wheat, rice, maize and sorghum respectively. In a mixture of wheat, rice and maize the numbers of eggs laid by 20 females in 60 grains of the mixture were 71, 10 and 10 . In a mixture of wheat, rice and sorghum the numbers of eggs were 82, 13 and 7. In a mixture of wheat , maize and sorghum the numbers of eggs were 57, 4 and 3. When wheat was excluded, the numbers of eggs were 40 , 32 and 2 in rice, maize and sorghum respectively.

In experiments when two cereals were tested together, the numbers of eggs laid by 10 females in 40 grains of the mixture were 60 and 7 in wheat and rice; 62 and 1 in wheat and maize ; 55 and 0 in wheat and sorghum; 25 and 24 in rice and maize; 20 and 14 in rice and sorghum; and 17 and 16 in maize and sorghum.

TABLE 17

Preferred Oviposition Sites of S. granarius on a mixture of different Cereals (Offered in their preferred positions).

Total numbers of eggs laid by 160 females in 560 grains in 48 hours				Significance of Preference (χ^2)
WHEAT (ENT)	RICE (EMB)	MAIZE (TAP)	SORGHUM (ENT)	
82	8	6	0	$P < 0.001$
71	10	10		$P < 0.001$
82	13		7	$P < 0.001$
57		4	3	$P < 0.001$
	40	32	2	$P < 0.001$
60	7			$P < 0.001$
62		1		$P < 0.001$
55			0	$P < 0.001$
	25	24		Not signif.
	20		14	Not signif.
		17	16	Not signif.
Total 469	123	94	42	$P < 0.001$

Significance of preference :

In all the experiments, the weevils exhibited a highly significant preference for ovipositing in wheat. A clear avoidance of laying eggs in sorghum was noticed when more than two cereals were tested together. No significant difference, how-ever, existed between the numbers of eggs laid in the following mixtures : rice and maize, rice and sorghum, and maize and sorghum . The total numbers of eggs laid in the four cereals were 469, 123, 94 and 42 in wheat, rice, maize and sorghum respectively (TABLE 17). The preference was highly significant ($P < 0.001$).

b) S. zea-mais

When the weevils were offered the four cereals in the same dishes, they laid their eggs in the following order : 50 in maize, 40 in wheat, 13 in rice and 5 in sorghum (TABLE 18). When the mixture consisted of wheat , rice and maize, more eggs were laid in maize, followed by wheat and then rice, the number of eggs being 46 , 38 and 18. In the absence of maize, the weevils preferred wheat, and then rice and finally sorghum (63, 32 and 12). In the absence of rice or of wheat, most of the eggs were laid in maize. In a mixture of two cereals only the following results were obtained : in wheat and rice mixture 45 and 19 eggs, in wheat and

TABLE 18

Preferred Oviposition Sites of S. zea-mais on a Mixture of Different Cereals

Total numbers of eggs laid by 160 females in 560 grains in 48 hours				Significance of Preference (X Test)
WHEAT (ENT)	RICE (KLD)	MAIZE (TAP)	SORGHUM (EMB)	
40	13	50	5	$P < 0.001$
38	18	46		$0.01 > p > 0.001$
63	32		12	$P < 0.001$
48		61	10	$P < 0.001$
	36	65	8	$P < 0.001$
45	19			$0.01 > P > 0.001$
18		42		$0.01 > P > 0.001$
44			12	$P < 0.001$
	21	40		$0.02 > P > 0.01$
	33		6	$P < 0.001$
		41	9	$P < 0.001$
TOTAL 296	172	345	62	$P < 0.001$

maize 18 and 42 ; in wheat and sorghum 44 and 12; in rice and maize 21 and 40 ; in rice and sorghum 33 and 6 ; and finally in maize and sorghum 41 and 9 . The total numbers of eggs laid in the four cereals were as follows : 345 eggs in maize, 296 in wheat , 172 in rice and 62 in sorghum.

Significance of preference :- In all the combinations of cereals the weevils showed a decided preference for certain sorts of grain. In the presence of maize, most of the eggs were laid in it. When maize was not available, wheat was strongly preferred. sorghum was the least attractive grain in all the combinations . The distribution of the eggs of S. zea-mais in the different cereals was far from random in all the tests i.e. the preference for oviposition sites was highly significant.

c) S. oryzae

The weevils when given the choice between the four cereals simultaneously, exhibited a marked ability to choose wheat , followed by rice, sorghum and finally by maize. The corresponding numbers of eggs laid in these cereals were 67, 24, 18 and 10 (TABLE 19). The prefere-nce for oviposition in wheat was significantly high in all the combinations, and the total

numbers of eggs obtained by summing up the data in all the experiments were 286, 148, 87 and 40 in wheat, rice, sorghum and in maize. When wheat was not available, the weevils preferred to oviposit in rice; and when maize and sorghum were offered together, the weevils significantly preferred the latter. The choice of the oviposition sites was significantly high in all the combinations of cereals offered.

d) Comparison between the preference for Oviposition Sites in the three Species.

The total numbers of eggs laid by the three species in the four cereals are given in Table 20. S. granarius showed a marked predilection for laying in wheat, followed by that for rice, maize and finally for sorghum. S. zea-mais preferred to oviposit in maize than in wheat, followed by rice and finally by sorghum. S. oryzae, on the other hand, were attracted more strongly to wheat, followed by rice, only slightly to sorghum and least of all to maize. The distribution of the eggs of these species in the four cereals differed highly significantly ($P < 0.001$).

TABLE 20

Comparison of the three species in their preference for oviposition in the four cereals

Species	Total numbers of eggs laid by 160 females in 560 grains in 48 hours			
	WHEAT	RICE	MAIZE	SORGHUM
S. granarius	469	123	94	42
S. zea-mais	296	172	345	62
S. oryzae	286	148	40	87

Significance of preference (X^2 Test)

Species compared	Significance
S. granarius and S. zea-mais	$P < 0.001$
S. granarius and S. oryzae	$P < 0.001$
S. zea-mais and S. oryzae	$P < 0.001$

D. THE OVIPOSITION BEHAVIOUR OF THE WEEVILS, AND THE POSSIBLE ROLE OF SOME SENSORY ORGANS.

The female weevil when ready to oviposit, prepares an egg-hole inside the grain by means of the strong mandibles located at the tip of the rostrum. The female normally chooses a rough surface such as the tapering end of the maize seed, or a hairy area similar to that of the wheat grain. These sites seem to be of great help in enabling the insect to grip the grain firmly throughout the elaborate process of preparing the egg-hole ; this may last for half an hour or more, apparently depending on the hardness of the grain. At the beginning of this process the weevil appears motionless when examined under the binocular microscope. The rostrum penetrates deeper and deeper until the antennae touch the surface of the grain and the movable head starts turning in a semi-circle around the longitudinal axis of the body. Consequently the curved rostrum causes the widening of the egg-hole near its base. Simultaneously, the weevil keeps dragging the first two pairs of legs towards the body, while the third pair holds on tightly to the grain. When the egg-hole is prepared, the female turns her longitudinal body axis through an angle of 180°, and the ovipositor, which is normally hidden inside the body is protruded. Some probings are made before the egg-hole is

found. The ovipositor (Fig. 5) makes an angle of about 90° with the last hidden tergum, which is also protruded during this process. The whole ovipositor is inserted inside the egg-hole, with the two coxites stretched apart, most probably touching the inner walls of the hole. A colourless secretion issuing from the ovipositor stoppers the hole after the egg has been deposited, and good sealing is ensured by some final touches of the ovipositor. The egg is laid and covered in about 1 - 2 minutes.

The weevils in the present series of experiments exhibited a marked ability in choosing their oviposition sites, for instance, S. granarius often laid their eggs in between the hairs of the wheat grain. S. zea-mais and S. oryzae laid their eggs near the hairy area but never in between the hairs themselves. The latter two species laid most of their eggs inside the embryo of the rice grain, whereas S. granarius normally prepared their egg-holes near the embryo but rarely right inside. The three species preferred the tapering ends of maize and sorghum grains, but very few eggs were laid inside the embryo itself.

The mechanisms involved in the behaviour of the females in selecting their oviposition sites may be either mechanical, tactile or chemical or co-ordination of these mechanisms.

The experimental evidence which supports these views was as follows :-

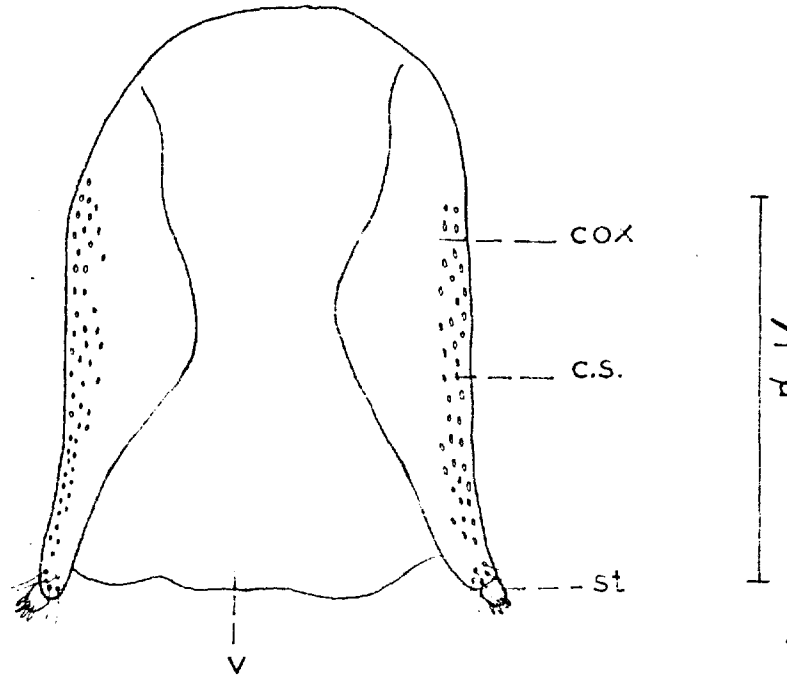


Fig. 5 : Ovipositor of S. zea-mais ; cox: coxite ; c.s.: campaniform sensilla ; st : stylus; v: vulva .

1) Mechanical and tactile sense:- The weevils showed a great tendency for laying their eggs in or near to certain areas of the grains, where they could hold on tightly to the surface during the elaborate process of preparing the egg-hole.

2) Chemical sense :- In the experiments with one type of cereal, the weevils avoided the embryo in wheat, but showed a marked preference for the embryo of the rice grain. In maize and sorghum the eggs were deposited very close to the embryo but rarely inside. In the experiments involving more than one kind of cereal, each species exhibited a decided selection of certain cereals regardless of the existing differences in the size and texture of the grains. It may be suggested, therefore, that certain chemical sense was involved in this behaviour, although the final proof would be in experiments on olfaction.

In order to locate the sensory organs responsible for detecting the preferred oviposition sites, a simple experiment was carried out with S. granarius which strongly preferred wheat and avoided laying their eggs in sorghum. The results were summarised in TABLE 21. In the first set of experiments 10 females with their antennae removed laid 51 eggs in wheat and 2 in sorghum in 48 hours (the number of grains used were 20 of each cereal). In the second set of experiments the females with their six tarsi amputated but the antennae

TABLE 21

Effect of different amputations on the preference of oviposition sites of S. granarius on wheat and sorghum mixture in 48 hours

Amputated Parts	Number of eggs laid by 10 females in 40 grains in 48 hours	
	W H E A T	S O R G H U M
Antennae	51	2
Tarsi	44	2
Antennae&Tarsi	45	0

intact, still showed a highly significant preference for wheat. When both antennae and tarsi were removed the weevils exhibited the same efficiency for selecting wheat as with these organs intact. Whole mounts of the ovipositor revealed the presence of a group of 7 minute peg organs located at the tip of each stylus (Fig. 5). Each peg, under high magnification, has a very thin double-wall with a more or less blunt apex (Fig. 6). Unlike ordinary setae, these pegs do not arise from sockets, and in a longitudinal section each passes through the very thin cuticle, and is innervated by at least two neurones (Fig. 7).

A large number of campaniform sensilla are found on the coxites of the ovipositor especially on the lateral sides (Figs. 5 & 6). They are also present on the last hidden abdominal segment (on the lateral sides of the tergum and on the reduced sternum). The longitudinal axes of the domes are parallel in all the sensilla, making an angle with the longitudinal axis of the coxite. These sensilla, most probably serve as proprioceptors and respond to mechanical stimuli such as touch and pressure. During the process of insertion of the ovipositor inside the grain, these sensilla most likely touch the .. inner walls of the egg-hole ; this may enable the insect to detect the suitability of the hole for receiving the egg.

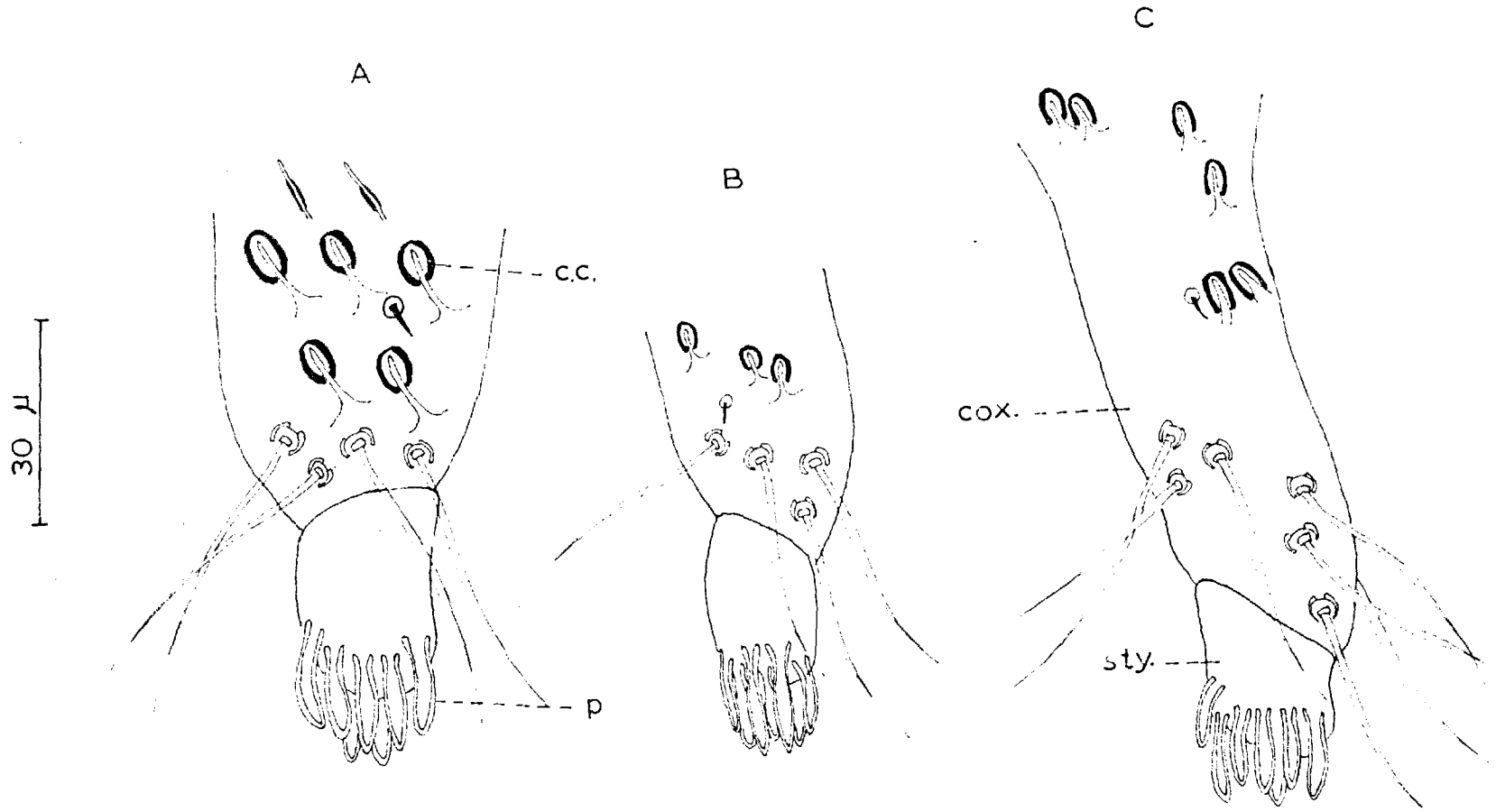


Fig. 6 : Distal end of the coxite of the ovipositor, A, S. granarius; B, S. oryzae; C, S. zea-mais; c.c., campaniform sensilla; cox., coxite; p, peg; sty., stylus.

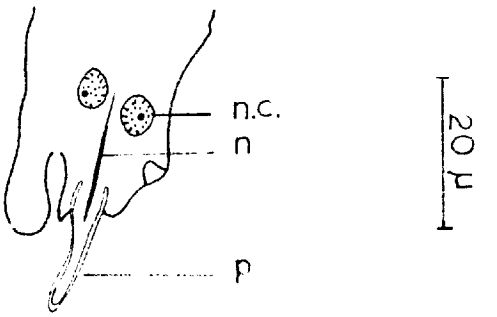


Fig. 7 : L.S. in the stylus of the ovipositor of S. granarius; n, nerve; n.c., nerve cell; p, peg.

In a profile through the grain the normal egg plug appears slightly larger in size than the egg, and the inner walls of the plug are fairly smooth (Fig. 8). The sensory organs on the ovipositor probably function as chemoreceptors, but their role in the selection of the oviposition sites is unlikely because the ovipositor is normally hidden inside the body, and is protruded just before the egg is laid. The peg organs may have another chemical function which is the detection of the amount of the sticky secretion which exudes from the ovipositor and covers the newly laid egg. This is suggested by the action of the ovipositor which repeatedly presses the secretion on top of the egg hole.

The possible chemoreceptors responsible for the choice of the egg-hole are the minute basiconic sensilla located in a group of about 16 pegs on the apex of the distal segment of the maxillary palp (Fig. 9). These may be the taste receptors which explain the efficiency with which the weevils choose the preferred cereal. The labial palps, on the other hand, can play no role in this mechanism since they are completely devoid of any setae or sensory organs (Fig. 9).

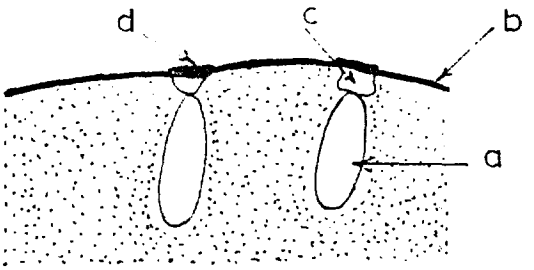


Fig. 8 : The position of the eggs of Sitophilus laid inside the grain; a, egg; b, surface layer of grain; c, sticky secretion; d, stained layer.

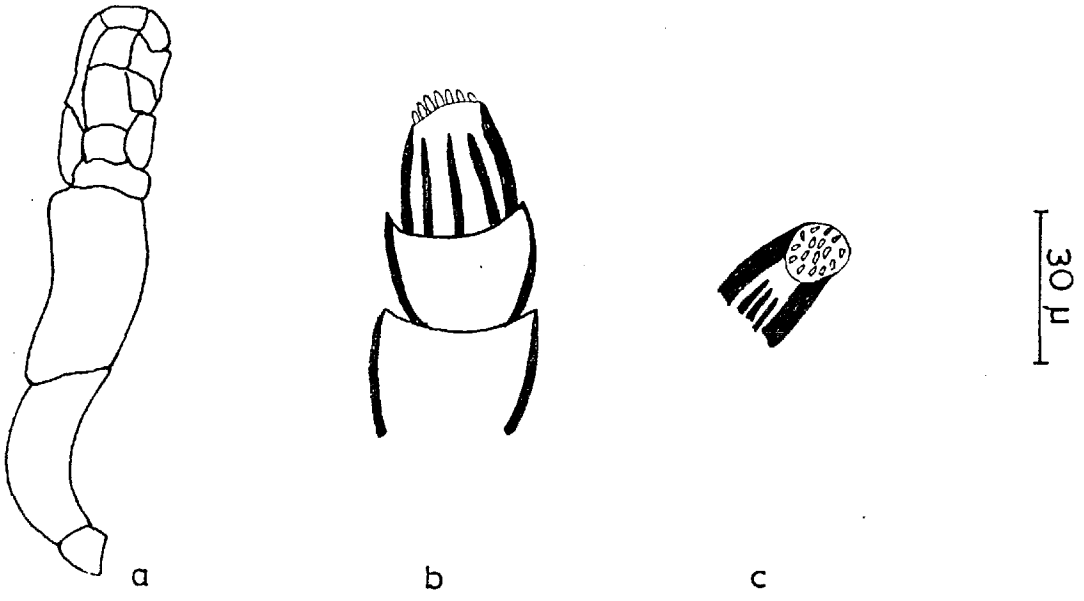


Fig. 9 : S. granarius adult : a, labial palp ; b, maxillary palp ; c, distal segment of maxillary palp (apical view) .

E. DISCUSSION

Sitophilus weevils were able to choose their oviposition sites with great efficiency. When the females were offered grains of one type of cereal placed in four different positions showed a marked ability to select certain parts of the grain. In wheat the three species preferred the hairy end of the grain to the embryo end, both when the grain was presented vertically or horizontally. In maize the three species exhibited a strong tendency to lay their eggs in the tapering end of the seed. The broad end seemed to be very hard and smooth while the tapering end was wrinkled and offered a better foothold to the weevils during the elaborate process of preparing the egg hole. A possible difference in the chemical constitution of these two parts of the grain may also contribute to the preference shown by the weevils. In rice the females preferred the embryo end to the tapering end and the keeled side to the sutured side. The eggs of S. zea-mais and S. oryzae were often laid in the embryo itself and thus may indicate an existence of a sense of taste in these weevils. In sorghum, a clear avoidance of the broad end of the grain may be attributed to a mechanical factor since it is smooth compared to the tapering end. A chemical factor may also be involved as the embryo

inside the grain is near to the tapering end. The preference for certain oviposition sites in the grains of a certain cereal was highly significant in all the three species. This preference in S. zea-mais differed highly significantly from that in the other two species. S. granarius and S. oryzae, on the other hand, exhibited more or less the same order of preference for the different parts of grains of wheat, maize and of sorghum.

When offered the choice between two or more cereals, the three species differed highly significantly in their preference for oviposition sites. The distribution of the eggs was far from random in every species. S.granarius selected wheat in any mixture of cereals. In the absence of wheat the preference for one of the other three cereals was not clear. However, the sum total numbers of eggs laid in the grains of the four cereals in all the experiments showed preference in the following decreasing order: wheat, rice, maize, sorghum. In S. zea-mais the significance of the discriminating power was high in all the combinations tested. The order of decreasing preference was as follows :- maize, wheat, rice, sorghum. In S.oryzae the weevils selected grains of different cereals in the following declining order of preference :- wheat , rice, sorghum , maize.

An interesting finding was in the difference in behaviour of S. zea-mais and S. oryzae which previously

have been considered to be a single species. While S.zeamais showed a preference for maize, S. oryzae was found to be least attracted to the seeds of this cereal.

The highly efficient ability with which the female weevils choose their oviposition sites, may be accomplished by mechanical means and / or through their chemical senses. Unfortunately no experiments on olfaction were carried out, so no firm statement can be made about this. Vision did not play a part since the experiments were carried out in complete darkness. The two suggested types of reactions may act in co-ordination, or one may be preceded by the other in a response-chain process similar to that mentioned by Crombie (1941). He concluded that when Rhizopertha dominica was in an environment which had the odour of food, the sense of touch appeared to be paramount in the selection of oviposition sites. These beetles showed a definite preference for crevices. Makings (1958) described a response-chain reaction in Achroia grisella. The females were attracted by the olfactory sense of smell (located on the antennae), to the odour of beeswax which stimulated oviposition. The ovipositor alone is responsible for the selection of the crevice. Larson (1927) found a marked predilection of Bruchus quadrimaculatus for well filled seeds with a smooth polished seed-coat, but he could not locate the organs of touch responsible for selecting the oviposition sites. Tarsal receptors of Pediculus species

were suggested by Wigglesworth (1941) as more probably responsible for the clustering of lice on the rougher surface, when they were offered the alternative of silk and cotton stockinet on which to walk. Hefford (1936), found that various types of seeds stimulate the oviposition of Bruchus obtectus to a different degree. The beetles normally preferred Phaseolus vulgaris seeds, but when this was absent, the seeds which were more similar in texture and in form were chosen. He also mentioned that the " optimum hosts " had a high carbohydrate content. It may be concluded from his experiments that chemical and tactile senses were involved in the choice of the oviposition sites. Wallis (1962) found that the olfactory receptors which mediate oviposition of the blowfly, are situated on the antennae, labellum and on the ovipositor. Contact chemoreceptors were mentioned by Dethier(1947) on the ovipositor of certain Hymenoptera. In Sitophilus weevils, the basiconic sensilla located at the apex of the maxillary palps are most probably the chemoreceptor organs responsible for taste or for smell. The trichoid sensilla found on the antennal club segments are humidity receptors (see Section 4 on humidity reactions). These played no role in the mechanism of selecting the oviposition sites. This evidence has been obtained experimentally in amputation experiments. The removal of the tarsi seemed to have no effect on the

process of selection either. It may be suggested that the sensory hairs located at the tip of the stylus of the ovipositor, act as contact chemoreceptors for detecting the amount of the sticky substance, secreted through the ovipositor on to the top of the newly laid egg. This conclusion may be derived from observations on the repeated pressing action made by the ovipositor presumably to ensure that the egg is well covered with the secretion. The possibility that these sensory hairs have an olfactory function is not dismissed, but the ovipositor is always hidden inside the body of the female, and it is only protruded just before the laying of an egg.

The campaniform sensilla found on the coxites and the last hidded abdominal segment (which also protrudes during oviposition) most probably respond to mechanical stimuli or to touch. Their function may be to detect the position of the egg-hole and its " suitability " for receiving the egg.

The " Host Selection Principle " put forward by Walsh (1864) that " an insect has a tendency to select that particular plant on which it has fed for a great many generations to deposit its eggs ", was applied to some insects by several workers. Hopkins (1916) concluded from his experiments on some scolytid beetles that an insect species which breeds in two or more hosts, will prefer to

continue to breed in the host to which it has become adapted. This principle was not in agreement with the behaviour of some insects e.g. Rhizopertha showed no preference for the grain on which it was reared for two generations (Crombie, 1941). Larson (1927) concluded that Bruchus quadrimaculatus exhibited avoidance of certain cereals even after having bred in them for several generations i.e. it showed no inherited predilection for that host. Herford (1936) mentioned that the preference for oviposition by Bruchus obtectus on its favourite host was not affected by rearing it in other hosts in the course of five generations.

The " Selection Principle " in the light of more recent concepts of habituation may be considered from a different point of view. In the light of Thorpe's work (1938 and 1939) on Nemeritis canescens and Drosophila melanogaster, and Crombie's experiments (1944) on Calliphora species, it has been shown that the natural aversion to the odour of some repellents, can be transformed into a high degree of tolerance simply by exposing the adults, shortly after emergence, to an air stream bearing the odour of the repellent to which the insects became habituated. Cushing (1944) found that the natural preference of Drosophila guttifera for laying its eggs in a medium which contains fungal growth may be reduced if the larvae have been reared in a medium free of fungi. Several

other examples of habituation in animals, as an important phenomenon influencing their behaviour, have been reviewed by Thorpe (1956). It is evident that an adult insect may become habituated for life to the medium i.e. its host plant, on which the larvae have been reared. Thus attraction to the " host " may persist through life but it may not be inherited immediately, until the process of selection over many generations may intervene.

In Sitophilus species , it can be concluded that S. granarius and S. oryzae exhibited a great tendency to oviposit on wheat, in which they were bred for several years. The behaviour of S. zea-mais, on the other hand, was different, since they showed a marked preference for maize. It has been mentioned by Birch (1954) that the small strain of the rice weevils (S.oryzae)is common in stored wheat and rare in stored maize. The reverse is true for the large strain (S.zea-mais). It was also shown that when the two strains (species) occurred together in crowded cultures one always drove the other out. The small strain (S.oryzae) was the successful one in wheat and the large was the successful one in maize.

It should be noted that no experiments were carried out in the present work on Sitophilus weevils reared on other cereals for several generations to see whether this affected their powers of selection.

IV. THE CLIMBING ABILITY OF THE WEEVILS ON SMOOTH GLASS SURFACE

A. Introduction and Review of Literature :-

Insects , in general, exhibit a great variety of tarsal structures, being modified in one way or another to enable the individual to move about freely in a certain habitat in which it lives or to which it has been adapted. Normally the claws are used in climbing rough surfaces, they act as grappling-hooks, being more or less curved. On the other hand, the claws can hardly play any role in climbing smooth surfaces, a process which depends entirely on adhesive or climbing organs. These are common in many groups of insects as in Hymenoptera, Diptera and many Hemiptera, they take the form of empodia or pulvilli between the tarsal claws. In a few Hemiptera they occur at the lower end of the tibia in the form of a chitinous sole plate in which are set thousands of minute cylindrical tubes as in Rhodnius prolixus (Gillett & Wigglesworth 1932), while in many Coleoptera and Orthoptera it is the ventral surface of the tarsal segments themselves which is specially modified (Dewitz,1884).

In many Orthoptera the functioning organs are the aroliar pads on the ventral side of the pretarsus, and the euplantulae which are less elaborate pad-like struc-

tures on the ventral part of the rest of the tarsal segments. The euplantulae may play a minor role in the climbing mechanism of some roaches, but they are not brought in contact with the glass surface when the roaches are walking inverted (Roth and Willis, 1952).

In Coleoptera the adhesive organs are of variable types, the simplest usually being in the form of tenent hairs clothing the soles as described by West (1862) in many Carabids, Chrysomelids and Curculionids. The expanded apices were either spatulate, clavate or trumpet-shaped. A marked deviation from the normal types is found in the platella of many Harpalinae (Carabidae), in which the soles are provided with peculiar flattened scale-like processes referred to as " squamae " . These may be biseriate or pilose as in the males of Bi-, Tri- and Quadripalmati (Fowler,1887).

One of the most elaborate climbing organs found in male Dytiscus on the fore-leg was described by Miall (1903). The first three joints of the tarsus are enlarged to form a circular disc, its under surface is roughened by a number of minute stalked suckers or cupules, which are outgrowths of the chitinous integument. Plateau(1871) found by actual experiment that Dytiscus marginalis freshly killed by ether, could support more than 13 times its own weight when its suckers were applied to smooth glass.

The review of literature reveals the fact that little experimental work has been done to examine the climbing ability of insects on various surfaces. In the present work, the efficiency of adhesive organs on vertical glass surfaces was determined in three species of Sitophilus. The structure of the tarsi and of the climbing organs was also examined.

B. Methods and Technique :-

The climbing ability of the three species of Sitophilus was determined by measuring the speed at which individual insects climbed up a standard height of a smooth glass surface, measured in centimetres per minute(cm./min). Glass tubes 5feet in length and 2.8 cm. in diameter,were found suitable for these experiments.

A cage 170 X 75 X 30 cm. (Fig. 10) of white card-board was constructed in a corner of the constant temperature room and fixed in position with adhesive tape. The inner wall of the cage was marked at 5 cm. intervals. Two card-board sheets 75 X 30 cm. each, were fixed horizontally inside the cage by means of adhesive tape, the upper one 2 5 cm. below the roof the cage., and the lower one 5 cm. above the bottom. Each sheet possessed 5 circular perforations of 3 cm. in diameter, arranged in a median row at 10 cm. intervals. These perforations

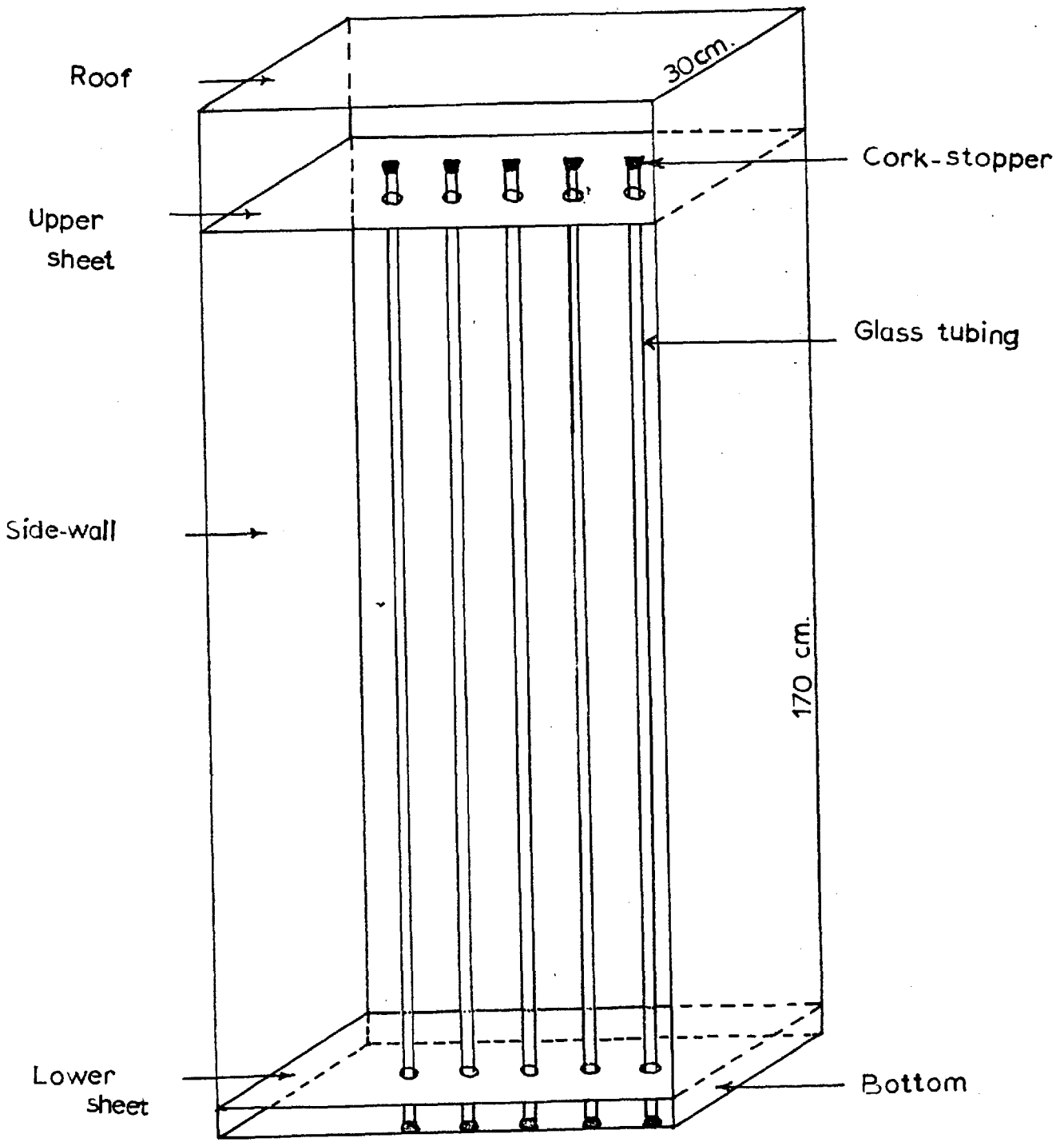


Fig. 10 :Cage for Determining Climbing Ability of Sitophilus Weevils

served to hold 5 glass tubes in a vertical position.

The tubes were thoroughly washed with water and soap solution, hot water, distilled water and finally benzene. When placed in a well ventilated room, no benzene odour was detected after a few hours. Each tube was closed at both ends with cork stoppers wrapped up in filter papers and muslin to prevent the insects from hiding inside the cork crevices ; the white colour matched the other parts of the cage. The muslin was fixed from the outer side of the stopper by adhesive tape. Two sheets of muslin, 40 cm. wide each, were fixed to the top of the cage and covered the whole front part. These allowed for a) ease of putting in or removing the glass tubes, b) clear observation of the climbing insects , c) even illumination inside the cage which was $\bar{1}$.0 Log Foot Lamberts (as measured by S.E.I. Exposure Photometer). Even illumination of the constant temperature room itself was obtained by directing diffused light towards the ceiling.

The experimental insects were 4 - 6 weeks old, and were physiologically mature, with regard to the development of the muscular system and to the full functioning of the climbing organs.

Both intact and operated weevils were experimented with, but as a control measure, both sets were anaesthetized before their climbing ability was determined. The

weevils were anaesthetised under a continuous stream of carbon dioxide for 3 minutes, and then kept over wheat grain in the constant temperature room for 24 hours, then allowed to walk about for a few minutes over cotton wool to brush off any wheat dust sticking to the tarsi. A single weevil was then introduced inside each glass tube by placing it on the stopper which was fitted to the lower end. The tube was then held in a vertical position by placing it inside the cage through one of the perforations in the upper cardboard sheet and then through the corresponding lower one. The insects were transferred from one container to another by means of a suction tube. The disturbance caused to the weevils seemed to be the main factor inducing them to climb.

The time taken by each weevil to climb 140 cm. of the glass tube was recorded, using a stopwatch. The insects were allowed to climb the first 10 cm. without recording the time, in order to be able to watch five climbing insects at almost the same time. The weevils often stayed for varying lengths of time making several trials to escape by turning around the edge of the stopper before starting to climb upwards.

Every insect was then transferred to a marked flat bottom glass tube, with bored cork and muslin, weighed individually in a tiny specimen tube on an Oertling balance

reading to 0.2 mgm. and approximated to 0.1 mgm. The weevils were then anaesthetised by carbon dioxide and the fifth tarsal segment bearing the claws was then removed from all the legs. Each insect was confined in its own corresponding glass tube containing a few wheat grain, and allowed to recover for 24 hours in the constant temperature room.

The speed of the operated weevils was determined once again, and then they were dissected in order to sex them. The tarsi were dehydrated, cleared in xylol and mounted in Canada balsam, and the maximum widths of the third tarsomeres of the pro-, mid- and hind-legs of one side were measured under the microscope by means of an eye-piece micrometer using the high power.

For counting the number of tenent hairs on the third tarsomeres, the tarsi of newly emerged adults were heated in KOH solution, washed in distilled water, then the 5th. tarsomeres were pulled out by means of a fine pair of forceps to facilitate the count. Immersion in diaphanol for a few minutes bleached the chitin to a great extent. The material was then dehydrated, stained with basic fuchsin, cleared in methyl cellosolve and mounted in Euparal. The hairs were counted under the microscope at 400 X magnification.

Histological sections of the tarsi were prepared by placing the material in Bouin's fixative and embedded by

the paraffin method. Sections were cut at 4 u and stained with Ehrlich's haematoxylin and eosin.

C. Description of the Tarsus :-

The tarsal segments are extremely variable in form and in number and afford valuable family and superfamily characters in Coleoptera (Imms,1957). The primitive 5-segmented condition is characteristic of the Adephaga , the Scarabaeids and many other Polyphaga. Among the Heteromera the fore and the middle tarsi are 5-segmented and the hind pair 4-segmented. In the Chrysomelidae and Curculionidae the fourth and fifth segments are anchylosed, the fourth being very small.

In Sitophilus weevils , the first tarsal segment is nearly twice the length of the second one(Fig. 11) ; they are roughly cylindrical in shape and increasing in diameter from base to apex. The third joint is slightly modified, tending at first to become somewhat flattened and widened triangularly (in S.granarius it is more or less oval in surface view, Fig. 11 ,c), with a notch arising at its apex, and as a result two lobes being formed distally. In length it is intermediate between the first and the second tarsomere. The fourth and fifth segments are anchylosed, the former being vestigial and

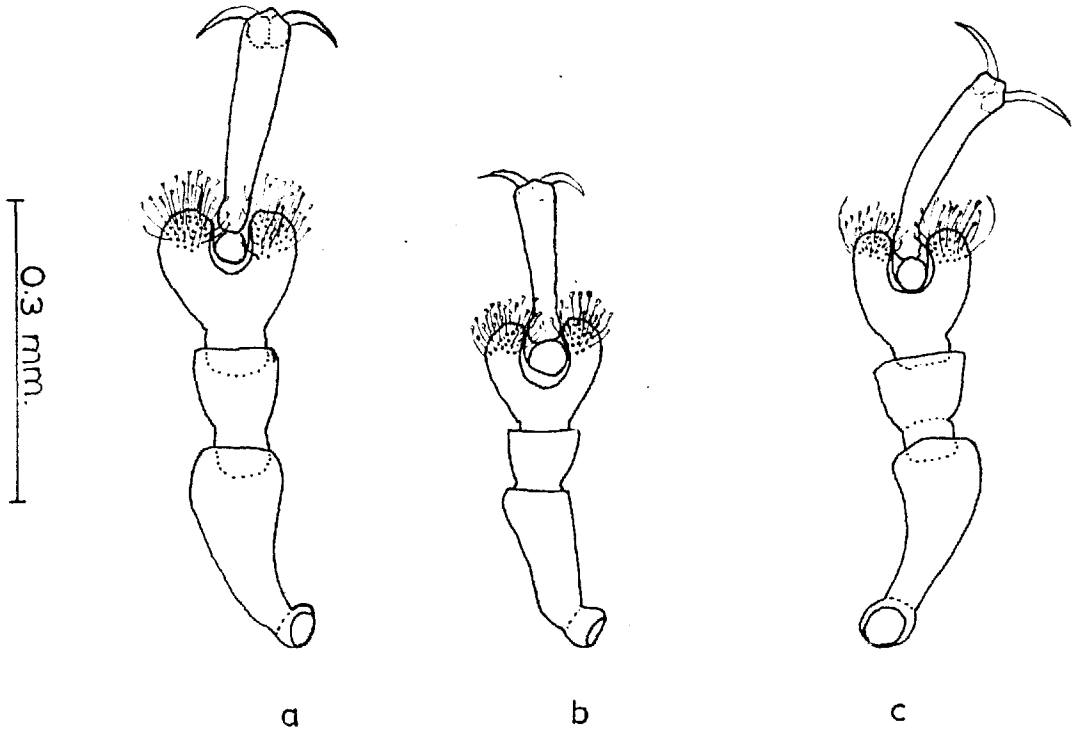


Fig. 11 : Tarsus of Sitophilus weevils : a, S. zea-mais ; b, S. oryzae ; c, S. granarius.

rounded and embedded between the two lobes of the functioning penultimate segment. The onychium is slender , slightly enlarged distally and may reach the length of the basal segment. It bears two equal claws, which are simple and slightly curved. The arolium of the pretarsus is vestigial.

The tarsal segments, as well as the other parts of the body, are clothed with various types of hairs or setae, which are simple, branched or feather-like and of unknown function. Their orientation and size differ from one pair of legs to another in the same species.

D. The Structure of the Climbing Organ

It has been clearly investigated that the adults of Sitophilus possess adhesive organs which enable them to grip smooth surfaces. The following facts suggested the importance of the third tarsal segment. Careful watching under the binocular microscope of the weevils walking inverted inside glass tubes, revealed that the terminal claws and the tuft of hairs clothing the ventral surface of the third tarsomeres were the only structures which were in contact with the glass surface. Further, after removing the onychium bearing the claws from the six legs the climbing efficiency of the insects seemed to be uneffected. On the other hand, when the third tarsomeres were

amputated from two pairs of legs or more, the insects could no longer proceed on a vertical glass surface.

By carefully examining the third tarsal segment under the microscope (H.P.), two distinct areas were identified occupying the ventral side of the bilobed part which formed the sole (Fig. 12,a). They looked identical in shape and surface area, each bearing a uniform tuft of tenent hairs. The apical hairs are nearly straight, but those directed towards the median tarsal notch are usually curved. When the weevil is climbing a smooth surface, the tenent hairs make an angle of about 45° with the wall as can be seen in lateral view (Fig. 12,b). It was also noticed that the apical hairs are slightly longer than the rest so that they all make contact with the substratum.

Each hair is fine, slender and tubular with a slightly swollen tip. In S.zea-mais and S.oryzae, the tips are more or less funnel-shaped with blunt apices (Fig. 13, a & b), While in S.granarius they are rather oval in shape and slightly smaller in size (Fig. 13,c). The width of the tenent hair is approximately $1\ \mu$, and the width of the glandular tip is about $3\ \mu$ in S.zea-mais and S.oryzae, and about $2\ \mu$ in S.granarius.

Each hair is provided with an inner minute canal which widens near the apex, apparently for the passage of

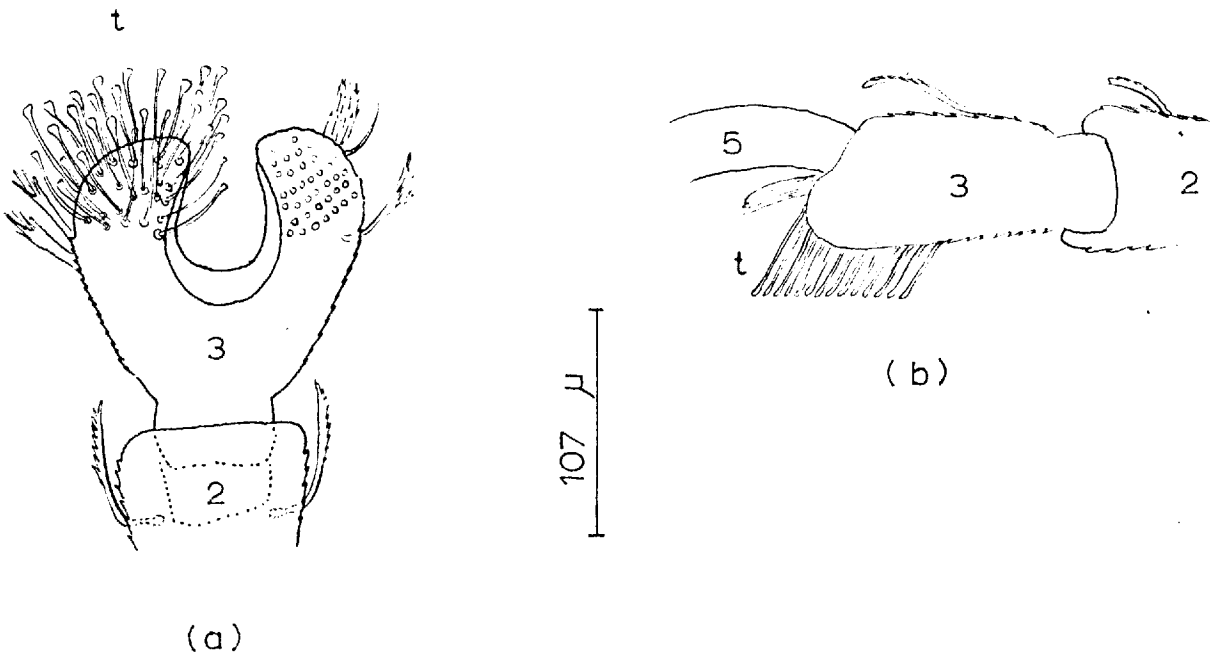


Fig. 12 : Third tarsomere of S. zea-mais weevils : (a) Ventral view ; (b) Lateral view; t, tenent hairs.

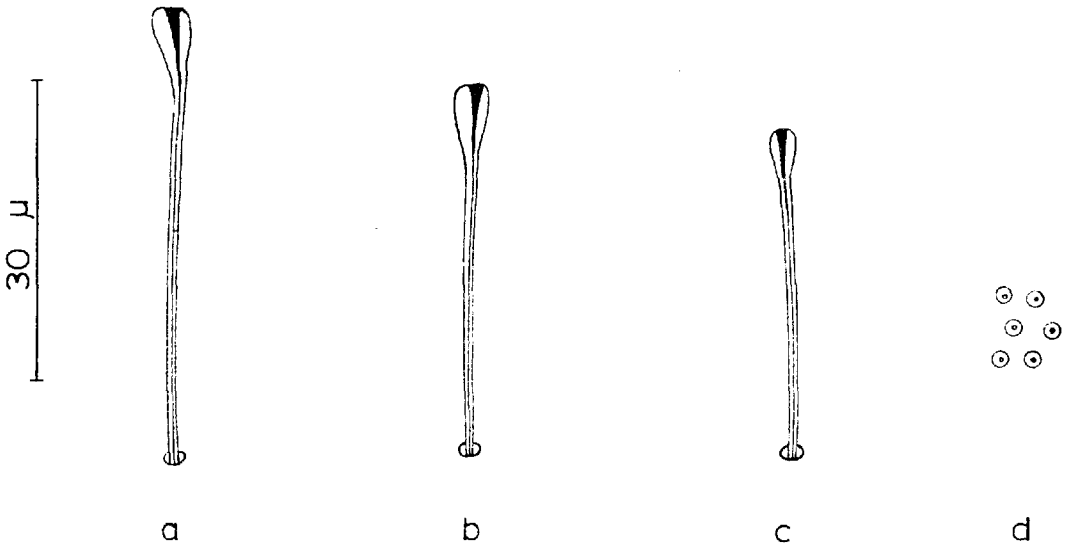


Fig. 13 : Tenent hairs on third tarsomeres of Sitophilus weevils (highly magnified) ; a, S. zeamais ; S. oryzae ; c, S. granarius ; d, Transverse section in tenent hairs.

the glandular secretion. The hair is circular in transverse section, with a minute canal lying right in the centre (Fig, 13,d). The tenent hairs do not arise from sockets like ordinary setae, but each runs through a deep invagination in the chitinous sole plate as shown in a longitudinal section in the third tarsomere of S.zea-mais (Fig. 14). A number of elongated glandular cells are found , each one being attached to the base of each hair.

E. Observations on the Nature of Secretion from the Tenent Hairs.

Gillett and Wigglesworth (1932) have discussed the suggestion that the climbing organs of many insects secrete a fluid which plays an essential part in their mechanism. Such a fluid might have the wetting properties of water or of oil, or it might be a sticky or cohesive substance. Some evidence as to whether the hypothetical fluid is oily or watery may be gained by testing the ability of the insect to climb a waxed surface ; for a watery fluid should not adhere to wax.

In the present set of experiments, Sitophilus weevils, however, showed a marked officiency when allowed to climb a vertical waxed glass surface. This applied to the three species experimented with.

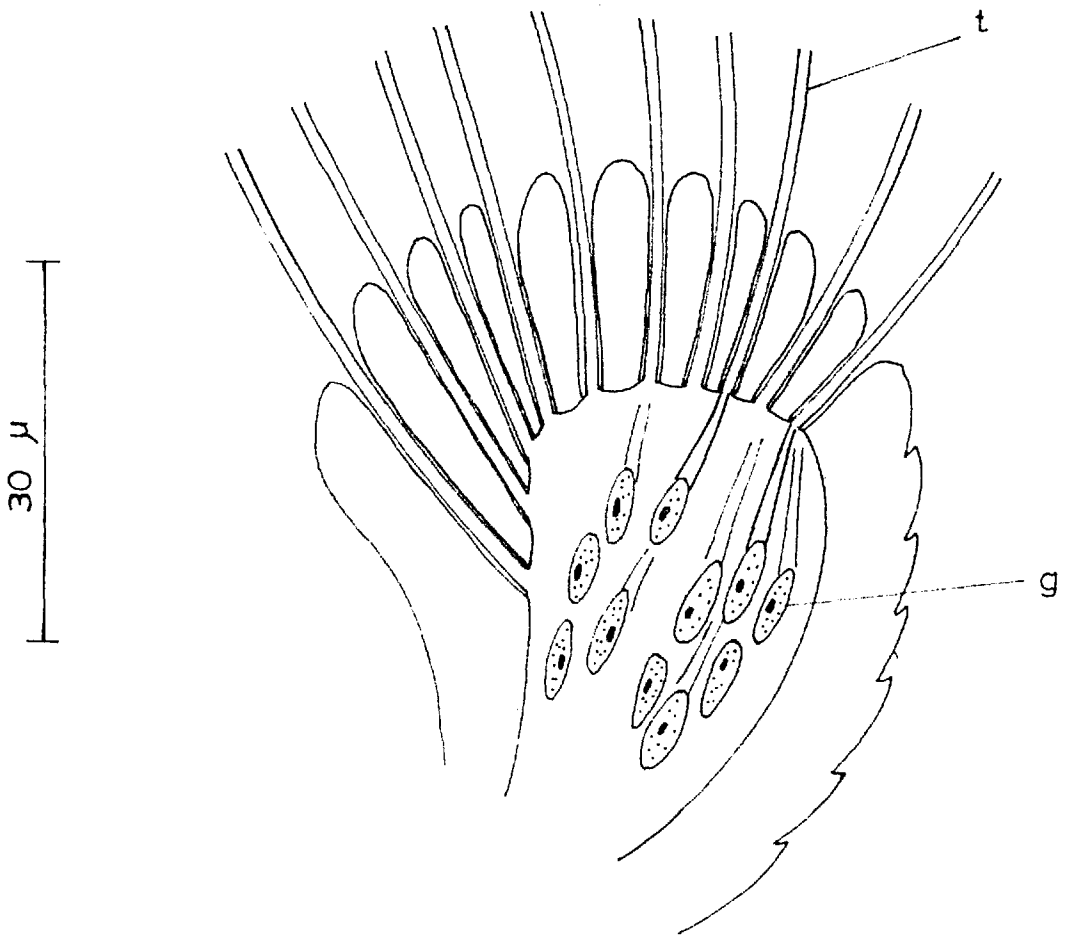


Fig. 14 : Section in third tarsomere of S.zea-mais weevil; t, tenent hair; g, gland cell.

Another simple experiment which contributes to the fact that the fluid secretion of the glandular hairs is not watery was carried out as follows :- the weevils were allowed to walk about on a horizontal smooth glass plate and then a strong current of water was directed so as to sweep the glass surface. In this state, the weevils were found to grip firmly to the substratum, regardless of the direction of the water current in relation to the body axis.

F. Results

Part 1. The Number of the Glandular Hairs and their Length.

The right and left lobes of the third tarsal segments were found to be , almost always, provided with the same number of tenent hairs. This applied to the three species of Sitophilus. Another interesting point is that the number of hairs on the second and third pairs of legs were more or less the same and considerably lower than those on the tarsi of the fore legs. This is clearly seen in TABLE 22, which gives the mean values of the number of hairs on the legs of the three species. In S.zea-mais , the mean number of hairs on the fore legs is 78.1 $\pm$ 2.2 and is 59.1 $\pm$ 1.9 and 55.4 $\pm$ 0.6 for the mid and the

hind legs respectively (TABLES 22 & 24). In the same order the mean values for S.oryzae were 47.4 ± 1.5 , 37.8 ± 1.0 and 37.8 ± 1.0 (TABLES 22 & 25) ; and for S.granarius they were 41.9 ± 1.1, 32.4 ± 0.9 and 31.4± 0.8 (TABLES 22 & 26).

Analyses of variance of means differed significantly when the number of tenent hairs on the fore legs and either mid or hind legs in the same species were compared. The significance was also high when the variance of means of corresponding tarsi of any two species was compared (TABLE 23). The mean number of hairs on the second and third pairs of legs were almost the same in S.oryzae and and S.granarius, but differed significantly in S.zea-mais.

The tenent hairs differed not only in number but also in their length in the same individual. In S.zea-mais the length of the hairs on the fore legs varied between 35.71 and 49.99 μ having a mean of 42.85 ± 2.1 μ.Those on mid and hind legs were 36.42 ± 1.5 and 36.78 ± 1.9 μ long respectively, ranging between 32.14 and 39.28 μ (TABLE 27).

Similarly, the mean lengths of S.oryzae hairs were 37.50 ± 1.1 , 33.92 ± 1.3 and 33.92 ± 1.3 μ ; and of S.granarius 32.14 ± 1.5 , 26.78 ± 1.2 and 26.78 ± 1.2 μ, for those on the fore, mid and hind legs respectively. The mean hair lengths of the three species are summarised in

TABLE 27 .

The analysis of variance of means between the hair lengths on the fore legs and either the second or third pairs of legs in the same species, and between the corresponding legs of any two species were all highly significantly different (TABLE 23).

TABLE 22

Mean Number of Tenent Hairs on Third Tarsomeres of the Three Species (10 individuals of each species)

Species	Mean Number of Tenent Hairs			
	Fore leg	Mid leg	Hind leg	Mean
S.zea-mais	78.1±2.2	59.1±1.9	55.4±0.6	64.2
S.Oryzae	47.4± 1.5	37.8±1.0	37.8±1.0	41.0
S.granarius	41.9±1.1	32.4±0.9	31.4±0.8	35.2

TABLE 23

Analysis of Variance of Means
(Ten individuals of each sex of each species)

Species compared	Number of tenent hairs on third tarsomeres	Length of hairs
Male&Female S.zea-mais	non-siggnificant	non-signif.
Male&Female S.oryzae	non-significant	non-signif.
Male&Female S.granarius	non-significant	non-signif.
S.zea-mais&S.oryzae	$P < 0.001$	$P < 0.001$
S.zea-mais&S.granarius	$P < 0.001$	$P < 0.001$
S.oryzae & S.granarius	$P < 0.001$	$P < 0.001$
S. zea-mais		
Tarsi I & II	$P < 0.001$	$P < 0.001$
Tarsi I & III	$P < 0.001$	$P < 0.001$
Tarsi II & III	$0.01 > P > 0.001$	non-signif.
S. oryzae		
Tarsi I & II	$P < 0.001$	$P < 0.001$
Tarsi I & III	$P < 0.001$	$P < 0.001$
Tarsi II & III	non-significant	non-significant
S. granarius		
Tarsi I & II	$P < 0.001$	$P < 0.001$
Tarsi I & III	$P < 0.001$	$P < 0.001$
Tarsi II & III	non-significant	non-significant

TABLE 24

Number of Tenent Hairs on Third Tarsomeres of S.zea-mais

(10 individuals of each sex)

Legs	Sex	Range	Mean	Total Mean
Fore	Males	72 - 84	76.4	78.1 ± 2.2
	Females	72 - 88	79.8	
Mid	Males	50 - 68	58.2	59.1 ± 1.9
	Females	58 - 64	60.0	
Hind	Males	50 - 60	56.0	55.4 ± 0.6
	Females	50 - 60	54.8	

Mean number of hairs on the three legs

Males	63.5
Females	64.9
Mean	64.2

TABLE 25

Number of Tenent Hairs on Third Tarsomeres of S. oryzae

(10 individuals of each sex)

Legs	Sex	Range	Mean	Total mean
Fore	Males	44 - 50	46.0	47.4 ± 1.5
	Females	44 - 56	48.8	
Mid	Males	34 - 44	38.2	37.8 ± 1.0
	Females	36 - 40	37.4	
Hind	Males	36 - 40	37.8	37.8 ± 1.0
	Females	36 - 40	37.8	

Mean number of hairs on the three legs

Males	40.7
Females	41.3
Mean	41.0

TABLE 26

Number of Tenent Hairs on the Third Tarsomeres of

S. granarius

(10 individuals of each sex)

Legs	Sex	Range	Mean	Total Mean
Fore	Males	38 - 44	41.2	41.9 ± 1.1
	Females	38 - 46	42.6	
Mid	Males	30 - 36	32.0	32.4
	Females	30 - 38	32.8	
Hind	Males	30 - 34	31.8	31.4 ± 0.8
	Females	28 - 34	31.0	

Mean number of hairs on the three legs

Males	35.0
Females	35.47
Mean	35.2

TABLE 27

Maximum Length of Tenent Hairs on Third Tarsomeres (μ)

Legs		S.zea-mais	S.oryzae	S.granarius
Fore	Range	35.71-49.99	35.71-39.28	28.57-35.71
	Mean	42.85 ± 2.1	37.50 ± 1.1	32.14 ± 1.5
Mid	Range	32.14-39.28	32.14-35.71	25.00-28.57
	Mean	36.42 ± 1.5	33.92 ± 1.3	26.78 ± 1.2
Hind	Range	32.14-39.28	32.14-35.71	25.00-28.57
	Mean	36.78 ± 1.9	33.92 ± 1.3	26.78 ± 1.2

Part 2. Climbing Experiments

a) Speed as related to weight of the weevil :-

1. S. zea-mais : The weight of the male weevils varied between 1.6 and 3.3 mg. , and of the females between 1.9 and 3.1 mg. ; the means being 2.42 and 2.55 mg. respectively (TABLE 29).

The minimum speed of the male weevils with their claws intact was 21.54 cm./min. and the maximum was 42.00 cm./min. having a mean value of 30.49 cm./min. which was slightly greater than the mean speed of the females which was 28.39 cm./min. ; the minimum and maximum were 22.70 and 40.00 cm./min. The analysis of variance of the two means was not highly significant $0.05 > P > 0.02$ (TABLE 31). By plotting the speed of the insects against the weight, the regression coefficient was found to be highly significant for the male weevils ($P < 0.001$), whereas for the females it was not significant (TABLE 32). The regression lines are shown in Figs. 15 and 16.

When the fifth tarsal segments bearing the claws were removed, the speed of the weevils seemed to be unaffected. This can be clearly illustrated by comparing the data in TABLE 29. The mean speed of the male weevils before and

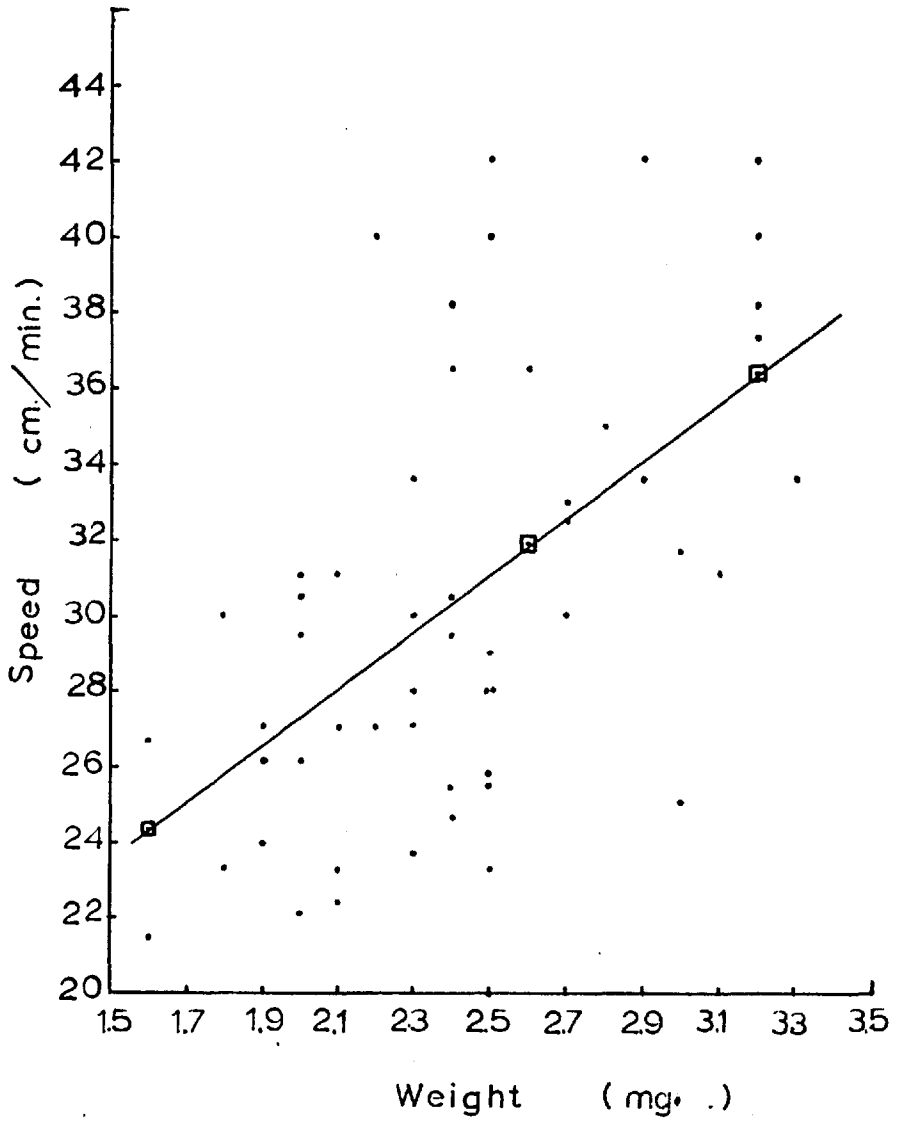


Fig. 15 : Regression line showing relation between weight and speed of male S. zea-mais weevils (claws intact).

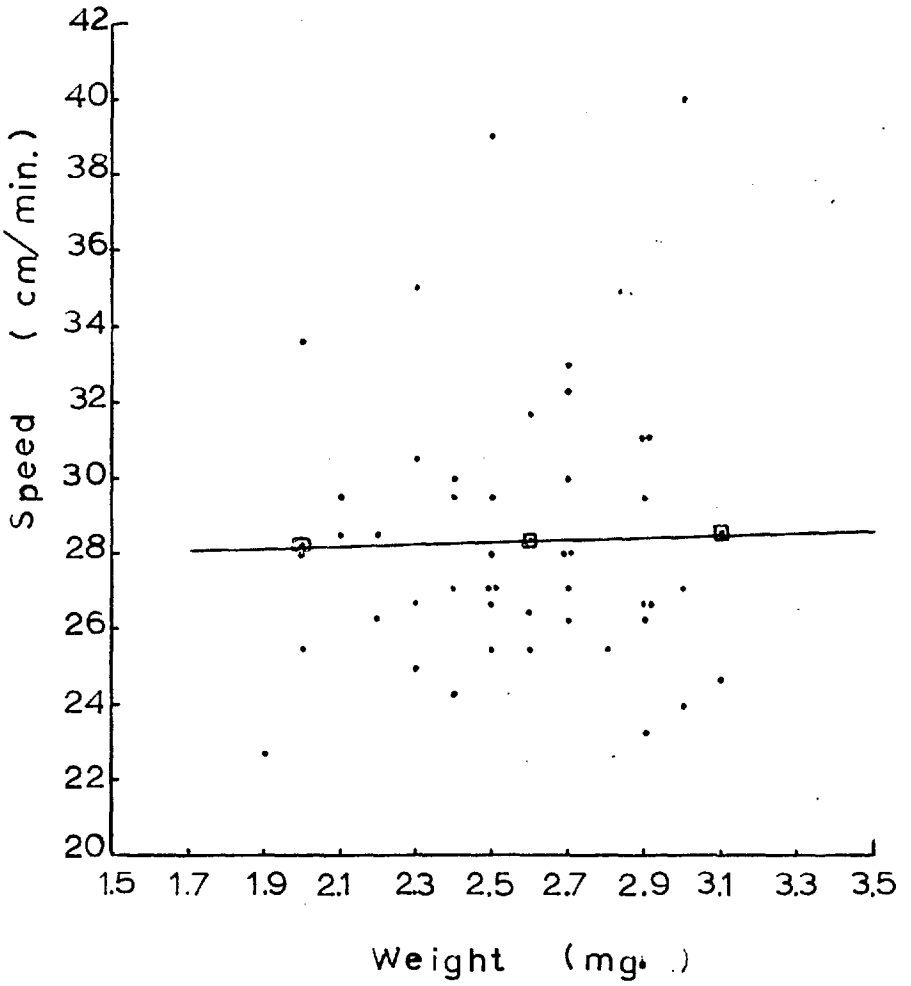


Fig. 16 : Regression line showing relation between weight and speed of female S. zea-mais weevils (claws intact).

after the operation was 30.49 and 30.58 cm./min. respectively. The variance of the means was not significantly different. The operated female weevils walked slightly faster than the intact ones, the mean speed being 29.47 and 28.39 cm./min. respectively. The variance of the two means did not differ significantly.

The regression coefficient obtained by plotting the speed of the operated insects against weight was highly significant in case of the males (Fig. 17) but not significant in the females (Fig. 18 and TABLE 32).

2. S. oryzae : The weight of the male weevils ranged between 0.8 and 2.4 mg., the mean being 1.55 mg. (TABLE 29). The mean value for the females was 1.59 mgm., while the minimum and maximum weights were 1.0 and 2.3 mg. The variance of means of the two sexes was not significantly different (TABLE 31).

The mean speed of the male weevils was 19.79 cm./min. (14.00 - 27.10) and was not significantly different from that of the females 20.68 cm./min. (14.74 - 28.00).

The regression coefficients calculated for the speed of the insects on their weight were significant in both sexes when the claws were intact (TABLE 32), but when the claws were removed the regression coefficient remained highly significant in the male weevils, but was not

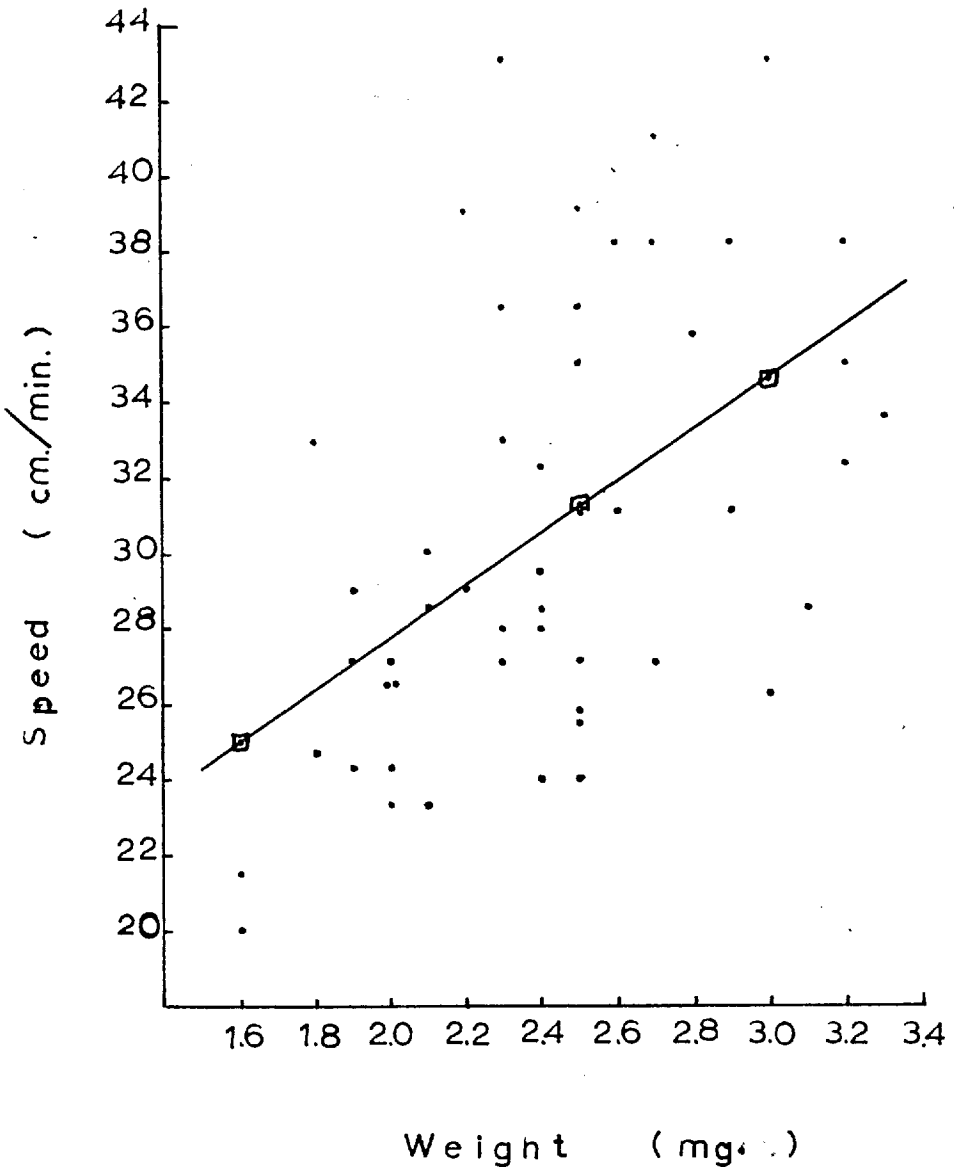


Fig. 17 : Regression line showing relation between weight and speed of male S. zea-mais weevils (claws removed).

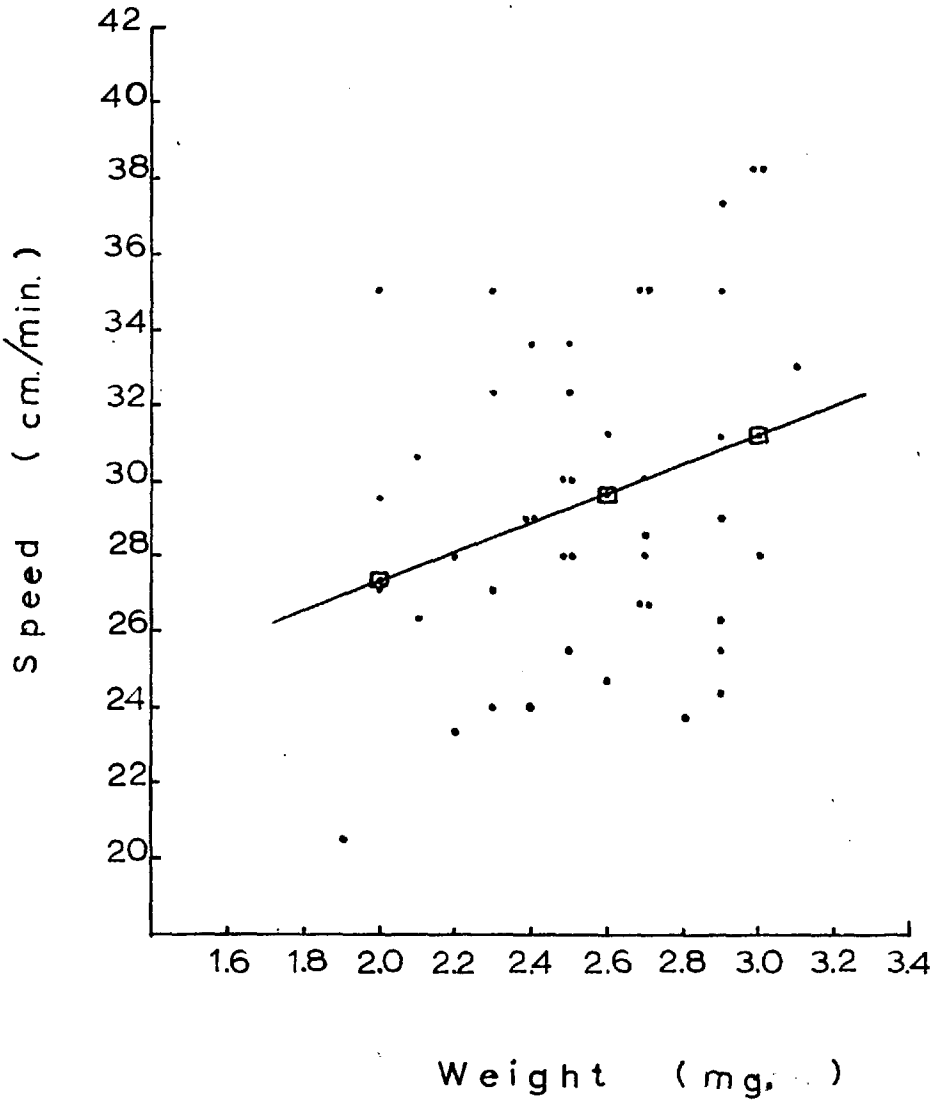


Fig. 18 : Regression line showing relation between weight and speed of female S. zea-mais weevils (claws removed).

significant in the females. The regression lines are shown in Figs. 19, 20, 21 & 22.

3. S. granarius : The weight of the weevils used in this experiment ranged between 2.0 and 3.3 mg. in the males, and 2.0 - 3.7 mg. in the females, the means being 2.8 and 2.95 mg. respectively, their variance not being significantly different.

As regards the speed of the weevils with claws intact, it varied between 6.89 and 18.06 cm./min. in the males, and between 5.49 and 20.99 cm./min. in the females (TABLE 29). The means were 12.81 and 12.73 cm./min. respectively, their variance of means in the two sexes was statistically not significantly different.

The relation between the weight of the insect and its speed was clearly illustrated by the regression lines (Figs. 23 and 25) in the male weevils before and after removal of the claws, the regression coefficients were highly significant ($P < 0.001$) in both cases. On the other hand, there was no significant relationship between the weight of the females (intact and operated) and their speed of climbing and this can be seen in Figs. 24 and 26.

The mean speeds of intact and of the operated weevils did not differ significantly in the three species. The data are summarised in TABLE 29. The analysis of variance of mean weights and speeds of the three species proved to

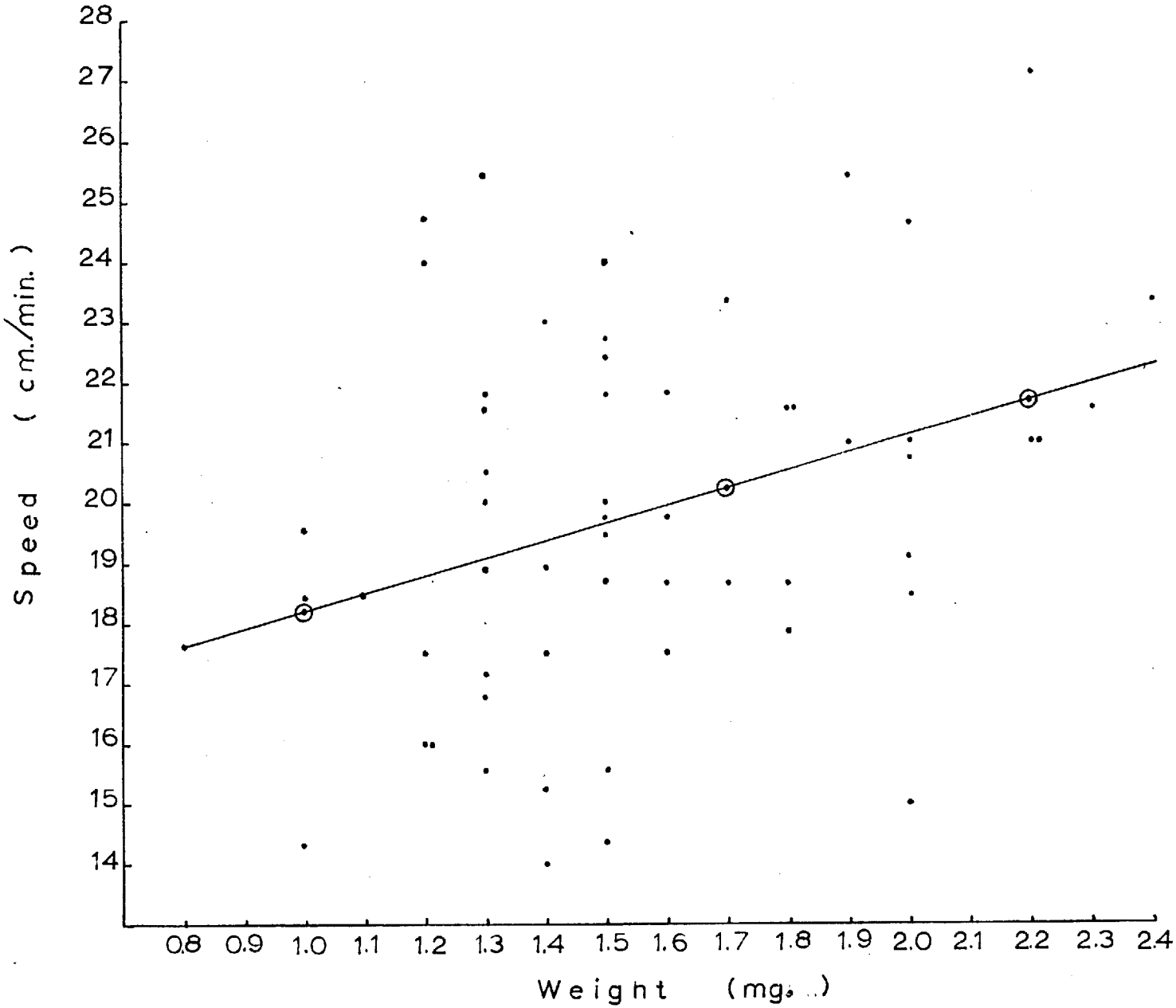


Fig. 19: Regression line showing relation between weight and speed of male S. oryzae weevils (claws intact).

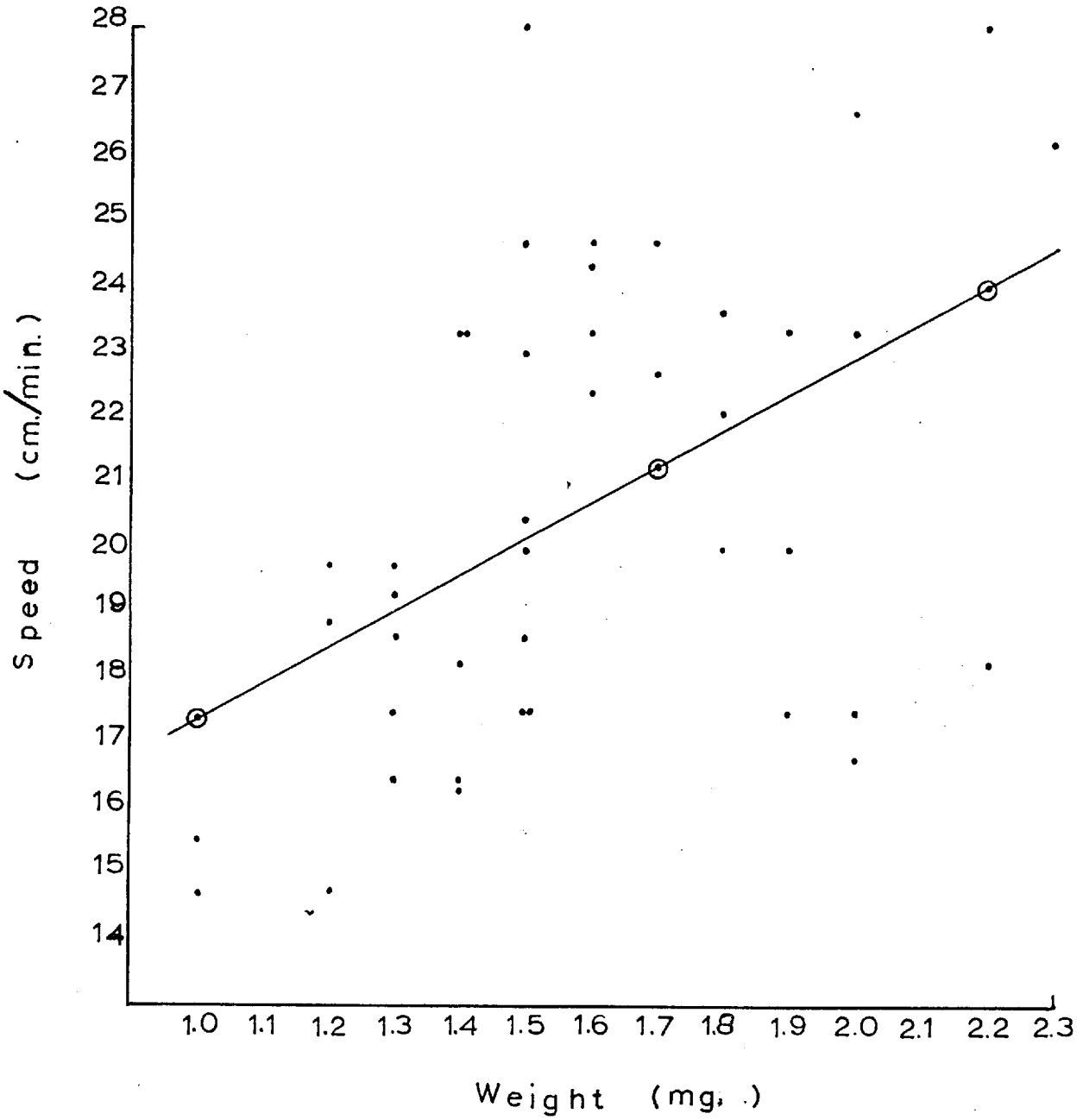


Fig. 20 : Regression line showing relation between weight and speed of female S. oryzae (claws intact).

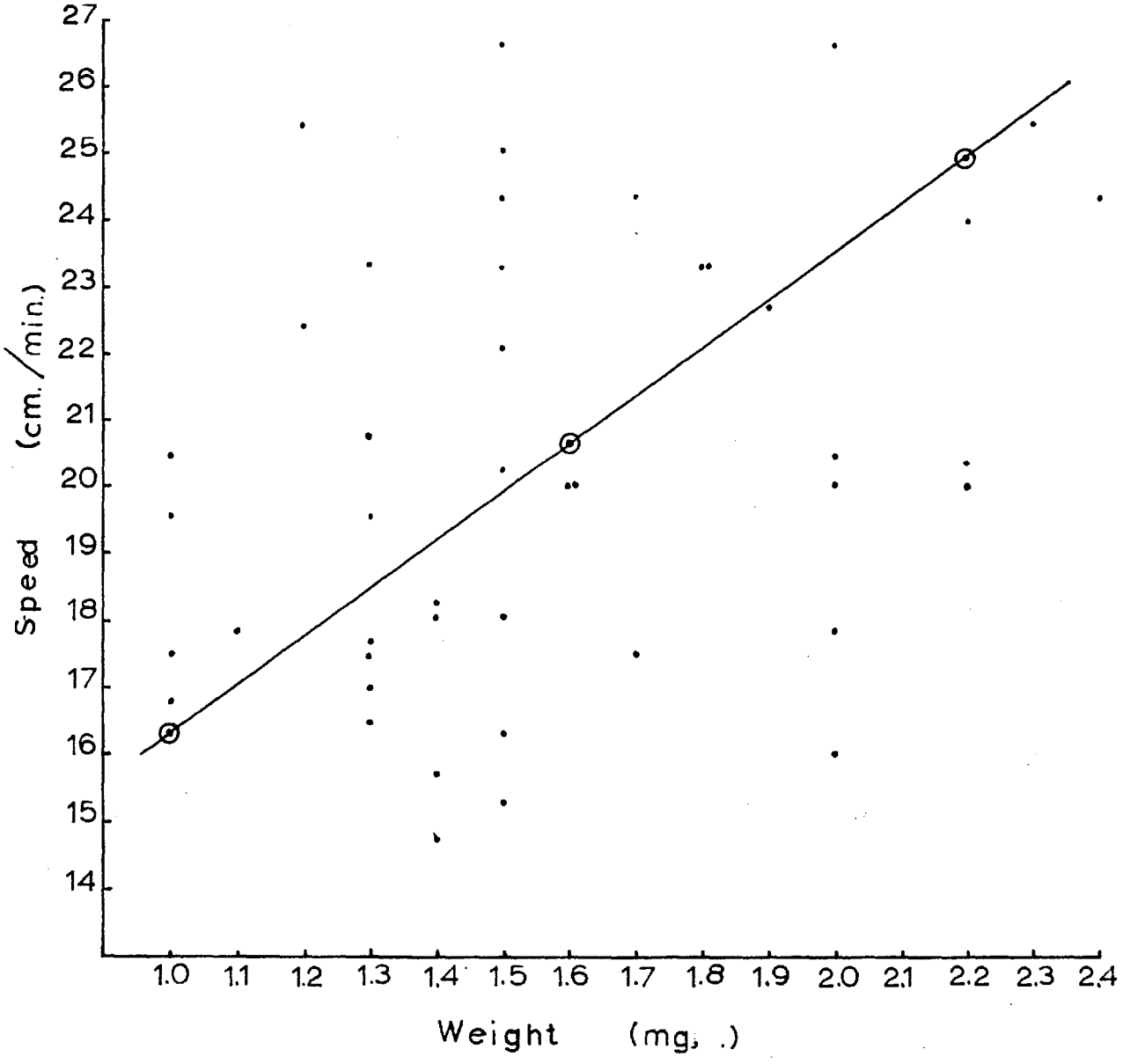


Fig. 21 : Regression line showing the relation between weight and speed of male S. oryzae (claws removed).

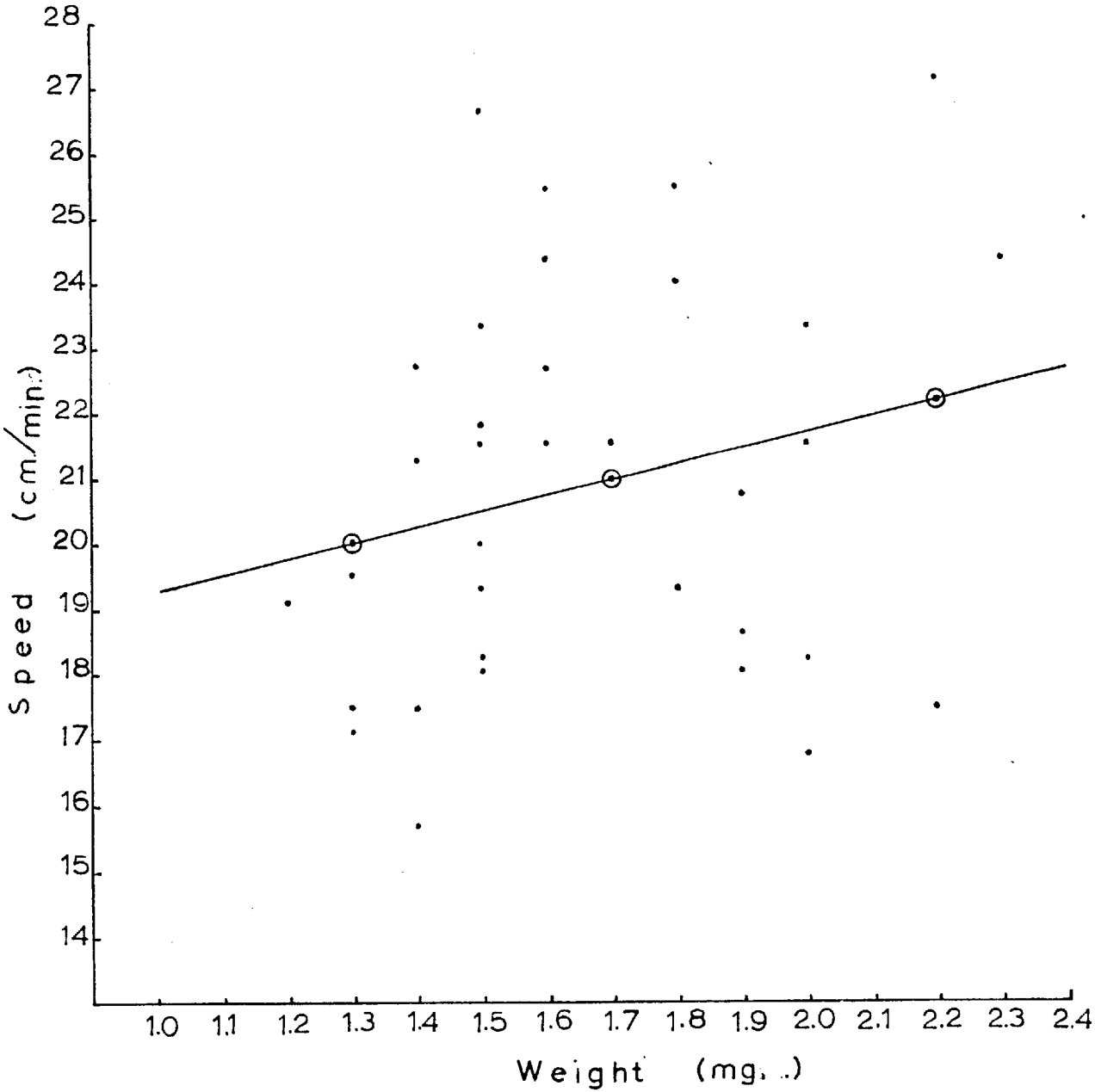


Fig. 22 : Regression line showing relation between weight and speed of female S. oryzae weevils (claws removed).

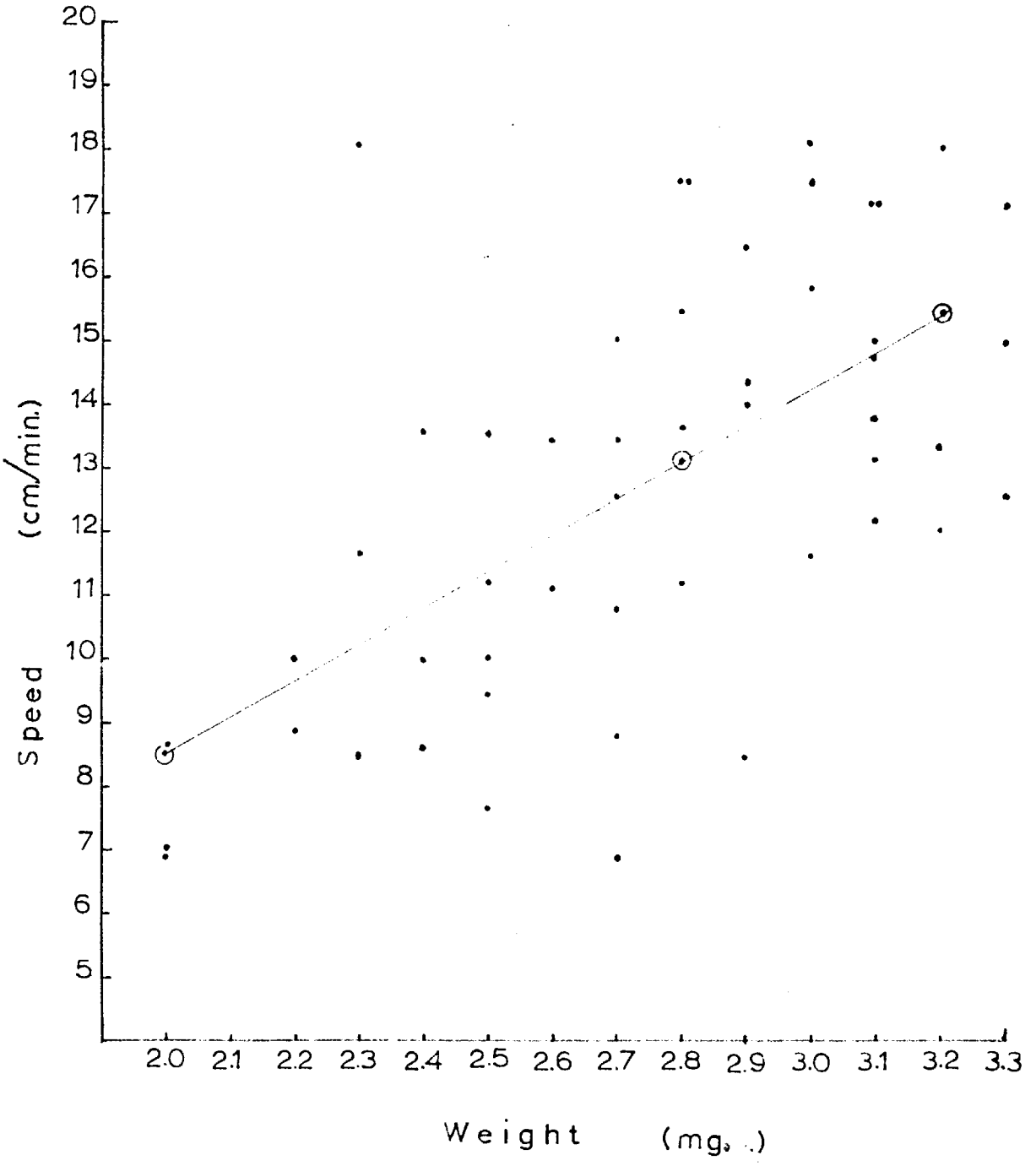


Fig. 23 : Regression line showing relation between weight and speed of male S.granarius weevils (claws intact).

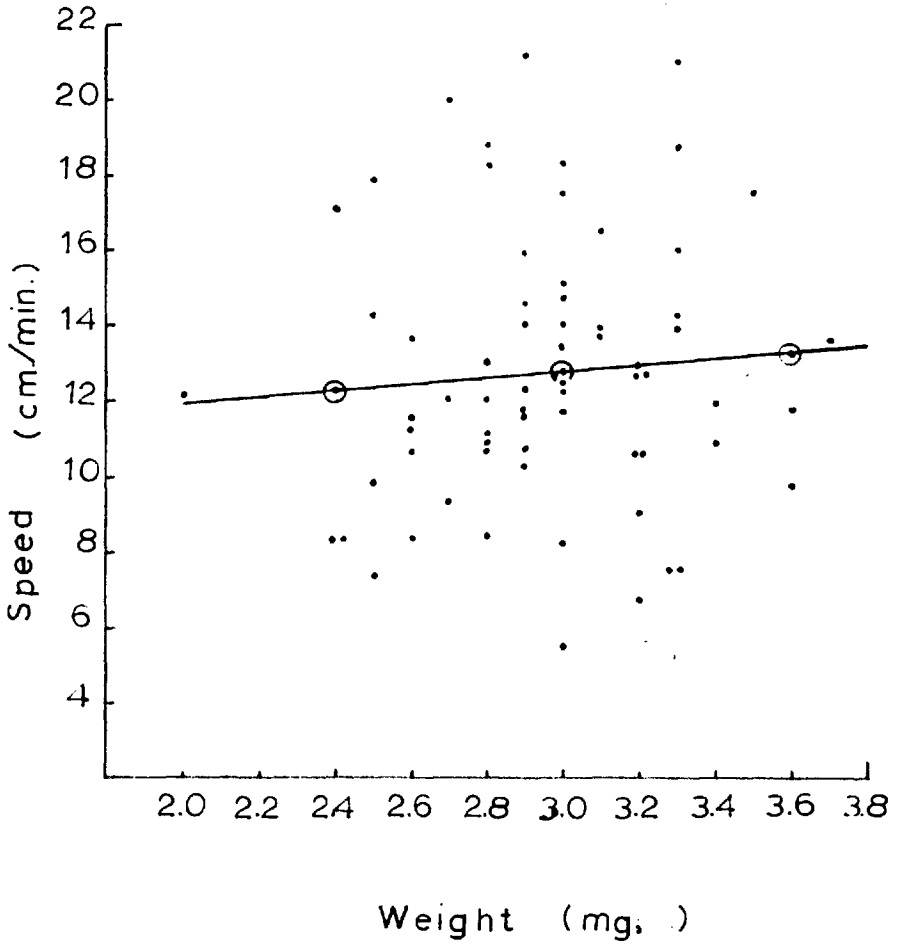


Fig. 24 : Regression line showing relation between weight and speed of female S.granarius weevils (claws intact).

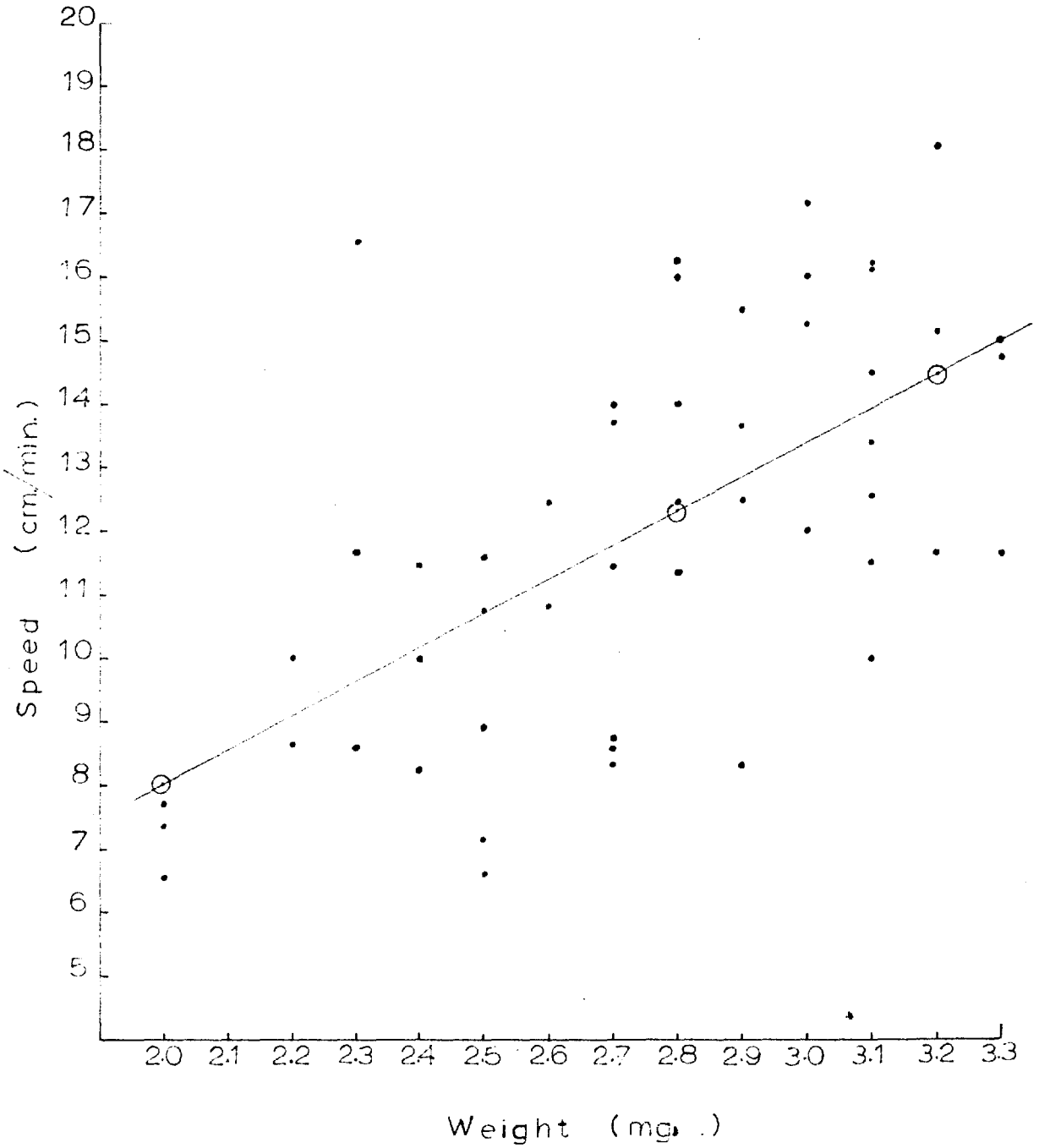


Fig. 25 : Regression line showing relation between weight and speed of male S.granarius weevils (claws removed).

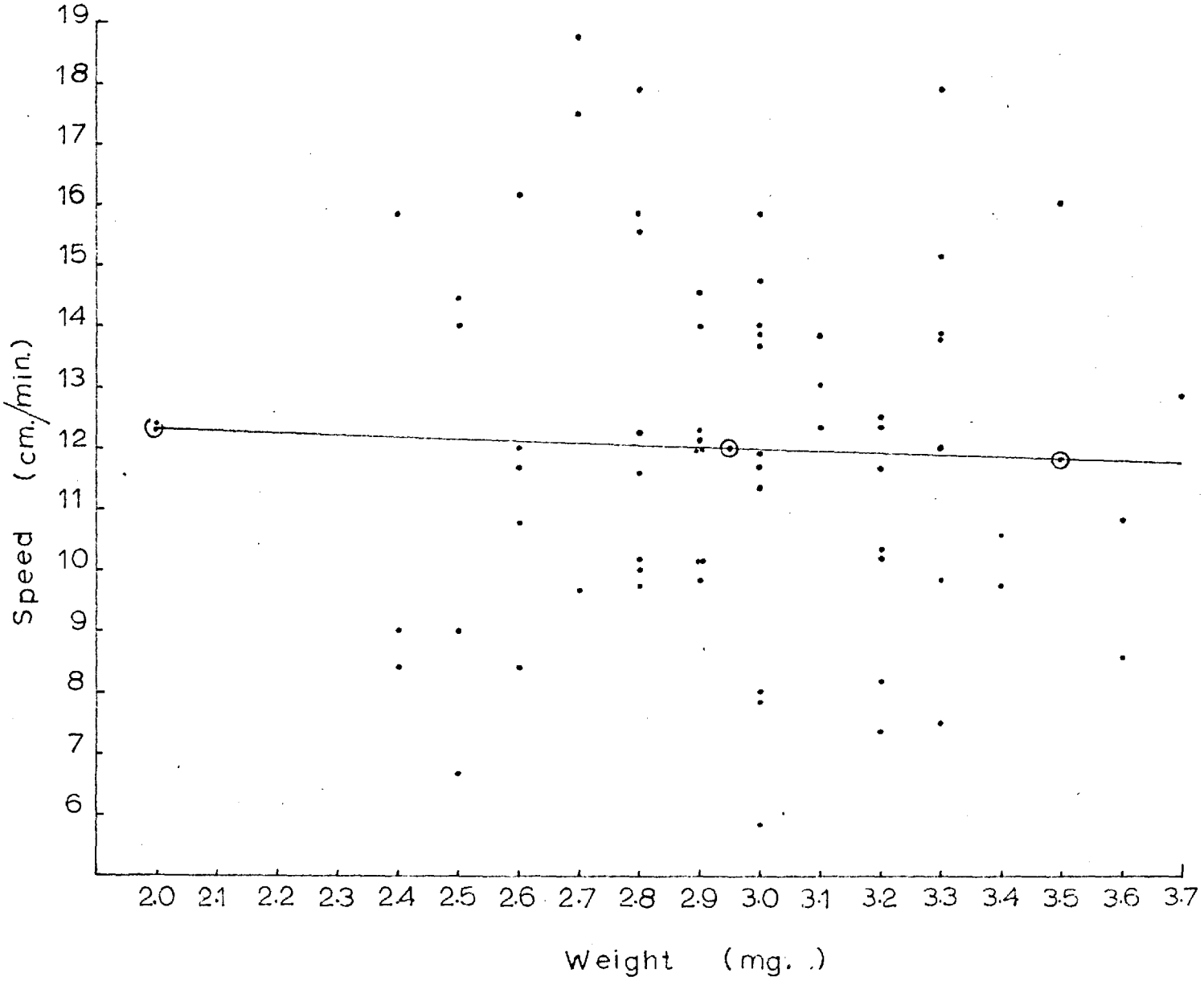


Fig. 26 : Regression line showing relation between weight and speed of female S. granarius weevils (claws removed).

be highly significant, when the same sexes were compared (TABLE 31).

b) Speed as related to Mean Tarsal Width of the Weevils:

In the three species the third tarsal segments on the fore legs are distinctly broader than those on the mid and the hind legs, which have more or less the same width. The " tarsal width " of a certain weevil represents the arithmetic mean of the maximum tarsal width of the fore, mid and hind legs of one side.

1. S. zea-mais : The mean tarsal width of 53 male weevils was 114.64 μ and of 45 females was 114.08 μ. The variance of the two means was non-significant, but it can be noticed from TABLE 29 that the males have a wider range of tarsal widths than the females.

The mean width of the fore tarsi is 123.87 μ as compared with 110.33 μ and 109.72 μ for the mid and hind tarsi respectively. Similarly in the females the mean widths are 122.96 μ, 110.19 μ and 109.08 μ in the same order (TABLE 28). The analysis of variance of means are significantly different between the fore tarsi and either mid or hind ones.

The correlation between the tarsal width and the speed of the insects was clarified by the calculation of regression equations; they were highly significant in

the male weevils (Fig. 27) but not significant in the females (Fig. 28 and TABLE 32).

2. S. oryzae : The mean tarsal widths of the weevils were 95.84 μ and 95.72 μ for 58 males and 42 females respectively (TABLE 29) ; the variance between the two being non-significant (TABLE 31). The widths of the male tarsi have a slightly greater range than those of the females (85.11- 103.56 μ and 88.68 - 100.58 μ).The mean widths of the fore, mid and hind tarsi of the male weevils are 101.93 μ, 92.68 μ and 92.85 μ respectively. Those of the females 101.94, 92.42 and 92.76 μ (TABLE 28). The analysis of variance of means are significantly different between the fore tarsi and either mid or hind tarsi in both sexes.

The regression coefficients of the mean tarsal width on speed were highly significant in both sexes (Figs. 29 and 30, and TABLE 32).

3. S. granarius : The mean tarsal widths of 50 male weevils and 67 females were 98.12 μ and 97.68 μ respectively (TABLE 29) , the variance between the two means being non-significant (TABLE 31). The mean widths of the fore, mid and hind tarsi of the male weevils

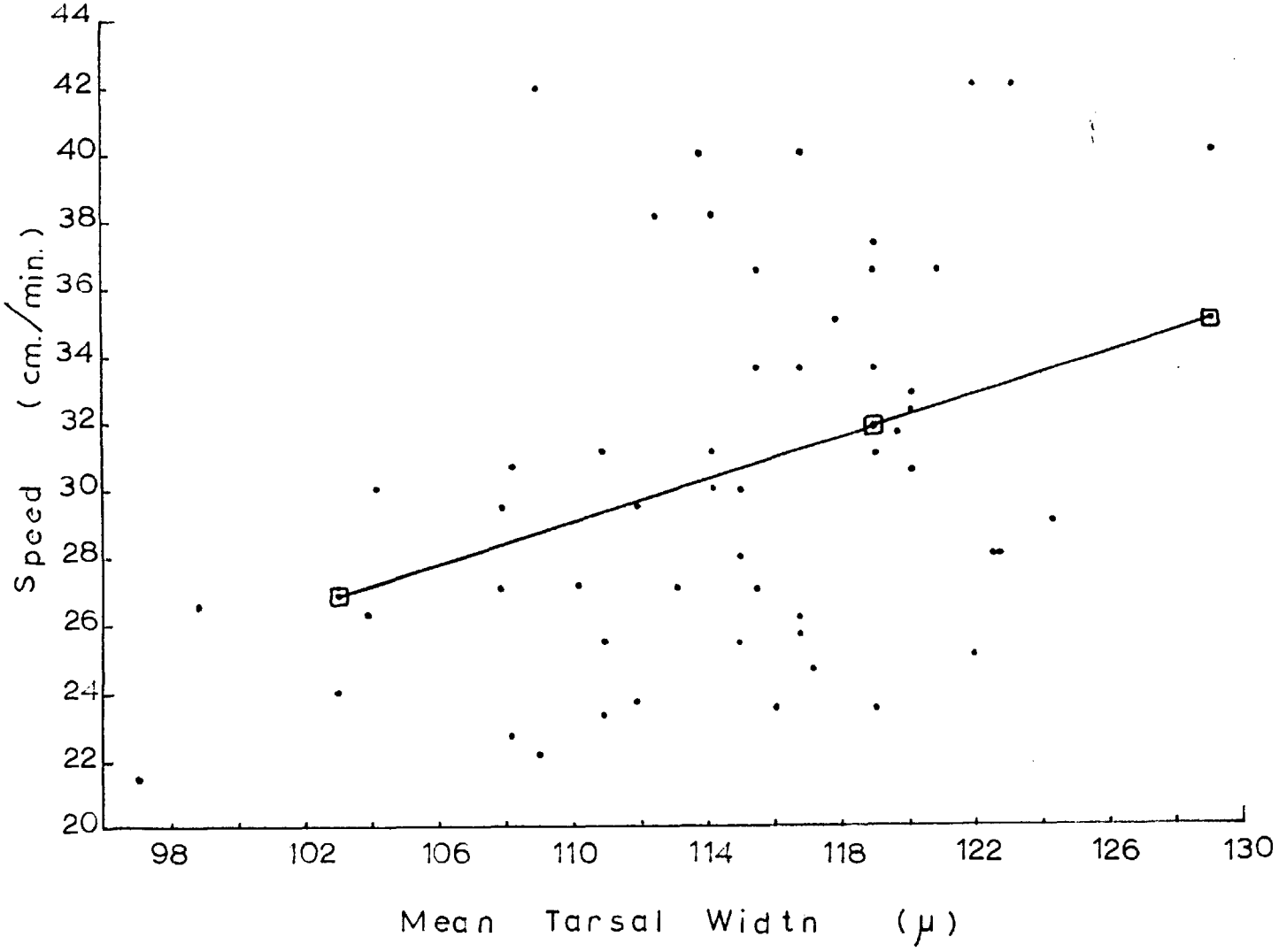


Fig. 27 : Regression line showing relation between mean tarsal width and speed of male S. zea-mais weevils (claws intact).

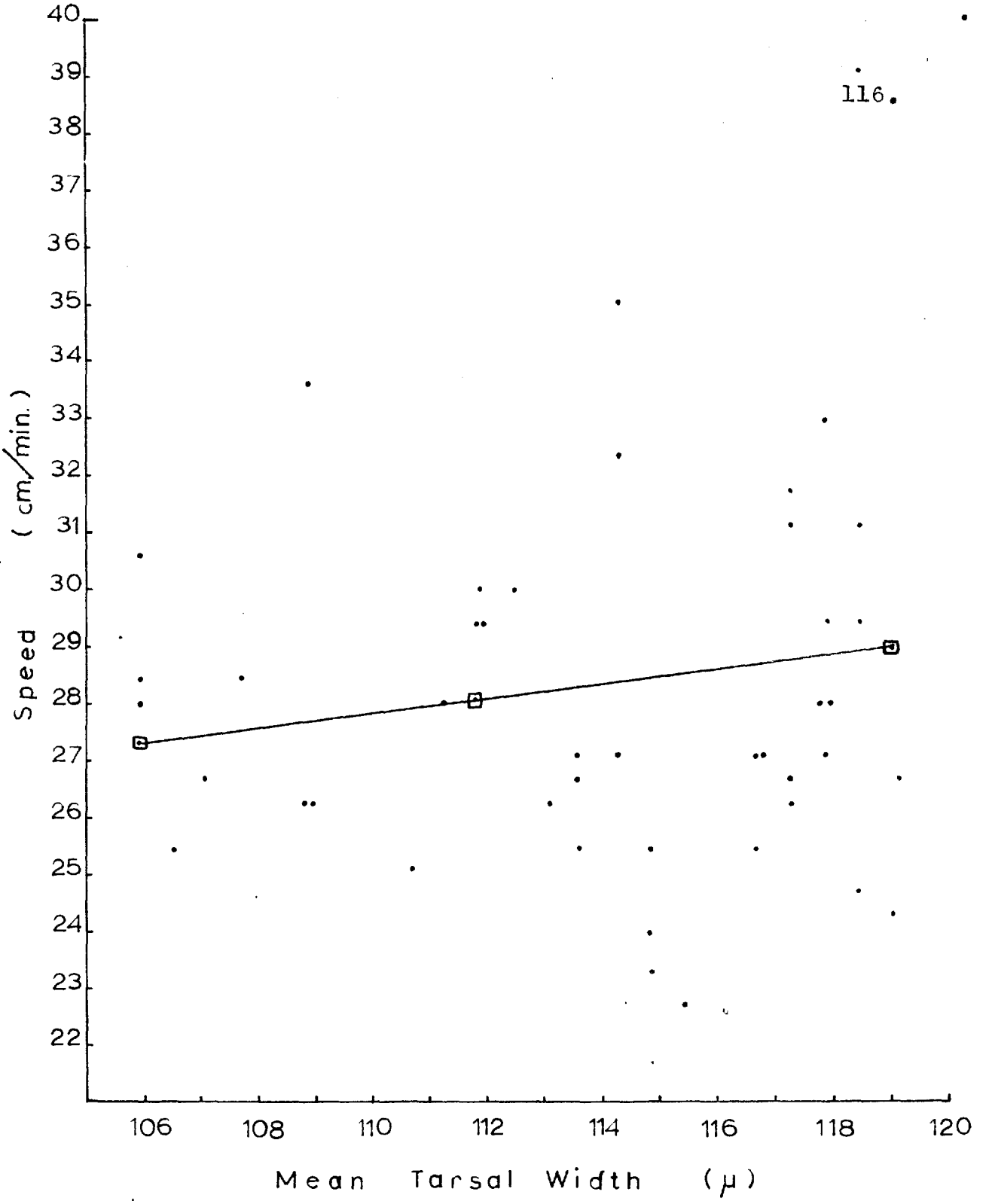


Fig. 28 : Regression line showing relation between mean tarsal width and speed of female S. zea-mais weevils (claws intact).

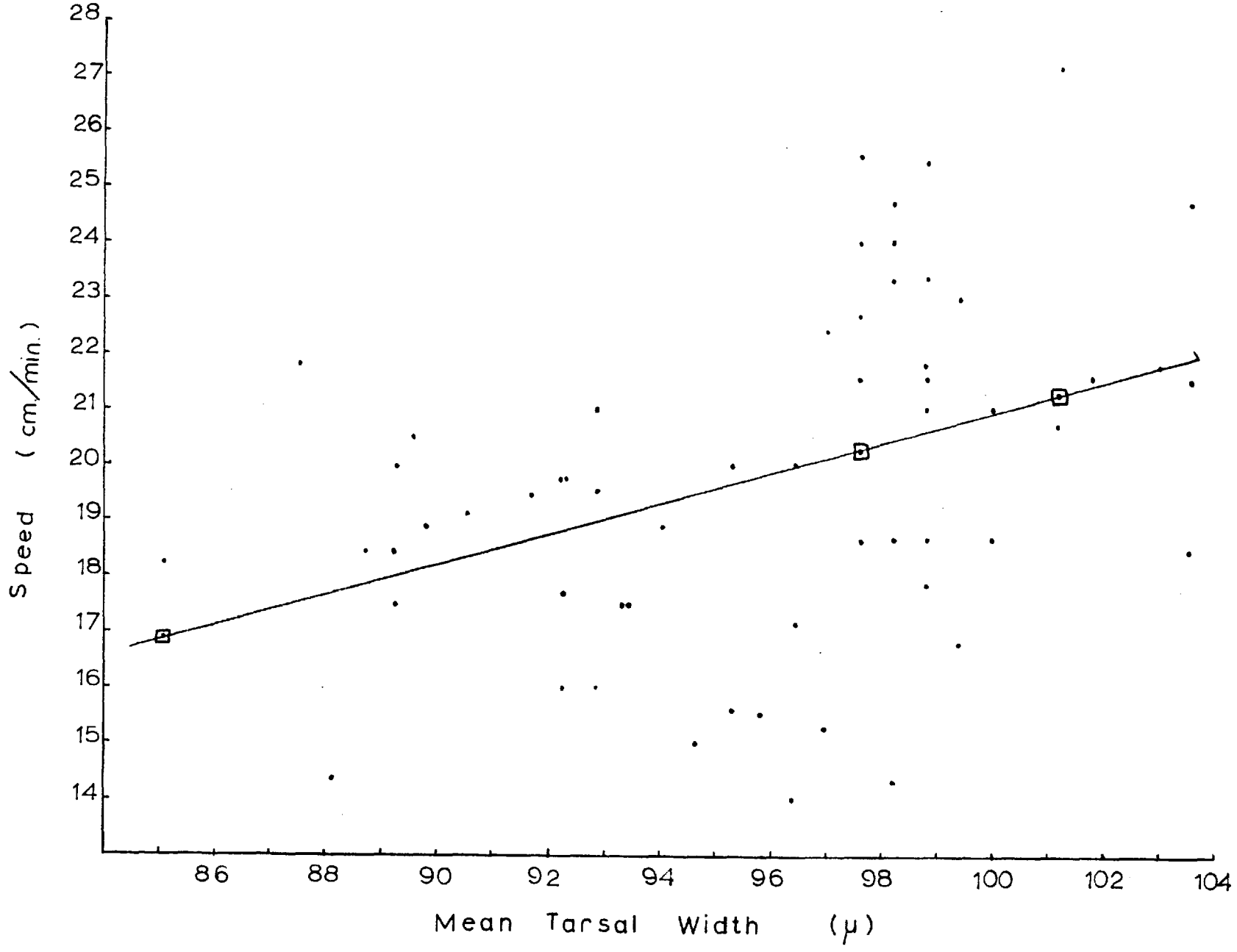


Fig. 29 : Regression line showing the relation between mean tarsal width and speed of male S. oryzae (claws intact).

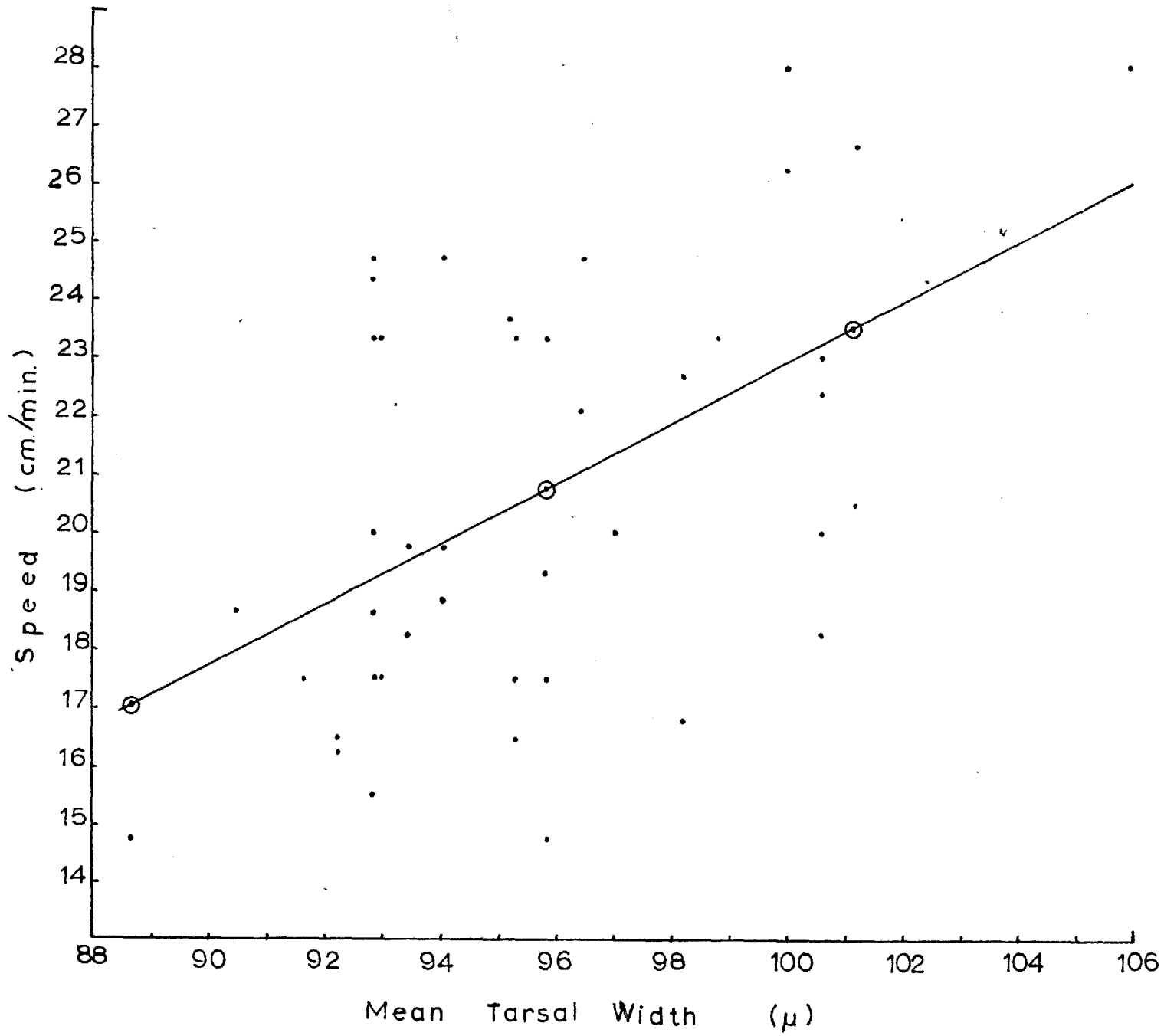


Fig. 30 : Regression line showing relation between mean tarsal width and speed of female S. oryzae (claws intact).

were 105.34 μ, 93.24μ and 94.10 μ respectively. Those of the females were 105.16, 93.96 and 93.93 μ (TABLE 28). The variance of means were significantly different in the fore tarsi and either mid or hind tarsi. The regression coefficients of the tarsal width on speed was highly significant ($P < 0.001$) in the male weevils (Fig. 31 and TABLE 32), but was not significant in the females (Fig. 32 and TABLE 32).

c) Distance climbed by S. granarius weevils as related to their body weight :-

The granary weevils are not as efficient in climbing smooth glass surfaces as the rice weevils. Apart from the fact that the adults of S. granarius, moved more slowly than the other two species, not all of them could climb the whole length of the 5-foot tubes. The minimum height that they reached was 50 cm. The percentage of the male weevils that could climb to the top was 48 % with their claws intact, and 42 % without the claws (TABLE 30). The mean distances climbed by the males with and without their claws were 126.6 and 123.9 cm. respectively. The variance of means of these two values being not significantly different.

The percentage of female weevils climbing the whole of the tube was 52.24 % with their claws intact, and of the

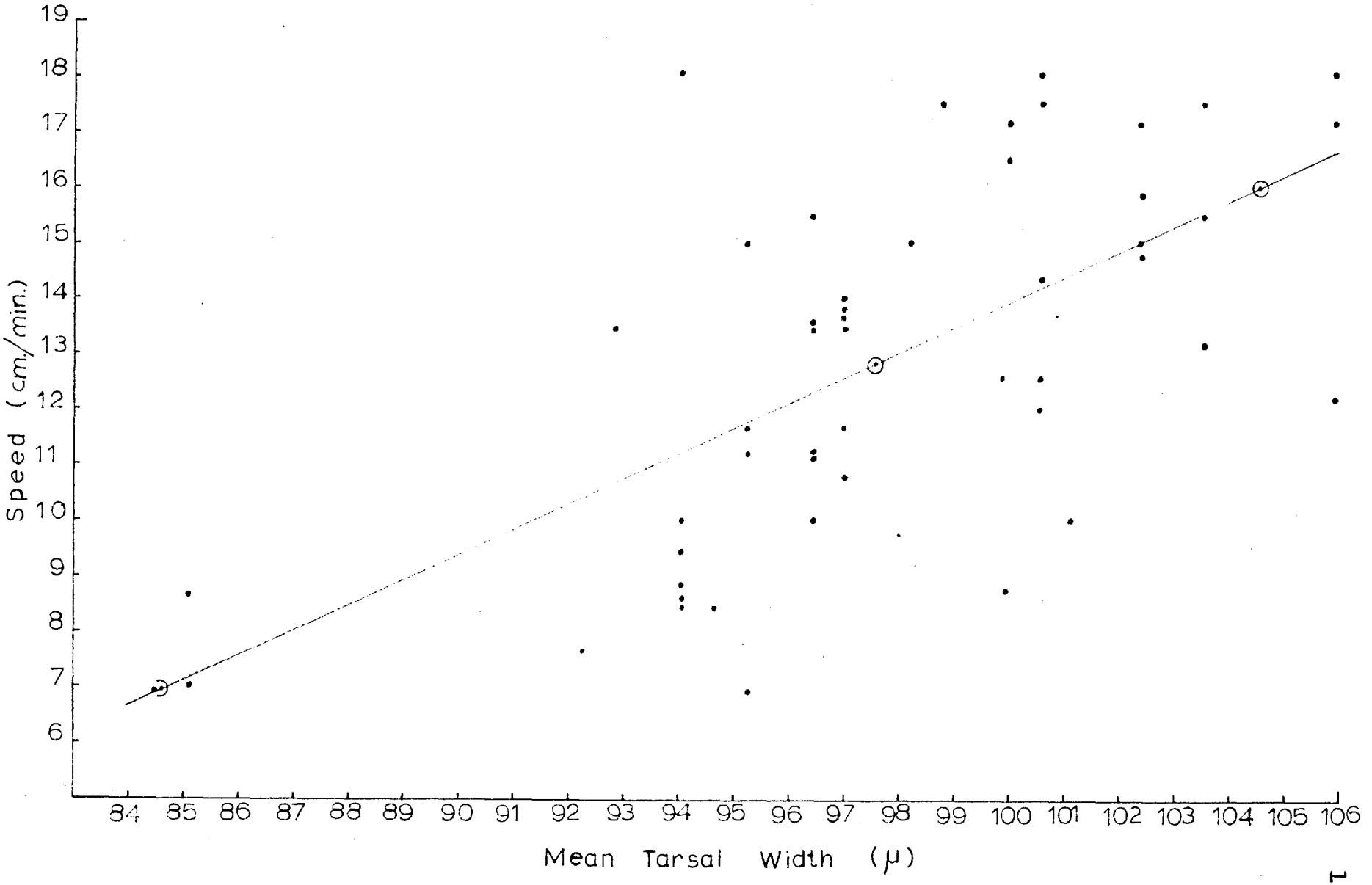


Fig. 31 : Regression line showing the relation between mean tarsal width and speed of male S. granarius weevils (claws intact).

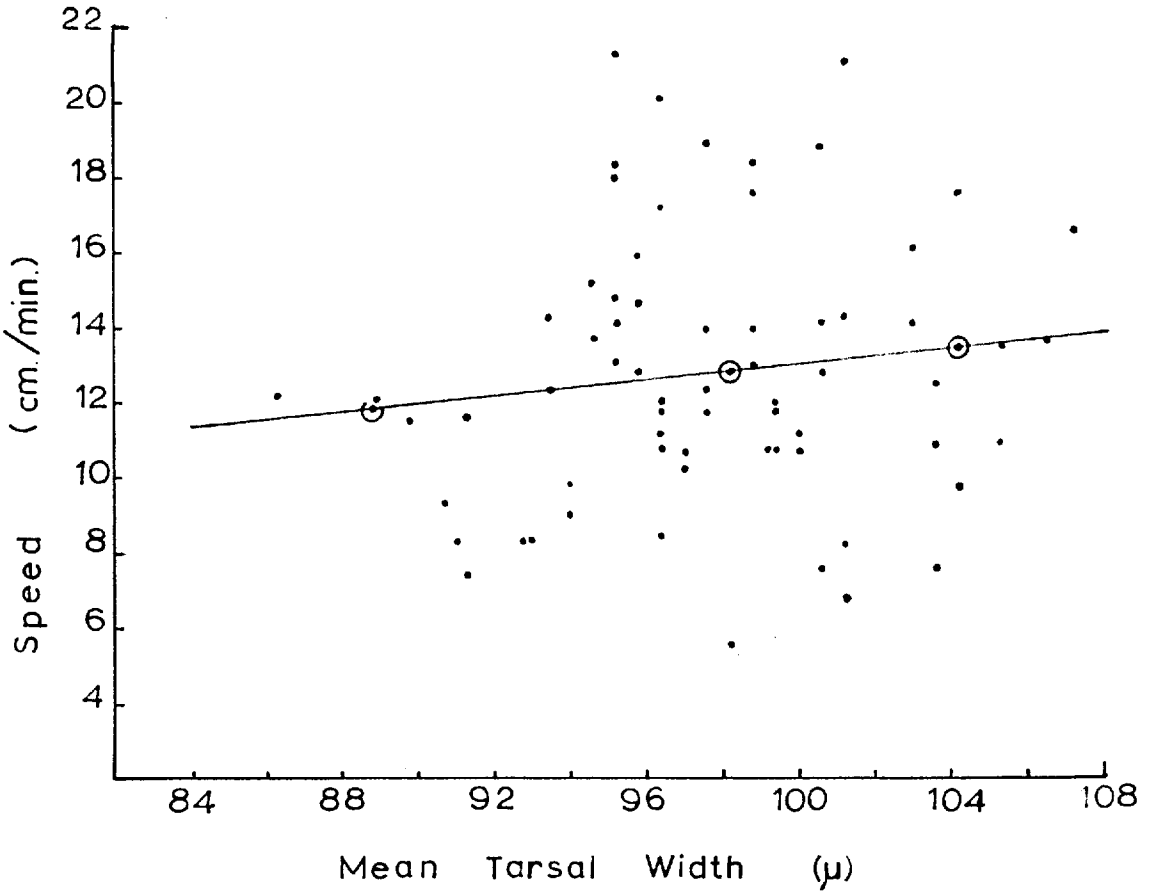


Fig. 32 : Regression line showing relation between mean tarsal width and speed of female S. granarius weevils (claws intact).

operated ones only 32.84 %. The mean distances climbed by the intact and operated females were 123.13 cm. and 112.39 cm., the variance of means of these values being non-significant, as well as that between the males and the females. The percentages of the weevils climbing varying heights are illustrated in Figs. 33 and 34. The regression coefficients relating body weight to the distance climbed were not statistically significant.

G. Discussion

The climbing ability of Sitophilus weevils seems to depend on a variety of factors, some of which were investigated, namely the weight of the weevil, the width of the third tarsomere and the number of tenent hairs involved in this mechanism. The latter, however, may be the main contributing factor explaining the significant difference in the climbing ability of the three species concerned.

Other factors may have an influence on the climbing ability but they were not studied. Such may be the variations in physiological conditions which themselves are possibly affected by the following :- a) difference in age of the weevils, b) previous breeding on different cereals

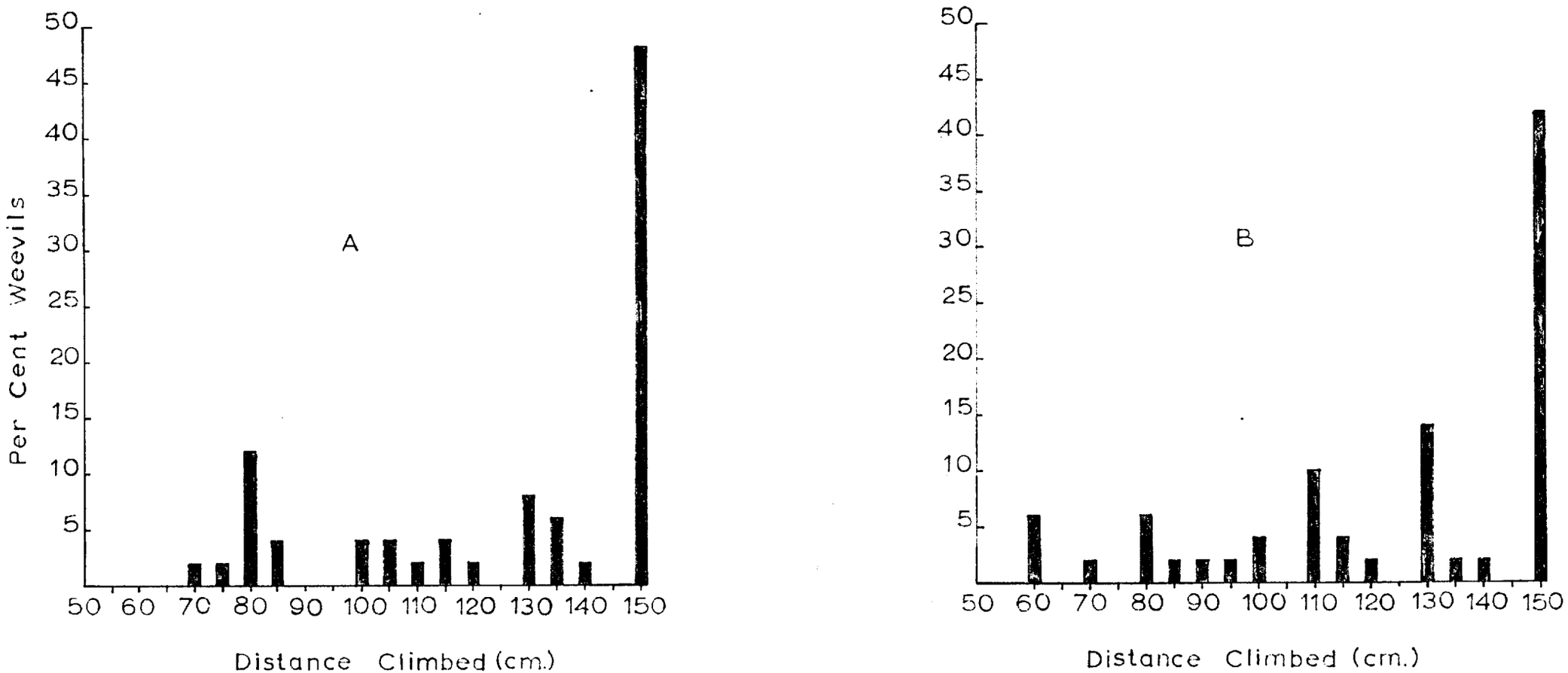


Fig. 33: Histogram showing the Percentage of Male S.granarius Weevils that Climbed Different Heights on Glass Surface : A, Claws Intact. B, Claws Removed.

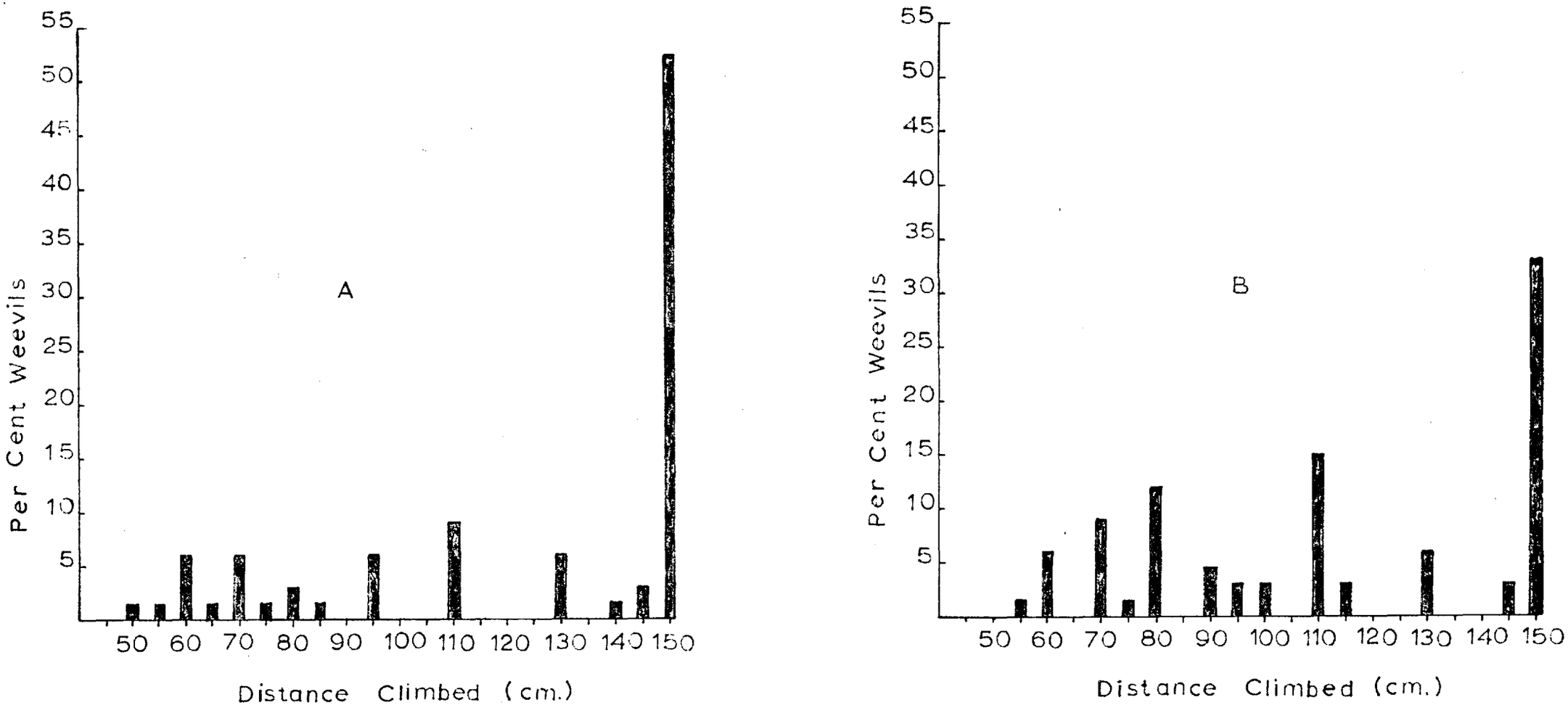


Fig. 34 : Histogram showing the Percentage of Female S.granarius Weevils that Climbed Different Heights on Glass Surface: A, Claws Intact. B, Claws Removed.

other than wheat or c) difference between strains of the same species in other countries.

From the ecological as well as physiological point of view, comparatively low and high temperatures have a definite strong influence on the activity of the weevils and hence on their speed of climbing. Other environmental factors such as humidity and air movements probably play a lesser role.

The three species concerned, exhibited a marked difference in their ability to climb a smooth glass surface ; the ability was measured by the speed of climbing in centimetres per minute. The granary weevils, however, were far less efficient than the two species of the rice weevils, which on the other hand, also differed significantly from one another (see TABLE 29). The highest speeds were recorded for S. zea-mais, the means for the males and the females being 30.49 cm./min. and 28.39 cm./min. respectively. This speed in S. oryzae was 19.79 cm./min. and 20.68 cm./min. for the males and the females , and 12.81 cm./min. and 12.73 cm./min. for the male and the female weevils of S. granarius. The differences between the variance of means were highly significant when the same sex of any two species were compared (TABLE 31). The variance between the two sexes of any one species was not significantly different except in S. zea-mais ($0.05 > P > 0.02$).

TABLE 28

Maximum width of third tarsomeres of the three species

Tarsus	Width	Maximum Width (μ)					
		S. zea-mais		S. oryzae		S. granarius	
		Male	Female	Male	Female	Male	Female
Fore leg	Minim.	103.56	114.27	91.06	94.63	89.28	92.85
	Maxim.	139.27	128.56	110.70	110.70	114.27	116.06
	Mean	123.87	122.96	101.93	101.94	105.34	105.16
Mid leg	Minim.	94.63	101.77	82.13	85.70	82.13	82.13
	Maxim.	124.99	116.06	99.99	103.56	99.99	101.77
	Mean	110.33	110.19	92.68	92.42	93.24	93.96
Hind leg	Minim.	94.63	99.99	82.13	85.70	82.13	83.91
	Maxim.	123.20	116.06	99.99	103.56	103.56	103.56
	Mean	109.72	109.08	92.85	92.76	94.10	93.93

TABLE 29

Weight, Speed, Tarsal Width and Number of Tenent Hairs of the Three Species

		S. zea-mais		S. oryzae		S. granarius	
		Male	Female	Male	Female	Male	Female
Weight (mg.)	Minim.	1.6	1.9	0.8	1.0	2.0	2.0
	Maxim.	3.3	3.1	2.4	2.3	3.3	3.7
	Mean	2.42	2.55	1.55	1.59	2.80	2.95
Mean Tarsal Width (μ)	Minim.	97.01	105.94	85.11	88.68	85.11	86.30
	Maxim.	129.15	120.23	103.56	100.58	105.94	107.13
	Mean	114.64	114.08	95.84	95.72	98.12	97.68
Mean Number Tenent Hairs	Minim.	50	50	34	36	30	28
	Maxim.	84	88	50	56	44	46
	Mean	63.53	64.87	40.67	41.33	35.00	35.47
Speed cm./min. Claws Intact	Minim.	21.54	22.70	14.00	14.74	6.89	5.49
	Maxim.	42.00	40.00	27.10	28.00	18.06	20.99
	Mean	30.49	28.39	19.79	20.68	12.81	12.73
Speed cm./min. Claws Removed	Minim.	20.00	20.49	14.74	15.70	6.54	5.83
	Maxim.	43.08	38.18	26.67	27.10	18.06	18.76
	Mean	30.58	29.47	20.45	20.89	12.01	12.00

TABLE 30

Maximum distance climbed by *S. granarius* weevils

Distance (cm.)	Males				Females			
	Claws Intact		Claws Removed		Claws Intact		Claws Removed	
	No.	%	No.	%	No.	%	No.	%
150	24	48	21	42	35	52.2	22	32.8
145					2	3.0	2	3.0
140	1	2	1	2	1	1.5		
135	3	6	1	2				
130	4	8	7	14	4	6.0	4	6.0
120	1	2	1	2				
115	2	4	2	4			2	3.0
110	1	2	5	10	6	9.0	10	14.9
105	2	4						
100	2	4	2	4			2	3.0
95			1	2	4	6.0	2	3.0
90			1	2			3	4.5
85	2	4	1	2	1	1.5		
80	6	12	3	6	2	3.0	8	11.9
75	1	2			1	1.5	1	1.5
70	1	2	1	2	4	6.0	6	9.0
65					1	1.5		
60			3	6	4	6.0	4	6.0
55					1	1.5	1	1.5
50					1	1.5		
Total	50		50		67		67	

TABLE 31

Analysis of Variance of Means of Weight, Speed and Tarsal Width of the three Species

Species and Sexes Compared	Weight	Speed (intact)	Tarsal Width
Male & Female *S.granarius*	not signif.	not signif.	not signif.
Male & Female *S.zea-mais*	not signif.	.05 > P > .02	not signif.
Male & Female *S.oryzae*	not signif.	not signif.	not signif.
Males			
S.granarius & *S.zea-mais*	P < 0.001	P < 0.001	P < 0.001
S.granarius & *S.oryzae*	P < 0.001	P < 0.001	.05 > P > .02
S.zea-mais & *S.oryzae*	P < 0.001	P < 0.001	P < 0.001
Females			
S.granarius & *S.zea-mais*	P < 0.001	P < 0.001	P < 0.001
S.granarius & *S.oryzae*	P < 0.001	P < 0.001	.02 > P > .01
S.zea-mais & *S.oryzae*	P < 0.001	P < 0.001	P < 0.001

TABLE 32

Significance of Regression Coefficients Representing the Relations between Weight, Tarsal Width and Speed of the Three Species

Species	Sex	Claws Intact		Claws Removed	
		Weight and speed	Tarsal width and speed	Weight and distance	Weight and speed
S. granarius	♂	$P < 0.001$	$P < 0.001$	not signif.	$P < 0.001$
	♀	not sign.	not sign.	not signif.	not sign.
S. zea-mais	♂	$P < 0.001$	$.01 > P > .001$		$P < 0.001$
	♀	not sign.	not sign.		not sign.
S. oryzae	♂	$.01 > P > .001$	$.01 > P > .001$		$P < 0.001$
	♀	$.01 > P > .001$	$P < 0.001$		not sign.

The variation in the speed of the three species was found to be directly proportional to the number of the tenent hairs found on the third tarsal segments. The mean number of tenent hairs on the three pairs of legs of S.zea-mais was 63.53 in the males and 64.87 in the females (TABLE 29). The mean numbers in the male and the female weevils of S. oryzae were 40.67 and 41.33. Those for S.granarius were 35.00 and 35.47 (Data in detail in TABLES 22,24,25 & 26). No difference was found between the two sexes of any one species, but the variance between the different species was highly significant.

By comparing the tarsal width of the three species it was found that S.zea-mais weevils possess the highest mean values (114.64 μ for the males and 114.08 μ for the females). The fact that S.granarius weevils have bigger mean tarsal width than S.oryzae and yet are less efficient in climbing , may be attributed to the following three main factors : 1) The number of tenent hairs is significantly lower in S.granarius than in S.oryzae. 2) The ratio between the mean tarsal width and body weight was 61.00 in S.oryzae, which is much higher than that in S.granarius which is only 34.05 (TABLE 33). 3) The ratio between the mean number of tenent hairs and body weight of S.oryzae was 25.48 compared with 12.24 in S.granarius.

TABLE · 33

Ratios of Mean Tarsal Width to Body weight of the Weevils, and of the Mean Number of Tenent Hairs to \' Weight in the three Species.

Species	Mean tarsal width / Body weight	Mean number of hairs / Body weight
S. zea-mais	46.02	25.83
S. oryzae	61.00	25.48
S. granarius	34.05	12.24

This comparison was based on the assumption that the heavier the body as related to tarsal width and the number of tenent hairs, the less efficient will be the climbing ability of the weevils. The variance of mean weights of the three species differed highly significantly TABLES 29 & 31; S. granarius weevils being much heavier than S. oryzae.

When applying these ratios for the two species of the rice weevils, we find that they have identical values of the ratio of mean number of tenent hairs to weight, and higher value in S.oryzae of the ratio of mean tarsal width to weight. The explanation for the greater efficiency of S. zea-mais in climbing may lie in its more(muscular)powerful muscular system, or any other unknown factor which would need further investigation.

Weevils with the fifth tarsomeres bearing the claws removed showed the same efficiency in climbing on glass as the intact ones. The analysis of variance of mean speeds of intact and operated weevils showed that it did not vary significantly in any one of the three species (TABLE 29). The arolium between the claws, being rudimentary, seemed to play no role in gripping to the smooth surface. On the other hand, when the third tarsomere, bearing the tenent hairs, was amputated from more than three legs, then even the most efficient S.zea-mais climbers, could no longer

proceed on vertical glass surfaces.

The relations between the speed of the weevils and their body weights, on the one hand, and their mean tarsal width on the other, were further analysed in calculations of regression equations. The coefficients were found to be highly significant in the male weevils of the three species, both before and after amputation (TABLE 32) ; but this relation was not significant in the females except in the intact S.oryzae. The regression lines are illustrated in Figs. 35,36 & 37. The difference in behaviour between the males and the females is possibly due to an unknown physiological factor, but in S.zea-mais an explanation may be found in the fact that the males have a wider range of body weights and tarsal widths than do the females, although the means are not significantly different.

The downward climbing of the weevils on glass seemed to be as efficient as the upward one, but the natural tendency of the insects was to climb up the walls of the container when disturbed, and the experiments were restricted to the upward movements. The weevils, however, when confined in a horizontally placed glass tube, climbed up and down without any detectable difference in their speed.

Several hypotheses have been put forward to explain the action of climbing organs in insects. Gillett and Wigglesworth (1932) gave a brief account of the ideas

advanced by earlier workers such as West (1862), Dahl (1884-5), Dewitz (1884), Simmermacher (1884) and Rombouts (1884).

Some workers have claimed that the organs are held to the surface by atmospheric pressure and that any fluid present would serve to make an airtight seal between the organ and the substratum. Surface tension of the fluid secretion around tenent hairs, cohesion of a sticky secretion, or adhesion between tenent hairs and the surface have all been suggested as the forces which are concerned in the climbing mechanism of the organs. There are indications that the force operating is not the same in all cases, and depends on the structure of the adhesive organ itself, and further that different forces may act together to enhance the effect.

Considering Sitophilus weevils, one could suggest adhesion, or less probably cohesion, as the main force involved in the mechanism of gripping on to the smooth surfaces. This suggestion springs from the fact that the tenent hairs possess minute canals which open at their apices and it is possible that a certain fluid is secreted to allow for gripping. This would cancel any possibility that they may act as suckers.

As regards the nature of the fluid, whether it is watery or oily (if adhesion is the phenomenon concerned), some evidence may be gained by testing the ability of the insects to

climb on a waxy surface ; for a watery fluid would not adhere to wax (Gillett and Wigglesworth, 1932) . In fact, Sitophilus weevils showed a marked efficiency in climbing waxy surfaces, and another interesting observation was that once they gripped on to a horizontal smooth glass surface, they exhibited a great resistance to a strong current of water. This indicated that the adhesive fluid is not watery.

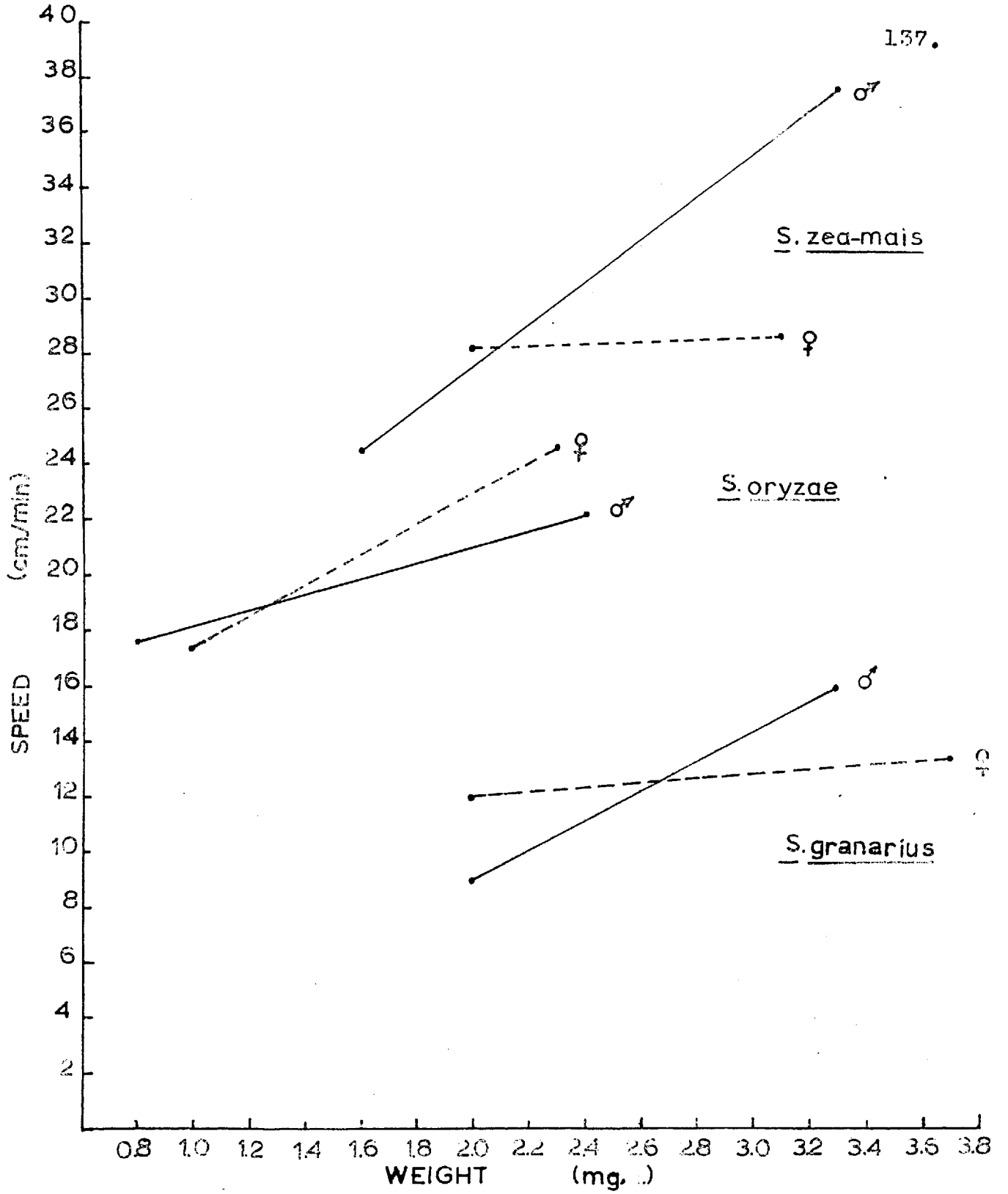


Fig. 35 : Regression lines showing the relation between weight and speed of the weevils (claws intact).

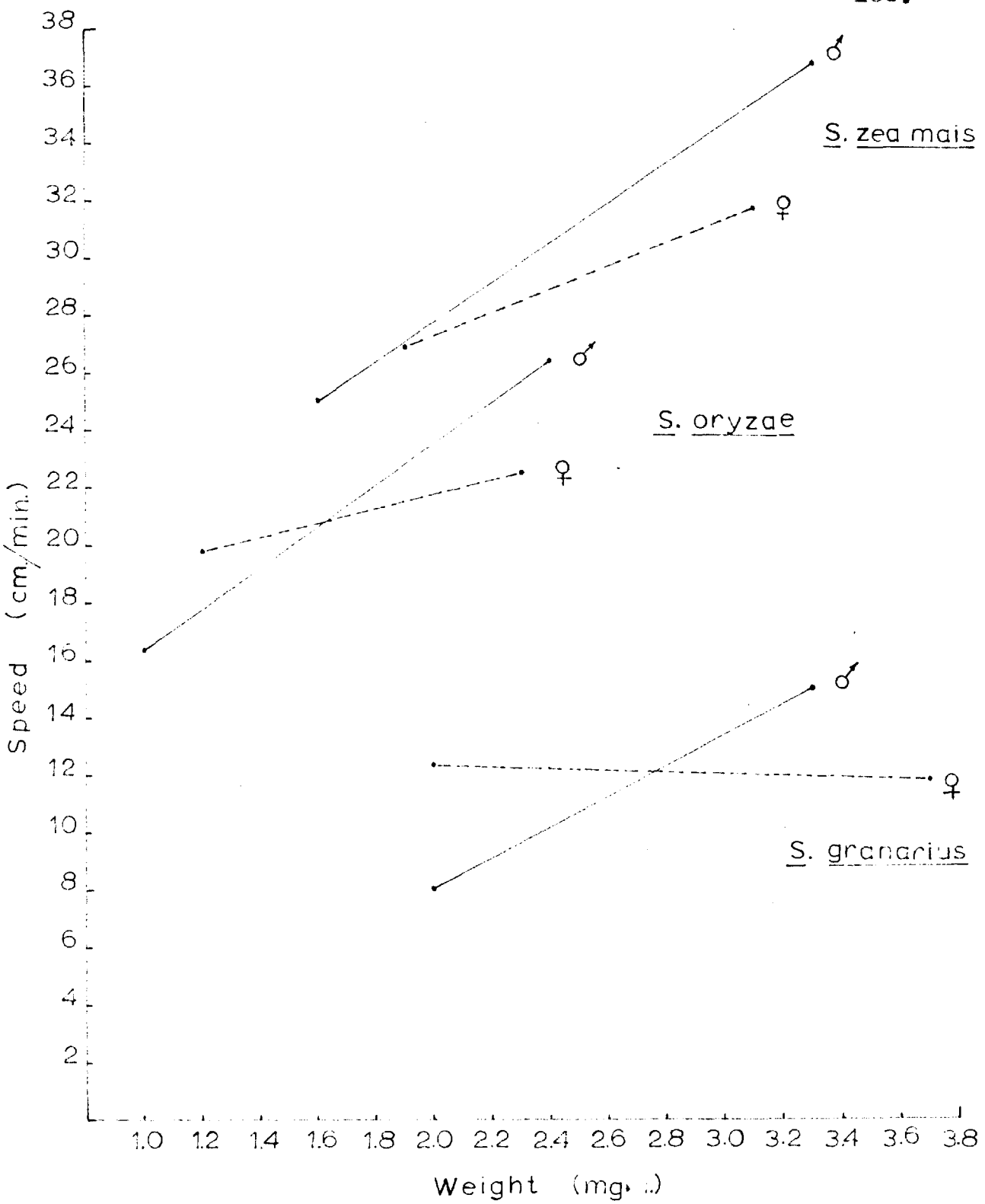


Fig. 36 : Regression lines showing the relation between weight and speed of the weevils (claws removed).

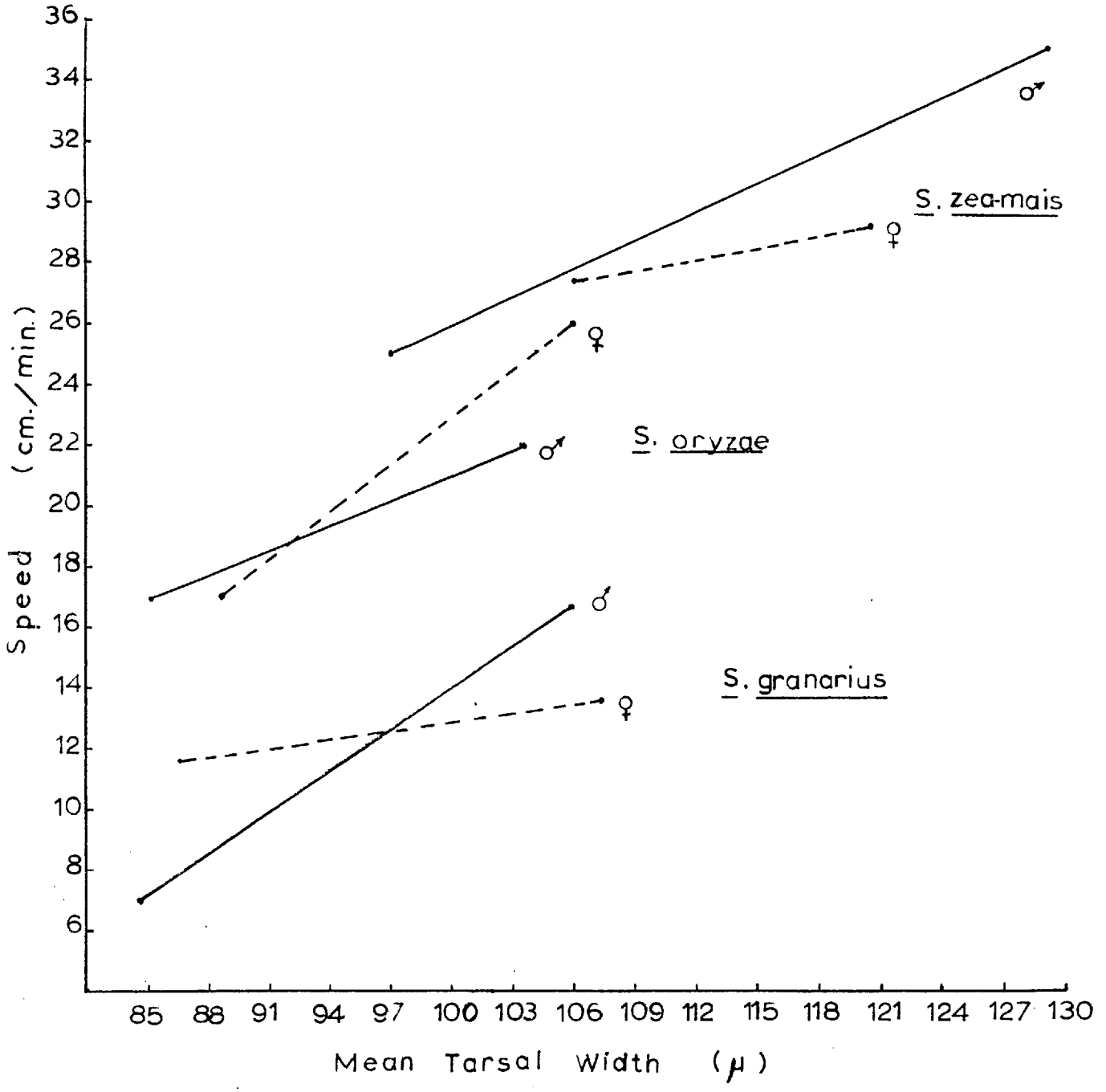


Fig. 37 : Regression Lines of Mean Tarsal Width & Speed

(Claws Intact)

V. COMPARISON OF SOME ASPECTS OF FLIGHT ACTIVITY OF SITOPHILUS SPECIES

A. Introduction and Review of Literature:

In a further study of the comparative behaviour of the three species of Sitophilus, some aspects of their flight behaviour were analysed. S.granarius is a species which is unable to fly, since the hind wings are vestigial and the following experiments were carried out on S.zeamais and S.oryzae only.

It is not presumed that all the factors inducing flight have been analysed, but the experiments were confined to the effects(~~to the effects~~) of temperature and of light intensity on the time taken to initiate flight of the suspended and of freely moving weevils and the duration of single flight periods in the suspended weevils and the frequency of flights per unit time in both the suspended and the free moving weevils. The effects of age, the relation of body weight to the size of the wing and that of the length of the hind wing to that of the elytron were also examined and compared in the two species.

Some observations on the mechanism of flight were also described.

It has been repeatedly reported that standing crops in the field are at times attacked by the rice weevils (Hinds,1914; Wenholz, 1917,1927; Kyle, 1918; Back,1919;

Cartwright, 1930, 1936; Veitch,1934; Mossop,1940 and Eden, 1952). All these observations were limited to maize,and indicate that the weevils were in flight in summer or late in the season at harvest time. However, there is no information in literature whether this flight occurs during the day or at night, nor about the environmental conditions or any other factors that may be connected with its occurrence. Schwitzgebel & Walkden (1944) , recorded that only low numbers of S.oryzae were attracted to three types of insect traps during the period of July to September in U.S.A. Kiritani (1959) working on the flying ability of four different strains of S.zea-mais and on six strains of S.oryzae concluded that the weevils collected from different countries of the world show differences in both physiological and ecological characters, and that these differences among inter-geographical strains often exceed those between the species. Although his laboratory work did not deal with the factors that induced flight yet the results obtained were extremely interesting. He found that the Japanese strain of S.zea-mais was a weak flyer when it was compared with the highly efficient Portugese and Indonesian strains. The ability of S.oryzae to fly was generally poor except the Argentine strain. The strains from Japan and Formosa seemed to have lost the ability to fly ; in fact the damage caused by S.oryzae in

Japan was reported to be restricted to the stored cereals only (see Kiritani, 1956 and Kiritani et al., 1957).

B. Material and Methods :

The insects used in this experiment were brought from standard cultures reared on English wheat of 14.2 % moisture content in equilibrium with 70 % R.H. at 25°C., for several years. It was impossible to find out with certainty from which country they originated.

The two following sets of experiments were conducted: a) Firstly, the weevils were suspended from the pronotum, and the time needed to initiate flight was recorded, at two light intensities, and at the temperatures ranging between 26° and 40° C. b) Secondly, the weevils were released inside a plastic cage and the number of flights (and attempts of flights) made by groups of 10 weevils were recorded over periods of 15 minutes, the temperatures and light intensities being constant.

The experimental weevils were of two ages i.e. they were 2 weeks old and 4 weeks old. They were obtained by sifting the original cultures twice a day, and keeping the newly emerged adults in groups of 100 in 2-lb. jars half filled with English wheat, and kept at constant temperature of 25°C. and in complete darkness.

1) The behaviour of suspended weevils in conditions of constant temperature and humidity was observed in the following apparatus :- A cylindrical aluminium box(Fig.38,a) 18 cm. high and 16 cm. in diameter was divided into an upper and a lower compartment by means of an inner circular ridge on which a thin asbestos layer was placed. A 25-watt bulb (b) was fixed through a hole in the lower compartment to heat the upper one (c), which was lined with white cardboard (d). A compact layer of cotton wool (e) was put between the two compartments to allow slow heating and cooling of (c). The latter was covered by a glass plate (f) having a central hole through which the suspended insect was introduced. The wweevil was fixed by the pronotum to a sharpened cocktail stick with a mixture of beeswax + rosin in proportion of 2 : 1 (Sawyer's formula). The cocktail stick (i) was firmly held by a clamp. The whole apparatus was placed inside a white cubic wooden cage (h) 25 cm. high with ground glass top (g) which allow-ed penetration of only diffusing light from the bulb (j). A 100-watt bulb held at the height of 36 cm. from the bottom of the compartment (c) gave a light intensity of 1.85 L.F.L. which was measured with an SEI exposure photometer. A 200-watt bulb (Siemens Sieray unit) giving a balanced solar-spectrum simulating natural sunlight gave a light intensity of 2.6 L.F.L. when held at the height of 40 cm. above the floor.

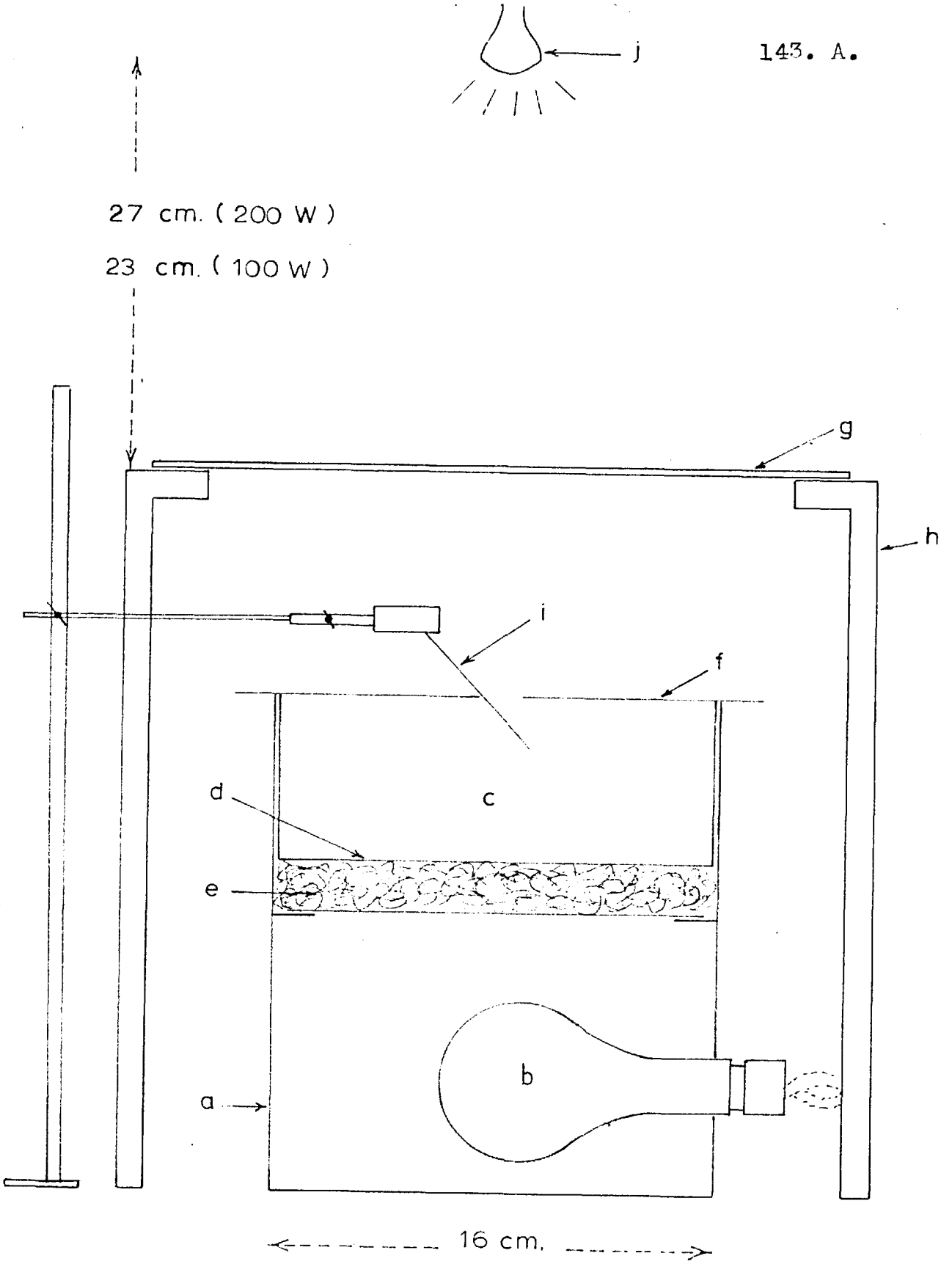


Fig. 38

The temperature inside the compartment (c) increased slowly from 26° C. to 40°C. and was measured by means of a thermocouple. The temperature which could be altered by putting the bulb (b) on and off, remained fairly constant for any single test lasting for 3 minutes.

The weevil of known age and sex, was suspended for 3 minutes, and the time needed to initiate flight was recorded at the corresponding temperature and light intensity.

2) In the second set of experiments, groups of 10 weevils of the same sex and age were released inside a cylindrical plastic cage 10 cm. high and 8 cm. in diameter (Fig. 39,a). This cage was placed with its open side directed downwards, on a double layer of muslin well stretched around a glass sheet (b). This helped the insects to upturn when they fell on their backs. A white cubic wooden cage (d) 25 cm. high, with a ground glass top (e), covered the apparatus which was placed on a white cardboard sheet (c). This ensured even illumination. The ability of the weevils to fly was tested at two constant temperatures, and at two levels of light intensity. Thus there were four combinations of the two factors, namely : 1) Low temperature and low light intensity. 2) Low temperature and high light intensity.3) High temperature and low light intensity. 4) High temperature and high light intensity. The two light intensities used in these experiments were 1.85 L.F.L. and 2.6 L.F.L. They were achieved

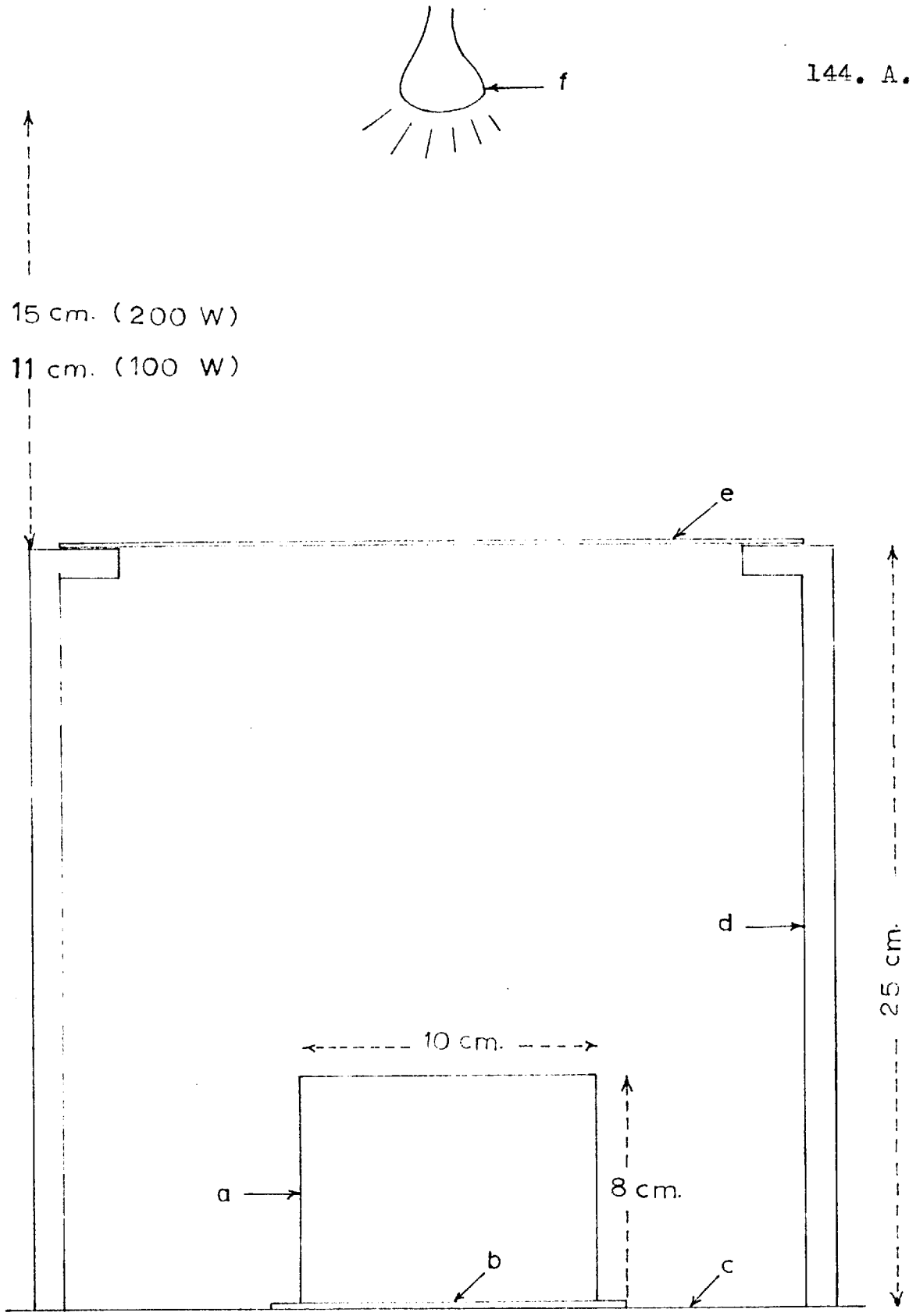


Fig. 39

by the means described above.

The temperature inside the cage (a) was 31 ± 0.5° C. when the two bulbs were uncovered; but when it was covered by a cardboard box placed on top of the cage (d), the temperature remained fairly constant at 36 ± 0.5°C. Equilibrium was reached within half an hour in all the experiments which were conducted in a constant temperature room. The number of flights and of attempts to fly per minute was recorded over a period of quarter of an hour for 10 groups of 10 weevils in every set of experiments. A confirmatory test for each set was carried out , recording the number of flights and of attempts at the 31-st. to the 35-th. minute.

3) An attempt was made to see whether the size of the wing and the weight of the body was correlated with flight ability. Individual weevils, freshly narcotized, were weighed on a torsion balance reading to 0.01 mg. The surface area of an expanded wing was measured under the microscope by a calibrated square eye-piece micrometer, and by drawing the wing on square millimeter paper.

4) The duration of flight of some suspended weevils was estimated with a stop-watch over a period of 5 minutes in 2.6 L.F.L. light intensity, and at 32° C. and 70 % R.H.

5) The wingbeat of suspended weevils was measured by means of a Stroboflash Type No. 1200 C (Dawe Instruments Ltd. England). The weevils were suspended from the pronotum

by means of a sharpened cocktail stick using Sawyer's Formula as a sticking material. The other tip of the stick was fixed to a cork stopper which was fitted to a 1" X 3" glass tube. The weevil thus flew inside the tube and the rate of wingbeat per minute (R.P.M.) could be measured in still air. The glass tube was held near the Stroboflash by means of a clamp. The experiments were carried out in the constant temperature room at 25°C., 70 % R.H. The light intensity was very low to allow better observations.

6) The length of the elytron along the long axis (E) and the direct length from the basal point to the tip of the expanded hind wing (H) were measured by means of an eye-piece micrometer, and a ratio H/E was calculated for about 40 weevils of each sex of the two species, and the differences between them were examined.

C. Some Observations on the Mechanism of Flight

1) A walking weevil, when ready to fly, pauses for a while ; it lifts alternate tarsi from the substratum two or three times, probably releasing the tenent hairs which grip the surface. It then prepares itself for the take-off by arranging its legs in a definite position. The mid-legs are raised upwards on both sides of the body and to a level higher than the body itself, while the tarsi are held upwards

in a vertical position. The body axis is then raised anteriorly making an angle of approximately 45° with the surface. The hind legs are stretched backwards, and one of the fore legs is kept touching the substratum and is stretched upwards while the other moves two or three times in the air anteriorly. Simultaneously the two elytra become slightly raised and open widely in a nearly horizontal plane making an angle of about 120° with each other. The time taken by the weevil to prepare itself for flight does not exceed three seconds.

2) By watching the weevils inside the plastic cage during the experiments, it was noticed that they were flying in nearly every direction. They had the ability of taking off while they were on a horizontal, or a vertical substratum, or even when they were in an inverted position on the roof of the cage. They flew from one side of the cage to the other , changing the axis of the body, and settling in the position corresponding to it.

3) The weevil when suspended from the pronotum, keeps waving the legs in the air strongly, and this may often be accompanied by a spiral movement of the abdomen. Just before flying, these movements disappear and the legs are retracted towards the body. This position is maintained during the whole period of flight. In S. oryzae the legs are brought closer to the body than in S. zea-mais.

4) The angle of divergence of the two elytra during flight was roughly 120° (it was not measured). This angle seemed to be insufficient to keep the elytra away from the path of the hind wings. As a result, the elytra vibrated continuously, and interfered with the up and down strokes of the hind wings. This hindering factor to the wingbeat consequently may have interfered with the flying ability of the weevils.

5) Tactile stimulation of suspended insects which had ceased flying, seemed to have no effect on the two species of the rice weevils. Chadwick (1953) speaks of it as a factor initiating flight in many insects but in fact, the tip of a needle when it was applied to any part of the body, induced the weevils to feign death.

D. Results

1. Experiments with Suspended Weevils

a) S. zea-mais :-

The time needed to initiate flight of suspended weevils seemed to be greatly influenced by two major factors namely by light intensity and by temperature.

Two weeks old male S.zea-mais weevils : At a light intensity 1.85 L.F.L., the mean time to initiate flight of 2 weeks old male S.zea-mais weevils was 105.0 seconds at 26°C. (TABLE 34, Fig. 40). There was a sudden drop in the duration of the pre-flight period at 28° C., and then the reaction became more

rapid as temperature increased to 40°C., when the mean time to initiation of flight was 23.1 seconds.

At the higher light intensity of 2.6 L.F.L. the mean time taken to initiate flight was much shorter than at 1.85 L.F.L. At 26°C. The mean time was 54.0 seconds, 23.3 seconds at 30°C. and 7.0 seconds at 40°C. (TABLE34, Fig. 40).

The mean values of the time needed to initiate flight at the two light intensities of 1.85 and of 2.6 L.F.L. along the whole temperature scale used in these experiments, were 53.4 and 29.5 seconds respectively. The variance of these two means was highly significant ($0.01 > P > 0.001$).

Two weeks old S.zea-mais female weevils : A similar behaviour was exhibited by the 2 weeks old female weevils(Fig.41). At the light intensity 1.85 L.F.L. there was a marked decrease in the mean of the time taken to initiate flight at 28°C. and at 36°C. The means ranged between 95.3 and 28.0 sec., with a total mean value of 52.7 sec. (TABLE 34). The latter was not significantly different from the mean of the total of all the values of the 2 weeks old male weevils at the same light intensity. At the higher light intensity 2.6 L.F.L. the mean of the ~~values~~ total values of time to initiate flight of the 2 weeks old female weevils was 36.1 sec. (the means ranging at different temperatures between 66.0 and 11.5 sec.), and this was significantly different from that of the same weevils at the lower light intensity 1.85 L.F.L.($0.05 > P > 0.02$).

TABLE 34

Mean Time to Initiate Flight of suspended Weevils at Different Temperatures and Light Intensites.

A- At Light Intensity 1.85 L.F.L.

Temperature ° C		26°	28°	30°	32°	36°	40°	Mean
Species	Sex Age	Mean Time to Initiate Flight (sec.)						
S.zea-mais	♂ 2 weeks	105.0	63.2	44.2	56.2	34.5	23.1	53,4
	♀	95.3	55.8	53.1	56.9	27.7	28.0	52.7
S.zea-mais	♂ 4 weeks	100.6	61.3	42.2	57.3	36.4	17.8	48.4
	♀	108.8	79.7	56.7	44.7	26.2	14.9	49.1
S.oryzae	♂	49.3	85.3	37.4	37.6	18.7	2.4	35.6
	♀	39.5	43.3	42.8	33.3	17.5	6.4	29.5

B- At Light Intensity 2.60 L.F.L.

S.zea-mais	♂ 2 weeks	54.0	57.8	23.3	31.0	15.4	7.0	29.5
	♀	66.0	51.0	37.6	40.2	21.3	11.5	36.1
S.zea-mais	♂ 4 weeks	21.0	21.3	7.8	6.4	4.8	2.8	10.1
	♀	33.0	21.2	16.8	8.2	6.4	3.0	13.9
S.oryzae	♂	75.0	69.8	44.8	33.4	11.8	4.7	35.7
	♀	57.0	33.4	36.3	39.0	13.5	5.5	30.4

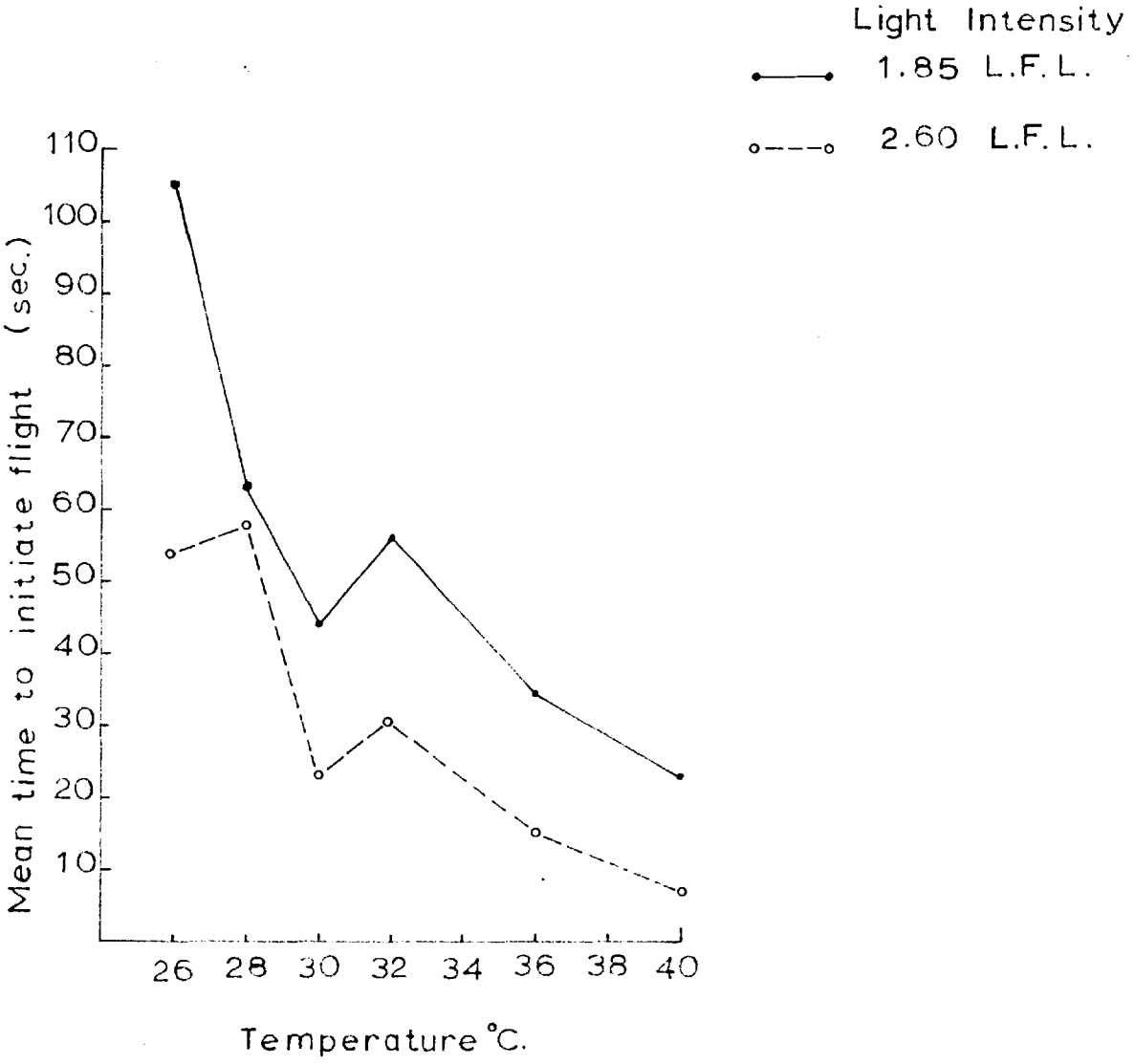


Fig. 40 : Relation between temperature and time to initiate flight of suspended male weevils of S.zea-mais (2 weeks old) at different light intensities.

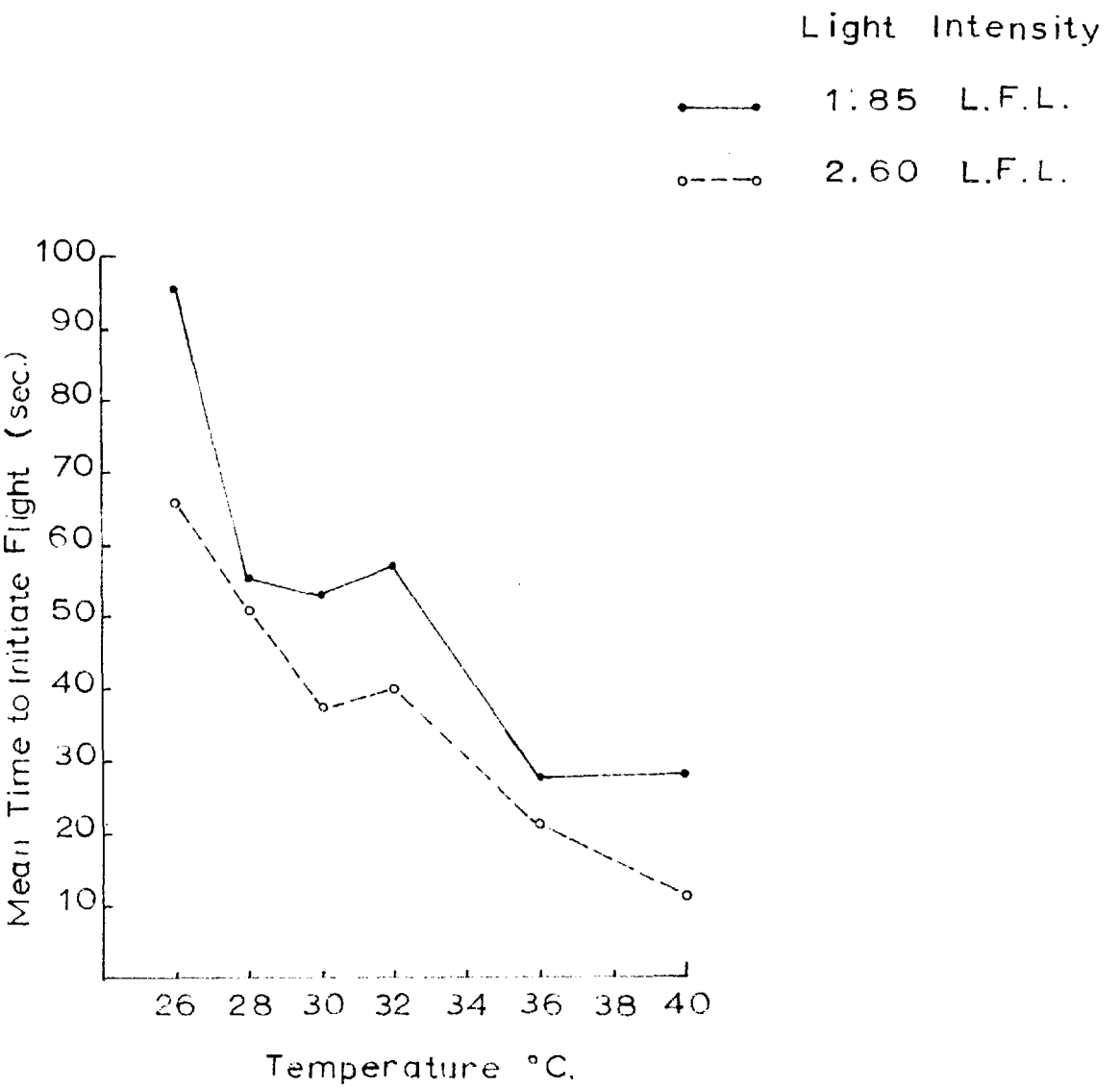


Fig. 41 : Relation between temperature and time to initiate flight of suspended female weevils of S. zea-mais (2 weeks old) at different light intensities.

Four weeks old S.zea-mais weevils : The behaviour of these weevils did not vary significantly from the 2 weeks old ones at the low light intensity of 1.85 L.F.L. The mean of the total values of the time taken to initiate flight of the male and the female weevils was 48.4 sec.(the means ranging between 100.6 and 17.8 sec. at different temperatures) and 49.1 sec. (the means ranging between 108.8 and 14.9) respectively (TABLE 34). A highly significant difference, however, existed when comparing the behaviour of similar sexes of the 4 weeks old weevils at the two light intensities ($P < 0.001$). The total mean time taken to initiate flight of the male w eevils at 2.6 L.F.L. was 10.1 sec. (21.0 - 2.4) and of the female weevils was 13.9 sec. (33.0 - 3.0) as is shown in TABLE 34. The variance of these two means was not significant .

Figs. 42 and 43, illustrated the strong effect of rise in temperature from 26° to 40°C. on the decrease of the time needed to initiate flight at the low light intensity of 1.85 L.F.L. In contrast to flight at the lower light intensity, at the higher light intensity the weevils of this age flew well at 26°C. The mean time taken to initiate flight at 2.6 L.F.L. was less than 10 sec. at 30°C. and at higher temperatures in the male w eevils, and at 32°C. and above in the female weevils.

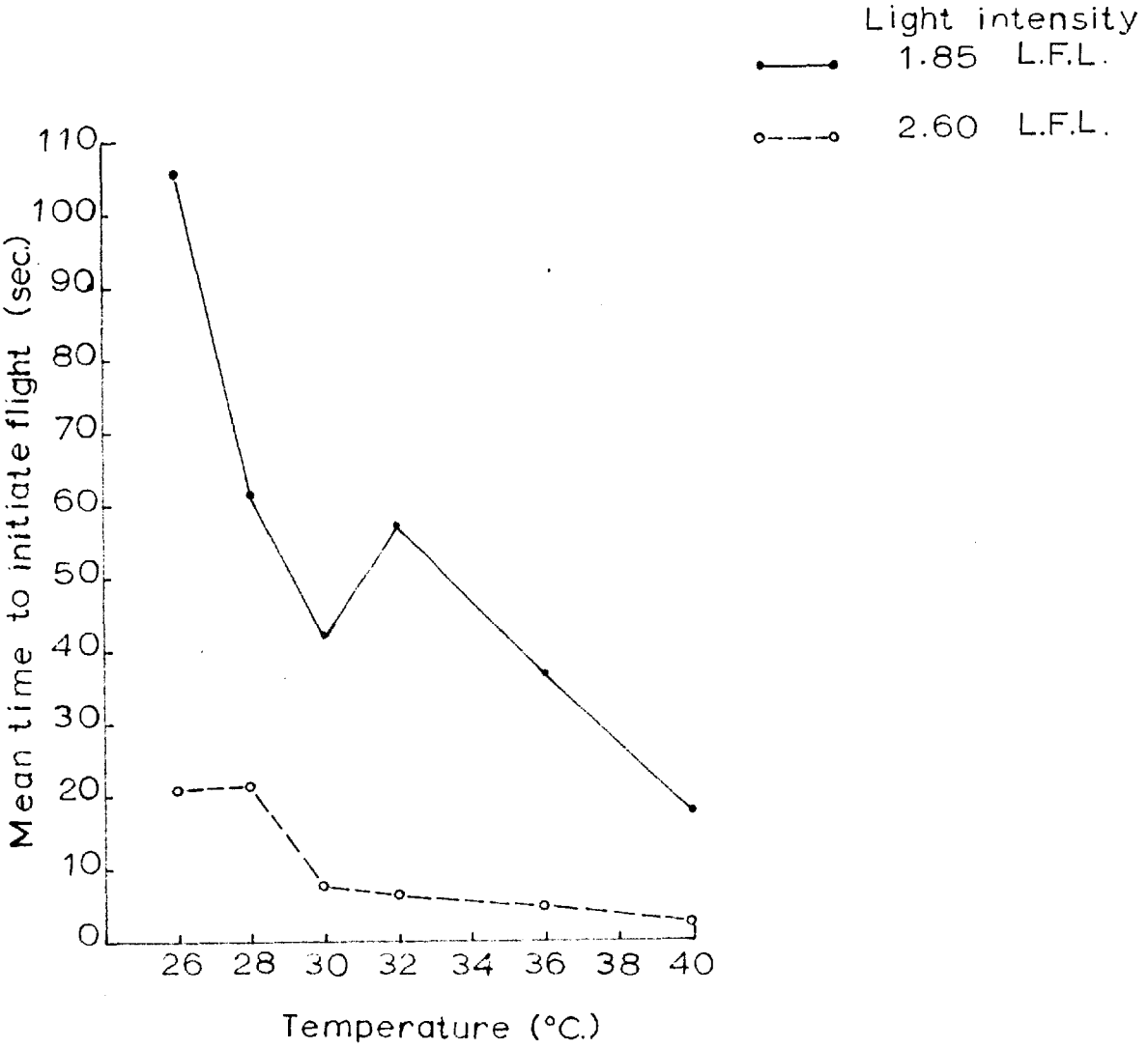


Fig. 42 : Relation between temperature and time to initiate flight of suspended male S. zea-mais weevils (4 weeks old) at different light intensities.

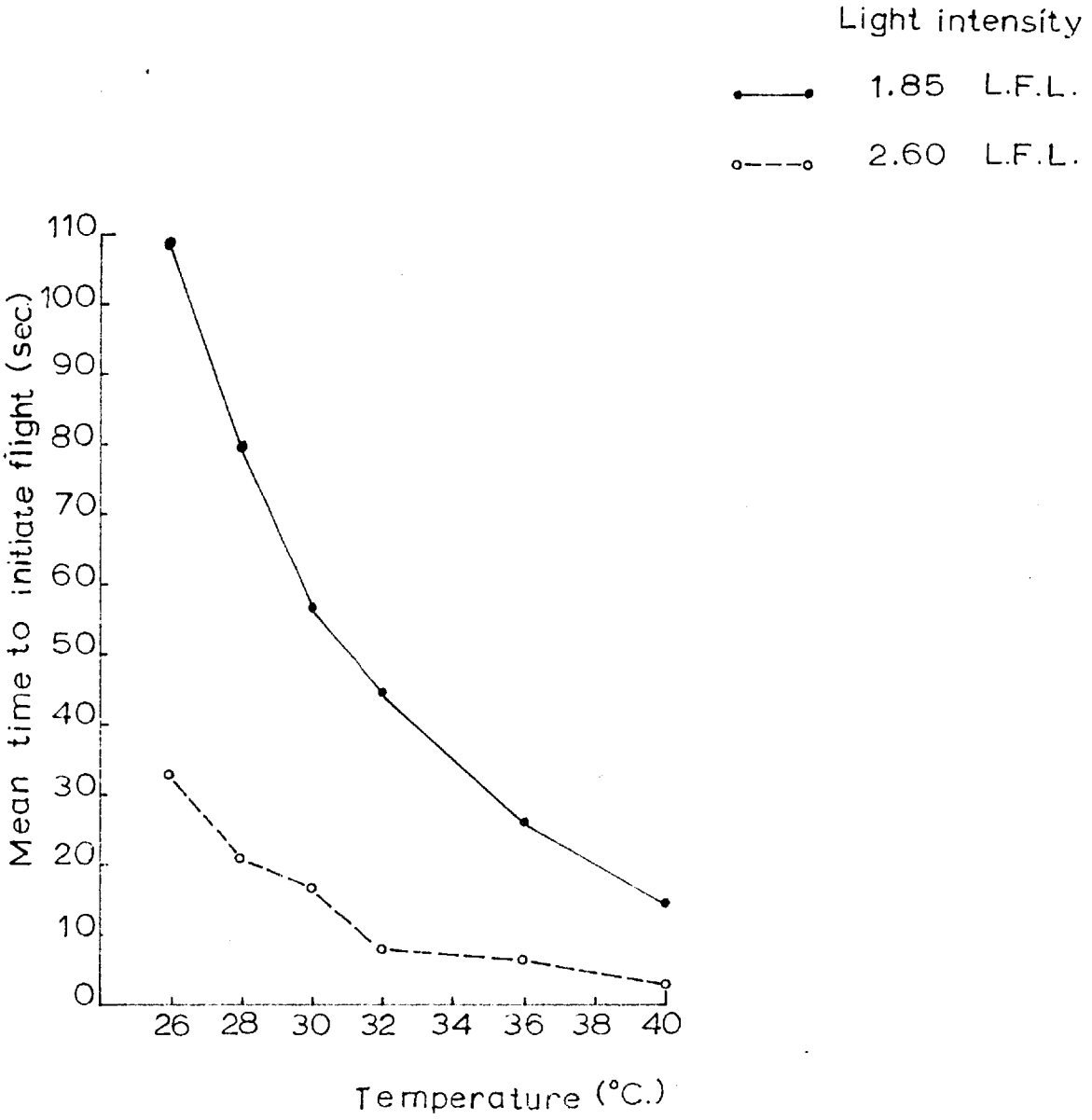


Fig. 43 : Relation between temperature and time to initiate flight of suspended female S. zea-mais weevils (4 weeks old) at different light intensities.

b) S. oryzae :

Two weeks old weevils were unable to fly when suspended from the pronotum. Several attempts to fly, however, were usually made, the elytra being widely diverged and the hind wings unfolded, but no actual flight occurred. A simple experiment was carried out to record the time needed to initiate the first attempts to fly, and the number of attempts made by suspended weevils at 36°C. and at a light intensity of 2.6 L.F.L. These observations lasted for 3 minutes. The aim of the experiment was to compare the efficiency of the two ~~species~~ sexes. The data in TABLE 35 indicated that the male weevils were more active than the females. The mean time taken to initiate the first attempt was 100.5 sec. in the males and 121.0 sec. in the females. The variance of the two means was not significant. The number of attempts to fly made by the male weevils ranged between 1 and 9 per 3 minutes, the mean being 4.4 . The mean number of attempts made by the female weevils was 2.6 ranging between 1 and 6.

S. oryzae weevils were fairly efficient flyers at the age of 4 weeks. The total mean time before flight was initiated in the suspended males was 35.6 sec. at the light intensity 1.85 L.F.L., and 35.7 sec. at the light intensity 2.6 L.F.L., but the variance of the two means was not significant. The female weevils gave total mean values of 29.5 sec. and 30.4 sec. at the lower a nd at the higher light intensities

TABLE 35

Number of Attempts to Fly per 3 minutes made by suspended *S.oryzae* weevils (2-weeks old), and the time to Initiation of First Attempt at 36°C. and 2.6 L.F.L. light intensity.

Number of Weevils	Time to Initiate First Attempt (sec.)		Number of Attempts per 3 minutes.	
	♂	♀	♂	♀
1	70	115	8	2
2	30	150	9	1
3	120	105	4	3
4	75	170	5	1
5	165	130	1	2
6	165	80	1	4
7	70	70	5	6
8	90	145	3	2
9	105	125	5	3
10	115	120	3	2
Mean	100.5	121.0	4.4	2.6

which are not significantly different from each other (TABLE 34). It was interesting to note that whereas the difference of 1.85 and 2.6 L.F.L. had an appreciable effect on the time of reaction of S.zea-mais, and none on that of S.oryzae. It is not presumed that higher light intensity (and possibly radiation) do not affect this reaction, but only that there was no detectable effect under experimental conditions. The similarity in behaviour at the two light intensities is illustrated in Figs. 44 and 45 . The relation between temperature and the time taken to initiate flight, on the other hand, was clear this time interval becoming shorter with the rise in temperature from 26° to 40°C. (see TABLE 34 and Figs. 44 and 45). Below 30°C. the mean of the time before flight was initiated was longer in the males than in the females, but above 30°C. both sexes of both species reacted more or less in the same way along the rest of the temperature scale. The variance of the total means of time taken to initiate flight of the male and the female weevils, was not significantly different at the two light intensities used.

S.oryzae weevils were flew more readily than S.zea-mais weevils of the same age when suspended at the low light intensity 1.85 L.F.L., but less readily at the high light intensity 2.6 L.F.L. The variance of the means of time taken to initiate flight was highly significant in both cases.

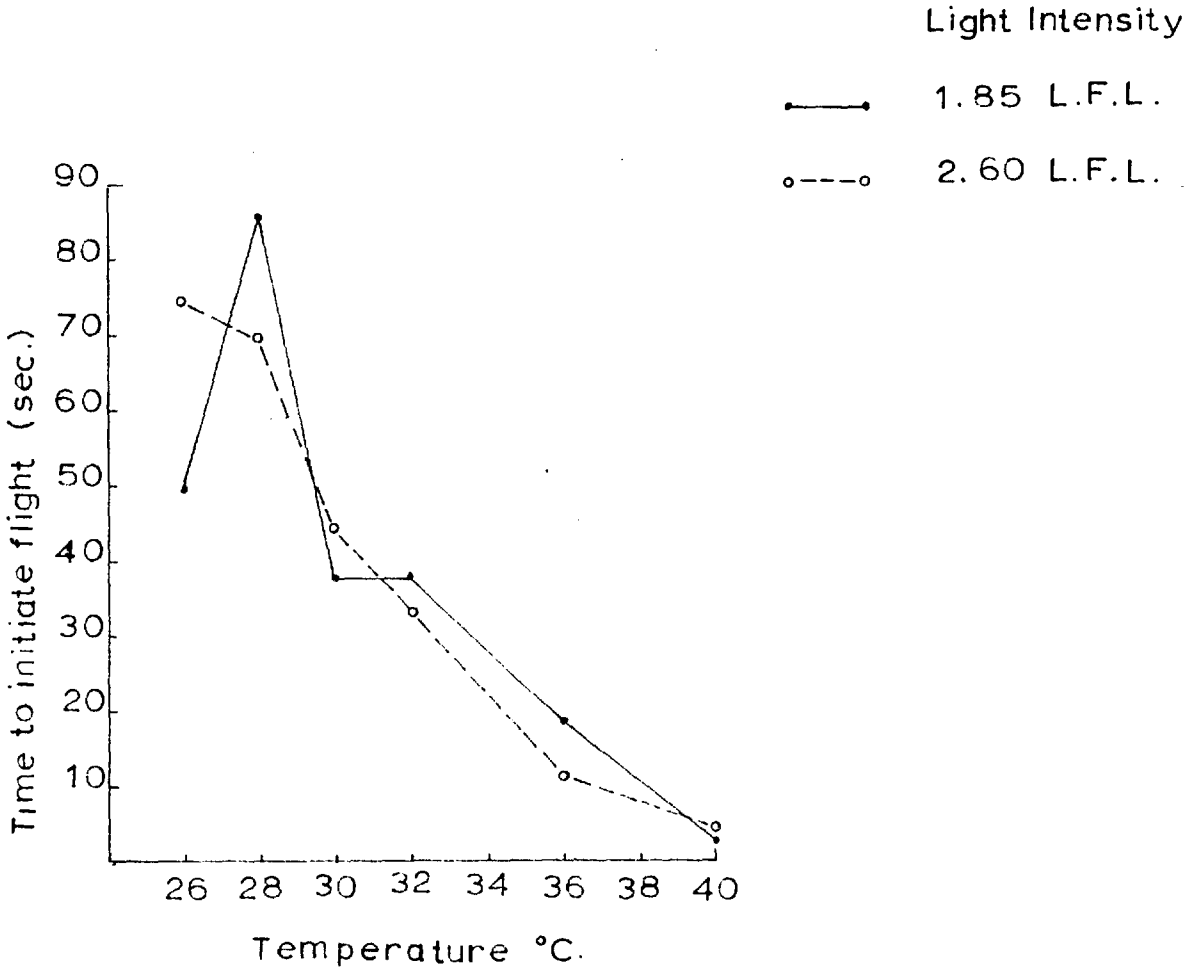


Fig. 44 : Relation between temperature and time to initiate flight of suspended male weevils of S. oryzae (4 weeks old) at different light intensities.

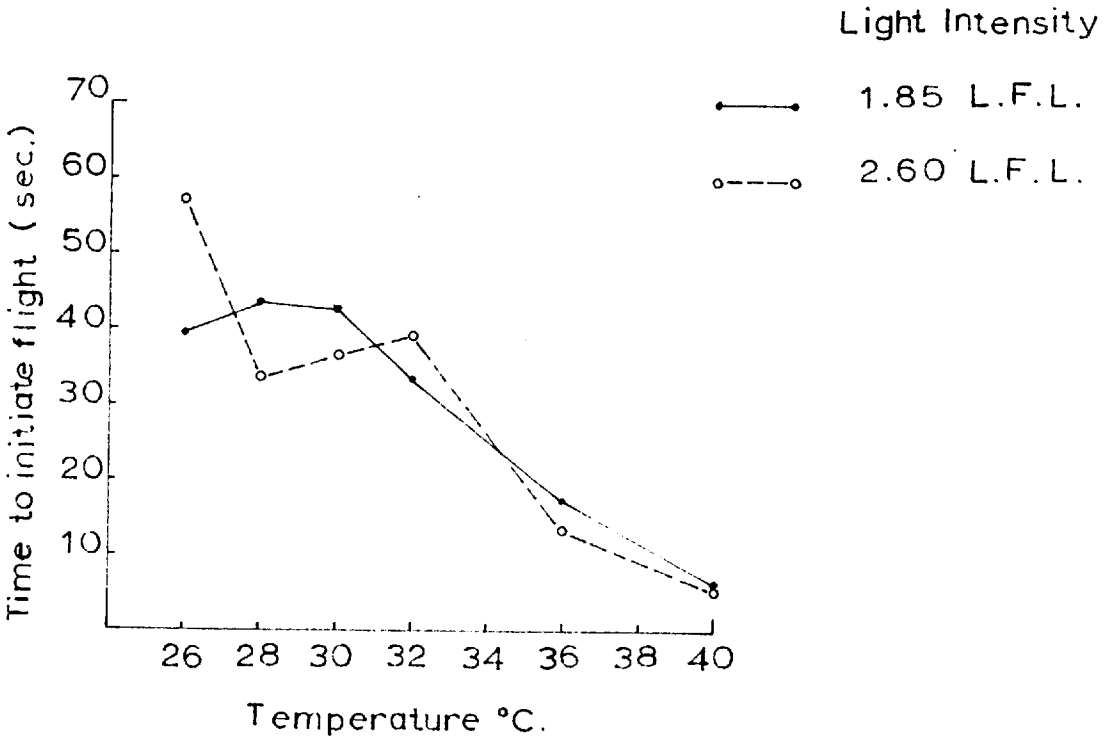


Fig. 45 : Relation between temperature and time to initiate flight of suspended female weevils of S. oryzae (4 weeks old) at different light intensities.

2. Experiments with Released Weevils

a) S. zea-mais :-

The total number of flights performed by a 100 weevils of each sex per 15 minutes, at constant temperatures and light intensities, are summarised in TABLE 36. The 2-week old male weevils of S.zea-mais flew far more readily than the corresponding females at the four combinations of temperature and light intensities in these experiments. At the low light intensity 1.85 L.F.L. and low temperature 31±0.5°C. the 2-week old male and female weevils made 151 and 105 flights per 15 minutes respectively. At the same light intensity but at higher temperature (36±0.5°C.) these were 259 and 128 flights per 15 minutes in the males and the females respectively. The effect of rise in temperature on the increase in the number of flights of the weevils was more significant in the males than in the females($0.05 > P > 0.02$). These data were analysed by the X^2 test.

At 31 ± 0.5°C. and the stronger light intensity 2.6 L.F.L., the numbers of flights of the male and the female weevils were 256 and 176 per 15 minutes. The effect of increasing the light intensity on inducing the weevils to make more flights was not significantly different in the males and the females. When both the light intensity and the temperature were high, the numbers of flights made by the male and the female weevils were 343 and 221 per 15

TABLE 36

Number of flights per minute made by 100 weevils of S. zea-mais in each set of experiments

Sex	Age (weeks)	Temperature (°C.)	Light intensity (L.F.L.)	Number of flights 1	2	3	4	per 100 weevils per minute 5	6	7	8	9	10	11	12	13	14	15	Total	Mean time to initiate 1st. flight (min.)
Males	2	31±0.5°	1.85	2	3	4	4	4	9	11	8	10	11	14	16	16	18	21	151	4.45
"	"	36±0.5°	1.85	11	6	9	9	12	13	14	13	19	19	26	23	27	25	33	259	1.51
"	"	31±0.5°	2.60	11	9	9	12	18	23	17	15	15	16	14	26	22	20	28	256	2.10
"	"	36±0.5°	2.60	11	9	11	11	10	13	16	20	31	25	31	37	37	37	44	343	1.71
Females	2	31±0.5°	1.85	-	3	-	3	4	3	8	10	12	11	10	8	7	12	14	105	5.00
"	"	36±0.5°	1.85	-	2	4	5	5	6	7	9	14	11	15	12	8	13	17	128	6.51
"	"	31±0.5°	2.60	5	3	3	4	11	8	16	12	10	16	12	16	15	18	27	176	3.45
"	"	36±0.5°	2.60	7	6	9	8	14	10	16	13	27	16	16	19	19	22	19	221	3.01
Males	4	31±0.5°	1.85	3	2	3	6	7	8	10	16	17	20	26	16	19	27	35	215	5.55
"	"	36±0.5°	1.85	7	3	4	5	13	9	20	14	26	33	36	41	39	52	67	369	3.73
"	"	31±0.5°	2.60	29	13	17	16	24	22	25	40	39	41	49	49	52	57	61	534	0.70
"	"	36±0.5°	2.60	29	23	31	32	43	74	50	60	59	44	68	67	82	63	74	799	0.18
Females	4	31±0.5°	1.85	2	-	1	5	7	7	14	14	15	15	16	21	27	22	37	203	6.01
"	"	36±0.5°	1.85	1	2	3	8	8	12	10	18	22	26	29	31	40	36	45	291	4.33
"	"	31±0.5°	2.60	9	8	10	19	18	18	27	33	35	28	34	35	32	36	45	387	1.53
"	"	36±0.5°	2.60	13	19	24	26	26	33	38	44	38	38	40	46	45	44	61	535	0.79

minutes respectively. Thus the numbers of flights were more than double those made at the low temperature and the low light intensity. The rates of increase in numbers of flights in the male and the female weevils were not significantly different.

The 4 weeks old weevils exhibited more efficiency in their flying ability than the two weeks old weevils. The number of flights made by the male weevils was also greater than the number of flights made by the females at the four experimental combinations of temperature and light. At the low temperature and the lower light intensity the number of flights per 15 min. made by the male and the female weevils were 215 and 203. At the higher temperature and the lower illumination the number of flights increased to 369 and 291 in the males and the females ; the rate of increase not being significantly different in the males and the females at the upper 5 % level of significance. When the low temperature and the strong light intensity were used, a great increase in the number of flights occurred in both the male and the female weevils ; the mean numbers of flights rising to 534 and 387 respectively. The rate of increase in the males was more significant than in the females at the upper 5 % level (X^2 test : $0.05 > P > 0.02$). When both the temperature and the light intensity were increased, the numbers of flights made by the male weevils were 799 and those by the

females 535 per 15 min. The rate of increase in the number of flights as compared with the corresponding ones at the lower light intensity and low temperature, was more significant in the male weevils than in the females ($0.01 > P > 0.001$).

The effect of the age of the weevils on their flying ability was clear. The sum total of flights in the four experiments, made by the male weevils was 1009 at the age of 2 weeks, and 1917 at the age of 4 weeks. The sum total number of flights made by the 2 weeks old females was 630 and by the 4 weeks old ones it was 1416 (TABLE 42). The rate of increase in the number of flights due to the increase in age was more significant in the males at the upper 5 % level ($0.01 > P > 0.001$).

The activity of the weevils was normally low, shortly after their introduction inside the arena. The frequency of flights gradually increased with time in all the experiments, reaching a maximum at the end of each test of 15 minutes. The total numbers of flights per minute made by sets of a 100 weevils of S.zea-mais are summarized in TABLE 36. The rate of increase in the number of flights per minute was higher in the male weevils than in the females of the same age; and in the 4 weeks old weevils flew more frequently than the 2 weeks old ones of the same sex (Figs. 46 - 49).

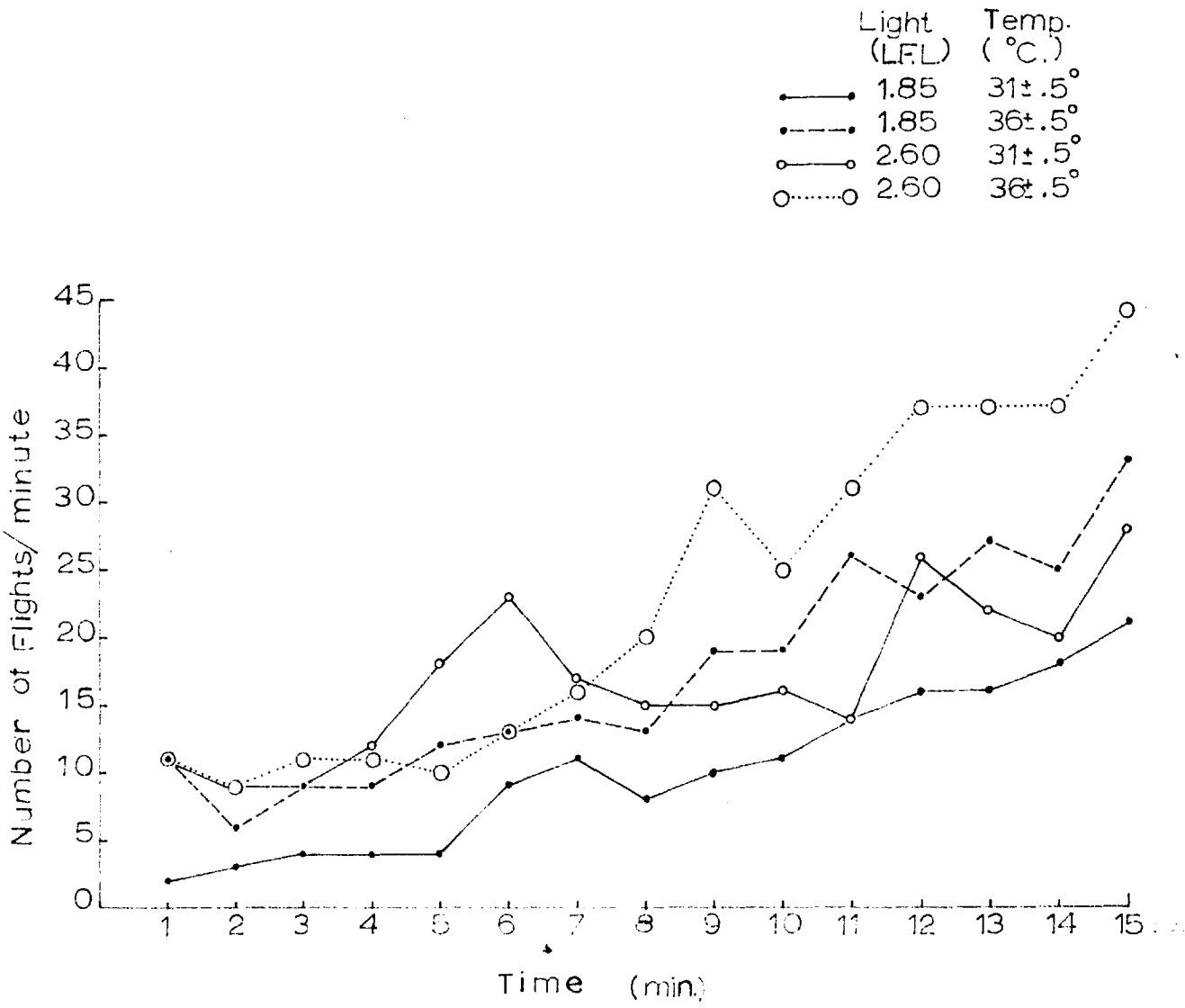


Fig. 46 : Number of flights per minute made by 100 male weevils of S. zea-mais (2 weeks old) at different temperatures and light intensities.

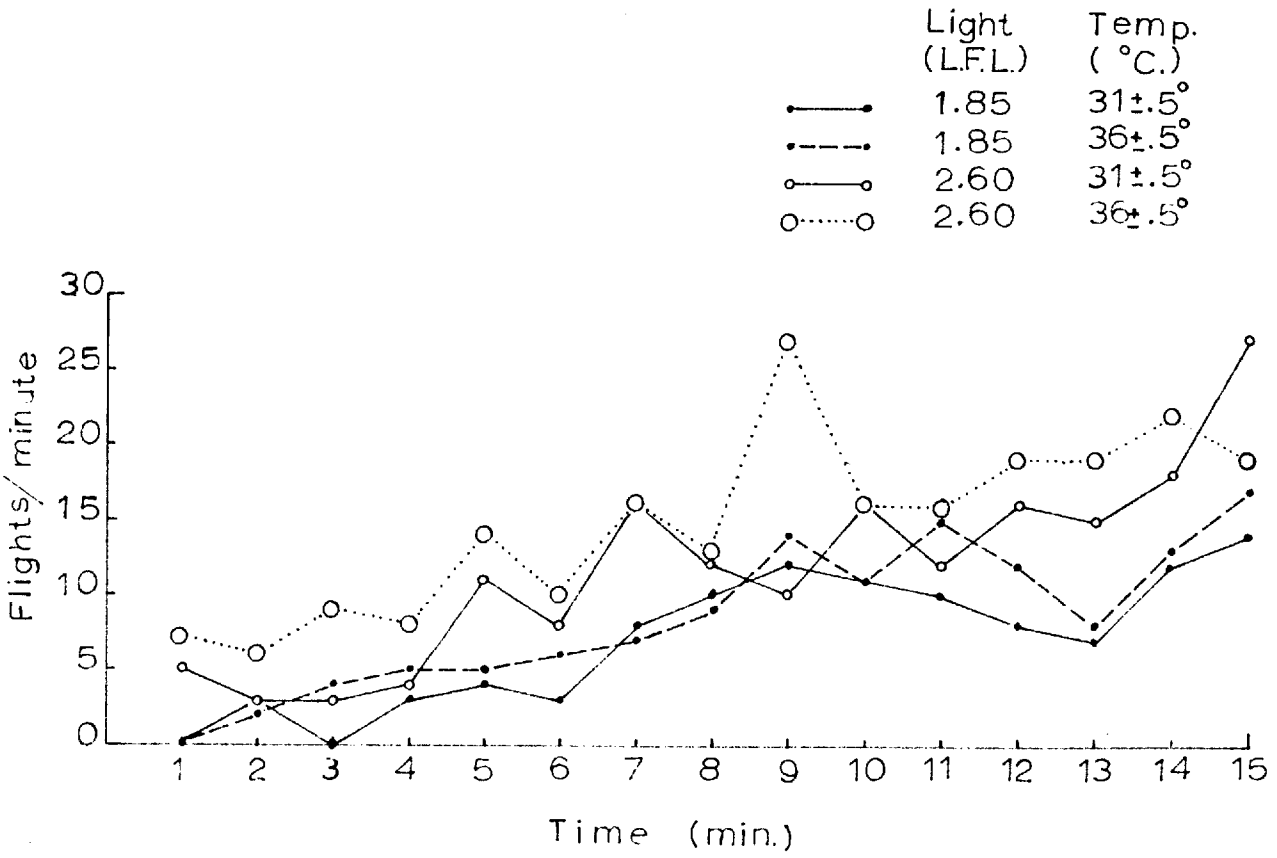


Fig. 47 : Number of flights per minute made by 100 female weevils of S.zea-mais (2 weeks old) at different temperatures and light intensities.

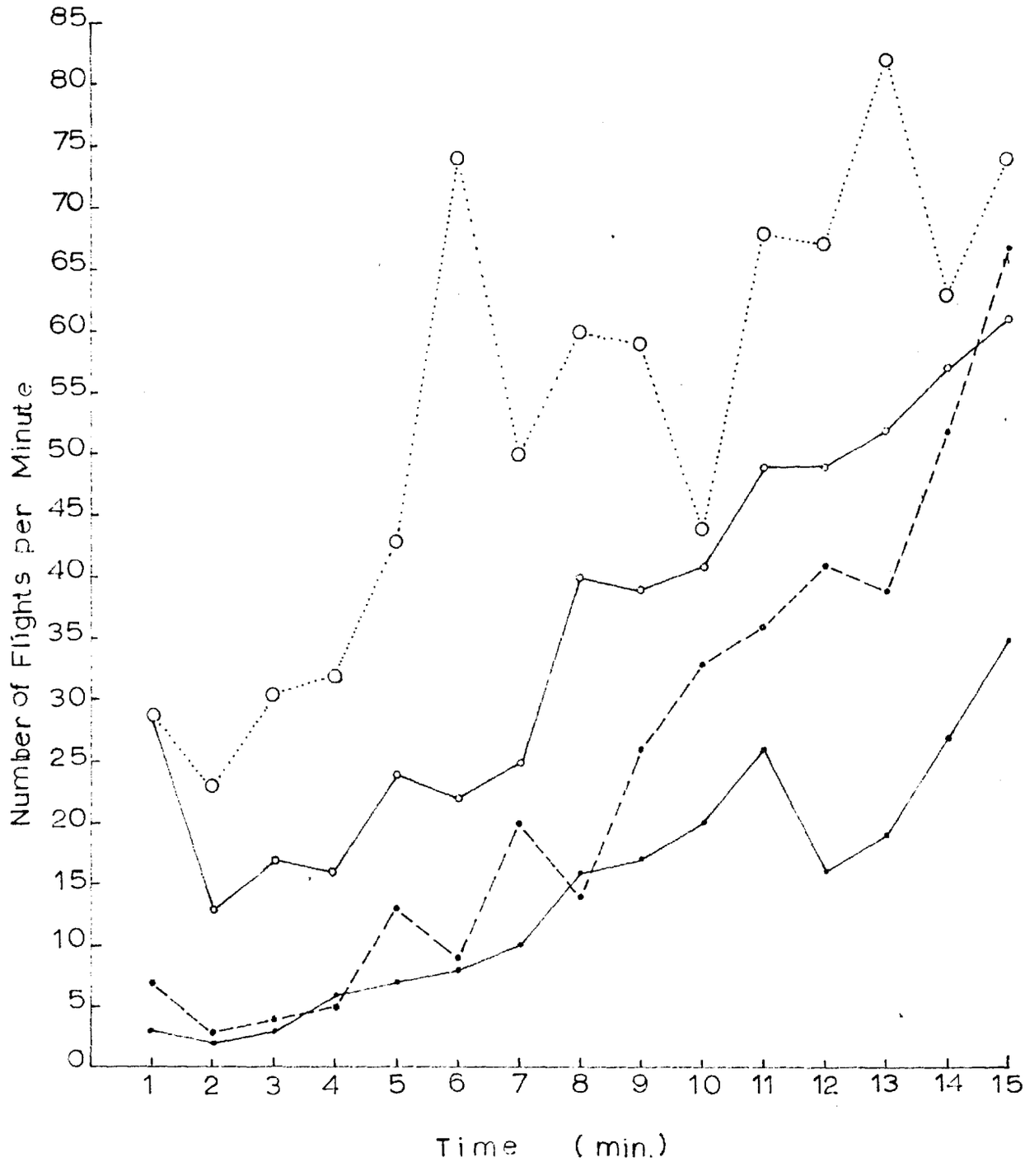


Fig. 48 : Number of flights per minute made by 100 male weevils of S. zea mais (4 weeks old) in 15 minutes at different temperatures and light intensities.

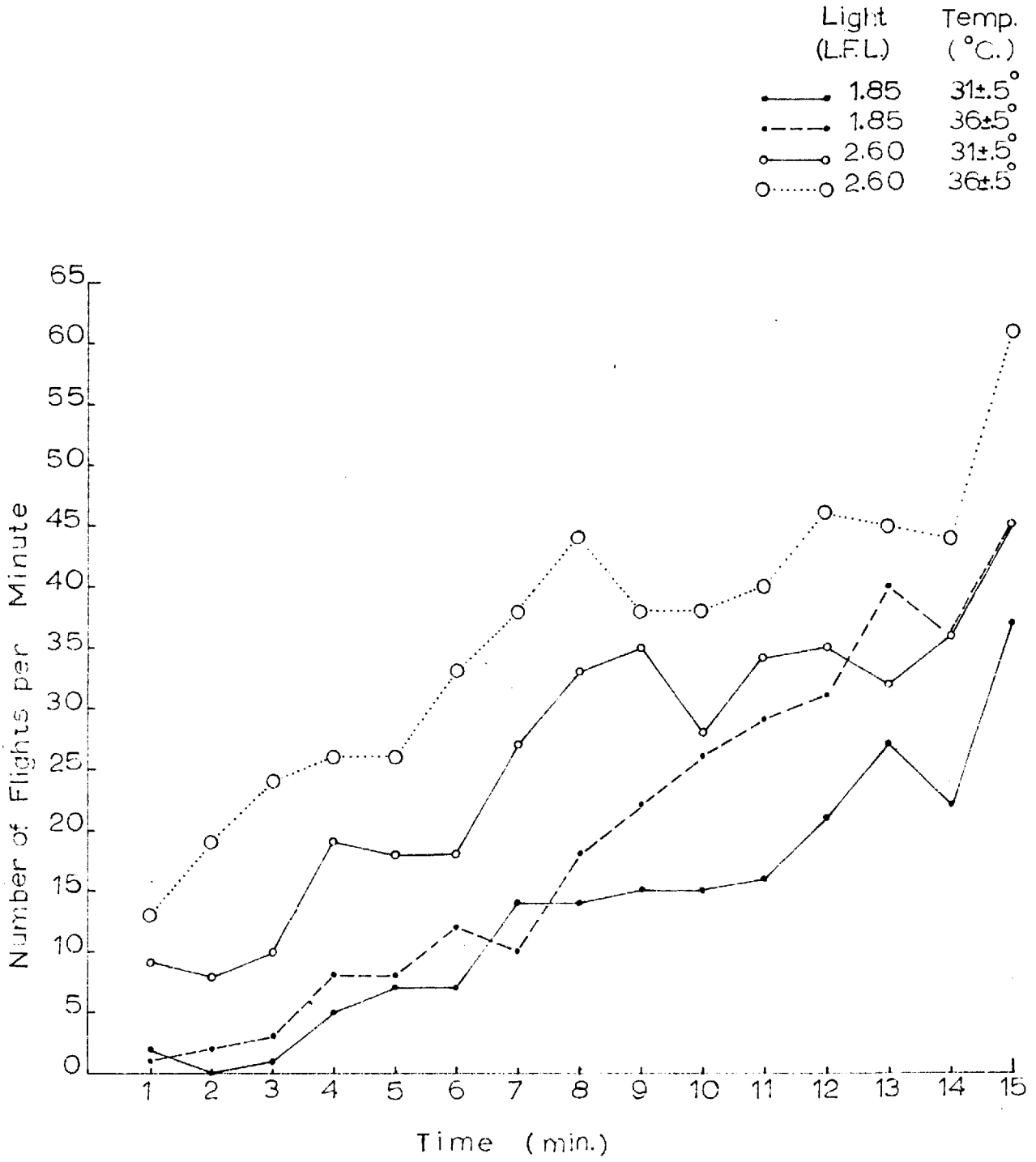


Fig. 49 : Number of flights per minute made by 100 Female weevils of S.zea mais (4-weeks old) in 15 minutes at different temperatures and light intensities.

The effect of different combinations of temperatures and light intensities on the time needed to initiate the first flight of S.zea-mais was determined. The means of time taken of each set of a 100 weevils are included in TABLE 36 . At the low temperature 31 ± 0.5°C. and the low light intensity 1.85 L.F.L., the means of time to initiate the first flight in the 2 weeks old male and female weevils were 4.45 a nd 5.00 minutes respectively. The variance of the two means was not significant. Under the same conditions of temperature and light intensity the 4 weeks old weevils of both sexes did not fly more readily than the corresponding 2 weeks old ones ; the means of time were 5.55 and 6.01 minutes respectively. The variance of the two means was not significant. Again, the variance of the means of time taken to initiate the first flight of the two different ages, was not significant when the same sexes were compared. The increase in temperature or in the light intensity or in both, showed a marked decrease in the means of time taken to initiate the first flight of the weevils in all the experiments. The response exhibited by the male weevils, however, was greater than that by the females; and the 4 weeks old weevils reacted more intensively than the corresponding 2 weeks old ones to the variayions in temperature and of light intensity (see TABLE 36).

In view of the fact that the number of flights of the weevils increased gradually with time, and reached a maximum near the end of the 15 minutes, a subsidiary test was carried out to determine this frequency at the 31-st. to 35-th. minute. The data in TABLE 37 show that the mean number of flights made by the weevils at the 31-st. to 35-th. minute did not vary significantly from that at the 15-th. minute in all the tests.

The number of attempts to fly per minute made by groups of 10 weevils, were recorded in the same experiments. The effect of different combinations of temperature and light intensity on the number of attempts to fly of 2-week and 4-week old weevils is given in TABLE 38. At 31 $\pm$ 0.5°C. and 1.85 L.F.L. the total number of attempts to fly per 100 weevils per 15 minutes were 20 and 25 in the 2-week old males and females respectively. A marked increase in the total number of attempts to fly occurred when higher temperature or the stronger light intensity were applied. The maximum frequencies were at 36 $\pm$ 0.5°C and 2.6 L.F.L., the total numbers of attempts being 69 in the male and 68 in the female weevils. An odd result, however, was obtained from observations on the 2-week old female weevils at 36 $\pm$ 0.5°C. and 1.85 L.F.L. i.e. there was no increase in frequency with the rise in temperature. Possibly this may have been due to variations

TABLE 37

Number of Flights per minute done by 10 Weevils of S.zea-mais in each set at the 31-35th minute, at four combinations of temperature and Light Intensity.

Sex	Age weeks	Temp. (°C.)	Light Intensity (L.F.L.)	No.Flights/10 Weevils/ minute 31	32	33	34	35	Mean No.Flights/ Weevil/minute At 31-35th min.	At 15th min.
Males	2	31°	1.85	1	2	2	1	3	0.18	0.21
"	2	36°	1.85	3	3	2	4	3	0.30	0.33
"	2	31°	2.60	3	1	4	3	2	0.26	0.28
"	2	36°	2.60	3	6	2	5	5	0.42	0.44
Females	2	31°	1.85	2	2	1	1	2	0.16	0.14
"	2	36°	1.85	1	3	1	2	2	0.18	0.17
"	2	31°	2.60	2	3	2	2	4	0.26	0.27
"	2	36°	2.60	3	1	2	2	3	0.22	0.19
Males	4	31°	1.85	4	3	5	2	4	0.36	0.35
"	4	36°	1.85	6	9	5	8	7	0.70	0.67
"	4	31°	2.60	7	6	7	4	5	0.58	0.61
"	4	36°	2.60	10	5	7	6	8	0.72	0.74
Females	4	31°	1.85	4	4	5	3	4	0.40	0.37
"	4	36°	1.85	6	3	3	5	5	0.44	0.45
"	4	31°	2.60	3	4	6	3	5	0.44	0.45
"	4	36°	2.60	8	7	4	6	4	0.58	0.61

in individual behaviour.

The 4 weeks old weevils showed a similar behaviour, but their total numbers of attempts to fly were much higher than those of the 2-week old ones. At the low temperature and low light intensity the total number of attempts to fly (per 100 weevils per 15 min.) of the 4-week old male and female weevils were 78 and 56 respectively (TABLE 38). At 36 ± 0.5°C. and 1.85 L.F.L. the totals were 108 and 80 , and at 31 ± 0.5°C and 2.6 L.F.L. the totals were 116 and 38, the maxima occurring at 36 ± 0.5°C. and 2.6 L.F.L., the totals being 128 in the males and 180 in the females. An odd result was recorded for the female weevils at 31±0.5°C. and 2.6 L.F.L. The two results in the females may indicate that they are more susceptible to the interaction of higher light and higher temperature than to one of these two factors by itself.

There was no regularity in the number of attempts to fly in the successive minutes. However, all the weevils exhibited a high activity in the first minute of the experiments at 36 ± 0.5°C. and 2.6 L.F.L. (TABLE 38). A similar response was also given by the 4-week old male weevils at 36 ± 0.5°C. and 1.85 L.F.L., and at 31 ± 0.5°C. and 2.6 L.F.L.

TABLE 38

Number of attempts to fly per minute made by 100 weevils of S.zea-mais in each set of experiments.

Sex	Age (weeks)	Tempe-rature (°C.)	Light intensity (L.F.L.)	Number of attempts to fly per 100 weevils per minute															
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
Males	2	31±0.5°	1.85	-	1	1	1	3	2	1	4	1	2	1	-	2	1	-	20
"	"	36± 0.5°	1.85	3	5	1	2	-	1	4	3	5	3	1	2	2	1	1	34
"	"	31± 0.5°	2.60	2	7	6	4	2	3	2	4	4	3	6	2	2	3	5	55
"	"	36± 0.5°	2.60	11	10	2	2	5	3	2	10	2	3	4	5	5	1	4	69
Females	2	31± 0.5°	1.85	-	-	1	2	1	1	3	1	2	2	2	1	5	1	3	25
"	"	36± 0.5°	1.85	-	-	2	2	1	1	2	3	-	1	-	1	-	3	2	18
"	"	31± 0.5°	2.60	4	9	6	-	6	2	3	4	-	1	-	1	2	2	2	42
"	"	36± 0.5°	2.60	12	3	4	4	1	1	5	3	9	7	3	5	6	2	3	68
Males	4	31± 0.5°	1.85	2	1	2	3	4	5	9	1	10	5	4	12	8	3	9	78
"	"	36± 0.5°	1.85	16	2	6	1	-	7	6	6	6	10	7	10	7	9	15	108
"	"	31± 0.5°	2.60	17	7	7	6	8	10	6	11	9	11	6	3	8	6	1	116
"	"	36± 0.5°	2.60	23	4	7	6	5	11	13	6	3	9	4	12	11	6	8	128
Females	4	31± 0.5°	1.85	2	1	4	3	1	1	3	4	1	5	7	9	5	6	4	56
"	"	36± 0.5°	1.85	3	1	6	5	6	5	8	9	5	12	5	6	5	3	1	80
"	"	31± 0.5°	2.60	2	1	1	-	1	1	4	1	2	2	4	8	5	3	3	38
"	"	36± 0.5°	2.60	21	9	13	11	17	11	14	5	11	15	8	19	12	11	3	180

b) S. oryzae :

The total numbers of flights made by a 100 weevils per 15 min., at constant temperatures and light intensities are summarized in TABLE 39. The 2 weeks old weevils were unable to fly nor to unfold the wings when released inside the cage, even at the high temperature and high light intensity. The 4 weeks old weevils, on the other hand, exhibited a marked ability to fly. At 31 $\pm$ 0.5°C. and 1.85 L.F.L. the total numbers of flights per 100 weevils per 15 min. were 84 and 62 in the males and the females. At the higher temperature of 36 $\pm$ 0.5°C. and the same low light intensity, the corresponding numbers were 150 and 149 flights per 100 weevils per 15 min. The effect of the rise in temperature on the increase in the numbers of flights of the weevils did not vary significantly in the males and the females at the upper 5 % level ($0.10 > P > 0.05$). At the lower temperature and higher light intensity the increase in the total numbers of flights was significantly greater than those in the previous set of experiments; the total numbers of flights in the males and the females were 324 and 289 per 100 weevils per 15 minutes respectively. The effect of increasing the light intensity on inducing the weevils to fly more frequently was not significantly different in the male from the female weevils at the upper 5 % level ($P > 0.10$). At the high temperature and high light intensity the weevils

TABLE 39

Total number of flights per minute made by 100 released weevils of S.oryzae (4-week old) in each test.

	Males				Females			
Temp. (°C.)	31°	36°	31°	36°	31°	36°	31°	36°
Light (L.F.L.)	1.85	1.85	2.6	2.6	1.85	1.85	2.6	2.6
Time (min.)	No. flights/100 weevils/minute							
1	--	--	5	22	--	--	4	13
2	--	--	4	11	--	1	4	10
3	--	2	6	19	--	1	7	17
4	--	3	12	27	--	3	8	20
5	1	7	10	25	1	6	14	28
6	2	2	22	37	--	7	20	30
7	3	8	18	33	2	10	13	26
8	4	8	25	34	3	6	29	28
9	4	9	24	45	2	14	21	28
10	4	13	28	37	6	10	22	33
11	8	12	31	41	7	17	21	35
12	12	22	31	36	6	15	29	44
13	14	23	29	45	9	20	31	38
14	16	21	39	32	15	18	28	45
15	16	20	40	49	11	21	38	57
Total	84	150	324	493	62	149	289	452
Mean time to initiate first flight (min.)	9.19	6.15	3.18	0.45	8.96	6.44	2.06	1.01

showed their maximal efficiency, within the range of these experiments; the total numbers of flights were 493 and 452 per 100 weevils per 15 minutes in the male and the female weevils. The increase in the rate of activity, as compared with that at the lower temperature and light intensity, was not significantly different in the male and the female weevils at the upper 5 % level of significance ($P > 0.10$).

The influence of changes in temperature and light intensity on the time needed to initiate the first flight of the weevils was strongly manifested. At the low temperature of 31 $\pm$ 0.5°C. and the low light intensity of 1.85 L.F.L. the means of time to initiate the first flight of the male and the female weevils were 9.19 and 8.96 minutes respectively (TABLE 39). At the low illumination and the higher temperature the corresponding means were 6.15 and 6.44 min. When the temperature was kept low but the stronger light intensity was applied, a marked decrease in the means of the time taken to initiate the first flight occurred, the means in the males and the females being 3.18 and 2.06 minutes. The shortest means of time occurred when both factors were raised; the mean values being 0.45 and 1.01 minutes in the male and the female weevils respectively. In TABLE 39 and Figs. 50 and 51, it can be seen that the number of flights of the weevils per minute increased gradually with time, the maximum values occurring near to or at the end

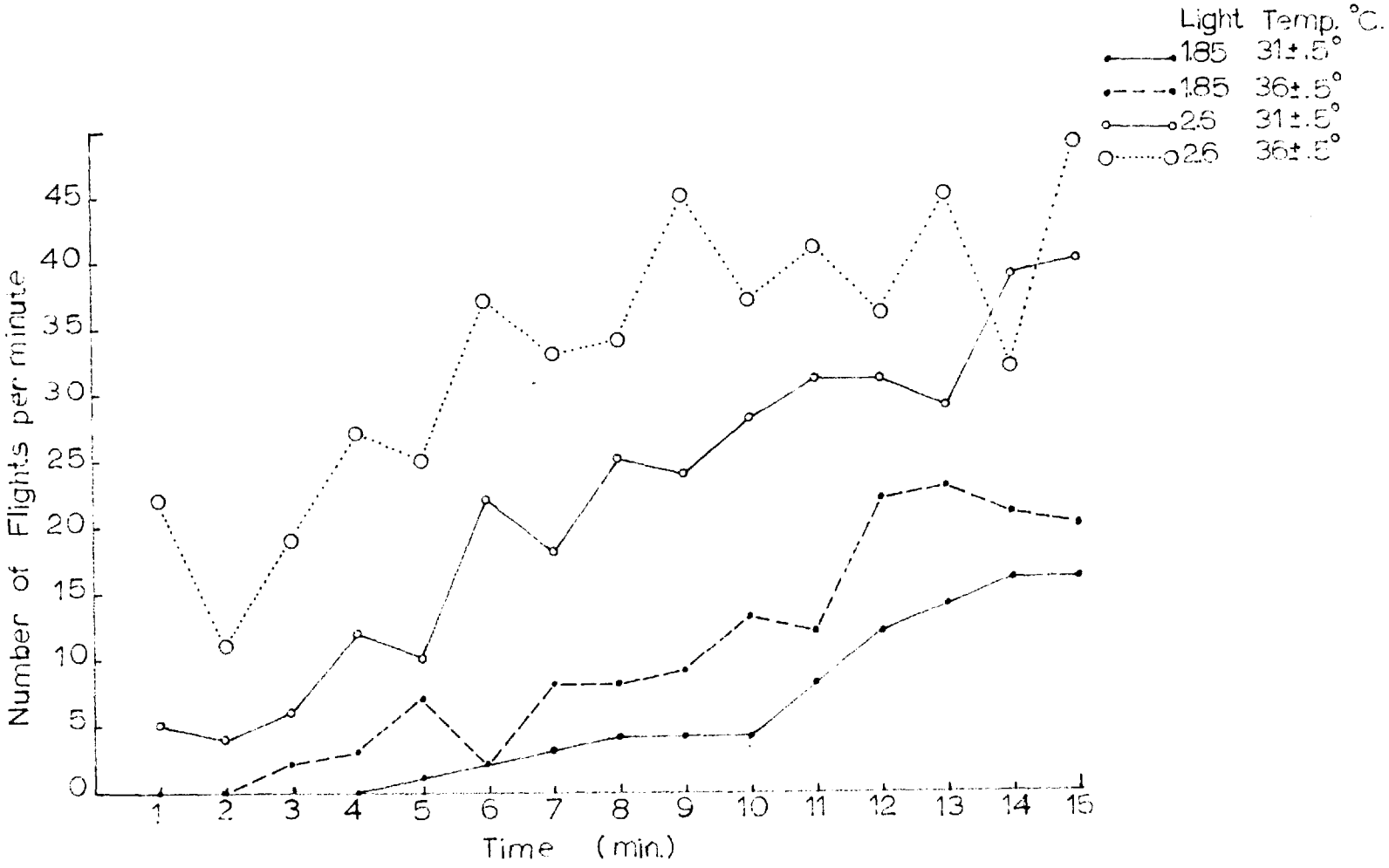


Fig. 50 : Number of flights/minute made by 100 Male weevils of S.oryzae (4-weeks old) at different temperatures and light intensities.

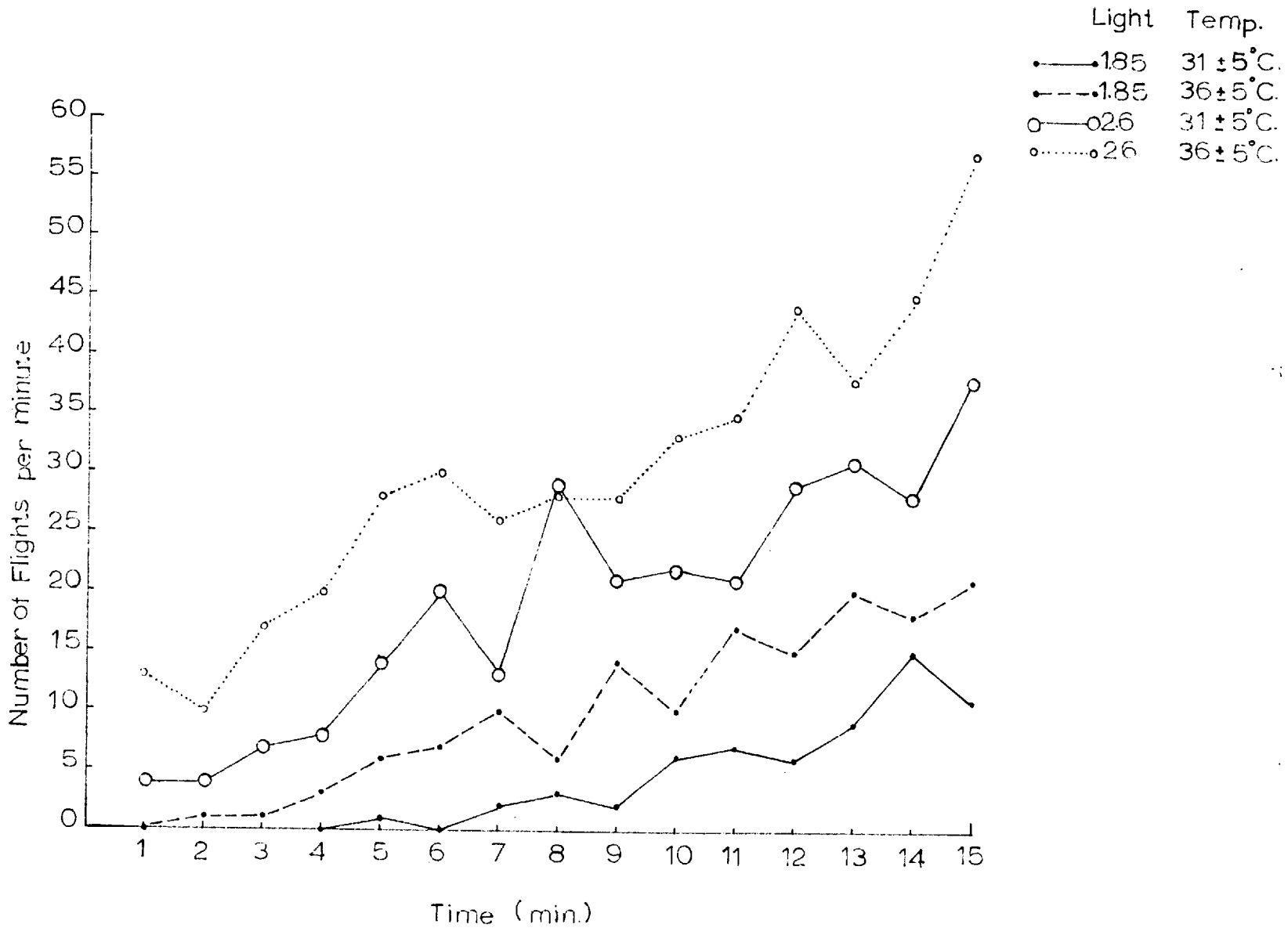


Fig. 51 : Number of flights per minute made by 100 ♀♀ weevils of S. oryzae (4-weeks old) at different temperatures and light intensities.

of the 15 minutes. This maximum rate was found to persist at more or less the same level after 31-35 minutes as was shown in the tests carried out in each set of experiments. The data are summarized in TABLE 40. The mean number of flights per weevil per minute at the 31-st. to-35 th. minute did not vary significantly from that during the 15-th. minute.

The effect of the different combinations of temperature and light intensity on the number of attempts to fly made by S.oryzae is illustrated in TABLE 41. At 31 ± 0.5°C. and 1.85 L.F.L., the total numbers of attempts per 100 weevils per 15 minutes were 45 and 25 in the males and the females. By raising the temperature alone, the corresponding total numbers were 98 and 93 . By raising the light intensity and keeping the temperature low, the intensity of flight activity increased tremendously and the total numbers of attempts to fly per 100 weevils per 15 min. reached 175 and 194 in the males and the fema-les respectively. At the higher temperature of 36 ± 0.5°C. and the strong light intensity of 2.6 L.F.L. the total numbers of attempts in the males and the females were 272 and 200 (per 100 weevils per 15 min.) respectively. As in the case of S.zea-mais, it was observed the S.oryzae weevils exhibited a rapid initial response at the higher temperature and the higher light intensity. The total numbers of attempts to fly per 100 weevils during the first minute of the experiments were 49

TABLE 40

Number of Flights per minute of S.oryzae Weevils (4-weeks old) at the 31st - 35th minute, at constant temperatures and light intensities

Sex	Temp. (°C.)	Light Intensity (L.F.L.)	No.of Flights/ 10 Weevils/ minute					Mean No. of Flights/ Weevils/ minute	
			31	32	33	34	35	At 31-35th min.	At 15th min.
Males	31°	1.85	2		2	3	2	0.18	0.16
"	36°	1.85	1	3	2	3	2	0.22	0.20
"	31°	2.60	5	2	4	4	6	0.42	0.40
"	36°	2.60	4	6	5	5	3	0.46	0.49
Females	31°	1.85	1	1	2	1	2	0.14	0.11
"	36°	1.85	2	1	4	2	2	0.22	0.21
"	31°	2.60	3	4	4	4	5	0.40	0.38
"	36°	2.60	6	5	3	7	6	0.54	0.57

TABLE 41

Number of attempts to fly per 100 weevils per minute of 4-week old S.oryzae weevils (released), at constant temperatures and light intensities.

	Males				Females			
Temp.(°C.)	31°	36°	31°	36°	31°	36°	31°	36°
ight (L.F.L.)	1.85	1.85	2.6	2.6	1.85	1.85	2.6	2.6
Time(min.)	No. attempts to fly/100 weevils/minute							
1	-	-	11	49	-	-	4	28
2	-	2	5	16	-	1	8	10
3	-	5	7	11	-	6	10	16
4	-	4	9	18	-	2	6	12
5	1	3	12	21	-	2	16	10
6	2	9	12	14	2	4	14	9
7	1	5	15	22	1	6	19	16
8	4	9	14	26	2	7	18	14
9	4	8	10	11	3	9	18	18
10	5	8	20	19	1	7	13	11
11	5	11	14	17	4	7	15	10
12	5	6	11	13	5	8	12	13
13	4	8	10	15	3	6	18	18
14	7	7	10	15	2	8	12	7
15	7	13	15	5	2	10	11	9
Total	45	98	175	272	25	93	194	200

in the males and '28 in the females (TABLE 41). These figures were followed by a sudden drop in the numbers of attempts to fly in the second minute. The rate per minute fluctuated during the rest of the experiment at a much lower level than the initial high frequency.

c) Comparison between S.zea-mais and S.oryzae weevils in experiments on released weevils :-

Conclusion from these data are summarized in TABLE 42. In contrast to S.zea-mais, the 2-week old S.oryzae weevils were apparently unable to fly. By comparing the 4-week old weevils of both species, it was found that the total numbers of flights (100 weevils per 15 min.) in the male and the female weevils of S.zea-mais were much higher than those in the corresponding sexes of S.oryzae. In both species the total numbers of flights at the high light intensity and low temperature were greater than the total numbers of flights at the low light intensity and the high temperature. The difference between the sum totals of flights of the two sexes of S.zea-mais was compared to that between the two sexes of S.oryzae and was found to be highly significant($P<0.001$). That is, the males and females behaved differently in S.zea-mais, but the two sexes behaved in a similar way in S.oryzae. At the low temperature and the lower light intensity the numbers of flights made by S.oryzae weevils were much lower

TABLE 42

Number of flights made by released weevils per 15 minutes at constant temperatures and light intensities.
(Four combinations)

Light intensity (L.F.L.)	Temperature (°C.)	Age (weeks)	No. flights/100 weevils/15 min.			
			S. zea-mais		S. oryzae	
			Males	Females	Males	Females
1.85	31°	2	151	105	-	-
1.85	36°	"	259	128	-	-
2.60	31°	"	256	176	-	-
2.60	36°	"	343	221	-	-
Total			1009	630	-	-
1.85	31°	4	215	203	84	62
1.85	36°	"	369	291	150	149
2.60	31°	"	534	387	324	289
2.60	36°	"	799	535	493	452
Total			1917	1416	1051	952

than those made by S.zea-mais. When one both or both of the factors applied were high, the increase in the rate of flights was significantly higher in S.oryzae than in S.zea-mais, at the upper 5% level ($P < 0.001$). The only exception was in the males of both species when temperature alone was raised ; the difference in the increase of the rates of flights was then not significant ($P > 0.10$).

When comparing the 4-week old weevils of S.oryzae with the two weeks old weevils of S.zea-mais, it was found that at the low light intensity the total numbers of flights of S.oryzae weevils were smaller in both sexes than in S.zea-mais. In contrast, at the higher light intensity, the total numbers of flights in both sexes of S.oryzae were greater than in the corresponding sexes of S.zea-mais. The sum total of the numbers of flights of the weevils in the 4 sets of experiments indicated a significant difference between the male and the female weevils of S.zea-mais, as compared with the difference between the two sexes of S.oryzae weevils at the upper 5% level ($P < 0.001$).

'Attempts to fly' as well as actual 'flights' were also recorded. The numbers of attempts to fly made by the weevils of the two species are summarized in TABLE 43. The 4-week old weevils of S.zea-mais were far more efficient than the 2-week old ones in all the sets of experiments. In both ages the additional total numbers of attempts to fly per 400 male

TABLE 43

Number of attempts to fly made by Released Weevils per 15 minutes at constant temperatures and light intensities (four combinations)

Light intensity (L.F.L.)	Temperature (°C.)	Age (weeks)	No. of Attempts to Fly/100 Weevils /15 minutes.			
			S.zea-mais		S.oryzae	
			♂♂	♀♀	♂♂	♀♀
1.85	31°	2	20	25	-	-
1.85	36°	2	34	18	-	-
2.60	31°	2	55	42	-	-
2.60	36°	2	69	68	-	-
Total per 400 Weevils			178	153		
1.85	31°	4	78	56	45	25
1.85	36°	4	108	80	98	93
2.60	31°	4	116	38	175	194
2.60	36°	4	128	180	272	200
Total per 400 Weevils			430	354	590	512

weevils were higher than in the females. On the other hand, the 4-week old weevils of S.oryzae were found to be less active flyers than the corresponding weevils of S.zea-mais at 31 ± 0.5°C. and 1.85 L.F.L. The rate of increase in the frequency of the attempts to fly of S.oryzae with the rise in temperature or of Light intensity or of both, was significantly higher than in S.zea-mais at the upper 5 % level. At the higher light intensity the total numbers of attempts made by S.oryzae were much greater than those by S.zea-mais. The sum total of attempts (400 weevils) were greater in S.oryzae than in S.zea-mais, but the inter-sexual differences were not significantly different in both species at the upper 5 % level.

3. Duration of Flight of Suspended Weevils

The behaviour of suspended weevils in flight was studied by recording the total duration of flight of individual weevils in tests lasting 5 minutes. The weevils did not fly continuously, but normally they flew for short periods which were interrupted by short intervals of rest. The maximum and minimum duration of single flights, and the number of flights made by the weevils in 5 minutes were also measured.

a) S.zea-mais :- The total duration of flights per test of the male weevils varied between 64 and 187 seconds in 5

minutes, the mean value being 118.5(sec. per 5 min.). The mean duration of flights of the female weevils was 109.9 sec. per 5 min. (ranging between 55 and 225 sec. per 5 min.) (TABLE 44). The variance of the two means was not significant.

The mean number of flights in 5 minutes was 38.9 in the males and 33.2 in the females ; the variance of the two means was not significant.

The maximum duration of single flights ranged between 4 and 8 seconds in the males , and between 4 and 15 seconds in the females, the means being 5.8 and 6.7 seconds respectively. These did not vary significantly from one another. The mean minimum duration of single flights was 1.6 seconds in both sexes (ranging between 1 and 2 seconds).

b) S.oryzae :- Suspended S.oryzae weevils showed a clear difference in behaviour from those of S.zea-mais. The mean numbers of flights in the male and the female weevils of S. oryzae were 15.7 and 14.5 per 5 minutes respectively (TABLE 45). The variance of these two means was not significant, but when compared with the corresponding mean values in the male and the female weevils of S.zea-mais the variances of means were highly significant ($P < 0.001$).

The mean maximum duration of single flights, on the contrary was much higher in S.oryzae than in S.zea-mais ; the means were 21.6 and 13.6 seconds in the males and the

YTABLE 44

Duration of flight per 5 minutes of Suspended Weevils of *S.zea-mais* (4- weeks old) at 32°C. and 2.6 L.F.L.

No. of Flights per 5 minutes		Duration of Single Flights (sec.)				Total Duration of Flights/ 5 minutes (sec.)	
		Maximum		Minimum			
♂	♀	♂	♀	♂	♀	♂	♀
42	30	5	5	1	2	88	69
27	24	4	5	1	1	64	55
40	28	8	15	2	2	187	225
37	48	6	5	2	2	162	110
49	38	5	7	2	2	94	105
35	42	7	4	2	1	105	120
34	29	5	7	1	2	95	150
42	32	4	8	1	1	115	105
44	35	6	6	2	2	130	78
39	26	8	5	2	1	145	82
Mean							
38.9	33.2	5.8	6.7	1.6	1.6	118.5	109.9

TABLE 45

Duration of flight per 5 minutes of suspended weevils of *S.oryzae* (4 weeks old), at 32°C. and 2.6 L.F.L.

No. of flights per 5 minutes		Duration of single flights (sec.)				Total duration of flights per 5 minutes (sec.)	
		Maximum		Minimum			
Males	Females	Males	Females	Males	Females	Males	Females
10	14	25	8	5	2	95	56
14	29	12	10	3	1	71	61
11	8	55	12	3	3	121	60
20	27	8	5	2	1	79	51
8	3	55	65	1	5	85	155
4	12	60	4	3	3	206	37
24	20	3	8	1	1	48	41
25	10	7	30	1	2	73	104
12	13	12	20	2	3	43	104
17	15	5	6	1	3	41	62
12	8	35	5	3	3	137	30
33	16	14	4	1	1	161	37
18	12	8	4	2	1	60	35
12	16	4	10	1	1	23	35
Mean 15.7	14.5	21.6	13.6	2.1	2.1	88.8	62.0

females of S.oryzae ; these did not vary significantly from one another. The variance of means of maximum durations of single flights in both species was highly significant ($0.01 > P > 0.001$), when the males were compared, but not significant in the females.

The minimum durations of single flights varied between 1 and 5 seconds in the males and the females, the mean being 2.1 in both sexes.

When comparing the same sexes of both species, the variance of means was found to be not significant in either sex.

The total durations of flights in 5 minutes were 88.8 sec. and 62.0 sec. in the males and the females of S.oryzae; the variance of the two means was not significant. The variance of these two means when compared with those of the corresponding sexes of S.zea-mais were found to be highly significant.

4. The Wingbeat of the Weevils

The rate of wingbeat at 25 C. and 70 % R.H., in still air and very low light intensity, of S.zea-mais weevils varied between 4300 and 4600 (R.P.M.) in both sexes ; the means being 4445 and 4420 in the males and the females respectively (TABLE 46). The variance of the two means was not significant. The mean rates per second (R.P.S.) were 74.08 and 73.67 in the males and in the females.

TABLE 46

The wingbeat of Sitophilus weevils at 25°C., 70 % R.H. in still air

Rate of wingbeat per minute (R.P.M.)			
S. zea-mais		*S. oryzae*	
Males	Females	Males	Females
4400	4300	5000	5200
4500	4500	5300	5100
4600	4400	5000	5300
4500	4300	5200	5900
4500	4450	5100	5100
4350	4400	5050	5350
4550	4600	5250	5000
4300	4350	5200	5250
4450	4400	5100	5000
4300	4500	5150	5100
Mean 4445	4420	5135	5220
Mean rate per second(R.P.S.)			
74.08	7367	85.58	87.00

The rate of wingbeat per minute of S.oryzae weevils in the same conditions , varied between 5000 and 5300 R.P.M. in the male weevils, and between 5000 and 5900 R.P.M. in the females ; the means were 5135 and 5220 R.P.M. respectively (TABLE 46). The variance of the two means was not significantly different. The rates per second were 88.58 and 87.00 R.P.S. in the males and the females.

5. The Relation between the Weight of the Weevil and the Size of the Hind Wing

The body weight of S.zea-mais weevils varied between 2.25 and 3.26 mg. in the males, and between 2.26 and 3.38 mg. in the females ; the corresponding mean values being 2.79 and 2.92 mg. (TABLE 47). The size of the wing varied between 3.131 and 3.766 square millimeters, in the male weevils and between 3.038 and 3.720 square millimetres in the females ; the corresponding means being 3.481 and 3.351 mm^2. The relation between the mean size of the wing and the mean body weight in the two sexes was not significantly different at the upper 5% level.

The body weight of S.oryzae weevils varied between 1.20 and 2.15 mg. in the males and between 1.21 and 2.26 mg. in the females ; the corresponding mean values being 1.607 and 1.714 mg. (TABLE 48). The size of the wing varied between 1.440 and 2.191 mm^2. in the males and between

TABLE 47

The body weight and the size of the wing of S.zea-mais

	Males		Females	
	Weight (mg.)	Size of wing (mm^2)	Weight (mg.)	Size of wing (mm^2)
	2.95	3.649	2.68	3.038
	2.57	3.483	2.99	3.544
	3.01	3.615	3.38	3.720
	3.24	3.644	2.56	3.260
	3.17	3.766	3.12	3.447
	2.41	3.197	2.78	3.167
	3.06	3.649	2.44	3.110
	2.30	3.068	2.26	3.068
	2.34	3.131	3.18	3.331
	2.82	3.580	2.86	3.200
	3.26	3.736	2.75	3.281
	2.90	3.615	2.94	3.475
	3.00	3.580	3.32	3.665
	2.63	3.341	3.25	3.491
	2.25	3.161	3.30	3.463
Mean	2.79	3.481	2.92	3.351

1.420 and 2.298 in the females, the means being 1.787 and 1.808 respectively. The relation between the mean size of the wing and the mean body weight in the two sexes was not significantly different at the upper 5% level of significance.

Next, the two species were compared, and the relation between the size of the wing and the body weight was not found to differ significantly in the same sexes at the upper 5 % level.

6. The Relative Length of the Hind Wing to the Elytron in Sitophilus Weevils

The ratio of the length of the hind wing to the elytron (H / E) in the male S. zea-mais weevils varied between 2.000 and 2.108, and in the females between 2.000 and 2.100 ; the corresponding mean values being 2.065 and 2.052 (TABLE 49). The H/E ratio in the male S.oryzae weevils ranged between 1.921 and 2.034, and in the females between 1.935 and 2.032; the means being 1.990 and 1.975 respectively (TABLE 49). The analyses of variance of the means, showed no significant difference between the two sexes of the same species. When the same sexes of different species were compared, the variances of the means were also not significant.

TABLE 48

The body weight and the size of the wing of S.oryzae Weevils

Males		Females	
Weight mgs.	Size of Wing mm^2.	Weight mgs.	Size of Wing mm^2.
1.20	1.440	1.21	1.420
1.24	1.450	1.24	1.434
1.32	1.494	1.32	1.464
1.34	1.614	1.38	1.523
1.36	1.681	1.50	1.694
1.48	1.691	1.62	1.715
1.50	1.782	1.68	1.772
1.52	1.786	1.78	1.802
1.64	1.843	1.82	1.863
1.68	1.812	1.85	1.883
1.75	1.89	1.86	1.904
1.86	1.952	1.95	1.932
1.94	1.989	2.08	2.185
2.12	2.187	2.16	2.232
2.15	2.191	2.23	2.298
Mean 1.607	1.787	1.714	1.808

TABLE 49

H / E ratio in *S. zea-mais* and *S. oryzae* weevils

H/E ratio	*S. zea-mais*		*S. oryzae*	
	Males	Females	Males	Females
Minimum	2.000	2.000	1.921	1.935
Maximum	2.108	2.100	2.034	2.032
Mean	2.065	2.052	1.990	1.975
Number of insects examined	32	43	44	40

H = Direct length of expanded hind wing from the basal point to the tip.

E = Length of elytron along the long axis

E. D I S C U S S I O N

It was of interest to find that 2-week old weevils of S. oryzae were unable to fly, even when suspended from the pronotum. Several attempts, however, were made by unfolding their hind-wings, but no real flight occurred. S.zea-mais weevils, on the other hand, were capable of flight at that age, when suspended or released, although not as efficiently as the 4-week old ones.

The ' tarsal reflex ' mentioned by Fraenkel (1932) , i.e. the initiation of flight due to the loss of contact by the tarsi, known in all the insects tested, was clearly seen in the two species of the rice weevils. The variance of means of time taken to initiate flight, and the number of flights per minute made by suspended and released weevils differed highly significantly in the two species in the same conditions of temperature and light intensity.

The present work shows that temperature and light intensity are among the major factors which induce the flight of the rice weevils. The increase in temperature from 26° to 40° C., strikingly decreased the mean time taken to initiate flight of the suspended weevils of both species. When the light intensity was increased from 1.85 to 2.60 L.F.L., S.oryzae weevils exhibited no difference in behaviour from that in the lower light intensity, whereas S.zea-mais weevils showed a marked

response to the high light intensity at lower temperatures. It is not informed that yet higher light intensities (e.g. those of bright sunlight) are unable to influence flight activity of S. oryzae , but only that no effects were detected under the experimental conditions. S. oryzae weevils were more efficient flyers than S. zea-mais of the same age when suspended at the low light intensity of 1.85 L.F.L. , but less efficient at the high light intensity of 2.6 L.F.L. The analysis of variance of means of the time taken to initiate flight differed highly significantly in both species.

Similarly, the released weevils exhibited a clear response to the increase in temperature or in light intensity. In both species , the total numbers of flights at the high light intensity 2.6 L.F.L. and the low temperature $31 \pm 0.5^{\circ}C$. were greaterthan the total numbers of flights at the low light intensity 1.85 L.F.L. and the high temperature $36 \pm 0.5^{\circ}C$. It may be concluded that light plays a more important role than temperature in controlling the flight of the weevils. By comparing the 4-week old weevils of both species, it was found that the total numbers of flights (of 100 weevils per 15 min.) in the male and the female weevils of S. zea-mais were much higher than those in the corresponding sexes of S. oryzae. The total numbers of flights made by the weevils indicated a highly significant difference between the two sexes of S. zea-mais (the males being more efficient) when compared with the

difference between the sexes of S.oryzae at the upper 5 % level ($P < 0.001$).

The numbers of attempts to flight made by S.oryzae weevils were less than those made by S.zea-mais at the low temperature and low light intensity, but the rate of increase in the frequency with the rise in temperature or in light intensity or in both was significantly higher in S.oryzae than in S.zea-mais at the upper 5 % level.

The mean durations of flights of suspended weevils were (were) not significantly different in the two species. The flights of the weevils were not continuous, but normally the single flights lasted for a few seconds and were interrupted by periods of rest.

Some factors which may affect the flying ability of insects such as the wingbeat, the relation between the size of the wing and the body weight, and the relation between the length of hind wing to the length of the elytron, were found to be not significantly different in the two species. The fact that S.zea-mais weevils are more efficient flyers than S.oryzae may be attributed to other physiological factors such as muscular power, internal body temperature or greater sensitivity to external stimuli, transmitted through the activity of sensory receptors such as those described by Reuter (1936) on the elytra and wings of Calandra species (Sitophilus). She described two types of branched

hairs accompanied by gland cells and sensory pit organs on the elytra ; and sensory hairs and sensory pit organs on the hind wings.

The effect of air currents on flight of some insects is of great importance, for instance in Muscina stabulans (Hollick,1940) , the deflection of the antennae is perceived by Johnston's organ, on the second antennal segment, which acts as an aerodynamic sense organ, which is sensitive to wind speed. Again, Schistocerca gregaria adult possesses five pairs of sensitive hair beds on the head, described by Weis-Fogh (1956), which are also wind-sensitive. The influence of air currents, of known wind-speed, on the flight activity of the rice weevils was not studied.

The importance of temperature on the flight of some insects was described by Waloff and Rainey (1951) who stated that the minimum thoracic temperature for forced flight of Schistocerca gregaria was 20°C. and that thoracic temperatures well above 25°C. were necessary for sustained flight. They concluded that sustained flight has been recorded in the absence of sunshine at air temperatures of 23°C. by day and at air temperatures of 25°C. or over by night. Weis-Fogh (1956), mentioned that in the absence of radiant heat, the thoracic temperature of Schistocerca gregaria corresponded to the air temperature plus an amount due to the metabolism of the wing muscles; at normal lift and flying speed this

this increase was 6° to 7°C. An alteration in air temperature should therefore produce a similar alteration in the thoracic temperature. Concerning the effect of light on the locust behaviour, he mentioned that illuminating the locust with short-wave ultraviolet light invariably disturbed and usually inhibited flight.

Mittelstaedt (1948 and 1950) in his experiments on the dragonflies concluded that they always flew with their dorsal surface toward the source of light.

Williams (1933) mentioned that high-pitched sounds immediately intensified the flight of the desert locusts but only for a short time.

The present work throws some light on the occurrence of the rice weevils in the corn fields mentioned in literature. Their presence in the fields in summer may be partially explained by stimulating the effects of the rise in temperature and of light intensity on their flight activity. The final attraction to the standing crops is probably linked with the olfactory sense, which has not been investigated in this connection.

VI. Reactions of Sitpphilus Weevils to Relative Humidity

A. Introduction and Review of Literature

The response of terrestrial arthropods to humidity varies greatly from one animal to another. A distinct difference in such behaviour, may exist even between species that are taxonomically comparatively closely related. Two major factors seem to control the humidity reactions of the nals:a)" long-range " reaction which has evolved as an adaptation to the condit-ions in which they normally survive and b) a "short-range" reaction to relative humidity which depends on the humidity at which the tested individuals are kept before the experiment (i.e. preconditioning).Most animals require to keep a certain more or less constant proportion of water in their bodies within fairly narrow limits. Some animals live in habitats which are so damp that they have to prevent the accumulation of excessive amounts of water in their tissues, while others live in places so dry that they can survive there only because they possess remarkably effective mechanisms for reducing the amount of water lost from the body (Andrewartha and Birch,1954). Dethier and Chadwick (1948) mentioned that the response to humidity is frequently determined by the state of water balance of the

insect and the degree of starvation.

Many workers have studied thoroughly the humidity reactions of many adult insects as well as that of some immature stages. Experiments usually involve observations on the reactions of insects placed in an apparatus which provides a humidity gradient, such as the alternative humidity chamber (Gunn & Kennedy, 1936), or in an elaborate olfactometer which provides the small arena with two streams of air at different relative humidities (Willis and Roth,1950,a) . In this way aggregation responses have been studied and the orientation of the insects in the arenas involved orthokinesis, klinokinesis and klinotaxis (Fraenkel and Gunn,1940).

Examples of insects that normally show a preference to the dry side of the humidity gradient are those of Anopheles gambiae and A. funestus (De Meillon,1937), Locusta migratoria migratorioides (Kennedy,1937), Culex fatigans(Thomson,1938), Blatta orientalis (Gunn and Cosway,1938), Tenebrio molitor (Pielou and Gunn,1940), Pediculus humanus corporis (Wigglesworth,1941), Tribolium castaneum (Willis and Roth,1950,a) , S.granarius (Roth and Willis,1951,b); Smereka and Hodson , 1959), Drosophila melanogaster (Syrjämäki,1962) and those of Tenebrio molitor larvae(.Perttunen and Lahermaa,1962).

Some of these insects when desiccated for different periods of time, showed a reverse reaction to humidity i.e. they moved to the wet side of the humidity gradient.

Desiccation for five hours at 24°C. reversed the dry reaction of Drosophila to a preference for moist air (Perttunen and Syrjamaki,1958), whereas Tenebrio larvae showed a preference for the wet side only after two weeks of desiccation. The fact that Tenebrio larvae are extremely resistant to severe dryness was attributed to their ability to form metabolic water from the body fats (Buxton,1930; Leclercq,1948). 40 % of the desiccated Tenebrio larvae were able to survive for five weeks according to Perttunen and Lahermaa(1962). The normally fed adults and larvae of the grasshoppers Melanoplus bivittatus (Say) and Camnula pellucida (Scudd.) preferred the drier side, and the starved ones and insects during moulting period, the wetter of two humidities (Riegert,1959).

On the other hand, certain undesiccated animals exhibited normally a positive reaction to higher humidities, for instance, Porcellio scaber (Gunn,1937 ; Waloff,1941), the wireworms of the genus Agriotes (Lees,1943), Musca domestica larvae (Hafez , 195), Stomoxys calcitrans larvae (Hafez and Gamal-eddin, 1961), and the first and the fourth-instar hoppers of Schistocerca gregaria (Aziz, 1957).

The instensity of humidity reaction of any particular species, depends on the alternatives offered and their position on the humidity gradient scale. For instance Musca larvae are indifferent to humidity below 50% R.H./while near saturation a difference of 5% is sufficient to ensure a complete avoidance of the drier side (Hafez, 1950). Culex

distinguishes difference of 1% R.H. at the highest range of the humidity scale, whereas between 30% and 35% R:H., a difference of 50% is necessary to elicit a significant response(Thomson, 1938). Tenebrio molitor larvae can discriminate between 100 % and 99.5 % R.H. (Perttunen and Lahermaa,1962). Schistocerca hoppers move to higher humidities below 66 % R.H., and to lower humidities in a gradient of 66 - 100 (Aziz,1957).

Several attempts have been made to identify humidity receptors in various arthropods. Blumenthal (1935) working with spiders concluded that the tarsal organs (deep pits enclosing one or more peg-like sensilla) received moisture stimuli. Gunn (1937) was unable to identify the hygroreceptors in the wood-louse Porcellio scaber, but found some indication that they were located in the thoracic region. Unsuccessful attempts to locate the sites of hygroreceptors have been made by Thomson (1938) in the mosquito Culex fatigans, and by Gunn and Cosway (1938) on Blatta orientalis ; the latter workers suggested that these receptors may be located on the antennae. Waloff (1941), suggested that in the isopods, loss of water through the integument, and the consequent concentration of the body fluids may initiate the humidity reaction and that the proprioceptors could be involved in this type of mechanism. In the wireworms Agriotes obscurus and A. lineatus the antennae and maxillary and labial palps were found to be necessary for normal humidity reactions to take place(Lees,1943).

The humidity receptors of the spider beetle Ptinus tectus have been localised on the antennae but not identified (Bentley,1944). Pielou (1940) identified the humidity receptors of the adults of the mealworm Tenebrio molitor as being the pit peg organs on segments 1 - 10 and peg organs on segments 6 - 11 of the antennae. Begg and Hogben (1946), suggested that surface cones on the antennae of Drosophila melanogaster were hygroreceptors and that humidity receptors on other parts of the body may also be present. Haller's organs on the fore-legs of the sheep tick Ixodes ricinus were found by Lees (1948) to be necessary for the humidity response ; some evidence was presented to indicate that the trichoid sensilla in the anterior pit of Haller's organ were the receptors. Bursell and Ewer (1950) located the sites of these receptors on the body surface and the antennae of the onychophoran Peripatopsis moseleyi. Bar-Zeev (1960), proved experimentally the presence of hygroreceptors on the antennae of Aedes aegypti but gave no description of these organs.

The humidity receptors have been investigated in a number of species morphologically and histologically. Experimental evidence, however, was gained by the amputation of the parts bearing these sense organs with the result that the animals lost their response to humidity. Most frequently they are located on the antennae in the form of tuft organs, each bearing four minute hairs, as in Pediculus humanus corporis

(Wigglesworth,1941), or on the ventral surface of the thorax as in Musca domestica larva (Hafez,1950); or in the form of thin-walled trichoid sensilla and basiconic sensilla (peg organs) as those found on the antennal club segments of Tribolium species (Roth and Willis,1951,a). The same authors (1951,b) located the hygroreceptors on the antennae of a number of coleopterous adults and larvae, and described them as trichoid sensilla on the apex of the terminal segment of S.granarius weevils, basiconic and trichoid sensilla on segments 9-11 of Dermestes ater and Attagenus piceus beetles, basiconic sensilla on segments 8-10 of Rhizopertha dominica beetles, trichoid sensilla on segments 9-11 of Laemophoeus ferrugineus beetles, placoid and basiconic sensilla on segments 9-11 of Latheticus oryzae beetles, placoid and basiconic sensilla on the second antennal segment of Tenebrio obscurus and Dermestes ater larvae. In the latter, coeloconic sensilla could be found on the second segment. Roth and Willis(1952,b) discovered trichoid and basiconic sensilla on the two last antennal segments of the male Aedes aegypti, while in the female they were present on the 13 flagellar segments. Differences between the sexes also existed in Blatella germanica where the trichoid and basiconic sensilla were more frequent on the male antennae (segments 3-13) than in the female ones (Roth and Willis,1952,b). Aziz (1958), concluded that the sensory organs responsible for the humidity reactions of the

first and fourth instar hoppers of Schistocerca gregaria are most probably the coeloconic and basiconic sensilla found on the antennae. The humidity receptors of the grasshoppers Melanoplus species and Camnula species were located on the first eight antennal segments by Riegert (1959). Syrjämäki (1962) came to the conclusion, from amputation experiments on Drosophila melanogaster that the importance of the appendages bearing humidity receptors was in the following order : 1) antennae, 2) maxillary palps, 3) proboscis.

In the present work the humidity reactions of the three species of Sitophilus namely S.granarius, S.zea-mais and S. oryzae were tested, and the sites of the hygroreceptors were identified. The behaviour of S.granarius weevils was also discussed and compared with the previous work on this species carried out by Roth and Willis (1951,b) and by Smereka and Hodson (1959) who used different types of humidity gradient apparatus.

B. Material and Methods

1) Humidity gradient apparatus: The method used for studying the humidity reactions was based on the same principle as that suggested by Gunn and Kennedy (1936); but the alternative chamber was designed to have a very small height so that the intermediate zone was rendered very narrow, and the relative humidity at the roof of the chamber was similar to that on the

false floor. The apparatus (Fig. 52) was constructed as follows : a circular perforated zinc plate 13 cm. in diameter was cut and covered with muslin which was fixed around the edges by means of " durofix ". The arena was enclosed by the lid of a plastic Petri dish 9.2 cm. in diameter and 7 mm. deep fixed to the false floor by durofix. In this lid there was a hole 1 cm. in diameter for inserting the insects onto the false floor. A similar lid from which the top had been cut off by means of a hot needle, was fixed to the lower side of the false floor. The durofix became odourless after a few days. A larger glass Petri dish 14 cm. in diameter, covered the entire apparatus so as to isolate the arena from the outside atmosphere. A glass rod 5 mm. in diameter embedded in wax, divided the lower compartment into two equal ones. On either side of it were placed 4 semicircular thicknesses of filter paper soaked in 3 cc. of KOH solution giving the required humidity (Solomon,1951). The lid of the large Petri dish contained a central hole just above that of the plastic one. Both holes were covered by small glass covers. The insects were transferred to the arena inside a dry glass funnel inserted through the two holes. It was possible to slide the inner glass cover by using a glass rod having a rubber tip, without raising the large lid which may have led to disturbance of the

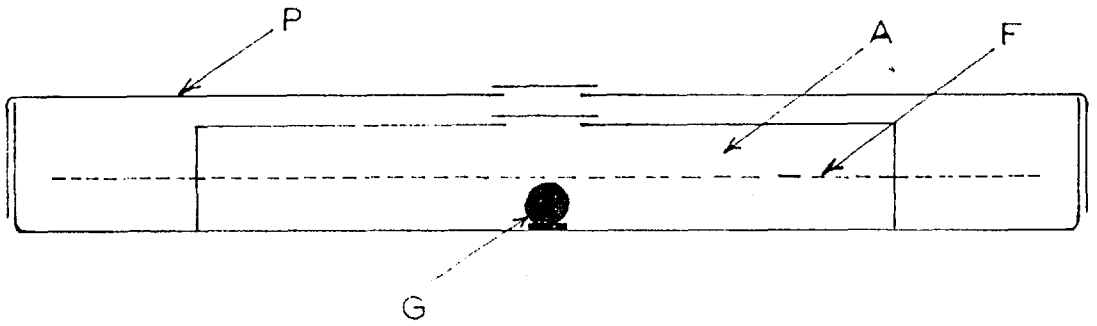


Fig. 52 : Section in alternative humidity chamber; A, arena; F, false floor ; G, glass rod ; P, petri dish.

humidity equilibrium once it has been established. After each experiment the insects were removed by shaking the apparatus or by a pair of forceps. Relative humidities in the two sides of the alternative chamber were measured by means of cobalt thiocyanate papers (Solomon,1957) . It was found that the observed humidities were very close to the theoretical values. The zone of sharpest gradient was about 1 cm. wide at the mid-line. The small height of the apparatus was the main factor in achieving such a narrow intermediate zone, on the false floor as well as on the roof of the chamber on which the weevils used to wander. Humidity equilibrium was found to be reached within half an hour.

The positions of the weevils were recorded every three minutes for a period of half an hour. The index of reaction or (I.R.), is a measure of the intensity of the humidity response, and signifies the mean excess percentage of position records in the lower humidity of the sum of readings in each experiment ; this index for each test was calculated from the formula :

$$\frac{(D - W)}{N} \times 100$$

in which ' D ' and ' W ' are the sums of successive positions occupied by the weevils in the dry and wet side

respectively, and ' N ' is the total possible number of position records per test (Willis and Roth,1950,a). Thus a positive I.R. value indicates preference to the drier side.

Experiments were carried out at room temperature of 20 ± 1°C., and uniform light intensity of 1.1 log foot lamberts, measured with an SEI exposure photometer. Uniform illumination was achieved by carrying out the experiments in a dark room with a constant source of light above the apparatus. The latter was placed below a white-painted cage, 25 X 25 X 25 cm., with a ground-glass top, provided with a narrow side-slit for watching the insects. The position of the apparatus was reversed, in each set of experiments, at four sets of 90 to cancel any bias due to variations in light.

2) Method of preconditioning the weevils : Three sets of experiments were conducted, on insects which were previously conditioned and starved for 24 hours in desiccators at 0 % R.H. and at 100 % R.H. and at 25°C. The other experiments were carried out on the weevils reared at 25°C. and at 70 % R.H. Every group of these preconditioned weevils was offered the following combinations : 0 - 100 % R.H. ; 0 - 20 % R.H. ; 40 - 60 % R.H. ; and 80 - 100 % R.H. The actual relative humidities differed

very slightly from these theoretical values. In each experiment 100 weevils were used, 10 at a time , so that every I.R. value represented 1000 position records. Control experiments were carried out using the same humidities on both sides of the alternative chamber (5 with the low, and 5 with the high relative humidity).

The experimental insects were 3-4 weeks old and chosen at random from standard cultures.

3) Amputation of antennal segments : In order to locate the position of the hygroreceptors in every species, the antennal segments were amputated by means of a tiny sharp " Paragon " blade number 15 . The weevils were operated while under continuous anaesthesia by carbon dioxide , which lasted about 1 or 2 minutes. The insects were then allowed to recover in the constant temperature room for 24 hours before their reaction to the humidity gradient of 0 - 100 % R.H. was tested.

Whole mounts of the antennae were partially bleached with Diaphanol, cleared in methyl cellosolve and mounted in Euparal.

4) Loss of weight on desiccation : In order to explain the significance of the difference in the humidity behaviour of the three species, especially of the desiccated weevils, another experiment was conducted to determine

the loss in weight of the weevils due to desiccation at 0 % R.H. and at 25°C. for several days. Simultaneously the number of dead weevils was recorded daily. The rate of loss in weight was calculated for the living insects only. For this purpose 100 weevils of each species were cleansed from wheat-dust by keeping them for a few minutes on thin layers of cotton wool, and then weighed in weighing bottles using an Oertling balance. The weevils were confined in 1 lb. jars covered with muslin fitted with rubber bands, placed inside the desiccators with KOH pellets. Every 24 hours the dead insects were counted and rejected and the living ones were weighed and replaced in the desiccators.

C. Results

1) S. zea-mais

a) Insects preconditioned at 100 % R.H. and 25°C. for 24 hours :- It was noticed that the weevils when kept in such a saturated atmosphere tended to aggregate in clusters, and that their activity diminished to a great extent. When they were introduced into the alternative chamber they showed a marked preference for the dry side within the first minute of the experiment. The highest

values for the index of reaction were obtained when the weevils were given the choice between the two extreme humidities of the gradient namely 0 % and 100 % R.H.; the mean I.R. being + 70.7 ± 4.7 (TABLE 50 and Fig. 53).

When the relative humidities differed by 20 % , the insects showed a definite reaction to the drier side , although this was less pronounced than in the gradient of a wide range. The I.R. values were 43.7 ± 5.1 , 43.5 ± 3.9 and 51.3 ± 4.6 , at the gradients 0 - 20 % , 40 - 60 % and 80 - 100 % respectively (TABLE 50 and Fig. 53).

b) Insects previously kept at 70 % R.H. and 25°C.: The reaction to the dry side was nearly as strong as in the previous experiment at the higher scale of the humidity gradient. The mean I.R. values were 63.9 ± 4.8 , 42.3 ± 2.4, 42.5 ± 3.5 and 31.8 ± 2.7 , at the gradients 0 - 100 % , 0 - 20 % , 40 - 60 % and 80 - 100 % (TABLE 51 and Fig. 54).

c) Insects preconditioned at 0 % R.H. and 25°C. for 24 hours : The reaction to the dry side disappeared after the weevils had been desiccated for 24 hours. Moreover, when they were offered the gradient of 0-100 %

TABLE 50

Index of reaction of S.zea-mais weevils preconditioned at 100 % R.H. and 25°C. at different humidity gradients

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 81	+ 56	+ 45	+ 40
6	66	34	38	56
9	78	39	43	54
12	68	34	36	42
15	74	44	51	44
18	76	49	48	51
21	68	52	36	57
24	61	52	54	50
27	59	41	40	60
30	76	36	44	59
Mean ± S.E.	+ 70.7±4.7	+ 43.7± 5.1	+43.5±3.9	+51.3±4.6
Mean control	- 1.3	+ 1.2	+ 2.0	+ 2.4

TABLE 51

Index of reaction of S. zea-mais weevils previously kept at 70 % R.H. and 25°C. offered different humidity gradients.

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 87	+ 46	+ 36	+ 31
6	69	41	46	31
9	58	41	43	35
12	72	39	52	27
15	62	47	49	37
18	59	41	40	31
21	52	35	42	32
24	59	47	44	30
27	65	43	34	25
30	56	43	39	39
Mean± S.E.	+63.9±4.8	+42.3±2.4	+42.5±3.5	+ 31.8±2.7
Mean control	+ 5.0	- 0.2	- 2.2	+ 1.0

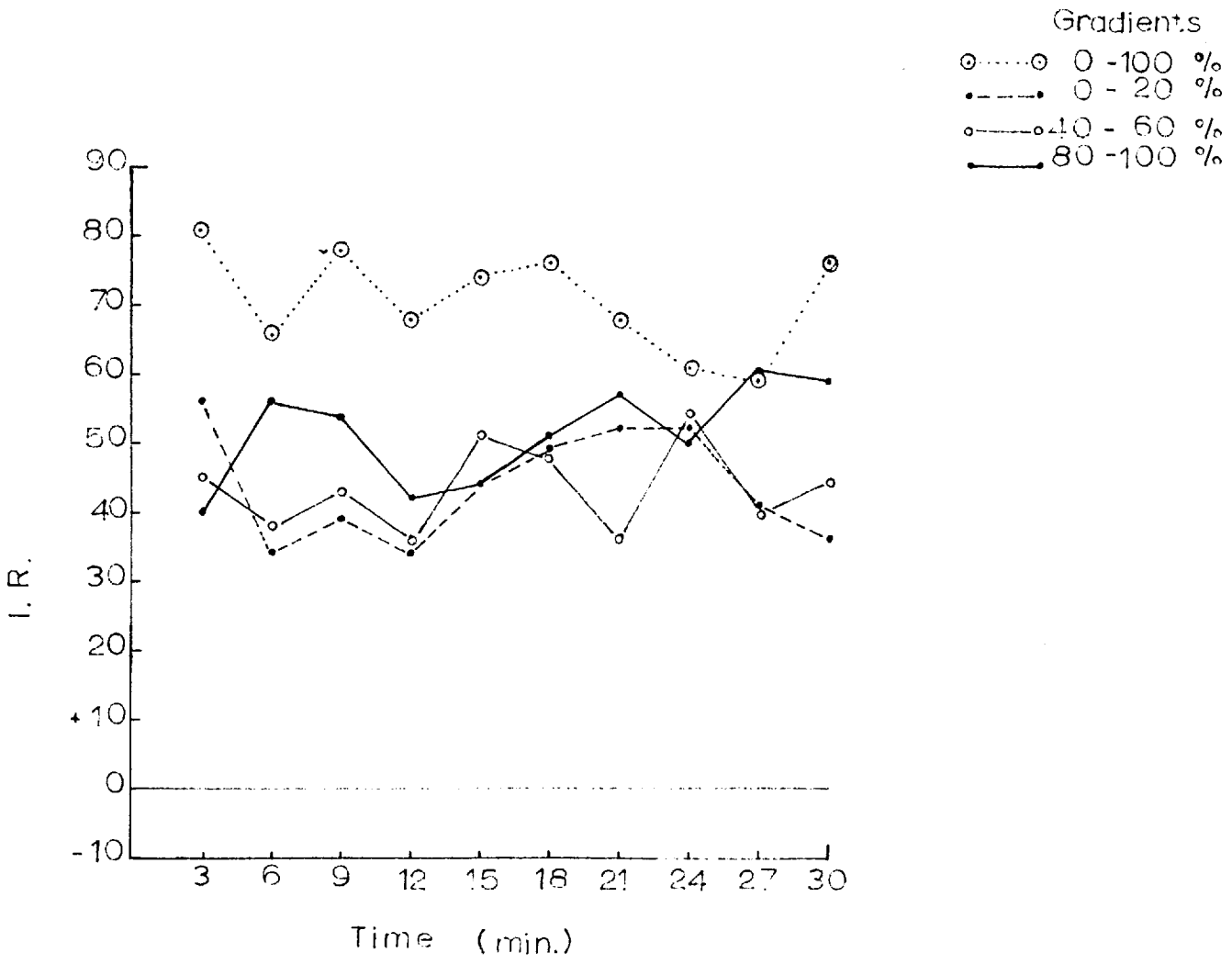


Fig. 53 : Index of reaction of Sitophilus weevils in different humidity gradients, and preconditioned at 100% R.H.

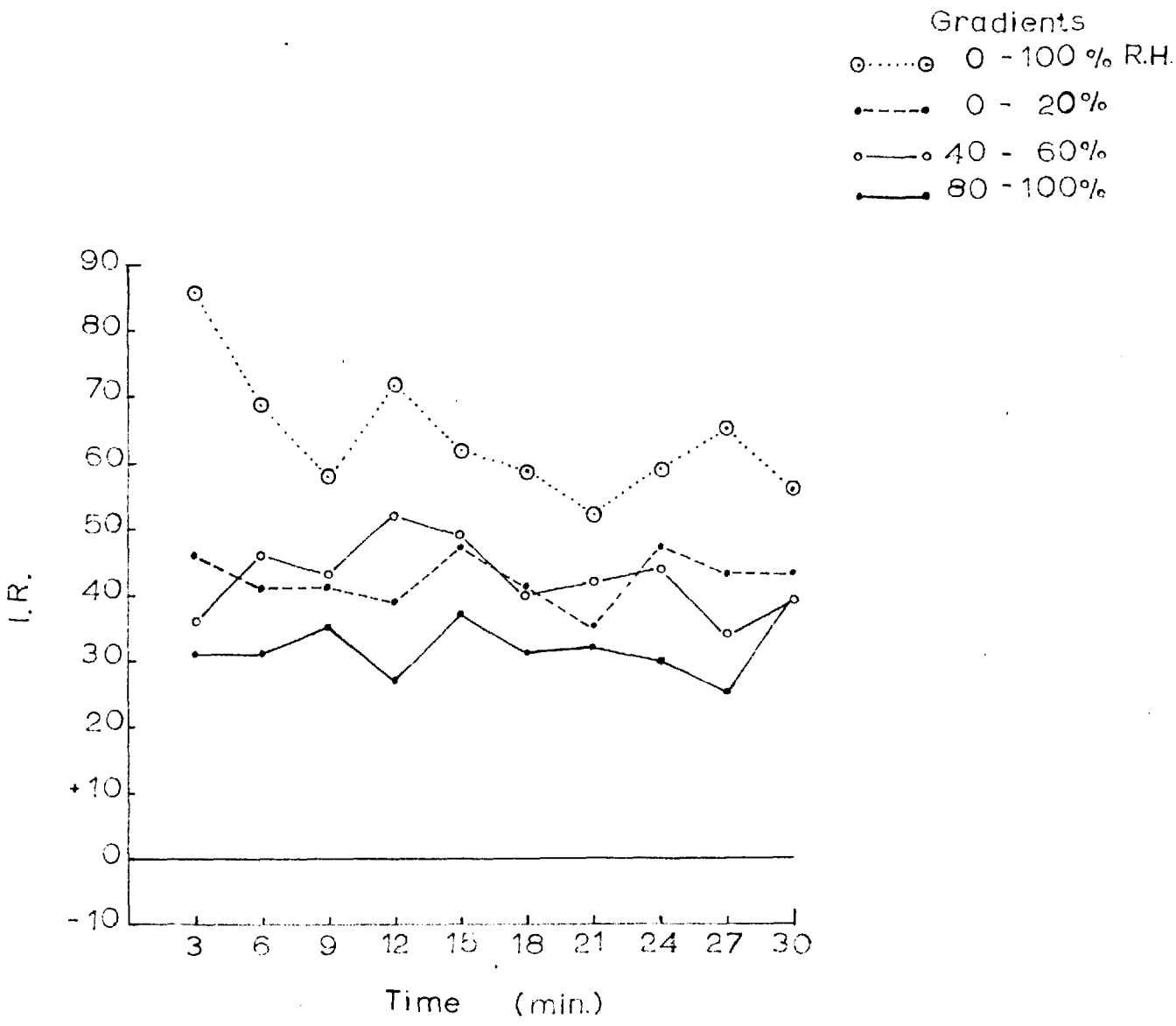


Fig. 54 : Index of reaction of S.zeamais weevils in different humidity gradients, and preconditioned at 70% R.H.

they did not show any preference for either side, the mean I.R. being + 0.2 ± 1.6 . However, a tendency to move towards the wet side was observed in the gradients of 0-20 % and 40 - 60 % , the mean I.R. values being - 11.8 ± 5.2 and - 12.6 ± 4.1 respectively. The strongest reaction to the wetter side was clearly achieved in the gradient of 80 - 100 % , where the mean I.R. reached the value of - 39.8 ± 5.6 (TABLE 52 and Fig. 55).

The effect of preconditioning on the behaviour of the insects can be illustrated in Fig. 56 which shows the reactions of weevils conditioned at different humidities and placed in the humidity gradient of 0 - 100 %.

2) S. oryzae

a) Insects preconditioned at 100 % R.H. and 25°C. for 24 hours :- The positive reaction to dry conditions of these weevils can be clearly observed in TABLE 53 and Fig. 57 ; the weevils were given the choice between 0 % and 100 % R.H. The ' index of reaction ' during the first 6 minutes of the experiment was over + 70 . This strong preference for the dry side, however, decreased gradually with time, until at the end of 30 minutes the

TABLE 52

Index of reaction of S. zea-mais weevils preconditioned at 0 % R.H. and 25°C. for 24 hours offered different humidity gradients.

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 5	-21	-14	-36
6	- 1	-15	-25	-53
9	- 6	- 1	-15	-52
12	- 2	-18	- 5	-43
15	+ 8	+ 2	- 5	-43
18	- 5	- 9	-21	-41
21	- 5	-19	-10	-36
24	- 1	- 9	-12	-27
27	- 8	- 7	-10	-27
30	+17	-21	- 9	-40
Mean± S.E.	+ 0.2±1.6	-11.8±5.2	-12.6±4.1	-39.8±5.6
Mean control	+ 0.6	+ 0.4	+ 0.6	- 0.8

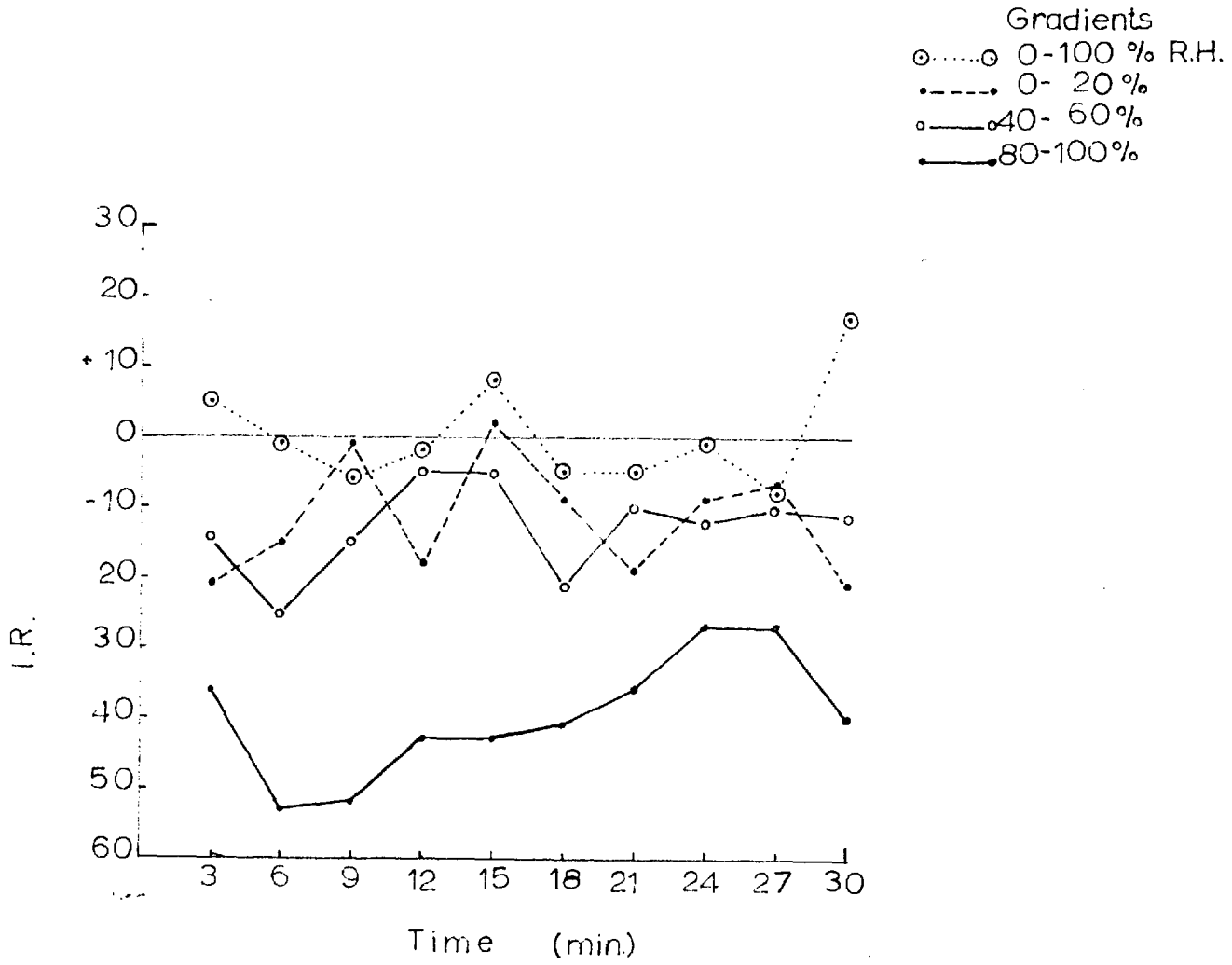


Fig. 55 : Index of reaction of Sitophilus oryzae weevils in different humidity gradients, and preconditioned at 0% R.H.

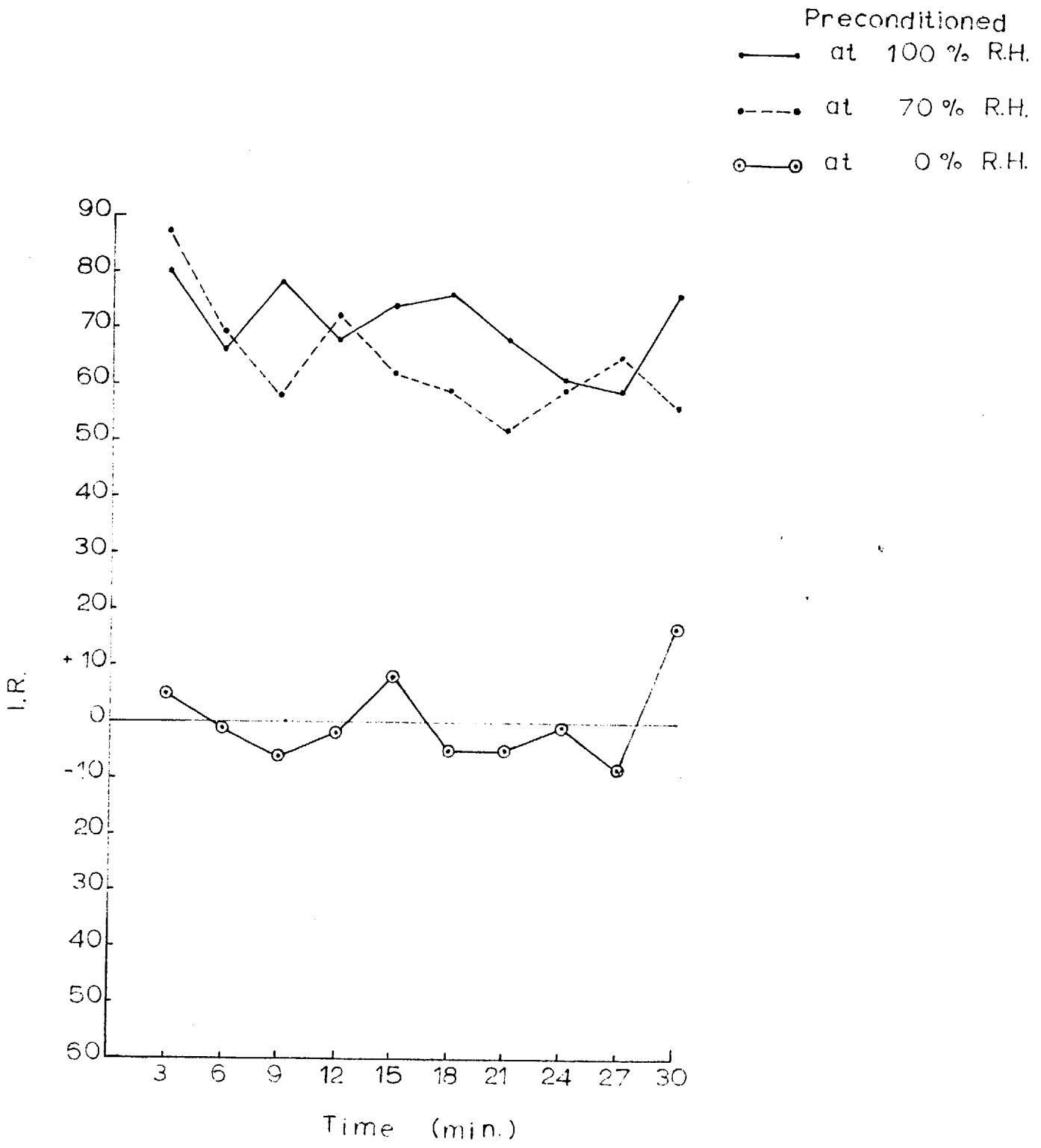


Fig. 56 : Index of reaction of S. zea mais weevils in 0-100 % Humidity Gradient , and preconditioned at 0 % , 70 % and 100 % R.H.

last three values of I.R. fell below + 40 ; the mean value of all the tests being + 55.4 ± 9.7 .

In the gradients between 0 - 20 % R.H. and 40 - 60 % R.H. the mean values of the ' index ' were +31.4±2.7 and 29.5 ± 2.8 respectively, i.e. they were low compared with those obtained in the experiments with S. zea-mais . The plotted values indicating these reactions (Fig. 57), fluctuated around a more or less constant level.

At the higher scale of the humidity gradient namely between 80 and 100 % R.H., an intermediate value of + 42.2 ± 4.9 was obtained. The index of reaction was high at first, then decreased after a few minutes and rose slightly at the end of the experiment (Fig. 57).

b) Insects previously kept at 70 % R.H. and 25°C. :

The weevils exhibited an extremely strong reaction to the dry side of the alternative chamber with a gradient of 0 - 100 % R.H. during the first few minutes of the experiment. A sudden change in the reaction (a drop in the I.R. value from + 90 to + 51) occurred after 6 minutes , and then the reaction stabilised around a mean (see Fig.58).

The data in TABLE 54 indicate that the highest mean I.R. was + 46.2 ± 10.5 at 0-100 % humidity gradient . The weevils reacted more or less to the same degree (+27.2 ± 6.5 and + 26.7 ±5.5), at the humidity gradients 0-20 %

TABLE 53.

Index of reaction of S.oryzae weevils preconditioned at 100 % R.H. and 25°C. for 24 hours, offered different humidity gradients.

Gradient	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 72	+ 31	+ 38	+ 59
6	74	28	30	50
9	69	29	29	42
12	64	40	31	37
15	64	31	27	39
18	50	26	28	32
21	53	29	26	39
24	38	37	30	39
27	33	30	34	46
30	37	33	22	39
Mean ± S.E.	+55.4±9.7	+31.4±2.7	+29.5±2.8	+42.2±4.9
Mean control	+ 0.6	+ 2.8	+ 1.6	+ 0.8

TABLE 54

Index of reaction of S. oryzae weevils previously kept at 70 % R.H. and 25°C., offered different humidity gradients.

Gradient	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min)	Index of Reaction			
3	+ 90	+ 51	+ 38	+ 41
6	51	31	30	45
9	40	35	40	45
12	54	18	19	53
15	37	18	22	41
18	37	31	19	27
21	40	22	32	43
24	37	20	32	28
27	34	22	16	25
30	42	24	19	13
Mean± S.E.	+46.2±10.5	+27.2±6.5	+ 26.7±5.5	+ 36.1±7.7
Mean control	+ 1.4	+ 0.2	- 2.6	+ 1.0

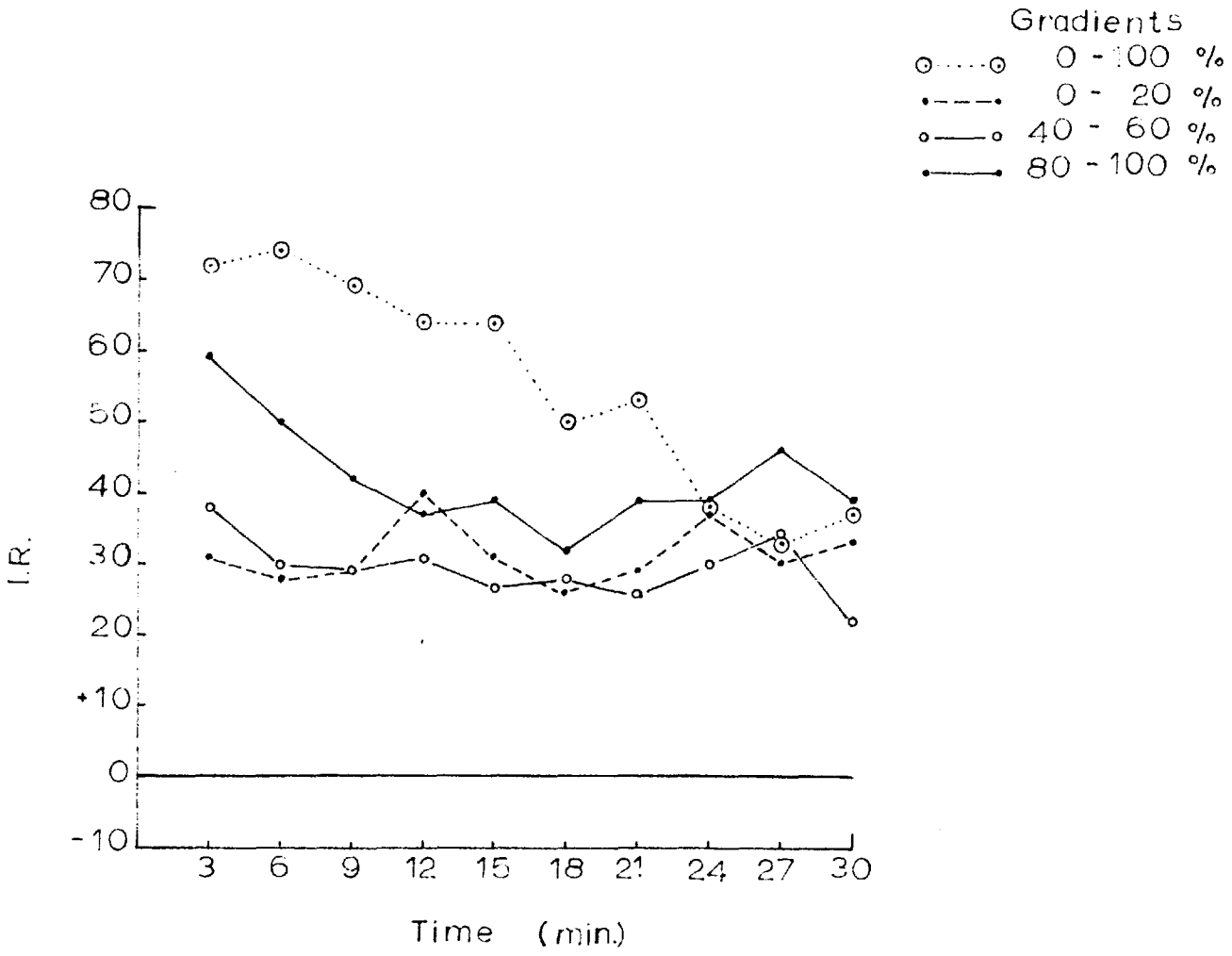


Fig. 57 : Index of reaction of S. oryzae weevils in different humidity gradients , and preconditioned at 100% R.H..

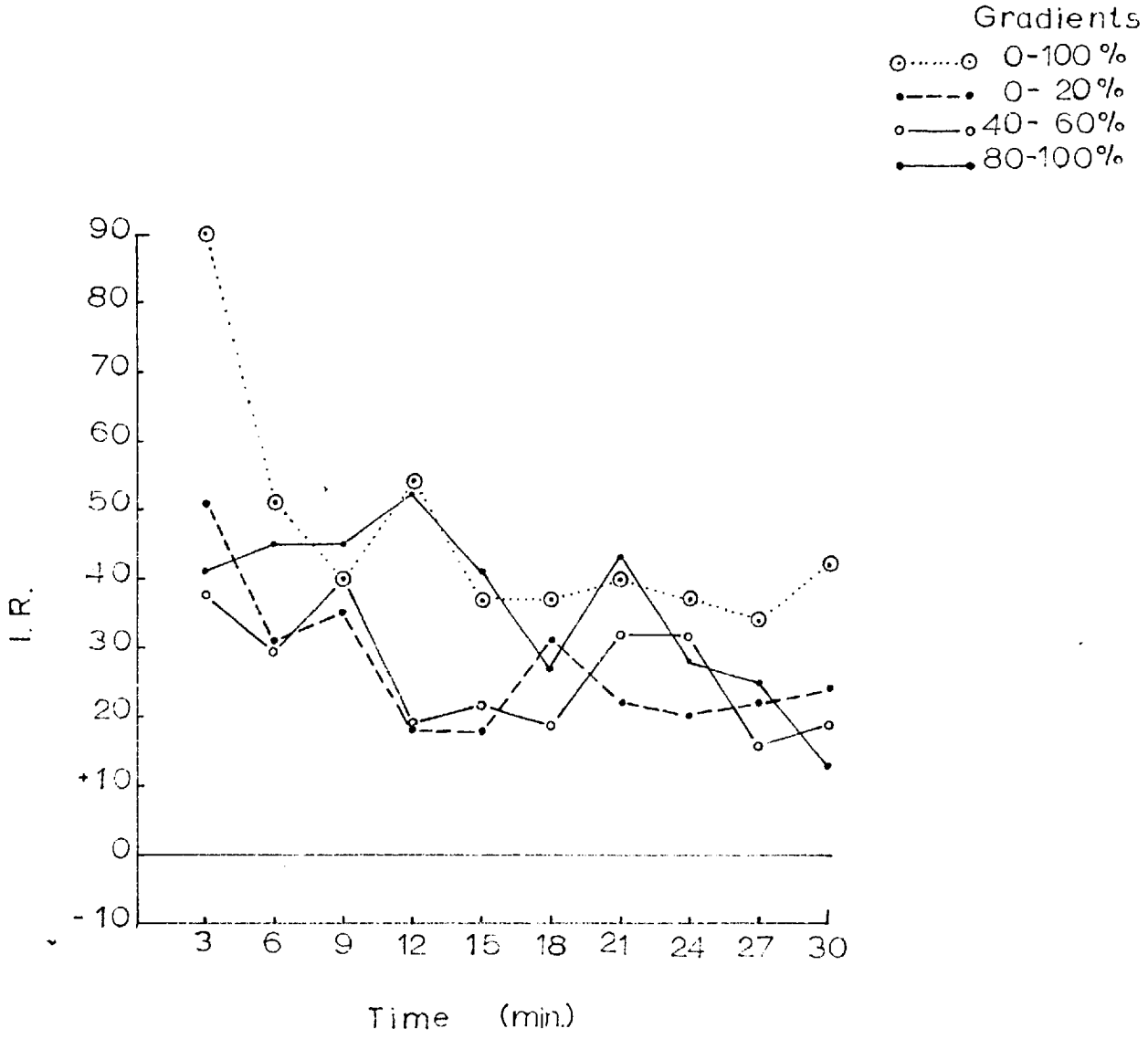


Fig. 58 : Index of reaction of S. oryzae weevils in different humidity gradients , and preconditioned at 70 % R.H.

and 40 - 60 %, and in a nearly similar manner. A slightly higher value, which was +36.1 ± 7.7, corresponds to the weevils' reaction at 80 - 100 % R.H. gradient.

Three of the four curves depicting the behaviour in these humidity gradients agreed in having lower values at the end of the experiment than at the beginning, i.e. under three sets of experimental conditions the reaction to drier air was strong at first and then dropped off with time. The exception to this was the behaviour in the gradient of 0 - 20 % R.H., where the reaction fluctuated around a constant mean to the end of the experiment.

c) Insects preconditioned at 0% R.H. and 25°C. for 24 hours: The humidity behaviour of S. oryzae weevils was greatly influenced by desiccation in such a dry atmosphere. They exhibited strong preference for the wet side of the humidity gradients between 0 - 100 % R.H. and 80 - 100 % R.H. The values of the mean index of reaction were - 48.2 ± 11.0 and - 52.5 ± 3.2 respectively. The reaction to the wet side, however, was also shown but to a lower extent when the weevils were offered 0 - 20 % R.H. and 40 - 60 % R.H. gradients; the means of the indices being -34.8 ± 4.2 and - 38.2 ± 5.0 respectively. These data are presented in TABLE 55 and Fig. 59. It can be seen that the weevils in the gradient of 0-100% R.H., gave a weak reaction to the wet side at the beginning of the experiment, the I.R. being - 10

TABLE 55

Index of reaction of S.oryzae weevils preconditioned at 0 % R.H. and 25°C. for 24 hours, offered different humidity gradients.

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	-10	- 39	- 38	- 52
6	32	33	54	46
9	45	35	33	51
12	44	37	49	53
15	41	21	37	48
18	63	34	36	60
21	57	39	30	50
24	58	27	33	50
27	64	39	41	53
30	68	44	31	62
Mean ± S.E.	-48.2±11.0	- 34.8±4.2	- 38.2±5.0	- 52.5±3.2
Mean control	+0.8	+ 3.4	- 1.0	- 0.6

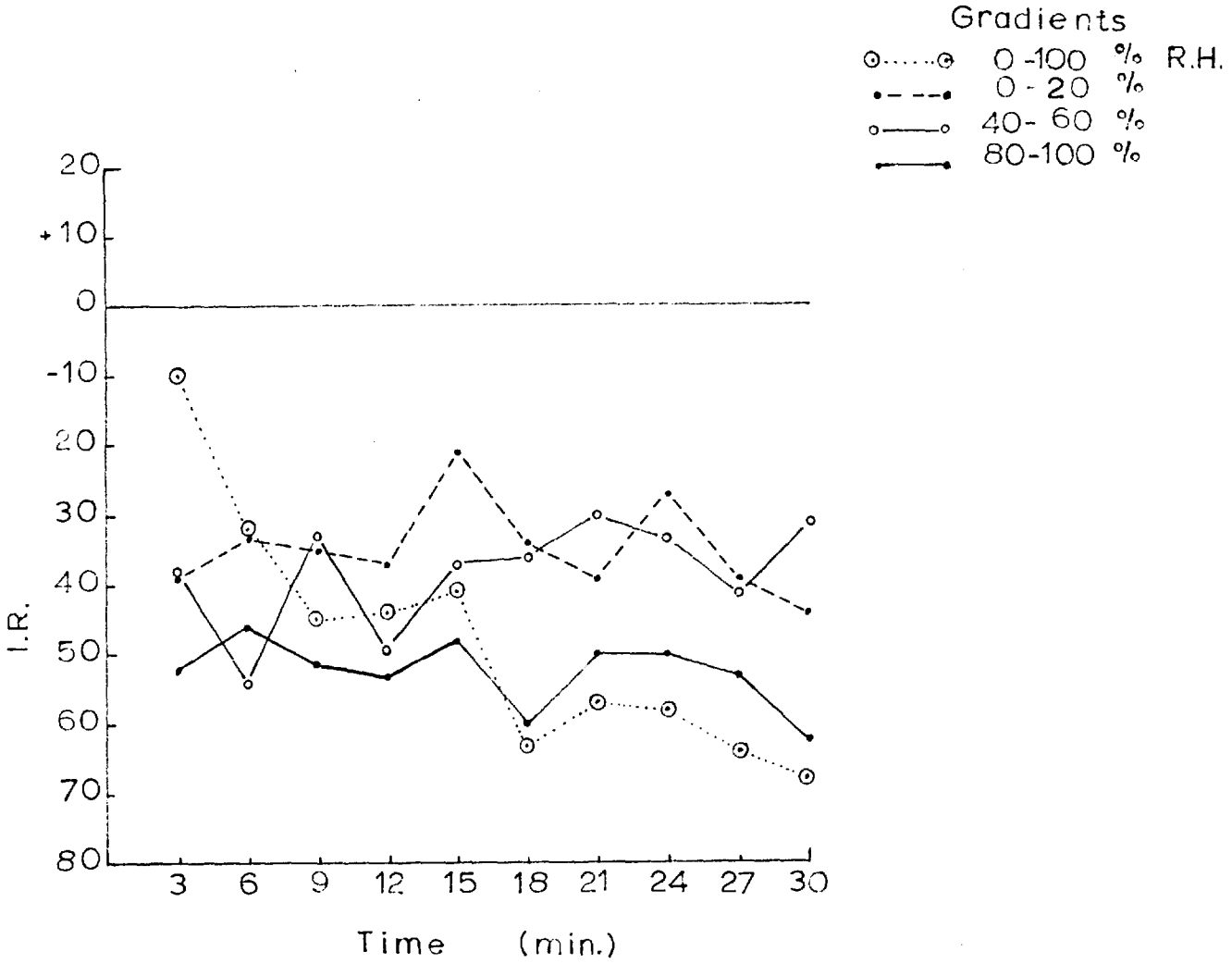


Fig. 59 : Index of reaction of S.oryzae weevils to different humidity gradients , and preconditioned at 0 % R.H.

after the first three minutes. The curve then steeply sloped and the figure of -63 was obtained after 18 minutes of the experiment, and after half an hour it reached -68.

The curves representing the behaviour of the desiccated weevils at 0 - 20 % , 40 - 60 % and 80 - 100 % R.H. gradients, indicate that the reaction to the wet side was fluctuating around the mean value of every experiment.

Fig. 60 clearly illustrates how the weevils reacted at 0 - 100 % R.H. gradient , when they were previously conditioned at three different relative humidities. The strong reaction to the dry air shown by the weevils preconditioned at 100 % R.H. and at 70 % R.H., became an extremely strong reaction to the wet side of the apparatus after desiccation at 0 % R.H. for 24 hours.

3) S. granarius

a) Insects preconditioned at 100% R.H. and 25°C. for 24 hours :- The weevils gave a clear reaction to the dry side in the alternative relative humidities of 0 and 100%, the mean I.R. was + 49.2±1.4 (TABLE 56). In the 0 - 20 % and 40 - 60 % R.H. gradients, the weevils seemed to be unable to discriminate between the alternative humidities.

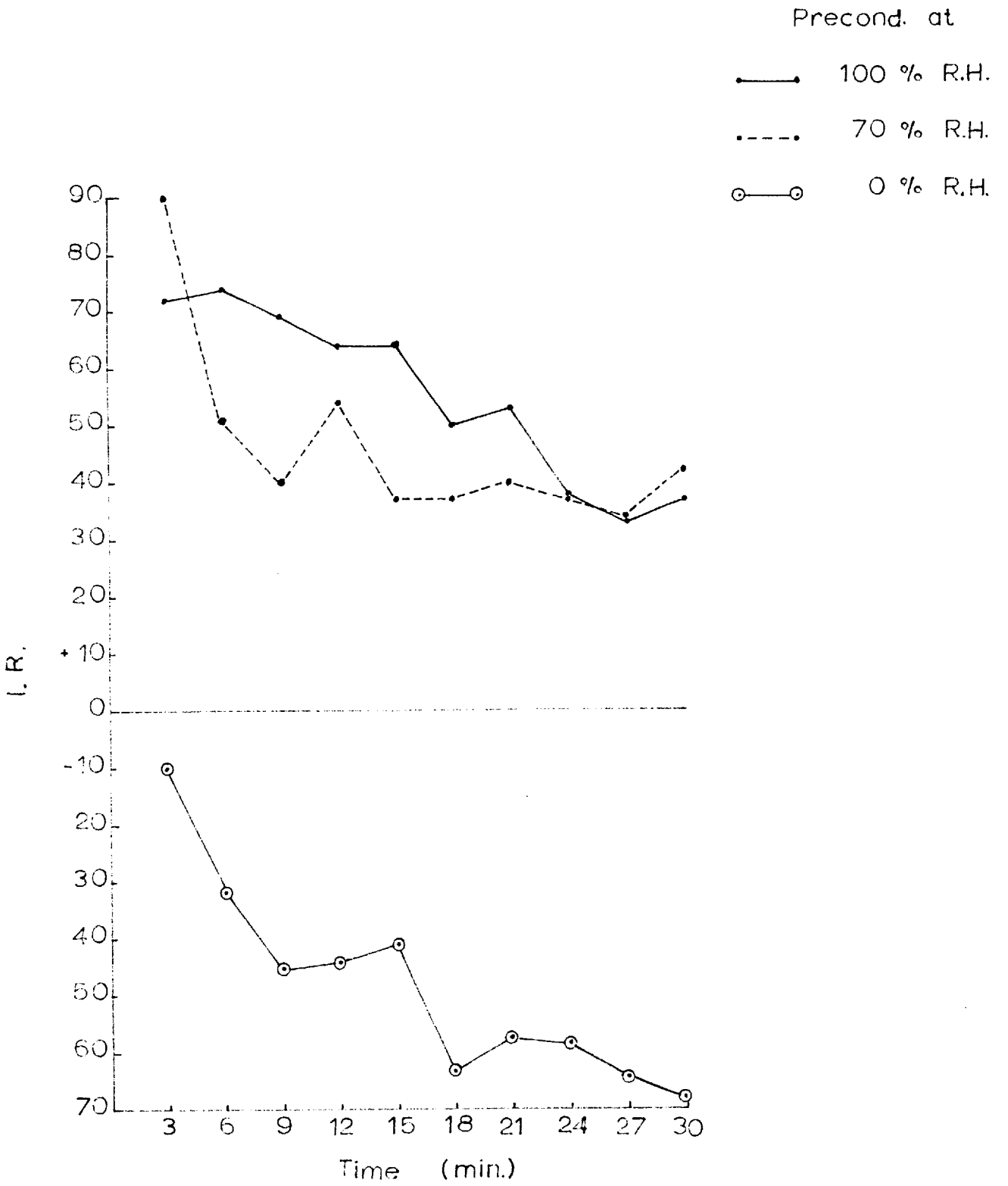


Fig. 60 : Index of reaction of S. oryzae in 0-100 % humidity gradient, and preconditioned 0, 70 & 100 % R.H.

The mean I.R. values were + 3.2 ±1.5 and + 5.3±1.1 which were not significantly different from the control ones . At 80-100 % humidity gradient, however, the dry reaction could be slightly detected, the mean I.R. was + 13.2 ± 5.3. The curves representing these reactions are shown in Fig.61.

b) Insects previously kept at 70 % R.H. and 25°C. :- The behaviour of the weevils kept under these conditions did not differ much from the previous experiment when they were preconditioned at 100 % R.H. Thus the results in TABLE 57 and the curves representing them in Fig. 62 clearly illustrate this.

At 0 - 100 % humidity gradient the mean I.R. value was + 48.7 ± 5.6 indicating a strong reaction to the dry side. But at 0 - 20 % and 40 - 60 % humidity gradients the weevils were almost indifferent to the two alternatives giving mean I.R. values of + 8.0 ± 4.9 and + 5.7 ± 4.8 respectively.

The tendency of the movement to the dry side, however, was clearer at the higher scale of the humidity gradient .

TABLE 56

Index of reaction of S. granarius weevils preconditioned at 100 % R.H. and 25° C. for 24 hours, offered different humidity gradients.

Gradient	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 48	+ 5	- 3	- 5
6	+ 57	- 3	+ 8	+20
9	+ 38	+ 1	+ 6	+22
12	+49	+ 6	0	+10
15	+ 59	+ 6	+ 9	+15
18	+ 56	+ 3	+13	+ 6
21	+ 52	+ 3	+11	+11
24	+ 44	+ 3	- 7	+15
27	+ 46	+ 3	+ 11	+26
30	+ 43	+ 5	+ 5	+12
Mean ± S.E.	+ 49.2±1.4	+3.2±1.5	+ 5.3±1.1	+13.2±5.3
Mean control	- 1.6	+2.8	+ 0.2	+ 2.6

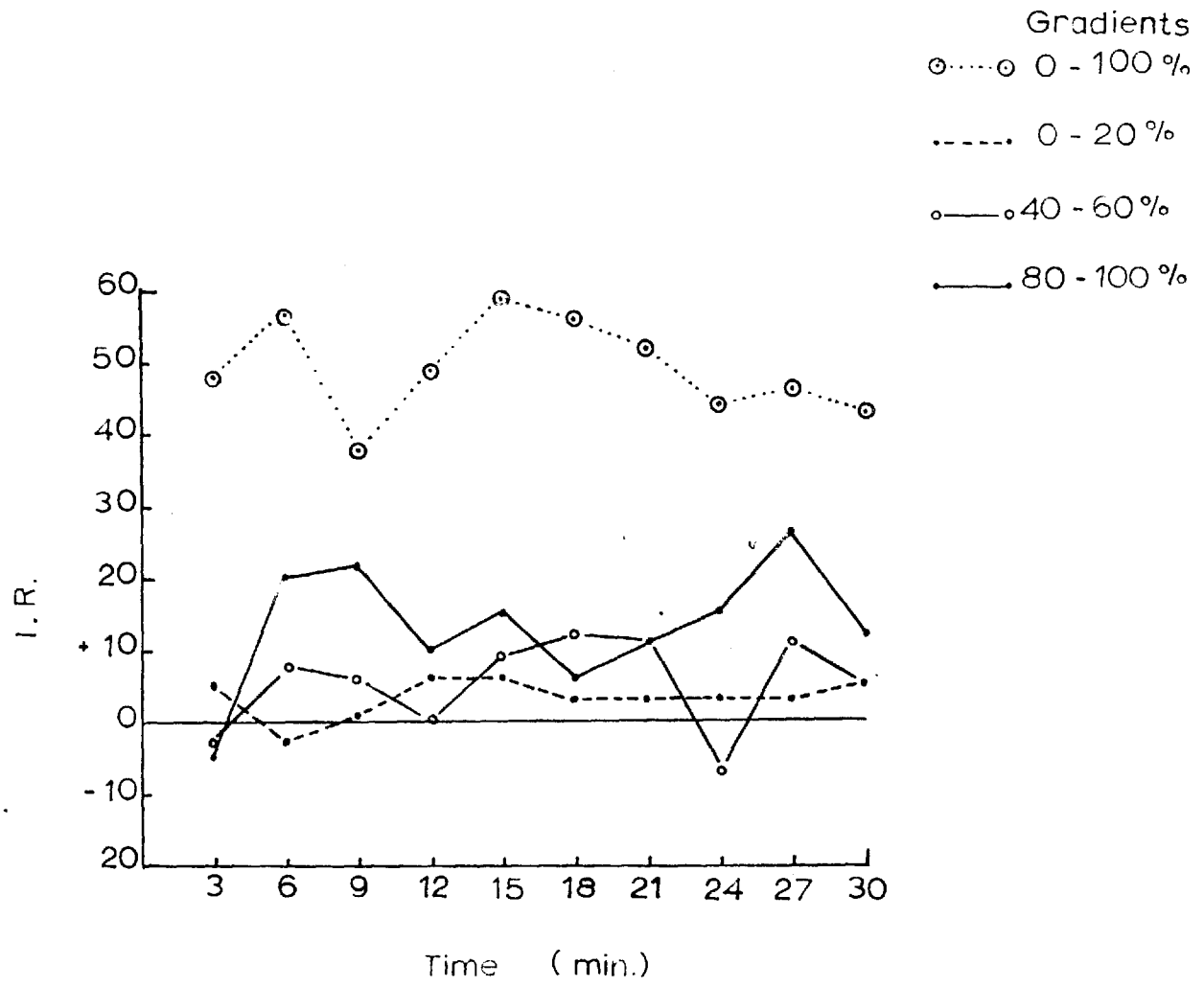


Fig. 61 : Index of Reaction of S.granarius Weevils in different Humidity Gradients , and preconditioned at 100 % R.H.

TABLE 57

Index of reaction of S. granarius weevils previously kept at 70 % R.H. and 25°C., offered different humidity gradients.

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 61	+ 7	- 6	+ 12
6	+ 52	+ 5	- 2	+ 20
9	+ 43	+23	+18	+ 11
12	+ 51	+ 9	- 7	+ 12
15	+ 49	+ 6	+ 7	+ 26
18	+ 45	+20	+ 5	+ 7
21	+ 61	-11	+ 9	+ 32
24	+ 50	+12	+ 4	+ 19
27	+ 31	+ 3	+11	+ 19
30	+ 44	+ 6	+18	+ 31
Mean± S.E.	+48.7±5.6	+ 8.0±4.9	+ 5.7±4.8	+18.9±5.5
Mean control	-4.3	+ 2.6	- 0.2	+ 1.4

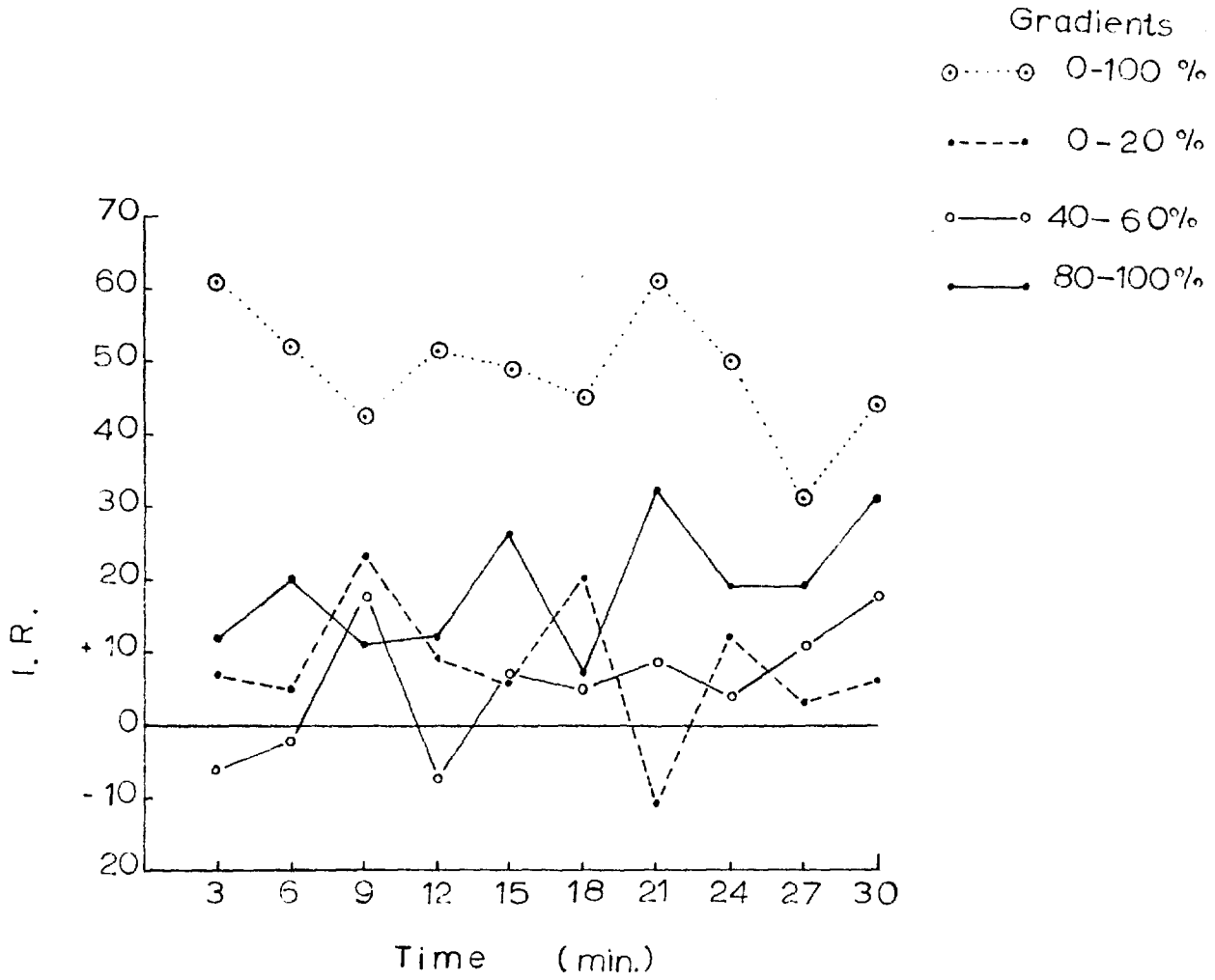


Fig. 62 : Index of reaction of S. granarius weevils in different humidity gradients, and preconditioned at 70 % R.H.

c) Insects preconditioned at 0 % R.H. and 25° C. for 24 hours :- The weevils which normally selected the dry side when they were previously kept in a humid atmosphere, exhibited a weak or negligible reaction to dry air after being desiccated for 24 hours. The mean I.R. was + 11.5 ± 7.8 at 0 - 100 % humidity gradient, and at 0 - 20 %, 40 - 60 % and 80 - 100 % gradients the indices were : -4.9±3.9, +1.4±3.9 and +3.6±5.0 which shows that there was no discrimination at all (TABLE 58) . Fig. 63 shows how this behaviour fluctuated around the non-reactive zone.

The effect of preconditioning at different relative humidities, on the behaviour of S.granarius weevils at 0 - 100 % humidity gradient is shown in Fig. 64. The desiccated weevils, showed a marked decrease in the reaction to the dry side , compared with those preconditioned in a wet atmosphere. Near the end of the experiment , however , the desiccated weevils seemed to have slightly gained the tendency to move to the dry side , the I.R. value of + 33 having been reached.

TABLE 58

Index of reaction of S.granarius weevils previously kept at 0 % R.H. , 25°C. for 24 hours, in different humidity gradients

Gradients	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
Time (min.)	Index of Reaction			
3	+ 19	- 4	0	- 6
6	+ 4	- 18	- 9	- 11
9	- 9	- 12	- 3	+ 13
12	+ 1	+ 8	+16	- 6
15	+ 22	- 6	- 6	- 2
18	+ 21	- 4	+ 2	+ 23
21	+ 1	- 8	+16	+ 4
24	+ 19	+ 1	+ 8	+ 5
27	+ 4	- 5	0	+ 5
30	+ 33	+ 4	-10	+ 11
Mean±S.E.	+11.5±7.8	-4.4±3.9	+1.4±3.9	+3.6±5.0
Mean control	+1.2	-1.2	-0.4	+2.4

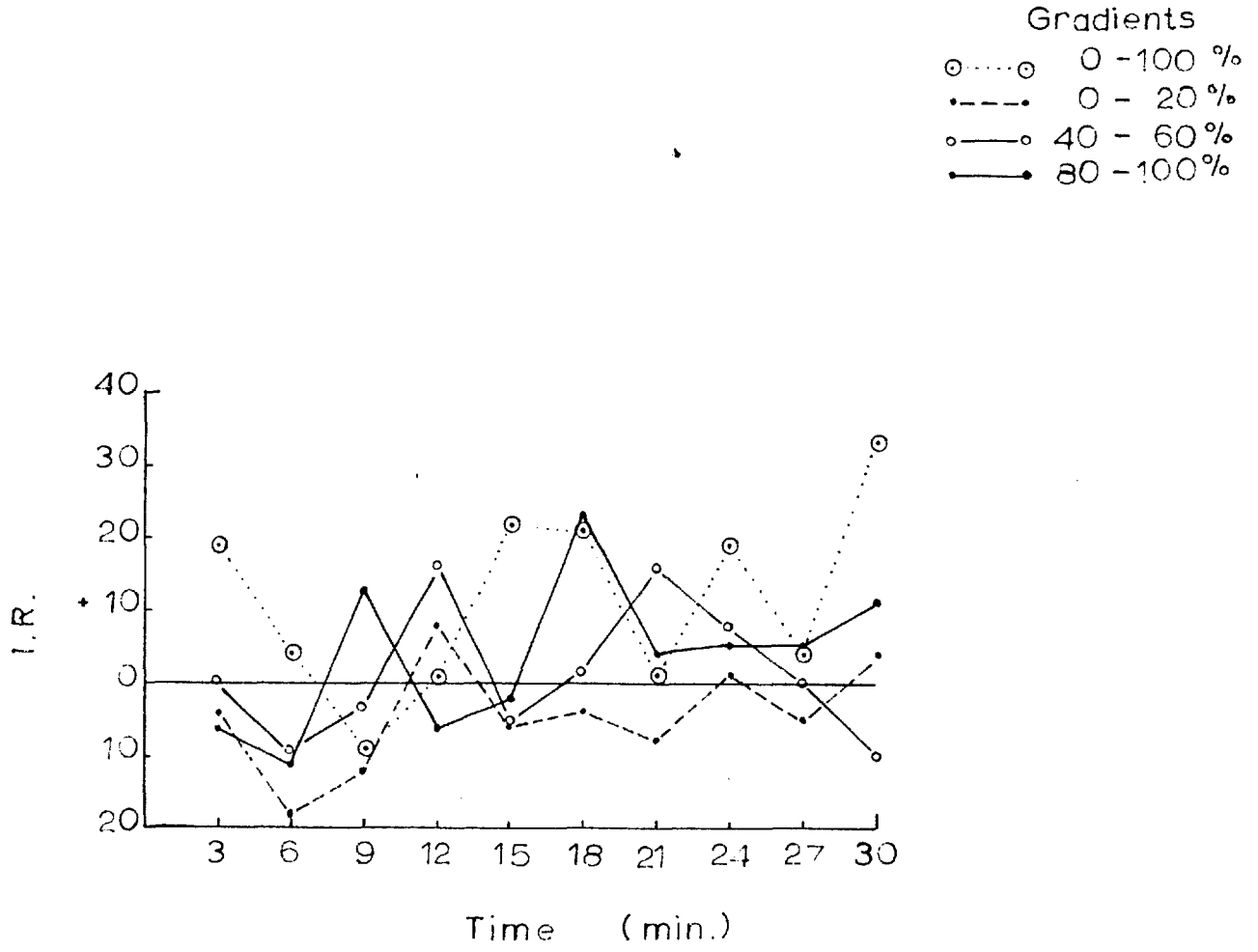


Fig. 63 : Index of Reaction of S. granarius Weevils in different Humidity Gradients , and preconditioned at 0 % R.H.

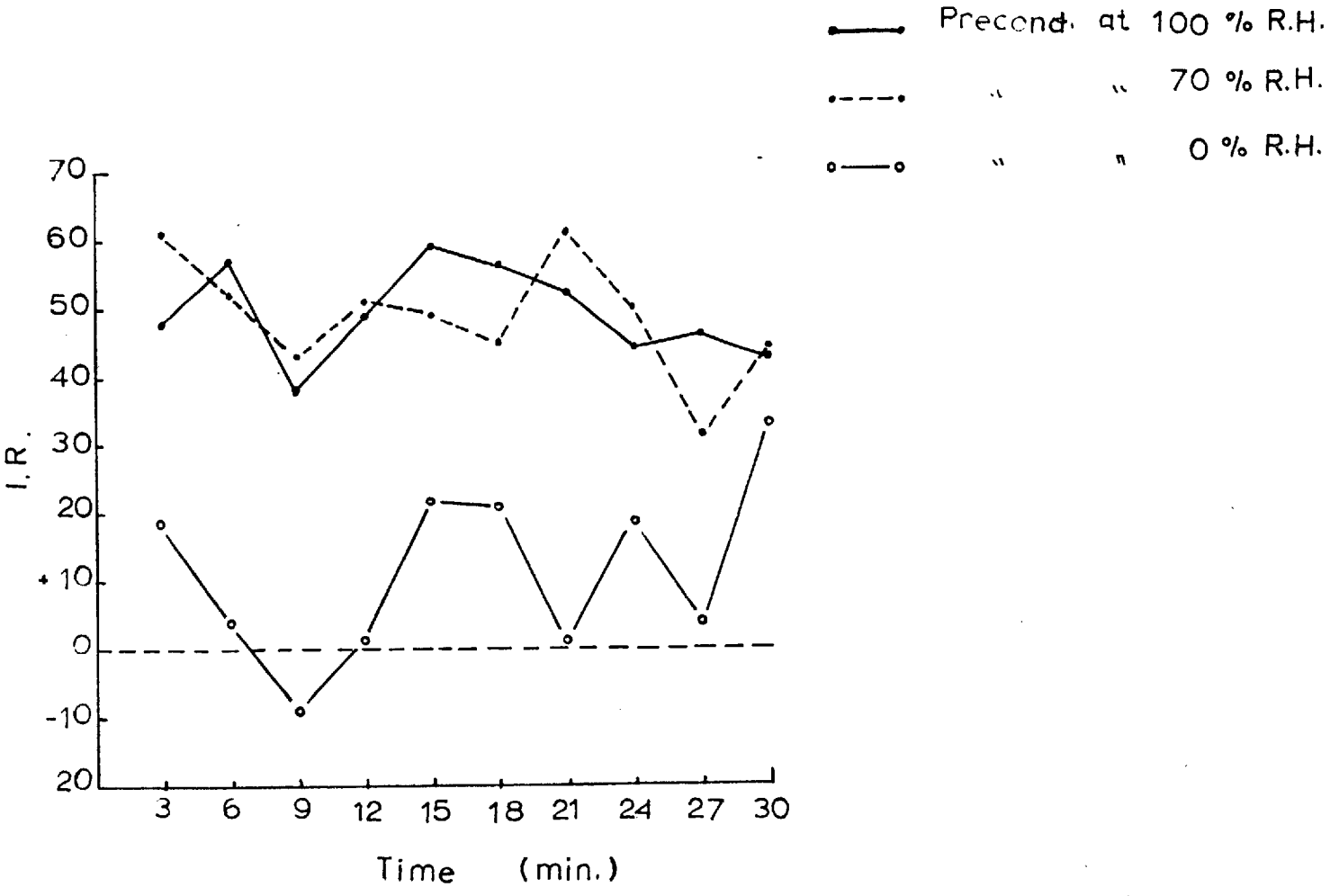


Fig. 64 : Index of Reaction of S. granarius Weevils in (0-100 %) R.H. Gradient.- Insects Preconditioned at different Relative Humidities.

4. The Humidity Receptors

Roth and Willis (1951,b), were able to locate the organs which control the humidity behaviour of S.granarius weevils. They gave a detailed description of the antenna as follows : geniculate and consists of eight segments . The first segment or'scape' is greatly elongated and about as long as ' pedicel ' (segment 2) and ' funicular segments ' (3-7) combined. The eighth segment is enlarged and forms a distinct club. Sensilla chaetica are found on all the antennal segments. Thin-walled long, slender, trichoid sensilla are found in a dense triangular patch interspersed among sensilla chaetica, at the apex of the eighth segment only.

After amputation of the club segments on both antennae of the weevils which normally showed a strong reaction to the dry side, the weevils became indifferent to humidity. This indicated that the hygroreceptors were only present on that segment.

In the present work sets of similar amputation experiments were conducted with S. granarius as with S.zeamais and S.oryzae, to see whether any differences in the distribution of the hygroreceptors exist, as those

that were found in different species of Tribolium by Roth and Willis (1951,a). The antennae of the three species of Sitophilus are illustrated in Fig. 65 . As far as the club segment is concerned, it was found that slight differences existed between that of S.granarius on one hand, and the rice weevils on the other. In the first species the club segment is elongated nearly oval in shape, and large as compared with the club segments of the rice weevils, in which it is more or less globose (Fig. 65, a' , b' and c'). The apical triangular dense patch of trichoid sensilla looked nearly identical in the three species. In the rice weevils, however, a number of minute pit organs, probably sensory in function, are dispersed near the apex of the club segment only. They vary in number from one individual to another of the same species. In S.zea-mais, 18-31 pit organs have been found, and in S.oryzae they ranged between 15 and 30 . No pit organs were found on the antennae of the granary weevils.

The three species, however, agreed in possessing hygroreceptors on the club segment only. This was confirmed experimentally. The weevils which normally showed a marked preference for the dry side of the humidity chamber, when previously kept in a humid atmosphere,

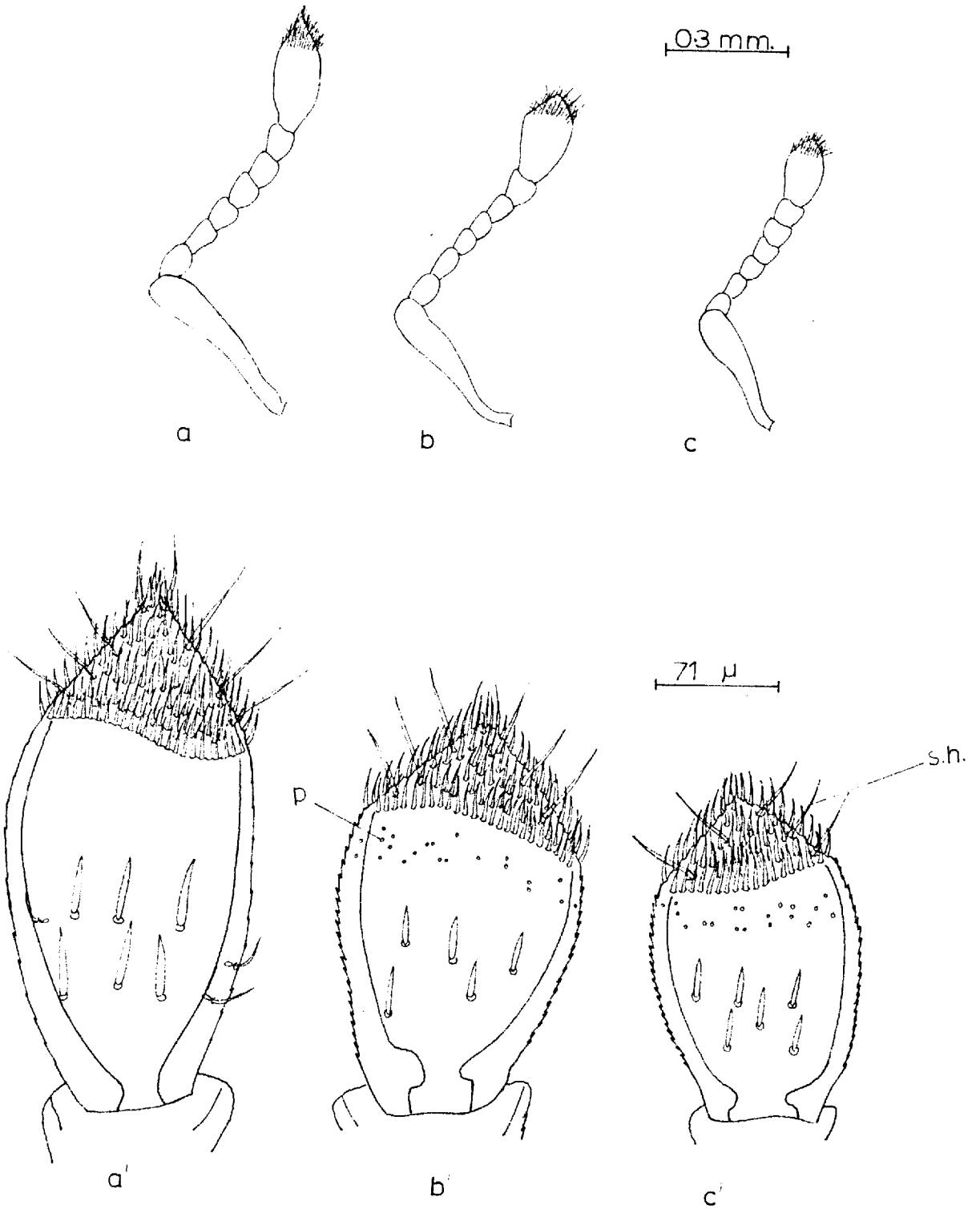


Fig. 65 : Antennae of the weevils, a) S.granarius, a', club ; b) S zeamais, b', club ; c) S oryzae, c', club ; s.h. sensory hairs; p, pit organs.

they were unable to discriminate between the two extreme humidities, when the club segment was amputated from both antennae. The reaction of weevils with amputated club segments, previously kept at 70 % R.H. and 25°C. is given in TABLE 59, and illustrated in Fig. 66 . The mean indices of reactions of weevils with club segments removed were - 4.9 ± 3.5, - 1.8 ± 0.6 and -0.9 ± 0.2 in S. zea-mais , S. oryzae and S. granarius respectively. This indiscriminate behaviour indicates that the weevils lost their ability to respond to humidity.

5. Effect of Desiccation on Loss in Weight and Rate of Death of the Weevils :-

This experiment was carried out as an attempt to explain the meaning of the difference in behaviour in reaction to humidity shown by the three species of weevils when they were desiccated for 24 hours at 0 % R.H., 25°C. (TABLE 61) , and to determine the ability of the weevils to resist desiccation.

Under absolutely dry conditions, the rate of water loss, indicated by the decrease in mean body weight , differed in the three species (TABLE 60 , Fig. 67) . After 24 hours of desiccation S.zea-mais lost 10.7 %

TABLE 59

Index of reaction of weevils with antennal club removed previously conditioned to 70 % R.H. and 25° C., and placed in a relative humidity gradient of 0 - 100 % .

Time (min.)	Index of reaction		
	S.zea-mais	S.oryzae	S.granarius
3	- 16	- 3	- 2
6	- 8	- 2	+ 2
9	- 7	- 5	+ 12
12	- 7	+ 8	+ 2
15	0	- 1	- 3
18	0	+ 1	+ 2
21	+ 1	- 7	- 6
24	- 6	- 6	- 3
27	- 8	- 2	- 5
30	+ 2	- 1	- 8
Mean ± S.E.	- 4.9 ± 3.5	- 1.8 ± 0.6	-0.9± 0.2
Mean control	- 0.8	+ 1.6	+ 0.6

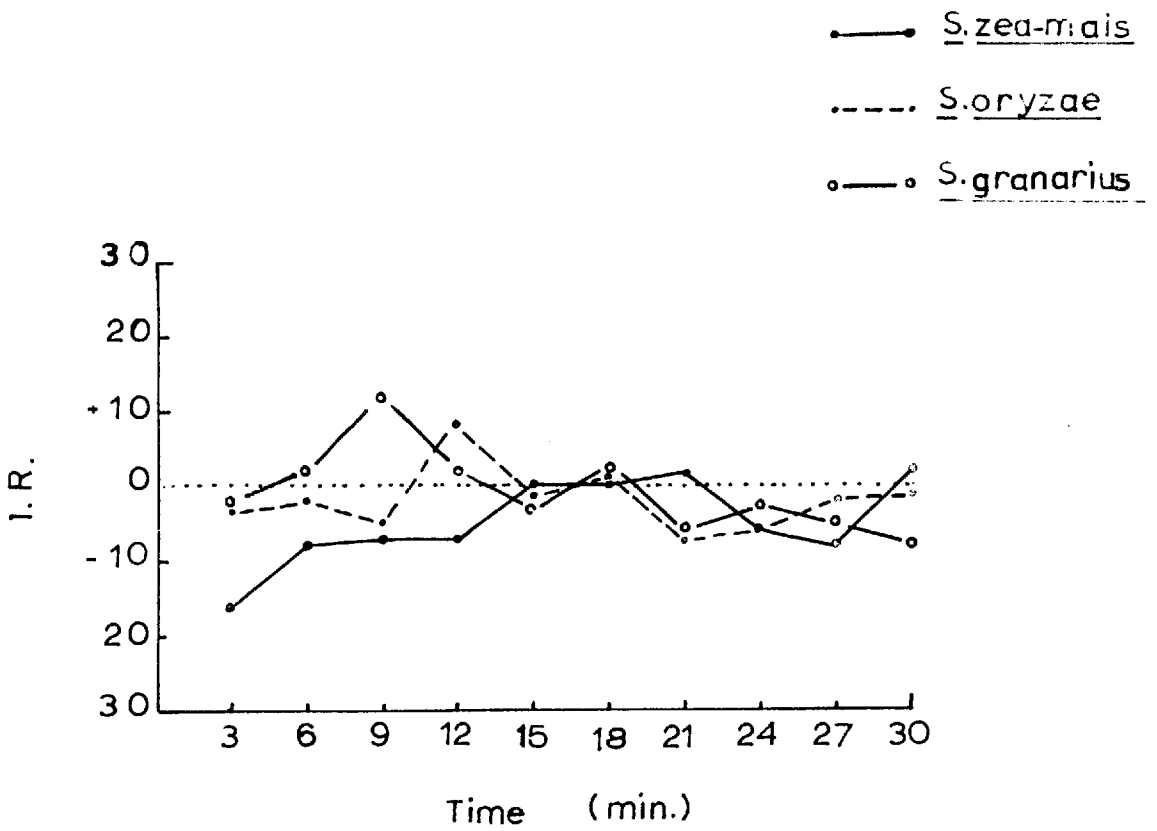


Fig. 66 : Index of Reaction of the Weevils in (0-100%) Humidity Gradient.- Antennal Club Removed.

of their original weight, while S.oryzae and S.granarius lost 13.7 % and 9.2 % respectively. This indicates that the highest loss was in S.oryzae, a species which showed the strongest reaction to moist air after desiccation at 0 % R.H. and 25°C. for 24 hours (TABLE 61 and Fig. 73). The slightly higher percentage of water loss in S.zea-mais than in S.granarius was also accompanied by a stronger preference for the wet side of the alternative humidities by the former species.

After 48 hours the percentages of total loss in weight were 21.1 % , 19.7 % and 18.3 % in S.zea-mais, S.oryzae and S.granarius respectively. The latter species still exhibited greater ability to withstand desiccation . The percentage of water lost from S.zea-mais weevils was higher than that from S.oryzae, yet the former species can be considered to be more resistant to dryness, since after 3 days of desiccation all S.oryzae weevils died, while 52% of S.zea-mais still remained alive (TABLE 60). After 4 days of desiccation all S.zea-mais weevils also died when the percentage loss reached over 23.1 % of the original weight. The corresponding figure for S.granarius weevils was a loss of 22.1 % of original weight, but after 4 days of desiccation 15 % of the weevils were still alive and died only on the sixth day. The sudden rise in mean weight

TABLE 60

Rate of death , and loss in weight of weevils due to desiccation at 0 % R.H. and 25° C.

Species	Days after desiccation	0	1	2	3	4	5	6
S.zea-mais	Number of insects found dead	-	-	4	44	52	-	-
	Cumulative percentage of original dying	-	-	4	48	100		
	Number of insects alive	100	100	96	52	-		
	Total weight of living insects (gm.)	.2417	.2155	.1833	.0969	-		
	Mean weight of living insect (mgm.)	2.42	2.16	1.91	1.86	-		
	Percentage of original average weight	100 %	89.3%	78.9%	76.9%	-		
S.oryzae	Number of insects found dead	-	7	53	40	-		
	Cumulative percentage of original dying	-	7	60	100	-		
	Number of insects alive	100	93	40	-			
	Total weight of living insects (gm.)	.1171	.0943	.0376	-			
	Mean weight of living insect (mgm.)	1.17	1.01	0.94	-			
	Percentage of original average weight	100 %	86.3 %	80.3 %	-			
S.granarius	Number of insects found dead	-	1	6	34	44	9	6
	Cumulative percentage of original dying	-	1	7	41	85	94	100
	Number of insects alive	100	99	93	59	15	6	-
	Total weight of living insects (gm.)	.2400	.2162	.1825	.1104	.0323	.0128	-
	Mean weight of living insect (mgm.)	2.40	2.18	1.96	1.87	2.15	2.13	-
	Percentage of original average weight	100 %	90.8 %	81.7 %	77.9 %	89.6 %	88.8%	-

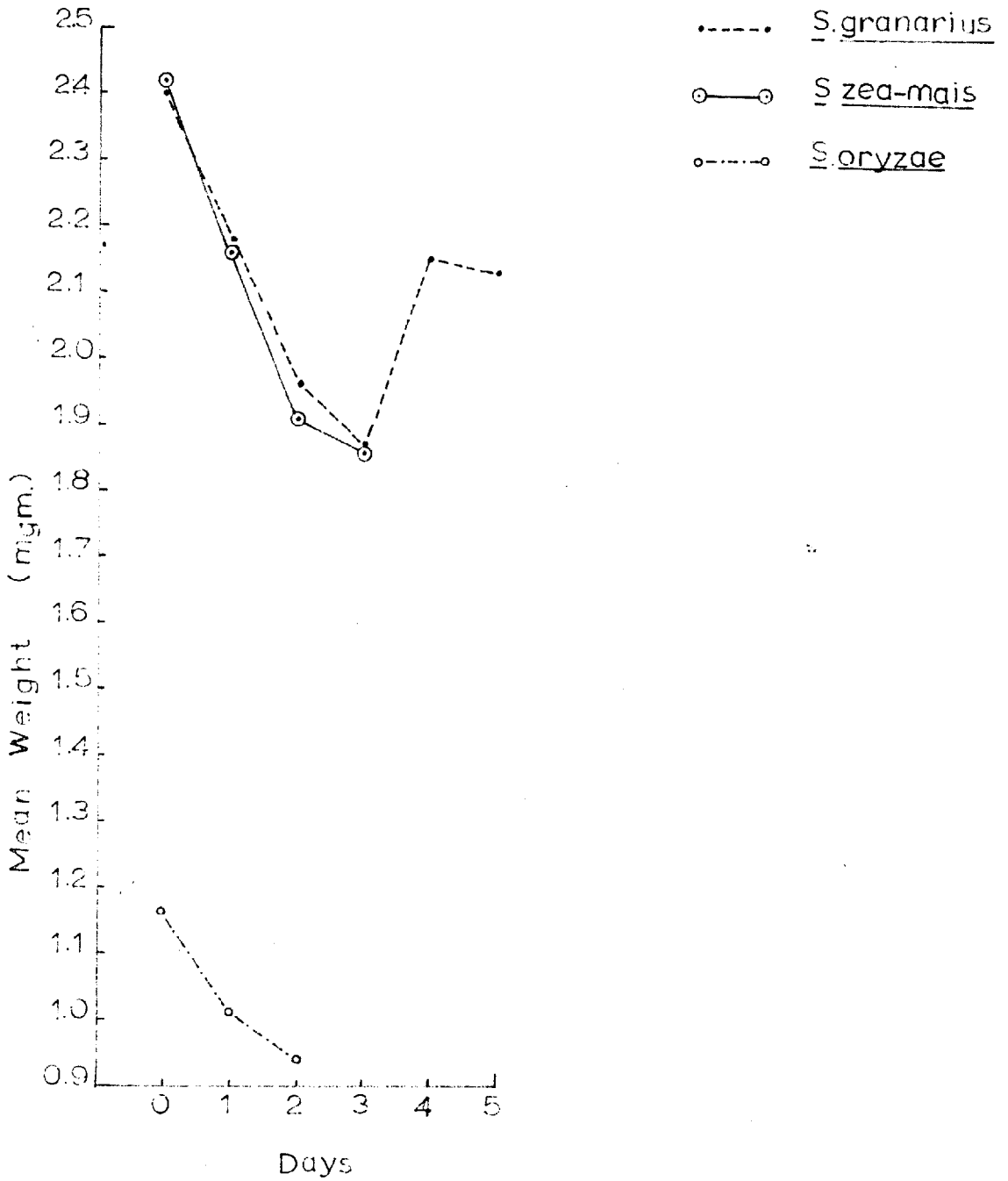


Fig. 67 : Loss in weight of the weevils on desiccation at 0% R.H. and 25° C.

of S.granarius weevils from 1.87 mg. after the third day of desiccation to 2.15 mg. after the fourth day indicates that only the heavier insects were able to survive for 4 - 5 days . This experiment exhibits differential survival of insects of varying weights. The rate of death of the three species of weevils are illustrated in Fig. 68 .

D. Discussion

Biological and ecological studies of Sitophilus species by some workers indicate that these insects reproduce ~~in~~ and survive more efficiently in higher humidities. Birch (1944) found that the number of eggs laid by the two strains of Calandra oryzae (=Sitophilus zea-mais and S.oryzae) is greater in wheat of higher moisture content. Richards (1947) concluded that oviposition of Calandra granaria (= S.granarius) weevils increases slowly as relative humidity rises from 70 % to 100 % R.H. , and falls rapidly if it is reduced below 70 % . Further, he showed the effect of the relative humidity on the length of the life cycle, the average numbers of days until the adult weevils leave the grain at 21°C. were 57 , 58, 64 and 71 days at the relative humidities 80 %, 70 %, 60 % and 50 % R.H. Reddy (1950) recorded the number of

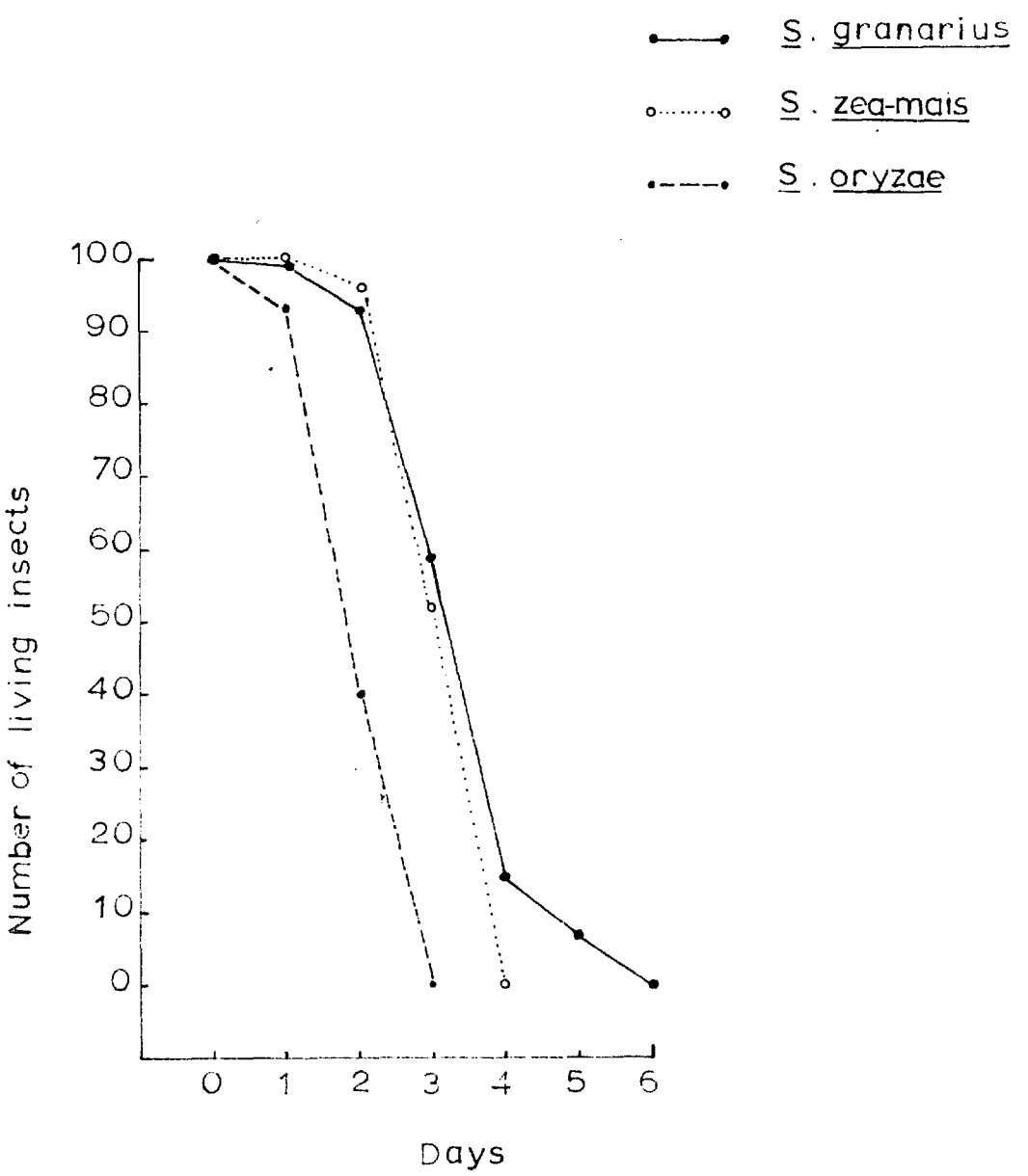


Fig. 68 : Rate of death of the weevils on desiccation at 0 % R.H. and 25°C.

eggs laid and the percentage hatch of S.oryzae , and came to the conclusion that the conditions most favourable for the activity of the weevils were 75 - 90 % R.H. and 28-30°C. Howe (1952) mentioned that oviposition of C.oryzae is poor at humidities below 70 % and that mortality of the immature stages is high below 60 % R.H.

The preference of the weevils for the dry side of the alternative humidity chamber in the present work was conclusive when the insects were preconditioned at 100 % and 70 % R.H. This behaviour results from the physiological effects of the water balance in the body. These insects which were previously kept at high humidities discriminate between high and low relative humidities and move to the latter. There is, however, a slight tendency for them to reverse this reaction at the end of the experimental half an hour. After 9 minutes, however, a marked decrease in the reaction to dry air occurred which was especially strong in S.oryzae, which proved to be the species least resistant to desiccation (Fig. 69). When the insects were desiccated for 24 hours at 0 % R.H., S. granarius and S. zea-mais weevils showed no preference for the dry side and S. oryzae gave a strong reaction to higher humidities of the gradient 0 - 100 % R.H. (Fig. 70). This interesting difference was further confirmed by determining the rate of loss in weight and the rate of death of

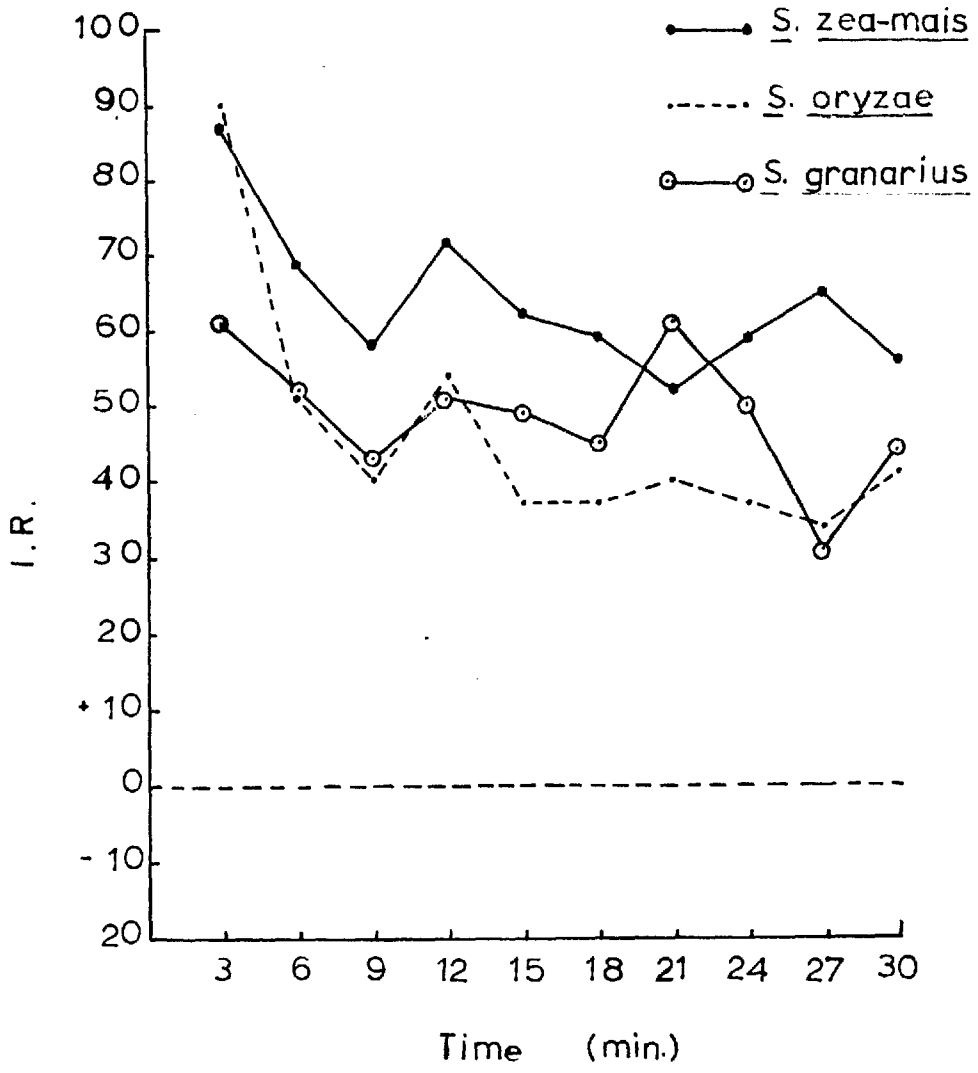


Fig. 69 : Index of Reaction of the Weevils in (0-100 %) Relative Humidity Gradient , and Preconditioned at 70 % RH.

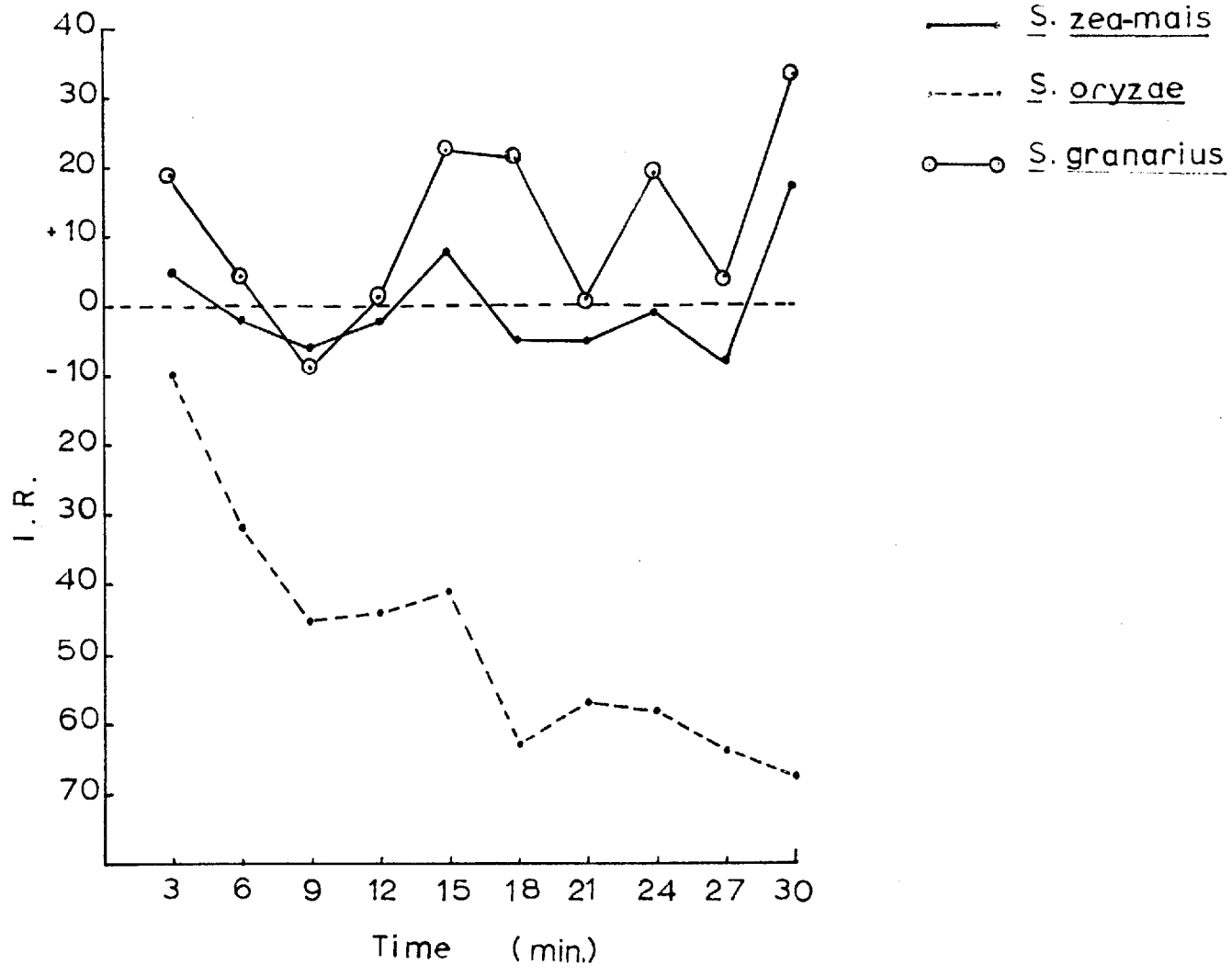


Fig. 70 : Index of Reaction of the Weevils in (0-100%) Relative Humidity Gradient , and Preconditioned at 0% R.H.

the weevils by desiccation for several days (TABLE 60 , Figs. 67 and 68). After 48 hours in extremely dry conditions, 60 % of S.oryzae weevils, and only 4 % of S.zea-mais and 7 % of S.granarius were found dead. The ability to withstand desiccation varied in the three species, and it was found that when on desiccation S.oryzae lost 19.7 % of their weight, all of them died. 23.1 % loss in weight of S.zea-mais weevils was found to be critical i.e. they were more resistant to dryness than S.oryzae. In S.granarius 85 % of the weevils died after 22.1 % loss in weight, and the following rise in the percentage of body weight of the living insects after 3 days of desiccation, led to the conclusion that only the heavier weevils could resist complete dryness for six days. 100 % death of S.zea-mais weevils occurred after 4 days, and of S.oryzae weevils after 3 days. The effect of starvation alone i.e. without desiccation on the mortality of the two species of the rice weevils was mentioned by Richards (1944) ; the mean number of days the weevils survived was 7.58 days in the large strain (=S.zea-mais) and 5.15 days in the small strain (=S.oryzae).

Humidity reactions of S.granarius weevils have been previously analysed by Roth and Willis (1951,b) who used an olfactometer with two air streams of extreme relative

humidities, and by Smereka and Hodson (1959) who used an alternative chamber with humidity gradients of 25 and 30 % R.H. In all essentials the results of the present experiments agree with those of the previous workers . The insects previously kept in favourable conditions of humidity (i.e. at 70 % R.H. or more), exhibited an initial reaction to the dry side which was followed by a slight decrease in the reaction over the test period, which was 20 minutes in the experiments of Roth and Willis (1951,b), and 30 minutes in the present work . Smereka and Hodson (1959) mentioned a reaction to the dry side during the first two hours, which gradually and clearly became a reaction to the wet side for the rest of the experimental time which lasted for 24 hours . This reversal of the reaction may be associated with the disturbance in the water balance in the weevils, which probably occurred during the first two hours which were spent in dry conditions.

The effect of 2-day desiccation on the humidity behaviour of S.granarius was found to produce a strong reaction to moist air (Roth and Willis , 1951,b), whereas in the present work 1-day desiccation decreased the reaction to dry air to a great extent, but there was no clear reversal in the reaction (TABLE 61 and Fig. 70).

The weevils when desiccated for 12 hours gave a clear reaction to the wet side in the experiments of Smereka and Hodson (1959).

From TABLE 61, in which all the humidity reactions of the three species are summarized, it can be seen that the intensities of reactions of the weevils preconditioned at 100 % R.H., were almost the same as those in the weevils which were preconditioned at 70 % R.H. A slight increase in the values of I.R., however, occurred in S.zea-mais and S.oryzae especially when they were offered 0-100 % a nd 80-100 % humidity gradients. In both cases of preconditioning, the highest figures of the indices of reactions were those of S.zea-mais, followed by S.oryzae and S.granarius. At 0-20 % and 40-60 % humidity gradients, the indices of reactions were remarkably low compared with these at the 0-100%R.H. gradient in both S. zea-mais and S.oryzae. In contrast to the other two species, S.granarius seemed to be unable to discriminate between gradients of 20 % R.H.

The graphs comparing the behaviour of the three species at 0-20 %, 40-60 % and 80-100 % R.H. gradients when the insects were preconditioned at 70 % R.H. are shown in Figs. 71 , 72 and 73.

TABLE 61

Mean 'Index of Reaction' of the weevils in different humidity gradients (+ indicates dry reaction)

Gradient	0 - 100 %	0 - 20 %	40 - 60 %	80 - 100 %
1. Insects preconditioned at 100% R.H. for 24 hours				
S. zea-mais	+70.7±4.7	+43.7±5.1	+43.5±3.9	+51.3±4.6
S. oryzae	+55.4±9.7	+31.4±2.7	+29.5±2.8	+42.2±4.9
S. granarius	+49.2±1.4	+ 3.2±1.5	+ 5.3±1.1	+13.2±5.3
2. Insects preconditioned at 70 % R.H.				
S. zea-mais	+63.9±4.8	+42.3±2.4	+42.5±3.5	+31.8±2.7
S. oryzae	+46.2±10.5	+27.2±6.5	+26.7±5.5	+36.1±7.7
S. granarius	+48.7±5.6	+ 8.0±4.9	+ 5.7±4.8	+18.9±5.5
3. Insects preconditioned at 0 % R.H. for 24 hours				
S. zea-mais	+ 0.2±1.6	-11.8±5.2	-12.6±4.1	-39.8±5.6
S. oryzae	-48.2±11.0	-34.8±4.2	-38.2±5.0	-52.5±3.2
S. granarius	+11.5±7.8	-4.4±3.9	+ 1.4±3.9	+ 3.6±5.0

4. Antennal club removed- Insects preconditioned at 70%R.H.	
S. zea-mais	- 4.9±3.5
S. oryzae	-1.8±0.6
S. granarius	- 0.9±0.2

When the insects were desiccated for 24 hours, on the other hand, S.granarius weevils were nearly non-responsive to the humidity gradients offered, while S.oryzae weevils showed a strong preference for the wet side in all the tests. A clear reaction to the wet side was seen in S.zea-mais at the higher range of the humidity scale, and a weaker response in 0-20 % and 40-60 % R.H. gradients, whereas in the 0-100 % R.H. gradient there was no discrimination between the two sides of the apparatus (TABLE 61) .

The role of the antennae in humidity perception was investigated in a number of arthropods (see Introduction). Removal of the club segment, however, abolished the humidity response completely (TABLE 61). This indicates that the trichoid sensilla found on that segment, are the only humidity receptors present on the body of the three species of weevils.

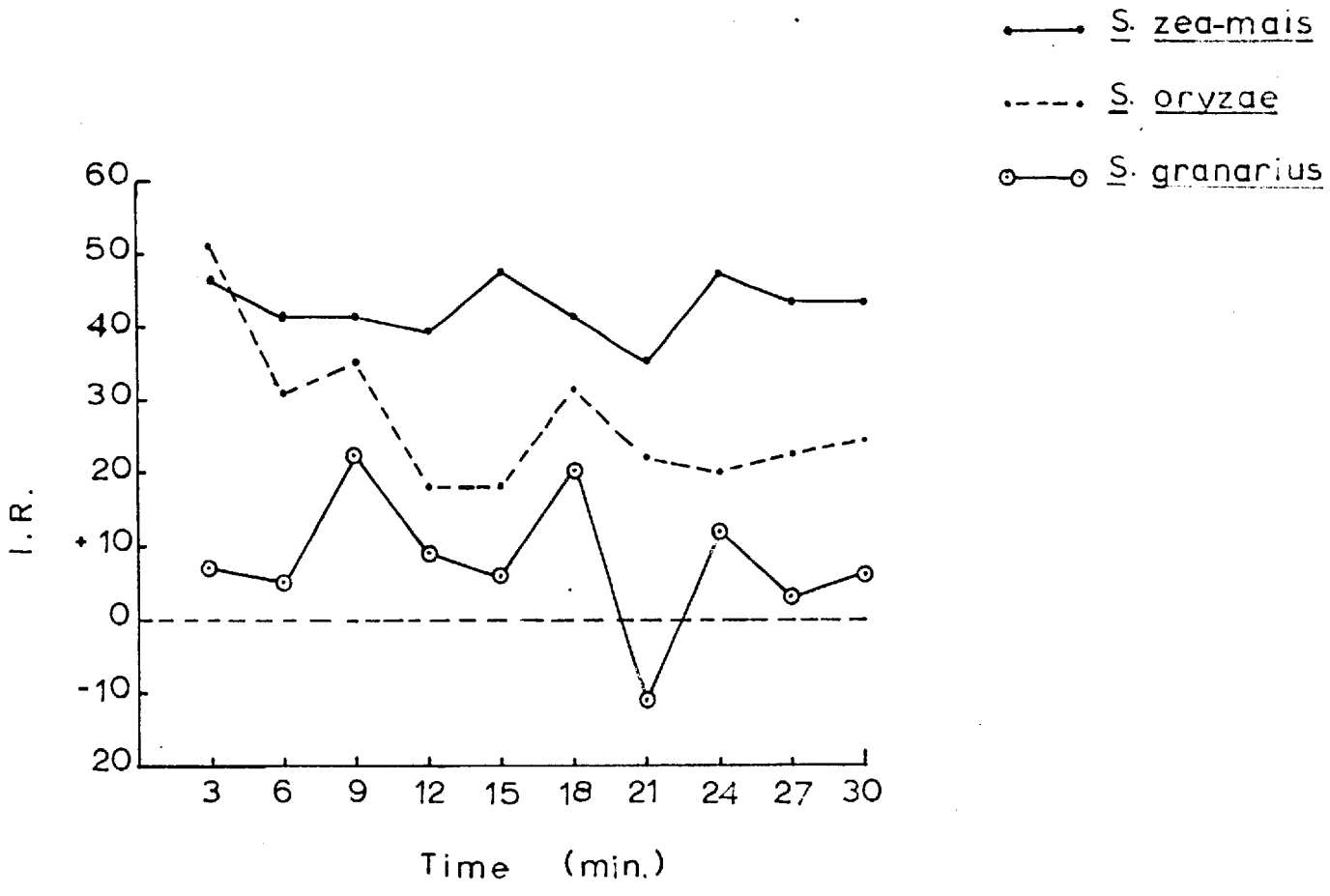


Fig. 71 : Index of Reaction of the Weevils in (0-20%) Relative Humidity Gradient, and Preconditioned at 70% R.H.

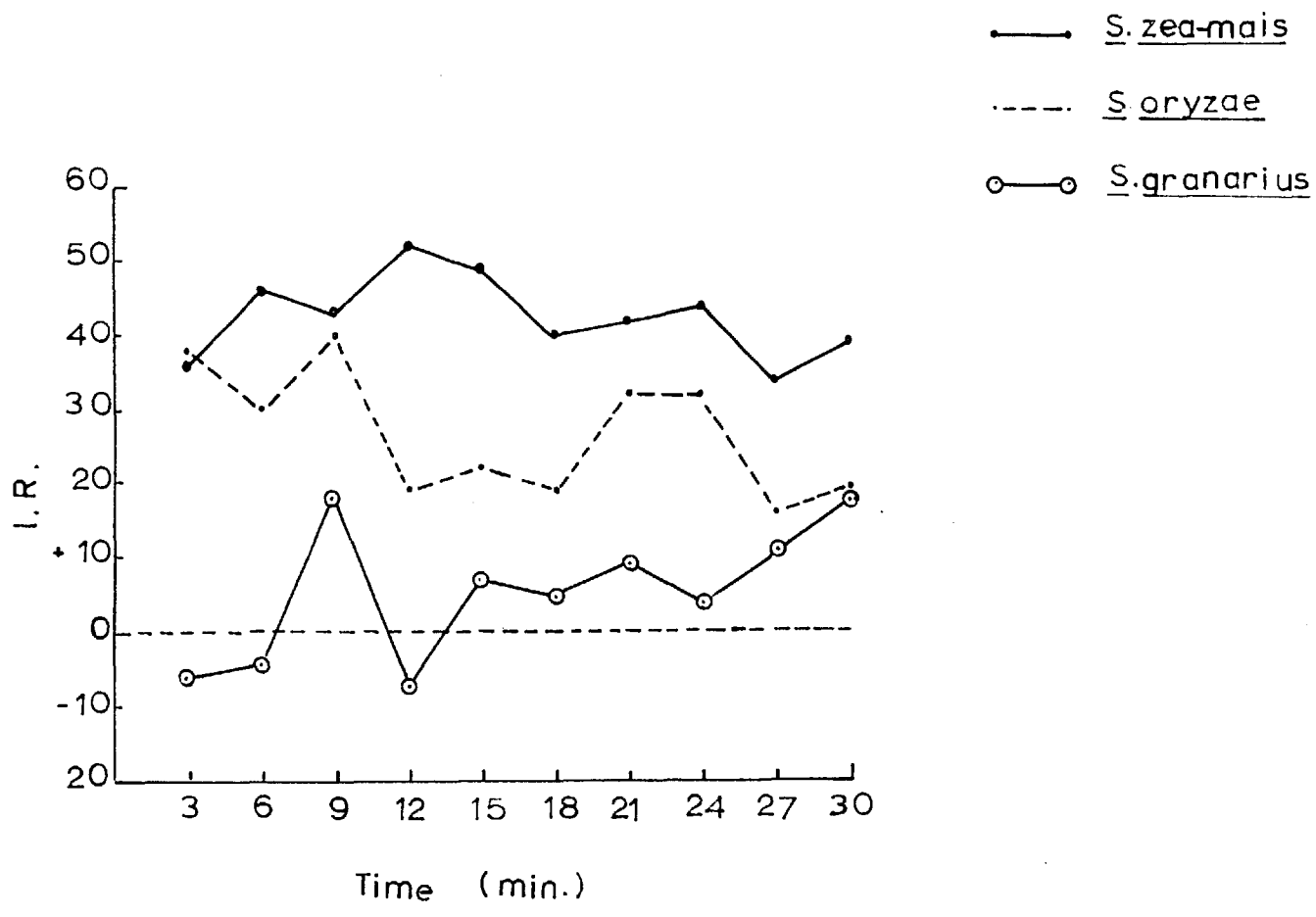


Fig. 72: Index of Reaction of the Weevils in (40-60%) Relative Humidity Gradient, and Preconditioned at 70% R.H.

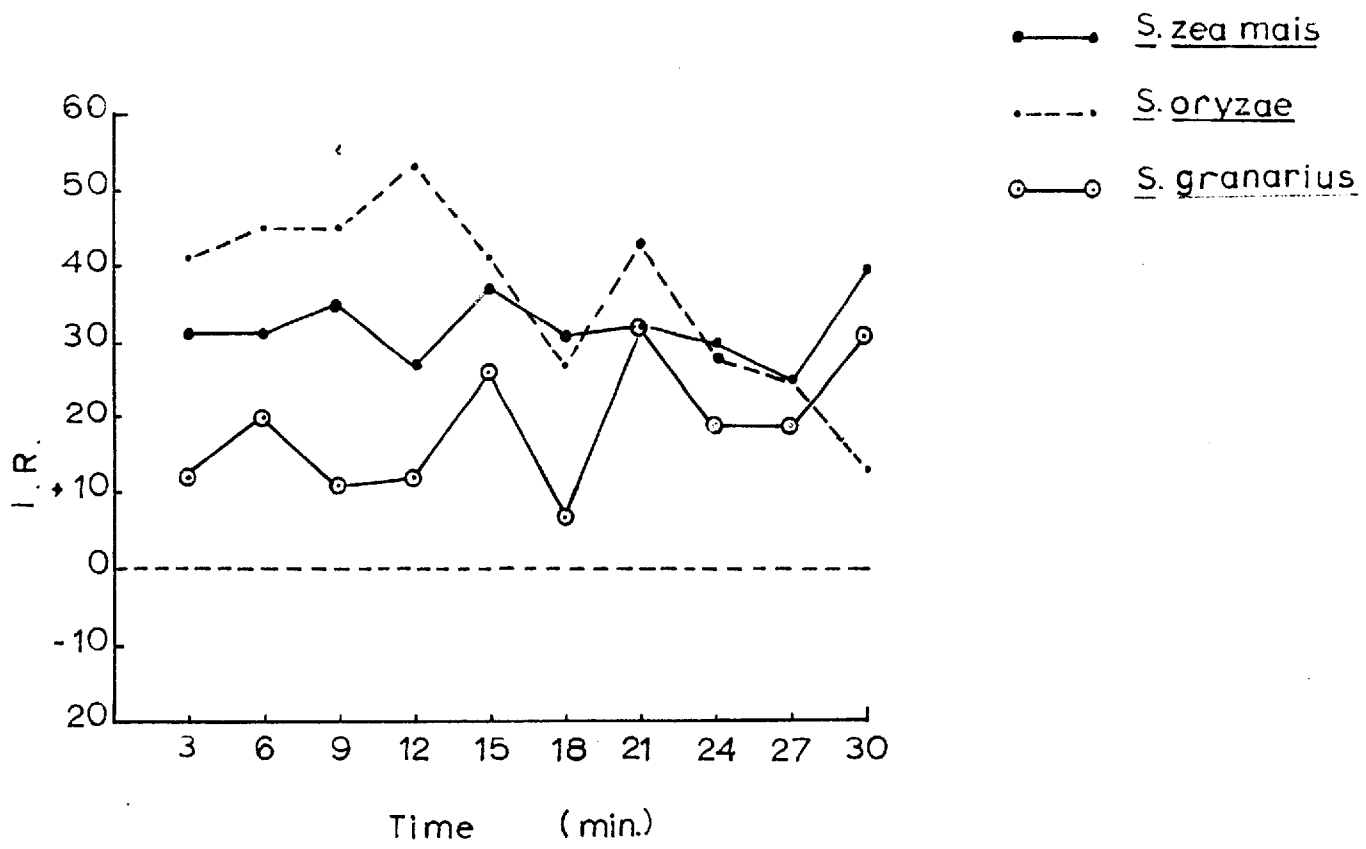


Fig. 73 : Index of Reaction of the Weevils in (80-100 %) Relative Humidity Gradient, and Preconditioned at 70 % R.H.

VII. TEMPERATURE PREFERENCE OF THE WEEVILS

A. Introduction and Review of Literature :-

The range of temperature within which an animal may live differs greatly in various species. It has been claimed by Brues (1939) that 52°C. is about the highest temperature at which any animal is known to thrive indefinitely. At the other extreme, the beetle Astagobius angustatus completes its life cycle at temperatures between -1.7° and +1.0°C. (Allee et al.,1949). Andrewartha and Birch (1954) concluded that aquatic animals live within narrow ranges of temperature (16°C. or less),whereas terrestrial or amphibious animals live in places where the temperature is more variable. Extensive work has been carried out dealing with the temperature preference of various species ; the subject has been reviewed by Deal (1941) and by Fraenkel and Gunn (1961). Most of the experiments on the reactions to temperature have involved gradients of floor temperature and the resulting gradients in the air. Whenever there is a gradient in temperature there are also, inevitably, gradients in the relative humidity of the atmosphere ; a difficulty which is encountered in the experiments on terrestrial animals.

While a definite preference for a certain range of temperature was exhibited by various species, in very few cases the role played by the temperature factor was not detected as in the larvae of Choristoneura fumiferana which responded only to differences in the relative humidity (Wellington, 1949).

Sensitivity to temperature typically plays an important part in the process of reaching and maintaining an optimal situation. Krogh (1914) suggested that the influence of temperature is twofold, it has a relatively prompt effect mediated by the central nervous system and a slower effect through the alteration of general metabolism. Homp (1938) found that the human body louse Pediculus humanus corporis, reached its optimal range (26.4°-29.7°C.) through restless movements and avoiding reactions in other parts of the gradient field. Herter (1924) mentioned that preadaptation to a higher or lower temperature may shift the preference upward or downward according to the species. Gunn (1934) found the preferred temperature range of normal male Blatta orientalis was 20°-29°C, while specimens desiccated to 70 % of their original weight showed a much lower preferred temperature, namely 12°-23°C. Agrell (1947) found that exposing the carabid beetle Harpalus pubescens to specific temperature during a fasting period led first to the selection of higher temperatures than in the control specimens.

The effect of preadaptation on the reaction of some insects to temperature was described by Mellanby (1939). He found that the " chill-coma temperature " for five species of insects belonging to three different orders was considerably affected by the temperature at which they had been living. Individuals of the same species from warm conditions were immobilized at higher temperatures than those from cool. Thomson (1938) found that the avoidance to high temperatures offered by Culex fatigans was strongest in the hungry females. Graham (1958) found two ranges of preferred temperature exhibited by Tribolium species, these were 28° and 14°C. He concluded that the intensity of reaction towards 28° or 14°C. was dependent upon the environmental temperature at which the population was previously kept; a colder environment initiated more intense warm end reaction. A T.castaneum population from a warm environment has a markedly more intense reaction towards 28°C than T.confusum (46 % as against 7%). Nicholson (1934) found that rising temperature causes activity of the sheep-tick to occur at a lower range of temperatures than does constant temperature. He further concluded that differences in the reactions to temperature of the closely related species Lucilia cuprina and L. sericata are very distinct . The difference in behaviour exhibited by the

same species at different developmental stages was illustrated by Thomsen and Thomsen (1937) in their experiments on Musca domestica . For young larvae in the feeding stage 30° - 37°C. was the preference zone, whereas that of mature larvae close to pupation fell below 15°C. Second-instar larvae of Aedes aegypti when subjected to a temperature gradient from 42°C to 8°C.,the majority of the larvae aggregated over the range of temperature 23° - 32°C., while third- and fourth-instar larvae and pupae showed a marked preference for the range of temperature 28° - 32°C. (Omardeen,1957).

Deal (1941) in his experiments on the granary and the rice weevils, apparently considered the latter as a single species (C.oryzae) . The present work was carried out in the light of the separation of the rice weevil complex into two definite species. Some modifications to Deal's technique were found to be essential, and thus S.granarius was also included in these experiments.

B. Methods and Techniques

The apparatus in which the temperature gradient was set up was a rectangular aluminium trough with wall and floor about 3 mm. thick and with internal dimensions of 24"X 2" X 1 " deep (Fig. 74). The trough was covered by a thick plastic cover through which 6 thermometers with their

bulbs touching the floor were inserted via small wooden tubes, with the result that 5 compartments were established, and the temperature range in each was measured.

An aluminium cylindrical rod (r) 7 cm. long and 3.5 cm. in diameter fixed to the floor of the trough near one end, was immersed inside a large thermos flask (f) filled with ice , and covered with a thick cardboard sheet. The other end was heated with a 60-watt bulb (b) covered by a sheet of black paper fixed to the reflector of the lamp. A wooden cage (c) supported the hot end of the apparatus. The apparatus was placed in a constant temperature room at 20°C. and 50 % R.H. A very constant gradient with a range of 12.5°C. (10° - 22.5°C.) was maintained. The steepness of the gradient was 2.5°C. in 2 inches. Equilibrium was reached within one hour. The five compartments were filled with two layers of English wheat grain. Two inches were left free of grain at each end of the trough to cancel any thigmotactic tendency of the weevils. In this manner , the weevils settled down inside the grain layer close to the aluminium floor, the temperature of which was known. The experiments were carried out in complete darkness to cancel any effects of light. The relative humidity of the air was measured by means of cobalt thiocyanate papers (Solomon , 1957). No detected difference existed between the relative humidities of the different compartments (i.e. any gradient

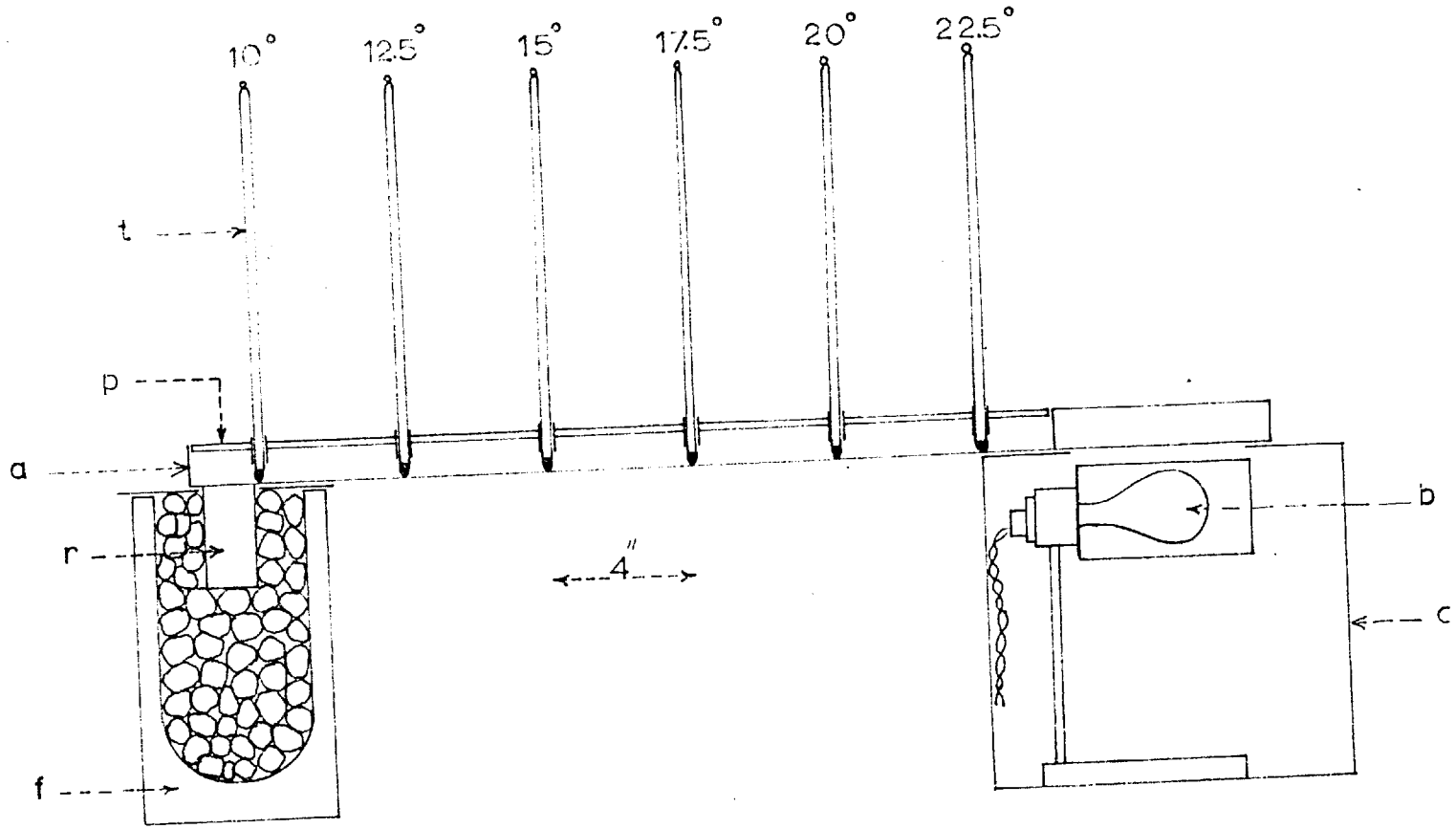


Fig. 74 : Temperature gradient apparatus ; a, aluminium trough ; b, bulb ; c cage; f, thermos flask; p, plastic lid ; r, rod ; t, thermometer.

that existed was below 5 % R.H.). The grain was conditioned at 50 % R.H., 20°C. for one week before using it in the experiments. The moisture content was 11.1 %.

The weevils tested were 2-week old, reared in English wheat at 25°C., 70 % R.H. 50 weevils, chosen at random, were introduced inside the apparatus through a hole in the plastic cover on top of the middle compartment. The number of the weevils in each temperature range was counted after one hour. Ten replicates were made in each set of experiments for the three species, the total number of insects used was 500 of each species. 4 control experiments with 50 insects in each, were carried out for each set of experiments at 20°C.

In some preliminary experiments, similar to those of Deal (1941), when a wide range of the temperature gradient was used, it was noticed that (1) The weevils exhibited a strong avoidance reaction of temperatures higher than 38°C. This was accompanied by lifting the tarsi in a nearly perpendicular position and using the tibiae in their rapid movements on the hot substratum. It is possible that these unfavourable conditions stimulate the weevils to show a strong reversal of the reaction i.e. to exhibit a preference for the other extreme end of the gradient. In fact a big percentage of the weevils aggregated in the coldest region.

(2) Another disadvantage was that all the weevils became immobile or ' cold trapped ' at temperatures below 10°C. ; a state from which they could never recover . (3) The wide range gradient of temperature was accompanied by a wide gradient of relative humidity of the air. The strong tendency of the weevils to move to drier atmospheres (see Section VI dealing with the humidity reactions of the weevils) must have interfered with their distribution in the temperature gradient appparatus, and the colder regions thus appeared to be favoured. (4) It was considered more reasonable to analyse the behaviour of the weevils within a small range of their preferred temperatures at the lower end of the range, and in a gradient which was not steep.

C. Results

The distribution of S.granarius weevils in the temperature gradient apparatus was far from random. The maximum number of weevils (TABLE 62 , Fig. 75) was found in the compartment number " V " where temperature ranged between 20° and 22.5°C. (32.6 % of the total weevils). A gradual decrease in preference, however, was observed towards the cooler end, 17.0 % , 12.4 % a nd 11.6 % were found in compartments " IV " , " III " and " II " respectively . A sudden increase in the percentage of the weevils, occurred

TABLE 62

Temperature preference of S. granarius adults in a gradient ranging between 10°- 22.5°C. at 50 % R.H. and in complete darkness. 500 2-week old weevils were used.

Compartment number and Temperature ranges				
I	II	III	IV	V
10°-12.5°C.	12.5°-15°C.	15°-17.5°C.	17.5°-20°C.	20°-22.5°C.
Total number of weevils and percentage				
132	58	62	85	163
26.4 %	11.6 %	12.4 %	17.0 %	32.6 %
Control experiments at 20°C., 50 % R.H. (200 weevils)				
44	38	37	38	43
22 %	19 %	18.5 %	19 %	21.5 %

in the coldest compartment number " I " where the temperature ranged between 10° and 12.5°C. The significance of the preference for the different regions of the gradient was high ($P < 0.001$). The weevils in the control experiments carried out at 20°C., 50 % R.H. showed no significant variation in their distribution in the different compartments.

In S.zea-mais (TABLE 63, and Fig. 75), an extremely strong preference for the coldest compartment was exhibited by the weevils (77.2 % of the total). A gradual decrease towards the hot end of the gradient occurred. The significance of the difference in distribution in the successive comparments was high ($P < 0.001$). The distribution of the weevils in the control experiments was not far from random.

In S.oryzae a gradual increase in the percentage of the weevils occurred in the direction of decreasing temperature, the peak being reached at the coldest region of the gradient " compartment I " , which contained 41.8 % of the total number of the weevils (TABLE 64, and Fig. 75).

D. Discussion

Within the limitations of the experimental methods used, the three species showed clear differences in their behaviour . The distribution of the weevils in the temperature gradient ranging between 10° and 22.5°C. differed highly significantly in the three species ($P < 0.001$). In S.granarius the

TABLE 63

Temperature preference of S.zea-mais weevils in a gradient ranging between 10° and 22.5° C. at 50 % R.H. and in complete darkness. The data from 500 2-week-old weevils

Compartment number and temperature ranges				
I	II	III	IV	V
10°- 12.5° C.	12.5°- 15°C.	15°- 17.5°C.	17.5°- 20°C.	20°- 22.5°C.
Total numbers of weevils and percentage				
386	78	18	12	6
77.2 %	15.6 %	3.6 %	2.4 %	1.2 %
Control experiments at 20° C. , 50 % R.H. (200 weevils)				
41	42	39	38	40
20.5 %	21 %	19.5 %	19 %	20 %

TABLE 64

Temperature preference of S.oryzae Weevils in a gradient ranging between 10° and 22.5° C. at 50% R.H. and in complete darkness. The data from 500 2-week old Weevils.

Compartment number and temperature ranges				
I	II	III	IV	V
10°- 12.5° C.	12.5°- 15° C.	15°-17.5° C.	17.5°-20° C.	20°- 22.5° C.
Total numbers of weevils and percentage				
209	115	76	53	47
41.8%	23.0 %	15.2 %	10.6 %	9.4 %
Control experiments at 20° C. , 50 % R.H. (200 weevils)				
42	39	41	39	39
21 %	19.5 %	20.5 %	19.5 %	19.5%

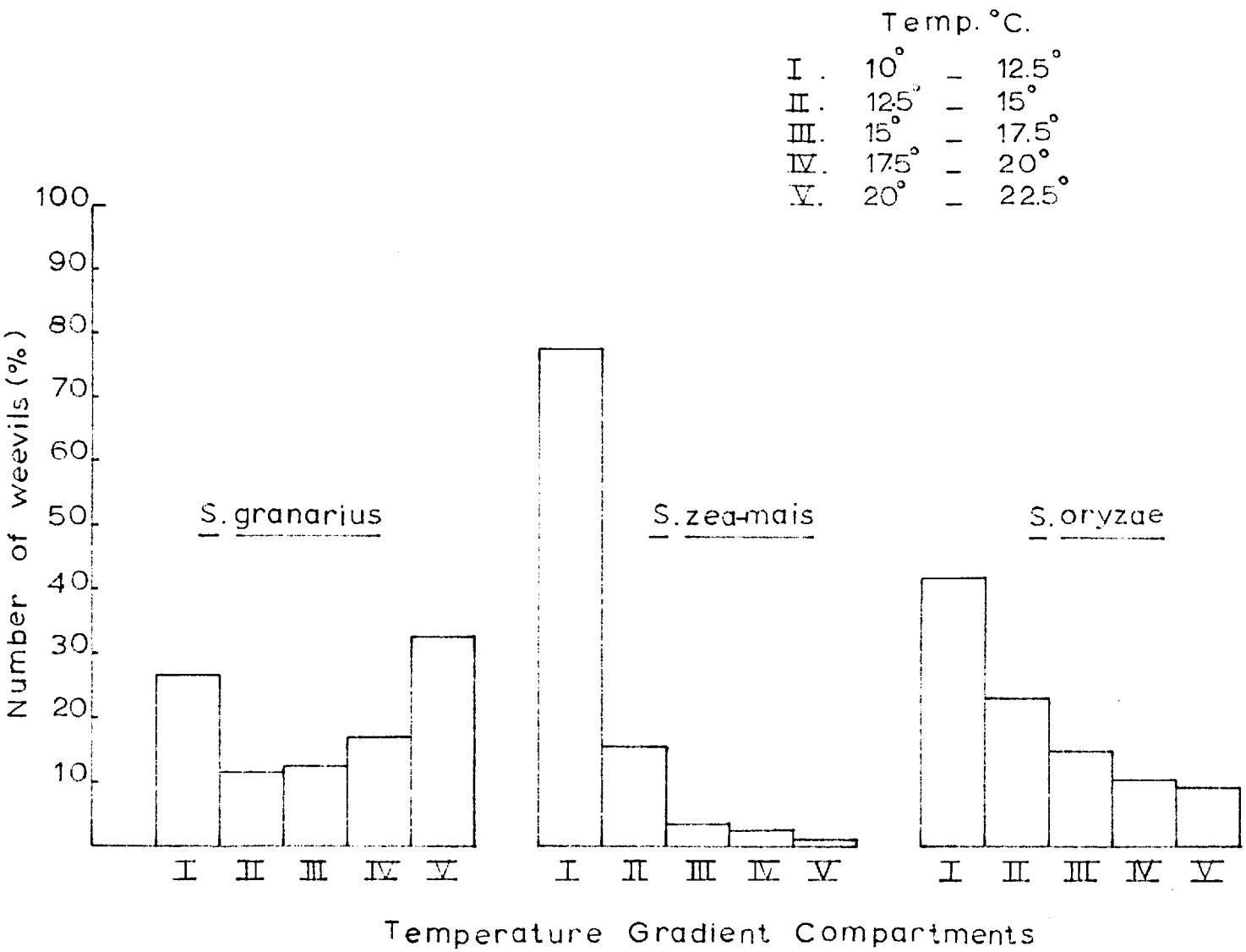


Fig. 75 : Histogram showing the distribution of the weevils in the temperature gradient apparatus.

maximum number of the weevils (32.6 % of the total) preferred the hottest region of the gradient (20°-22.5°C.), with a gradual decrease towards the cooler side, and the existence of another peak , but less conspicuous than the first, at the coldest compartment (10°-12.5°C.). This pattern of behaviour differed greatly from that of the two species of the rice weevils, both of which avoided the warm end of the gradient and exhibited a gradual increase in their preference for the regions with decreased temperature. The two latter species, on the other hand, differed significantly in the percentages present in the compartment number " I " i.e. at the coldest end of the temperature gradient ranging between 10°-12.5°C. It was found that 77.2 % of S.zea-mais weevils preferred the coldest region as compared to 41.8 % in S.oryzae.

The aggregation at the cold end of the gradient is puzzling. It can be suggested that the insects became less active at the lower temperatures and hence this is not a true " preferred temperature ". Similar results have been obtained by Deal (1941), in other insects than the granary and the rice weevils as e.g. Tribolium confusum, Ptinus tectus, Acanthomyops sp., and Cimex lectularius. Gunn and Walshe (1942) recorded two temperatures at which Ptinus tectus aggregated, these were 4° and 24°C. In a linear gradient extending from 8° - 45°C., the sheep-tick Ixodes ricinus aggregate rapidly in the coldest region after being

exposed to 25°C. Those remaining outside the coldest region show no definite preference within the range 11°-41°C.

It appears that S.zea-mais is the most sensitive to low temperatures, and the most readily immobilized by them. Back and Cotton (1924) working on the relative resistance of the granary and the rice weevils, found that the adults and the immature stages of S.granarius exhibited greater resistance to withstand very low temperatures than those of S.oryza (complex). It is known , however, that S.granarius can breed at 17°C. (Richards,1947), and that S.zea-mais is capable of breeding at the same temperature (Howe,1952), and S.oryzae even at a lower temperature,namely 15.2°C. (Birch,1945).

No attempts have been made to locate the organs responsible for the temperature sense, although there is an indication of their possible existence on the tarsi. This was suggested by the behaviour of the weevils on a warm metal surface (39° C. or more). The weevils lift their tarsi upward in a nearly vertical position .and the tips of the tibiae are used instead for walking on the hot substratum. Several types of hairs are found on the tarsal segments , some of them may be involved in the perception of variations in temperature. Another possibility is that the tenent hairs clothing the ventral surface of the third tarsomere, which normally touch the substratum (see Section IV on the climbing

ability of the weevils), may be influenced by the rise in temperature of that surface, through changes in the physical properties of their glandular secretion, which may either increase or decrease their adhering power. These changes may be detected by the insects and thus they avoid the unsuitable floor.

A temperature sensitive region was found in the pulvilli of the four tarsal segments and in the aroliar pad (between the claws) of Periplaneta americana (Kerkut and Taylor,1957). The activity of the roaches increased by the gradual cooling of the substratum. Later , the activity ceased and the insects exhibited a characteristic position with the claws and the distal ends of the tarsi raised from the ground. The sensitivity of the antennae to high temperatures was found in a number of insects, for example, in Phasmidae (Cappe de Baillon,1936), in Collembola(Strebel, 1932), in Rhodnius (Wigglesworth and Gillett,1934), and in Apis mellifica (Heran,1952) . In the sheep-tick Ixodes ricinus, the fore-legs bear sensilla sensitive to temperature (Lees,1948). Slifer (1951, 1953) described sensory structures situated on the head,thorax and abdomen of many grasshoppers, which function as thermo-receptors for radiant heat. Their existence was supported by experimental evidence.

VIII. REACTIONS OF THE WEEVILS TO LIGHT

A. Introduction and Review of Literature :-

Light as a physical factor plays a major role in the behaviour of animals. Discussions of the basic problem of orientation have centred around the reactions of various species to light, both because of the prevalence and adaptive scope of such reactions and because of their variety and range of elaboration. A convenient classification of orientation types (kineses and taxes) was given by Fraenkel and Gunn (1940), who reviewed the previous observations and theories, and whose classification was derived from that of Kühn (1919,1929). Since then a tremendous amount of work has appeared in literature involving the behaviour of animals in different types of light experiments. As examples of the most important light reactions worked out on insects, it may be mentioned a) the " klinotactic " behaviour of dipterous larvae (Mast,1911) which attain their orientation away of the light by regularly alternating lateral deviations of the head and comparing the light intensities on both sides ; b) the " tropotactic " behaviour of the photonegative Ephestia larvae (Brandt,1934) and the photo positive Eristalis flies (Mast,1923), which orientate themselves

directly away or directly towards a source of light by turning to more or to less stimulated side by simultaneous comparison of intensities of light on the two sides ; c) the " telotactic " behaviour of Apis (Minnich,1919 and Urban,1932), which attain their orientation to a source of light directly without deviations, the pattern of light being " fixed " on to certain ommatidia of the compound eye and ignoring any other source of light ; d) the "light-compass reaction " exhibited by the ant Lasius niger (Brun, 1914) and the honeybee Apis mellifica (Wolf,1927) and later by von Frisch (1946,a and b, 1948), which move at a temporarily fixed angle to light rays, which usually come from the sun, or to the plane of polarized light from the sky. The "dorsal light reaction" of dragonflies (Mittelstaedt, 1950) and locusts (Goodman,1959) are some of the types of reactions to light which have been discussed.

The light reactions of the granary weevils have been the subject of work of some authors. Törne (1941) studied the behaviour of Calandra granaria (= Sitophilus granarius) in a choice chamber apparatus offering the weevils seven compartments, illuminated with light of different wave lengths at the same time. The percentage of the weevils in the different compartments, five minutes after their introduction, was 29.4 % in the green light and 26.8 % in the yellow, and then in the decreasing order of 10.4 %,

9.9 % , 8.8 %, 8.7 % and 6 % , in three intensities of white light called'dark, faint and bright', blue and finally the red light. In another series of experiments lasting three hours and in which wheat grain was provided in the different compartments, the preference of the weevils for aggregation was as follows :- 20 % in the faint white light, 19.1 % in the bright white , 16.8 % in the yellow, 13.8 % in the green, 11.4 % in the blue, 10.9 % in the dark white and 8 % in the red light. In a long-range set of experiments lasting six days, most of the weevils were found in the dark compartment (33.3 %), followed by 23.7 % in the faint white light, 19.2 % in the blue, 14.3 % in the yellow and 9.5 % in the bright white light. No weevils were found in the red and the green compartments. From his experiments he concluded that light is as important a factor in the life cycle as temperature and humidity. In bright light, much more CO_2 was produced than in the darkness (the insects being more active in bright light), and the length of the life cycle was shorter. He also mentioned that the development of the granary weevils was greatly affected by unfavourable light conditions. Consequently development either stopped or sometimes it did not stop and dwarf types of offspring were produced. The optimum conditions of light for the development of the insects were 500 - 1250 Lux , which were of weak white light. Richards (1951) found that

when C.granaria weevils were disturbed, most of them moved away from the source of light and a small fraction of the population was photopositive. He was able to isolate two genetic types in the course of two generations, those which were negative to light and those which were almost indifferent to it. Smereka and Hodson (1959) mentioned that disturbed photonegative S.granarius weevils became photopositive when left undisturbed for 30 minutes or more, depending on the number of individuals participating in each experiment, since larger groups of weevils maintained themselves in an excited stage and thus remained photonegative for longer periods. A similar behaviour exhibited by the field crickets was observed by Chauvin (1941), who mentioned that individual field crickets were photopositive, but groups were photonegative.

In the present work, the reactions of newly emerged adults of the three species of Sitophilus towards a source of light were tested. The effect of unilateral blinding on the circus movements of some individuals showing a definite photopositive or photonegative reaction was also studied.

It should be emphasized that only one type of light experiment was tried, to see whether the three species behaved differently under identical experimental conditions. It is not assumed that all the complex reactions to light have been analysed or studied.

B. Methods and Techniques

Newly emerged weevils 0 - 2 hours old reared in a constant temperature room at 25° C., 70 % R.H. and in complete darkness, were obtained by sifting the cultures at a very low light intensity twice at 2-hour interval and choosing the weevils to be tested from the second sift. In this manner the behaviour of the weevils to a source of light for the first time in their lives could be examined. This precaution was found desirable since the work of Smereka and Hodson (1959) has shown that S.granarius weevils which were normally photonegative became photopositive after 30 minutes in the course of an experiment, when they were given the choice between a dark and a brightly lit chamber.

In the present work the reaction of the weevils to a horizontal beam of light was studied. The simple apparatus used was based on the same principle as that described by Richards (1951). Slight modofications, however, were found essential. A cage of dull black paper 30 X 20 X 20 cm. (Fig. 76, A) was constructed, having a side vertical slit 4 X 2 cm. (B) . A glass trough filled with water (C) was placed between the slit (B) and a 60-watt bulb (D), to prevent the heat of the bulb from reaching the arena (E) inside the cage. The arena was a circle 12 cm. in diameter, drawn

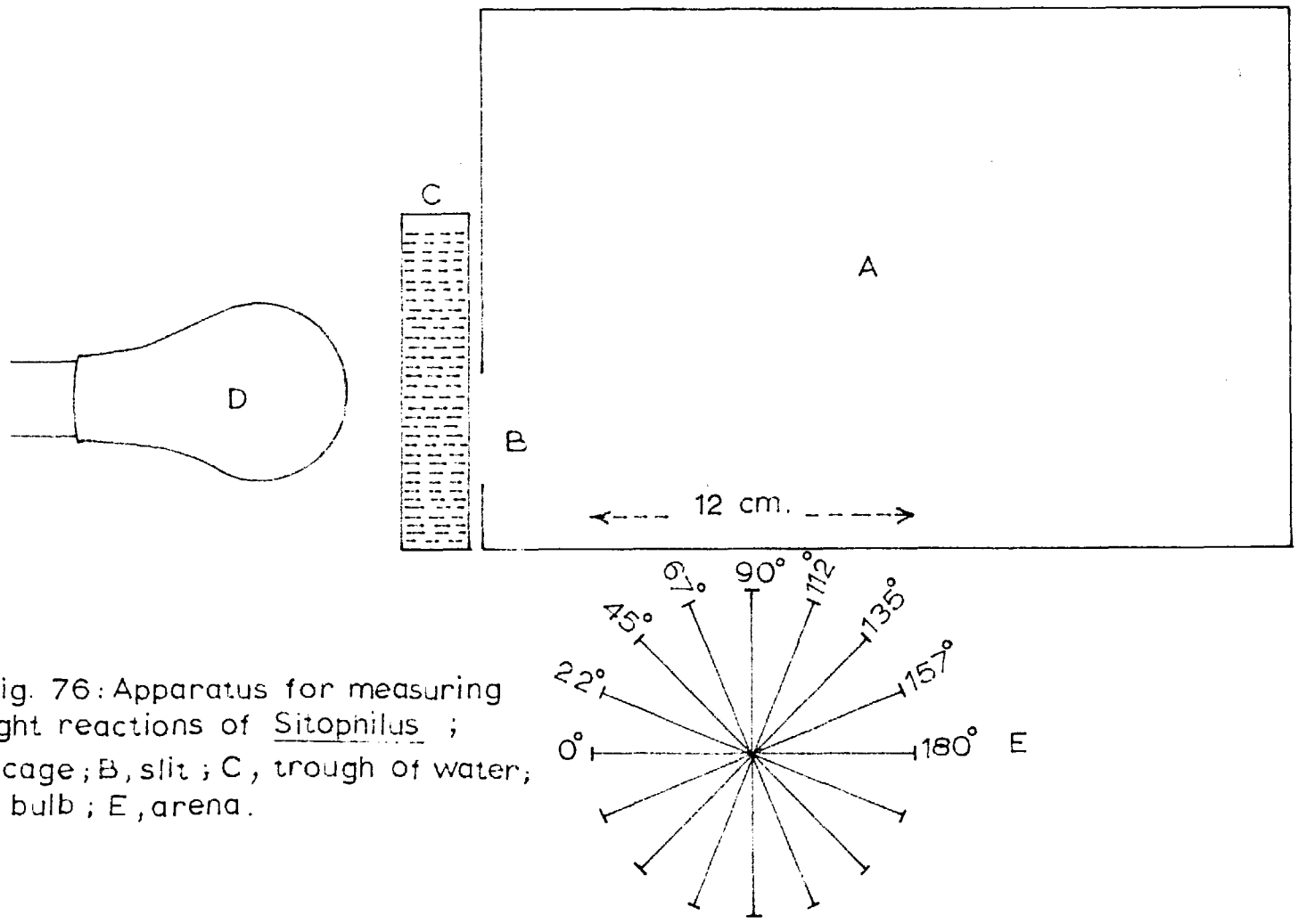


Fig. 76: Apparatus for measuring light reactions of Sitophilus ; A, cage ; B, slit ; C, trough of water; D, bulb ; E, arena.

with a red pencil on the floor of the cage. The centre of the circle was 10 cm. from the point vertically beneath the slit (B). Radii were drawn at intervals of $22\frac{1}{2}^{\circ}$ and the direction away from the light was called 180° and towards the light 0°. A weevil to be tested was placed on its back in the centre of the circle facing the light and allowed to walk 6 cm. The direction of the walk (or the angle of the track) was estimated to the nearest $22\frac{1}{2}^{\circ}$. In recording the tests the half degree was ignored i.e. $22\frac{1}{2}^{\circ}$ was taken as 22°, etc. All tests were made in a dark room , kept at 25° C., 70 % R.H. 200 weevils of each sex were tested in each set.

The effect of unilateral blinding on the behaviour of some individuals which exhibited a definite photopositive reaction in the first set of experiments was examined as follows :- The eyes on one side of the weevils were neatly covered with a layer of a black lacquer by means of a fine brush ; the weevils were held under a binocular microscope. The weevils were kept in the constant temperature room over night to recover before being tested. No inhibitory effect on the activity of the insects was noticed. A single weevil was placed on a white sheet of paper and covered with a white cubic wooden cage, 25 cm. each side, having a ground glass top which allowed only diffused light to penetrate from above. The behaviour of the weevil was observed through a narrow

slit near the top of the cage, and the track was drawn on a separate sheet of paper.

C. Results

1) Measurement of the angles of tracks made by the weevils in a horizontal beam of light :-

The angles of the tracks made by the weevils of each sex of the three species were summarized in TABLE 65 and Figs. 77 - 80 . In S.granarius the percentage of the male weevils which were photonegative to the source of light i.e. the angles of the tracks made by the weevils were 112^{c} or more away of the light was 81.5 %. The percentage of the female weevils that showed the same behaviour was 72 %. In S.zea-mais the percentage of the male weevils which exhibited a photonegative reaction was 31.5 %, while that of the females was 23.5 % . In S.oryzae the percentage of the male weevils which made tracks with an angle of 112° or more was 64 % , whereas that of the females which behaved similarly was 58 % . The three species agreed in that the percentage of the photonegative weevils was higher in the males than in the females of the same species. However, this difference in the behaviour of the two sexes of each species was not significant at P = 0.05 (TABLE 66).

TABLE 65

The angle of track made by the Weevils of the three species when placed facing a horizontal beam of light.

Angle		180°	157°	135°	112°	90°	67°	45°	22°	0°
1. S.granarius										
Frequency	♂	18	49	62	34	26	9	-	2	-
	♀	31	43	39	31	33	18	4	1	-
percentage	♂	9	24.5	31	17	13	4.5	-	1	-
	♀	15.5	21.5	19.5	15.5	16.5	9	2	0.5	-
	Mean	12.25	23	25.25	16.25	14.75	6.75	1.0	0.75	-
2. S.zea-mais										
Frequency	♂	4	9	17	33	28	49	28	20	12
	♀	-	6	20	21	57	34	27	17	20
Percentage	♂	2	4.5	8.5	16.5	14	24.5	14	10	6
	♀	-	3	10	10.5	28.5	17	13.5	7.5	10
	Mean	1.00	3.75	9.25	13.5	21.25	20.75	13.75	8.75	8.0
3. S.oryzae										
Frequency	♂	10	43	42	33	21	26	10	9	6
	♀	24	38	39	15	44	13	12	6	9
Percentage	♂	5	21.5	21	16.5	10.5	13	5	4.5	3
	♀	12	19	19.5	7.5	22	6.5	6	3	4.5
	Mean	8.5	20.25	20.25	12.00	16.25	9.75	5.50	3.75	3.75

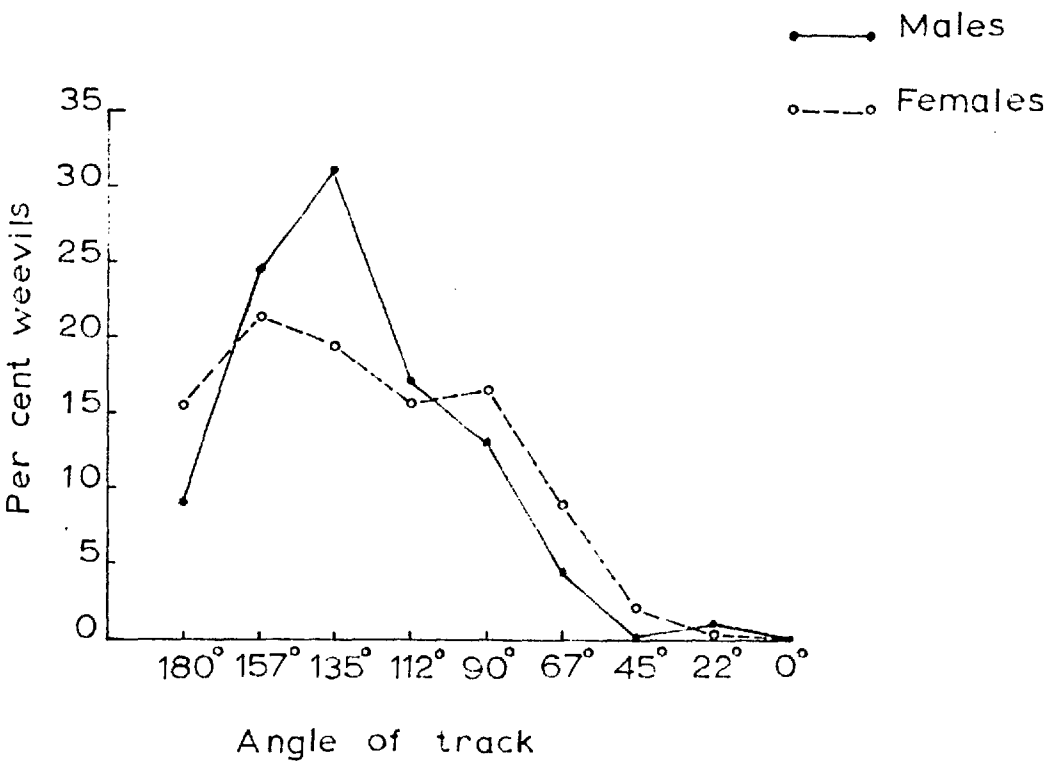


Fig. 77 : Angle of track made by S.granarius weevils in a horizontal beam of light.

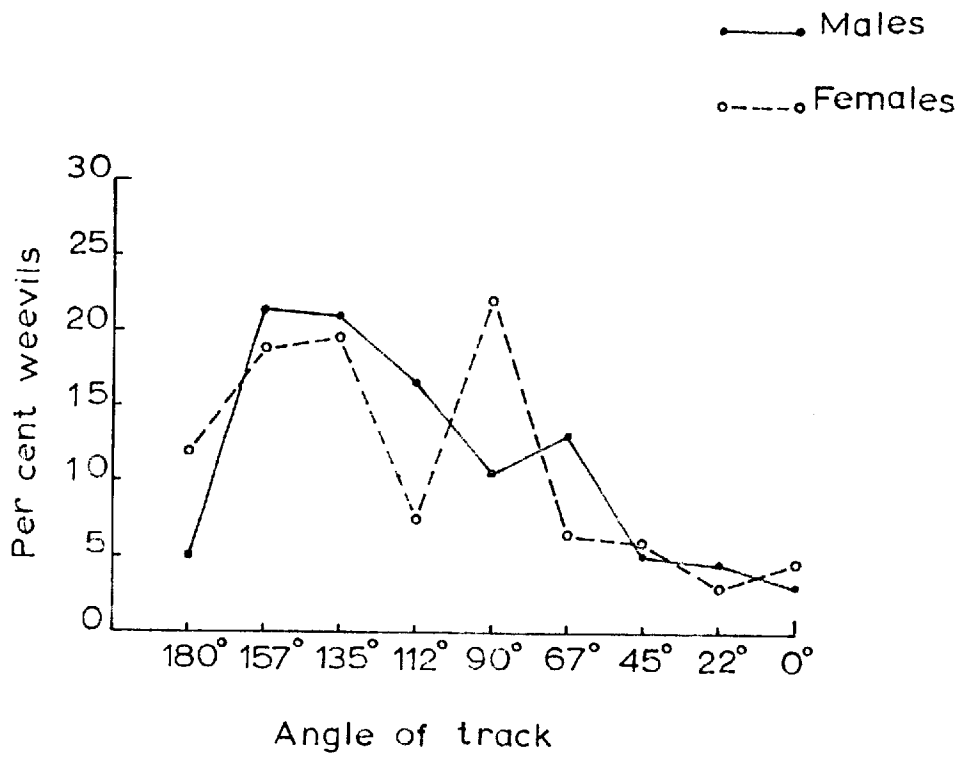


Fig. 78 : Angle of track made by S. oryzae weevils in a horizontal beam of light.

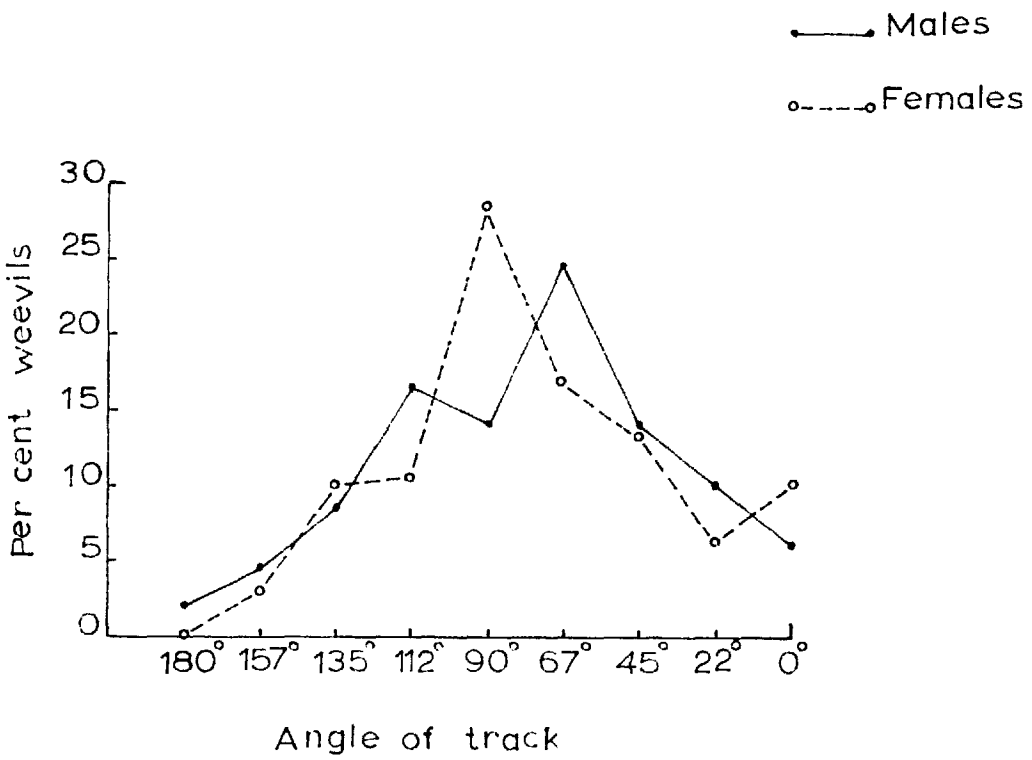


Fig. 79 : Angle of track made by S. zea-mais weevils in a horizontal beam of light.

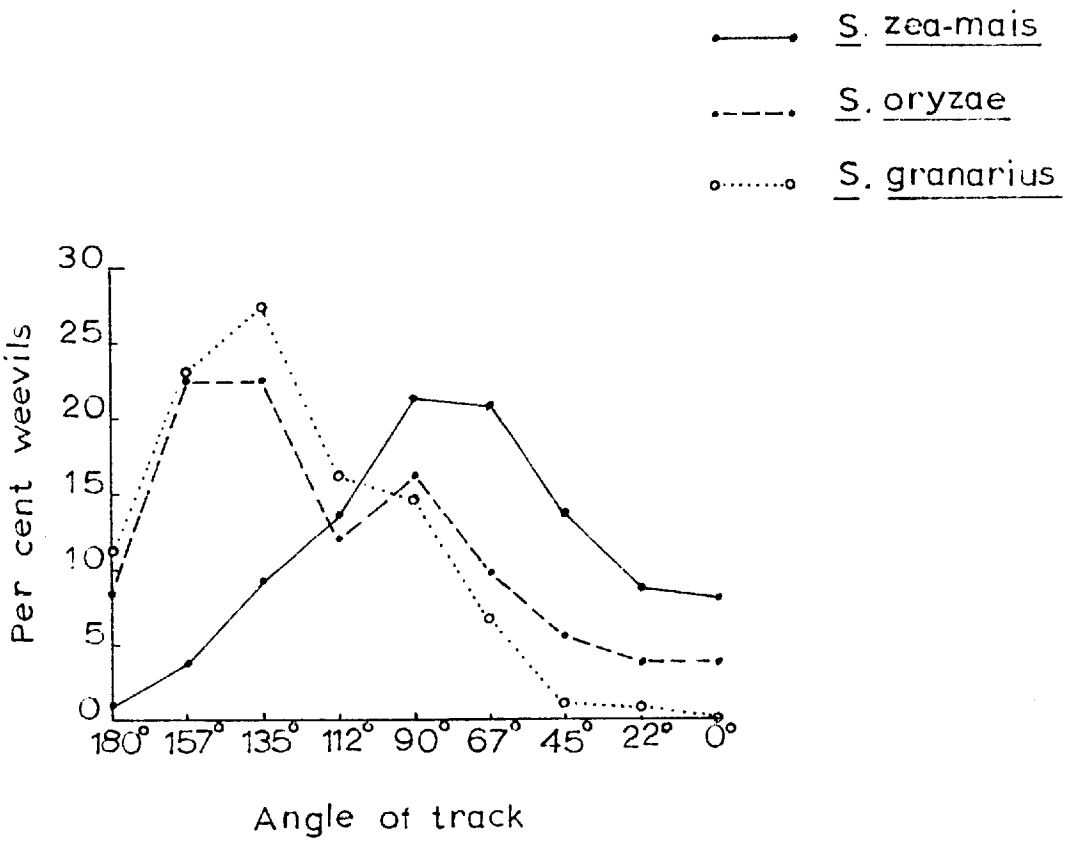


Fig. 80 : Angle of track made by the weevils of the three species in a horizontal beam of light.

When any two of the three species were compared, on the other hand, the variations in the frequency of the weevils making different angles of tracks were highly significant($P < 0.001$).

The total mean percentages of the photonegative weevils (making angles of tracks 112° or more) in S.granarius was 76.75 % compared with 61.00 % in S.oryzae and 27.40 % in S.zea-mais, in other words, within the limits of the experiment, S.granarius and S.oryzae were negative to light whereas S.zea-mais positive.

2) Observations on unilaterally blinded weevils :-

The behaviour of the weevils when blinded on one side and placed in a white cage with diffused light overhead was examined. Fig. 81 shows a typical track of a strongly photonegative S.granarius weevil with the right eye blackened out. It was observed that the weevil followed a frequently zigzaging path, but on the whole tending to make circus movements turning towards the blind side. Fig. 82 shows the track of a strongly photopositive S.zea-mais weevil exhibiting a clear tendency towards the unpainted eye. The track was not zigzaging and the curvature of the circles made was large i.e. the turnings were not frequent. S.oryzae weevils, on the other hand, showing a photonegative behaviour, made frequent turnings towards the covered eye, but no zigzaging movements were exhibited (Fig. 83).

TABLE 66

Significance of the difference in the frequency of the weevils making different angles of tracks (X^2 test)

Insects Compared	Significance
Males and females of S.granarius	not significant
Males and females of S.zea-mais	not significant
Males and females of S.oryzae	not significant
S.granarius and S.zea-mais	$P < 0.001$
S.granarius and S.oryzae	$P < 0.001$
S.zea-mais and S.oryzae	$P < 0.001$

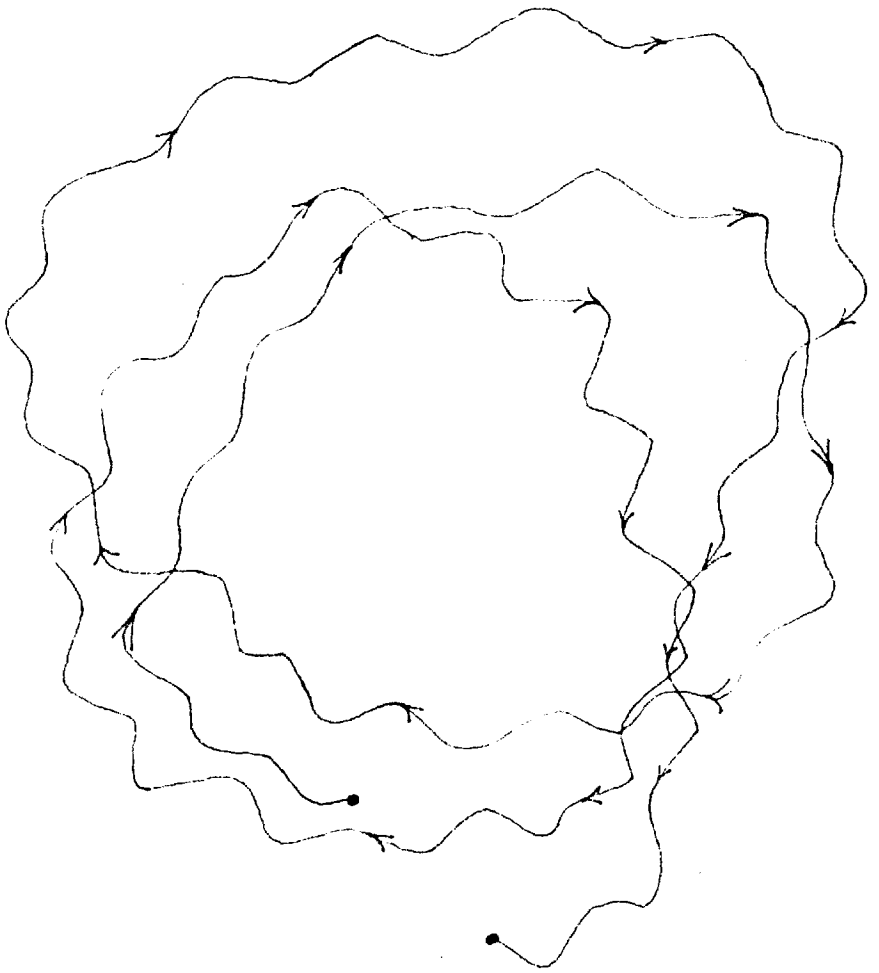


Fig. 81 : Track of a photo-negative weevil of S.granarius blinded on the right side, with the light overhead.

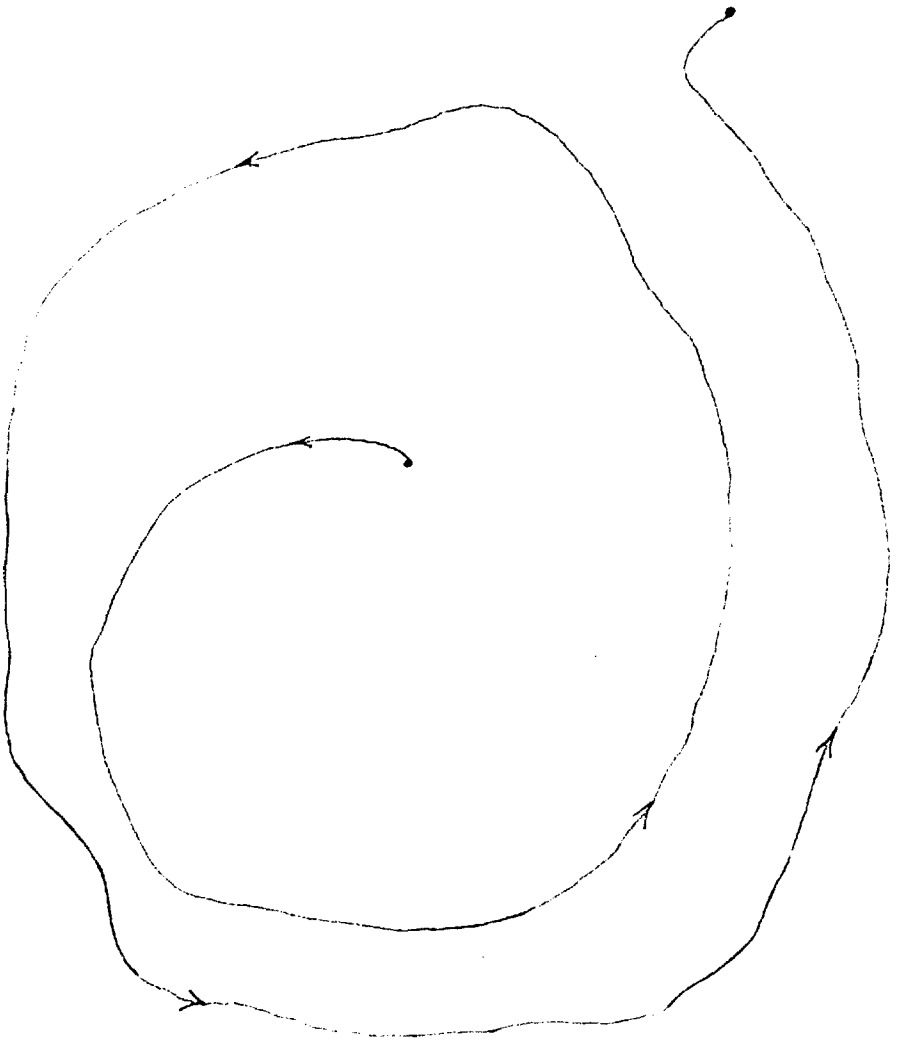


Fig. 82 : Track of a photo-positive weevil of S. zea-mais blinded on the right side, with the light overhead.

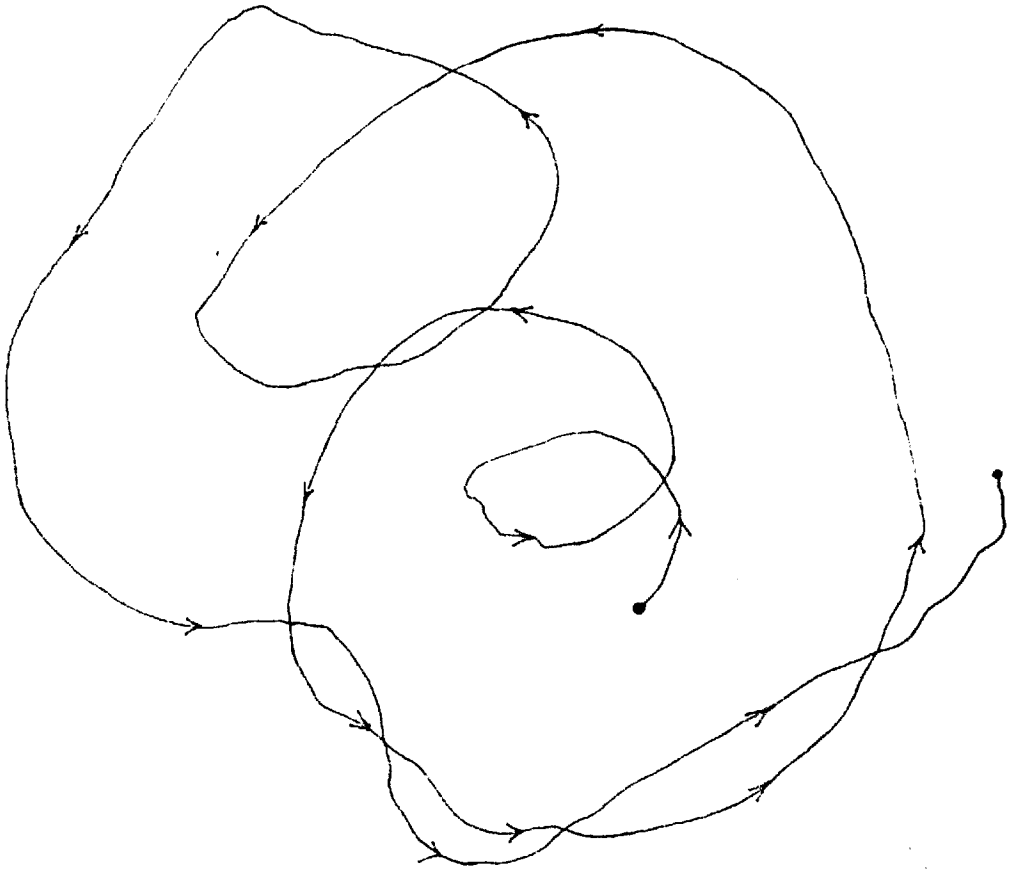


Fig. 83 : Track of a photo-negative weevil of S.oryzae blinded on the left side, with the light overhead.

An interesting observation was that S.granarius weevils, blinded on one side, when placed in a horizontal beam of light, followed a zigzag path ; a behaviour which was not shown by the other two species.

D. Discussion

The idea of studying the behaviour of the weevils just after their emergence from the grains (0 - 2 hours old) was to examine their natural tendency to react to light for the first time in their lives, when they were reared in complete darkness. The effect of preconditioning on the behaviour of S.granarius weevils to light has been emphasized by Smereka and Hodson (1959), who found that the photonegative weevils became photopositive with time when offered the choice between a dark and a bright place.

In these experiments it was found that the three species agreed in that the percentage of the weevils which showed a photonegative reaction i.e. which made angles of tracks 112° or more away of the light source, was higher in the males than in the females. This difference between the two sexes of the three species, however, was not significant at P=0.05 .

The three species, on the other hand, differed highly significantly from each other in their pattern of behaviour

in a horizontal beam of light ($P < 0.001$). The total mean percentages of the photonegative weevils was higher in S.granarius than in S.oryzae (76.75 % compared with 61.00 %) . The majority of the newly emerged weevils of both species can be considered as photonegative. In S.zea-mais, on the other hand, the newly emerged majority of the weevils were either photopositive or indifferent to light; the total mean percentages of the photonegative weevils being 27.4 % .

When the weevils were unilaterally blinded the three species exhibited circus movements on a white background and the light diffused from above. In S.granarius and S. oryzae, the strongly photonegative individuals turned towards the covered eye, and in S.zea-mais the strongly photopositive individuals made the turnings towards the seeing side. The path followed by S.granarius was zigzaging all the time, a behaviour which was not shown by the other two species ; and the reason for its existence in S.granarius is not obvious.

A slight difference between the two species of the rice weevils was that the curvature of the circles made by S. zea-mais weevils was large, while S.oryzae weevils made frequent turnings.

The importance of light as a physical factor affecting

the flying ability of the rice weevils has been clearly demonstrated in laboratory experiments (see Section V). It was found that the flight activity of the weevils increased with the increase in the light intensity, in other words positive photokinesis was noted in another set of experiments.

IX. HUMIDITY AND LIGHT REACTIONS OF THE FOURTH INSTAR LARVAE

A. Introduction and Review of Literature : -

The reactions of insect larvae to light and humidity have been investigated by a large number of workers. Much of larval behaviour, however, seemed to depend greatly on their phsiological condition at the time of the experiments. Starvation has been found to reverse or to modify the light reaction in certain lepidopterous and hymenopterous larvae (Wellington,1948; Sullivan and Wellington , 1953; Green, 1954 ; Wellington et al., 1954) . Choristoneura larvae which were photopositive at 25°C. became photonegative at higher temperatures depending on the larval instar examined (Wellington,1948). The same reaction was exhibited by Malacosoma larvae when they were overheated

in an alternative dark-light chamber, and this reversal was also seen in their field behaviour (Sullivan and Wellington, 1953) . Tenebrio larvae showed no reversal in their strong photonegative behaviour when they were desiccated for three weeks, while the adults when desiccated for six days became photopositive (Perttunen and Lahermaa,1958). It has been shown by Omardeen (1957) that the second and the third instar larvae of Aedes aegypti showed no marked preference for any one light intensity in a light gradient, whereas the fourth instar larvae and pupae aggregated in the darkest region of that gradient. Examples of the larvae which normally show a preference for the wet side of a humidity gradient are those of the genus Agriotes (Lees,1943) , Musca domestica (Hafez,1950), Stomoxys calcitrans (Hafez and Gamal-eddin,1961), and the first and fourth nymphal instars of Schistocerca gregaria (Aziz,1957) . A strong tendency to move to the dry side of the gradient was exhibited by Tenebrio molitor larvae, which can discriminate between 100 % and 99.5 % R.H. (Perttunen and Lahermaa, 1962).

The sensory organs involved in the behaviour of these immature stages have been located, and their role was elucidated by experimental evidence. Different types of olfactory sense organs were described, for instance a) the tuft organs situated on the ventral surface of the three thoracic segments

in Musca larva (Hafez,1950) ; b) the basiconic and styloconic sensilla on the antenna and the maxillary and labial palps of Leptinotarsa decemlineata larva, which function as olfactory organs, while the gustatory receptors are the sensilla placodea and sensilla trichoidea located on the inner surface of the labrum and the labium (Chin,1950) ; c) the placoid and basiconic sensilla on the second antennal segment of Tenebrio obscurus and Dermestes ater larvae. In the latter, coeloconic sensilla could be found on the second segment (Roth and Willis,1951,b) ; d) the coeloconic and basiconic sensilla found on the antennae of Schistocerca hoppers (Aziz,1958).

The larvae of Sitophilus normally develop inside the grain, i.e. inside the medium determined by the oviposition habits of their parents, and in which they themselves have no choice. However, their behaviour to light and in a steep humidity gradient was studied. The possible role played by some sensory organs in these reactions is also discussed.

B. Methods and Techniques

It has been mentioned by Howe and Oxley (1944) that the larvae of C.granaria (=S.granarius) begin to reach the fourth instar on the 16 th. day after egg-laying and that the maximum number of this instar is found between the 18th. and the 23 rd. day. Howe (1952) recorded the first appearance

of the fourth instar larvae of the large strain of C.oryzae (=S.zea-mais) on the 16 th. day after egg-laying and the first appearance of the pupae on the 24th. day . No information, however, is available in literature on the length of the larval stages of S.oryzae, but the difference in the length of the life cycle between this species and S. zea-mais was found to be small (Richards,1944) .

In the following behaviour experiments the larvae of the three species were chosen at the age of 20 days after egg-laying. This was achieved by establishing cultures of the three species on English wheat and kept at 25°C., 70 % R.H. The weevils were allowed to oviposit for 24 hours and then sifted out. On the 19th. day, the larvae were induced to leave the grains by applying carbon dioxide into the breeding jars, and rendering the cover rather tight. The jars were kept over night in the constant temperature room in complete darkness. The larvae were obtained the next day by sifting the grain. This method was applied successfully in S.granarius, but not in the other two species, in which the grains had to be dissected carefully by means of a sharp blade and the uninjured larvae were used in the experiments.

The behaviour of the larvae in a steep humidity gradient (0 - 100 % R.H.) was examined. The larvae, previously kept at 25°C.,70 % R.H. were tested in the alternative humidity

chamber used for studying the same reactions of the adults (see Section VI in Text), and at a light intensity 1.55 L.F.L. Owing to the extremely slow movements of the larvae, the number of the individuals present in both the wet and the dry sides of the apparatus was recorded every half an hour for 5 hours. 10 larvae were used in each set of experiments. The index of reaction of the larvae was calculated from the formula $I.R. = \frac{(D-W)}{N} \times 100$, in which D and W are the sums of successive positions occupied by the larvae in the dry and wet sides respectively, and N is the total possible number of position records. Thus a negative I.R. value indicates preference for the wet side (Willis and Roth, 1950, a).

The behaviour of the larvae in a horizontal beam of light was examined by placing them in the centre of the arena with radii drawn at $22\frac{1}{2}^{\circ}$ intervals (see Section VIII in Text), and their position was recorded after 2 hours. 10 larvae were used in each set of experiments. The possible sense organs were examined by making whole mounts of the mouth parts heated in KOH, cleared in methyl cellosolve and mounted in Euparal.

C. Results

The larva moves with great difficulty by means of irregular peristaltic movements which start from the caudal end of the body, but which rarely reach the head region, with the result that the body does not proceed forwards. In the position of rest, or during movement, the larva is almost always lying on one side. Unsuccessful attempts are made by the larva to raise its body and to move with the dorsal surface upwards, but usually it falls on one side. In doing this it shifts slightly from the original position.

1) Reactions of the larvae in a humidity gradient :

The larvae of the three species, previously kept at 70 % R.H., showed a definite preference for the wet side when placed in the humidity gradient 0 - 100 % R.H. The data in TABLE 67 represent the reaction of 30 larvae of S. granarius and 20 larvae of each of the other two species. It can be noticed that the larvae of S. zea-mais exhibited a strong reaction to the wet side, half an hour after being introduced in the alternative chamber. The index of reaction was - 55 . In S. oryzae and S. granarius the I.R. values at that stage were - 40 and - 33.3 respectively. This may be attributed to differences in their locomotory power. During the course of the experiments, however, a gradual increase in the reaction of the larvae in the wet side was observed(Fig.84) .

TABLE 67

The index of reactions of the fourth instar larvae of the three species, previously kept at 70 % R.H., when placed in the humidity gradient 0 - 100 % R.H. at 25°C.

Time (hours)	S.zea-mais	S.oryzae	S.granarius
	Index of Reaction		
½	- 55	- 40	- 33.3
1	- 70	- 40	- 43.3
1½	- 70	- 60	- 43.3
2	- 75	- 65	- 53.3
2½	- 75	- 70	- 53.3
3	- 80	- 70	- 63.3
3½	- 80	- 85	- 63.3
4	- 80	- 85	- 66.7
4½	- 80	- 85	- 66.7
5	- 80	- 85	- 73.3
Mean	- 74.5	- 69.0	- 56.0

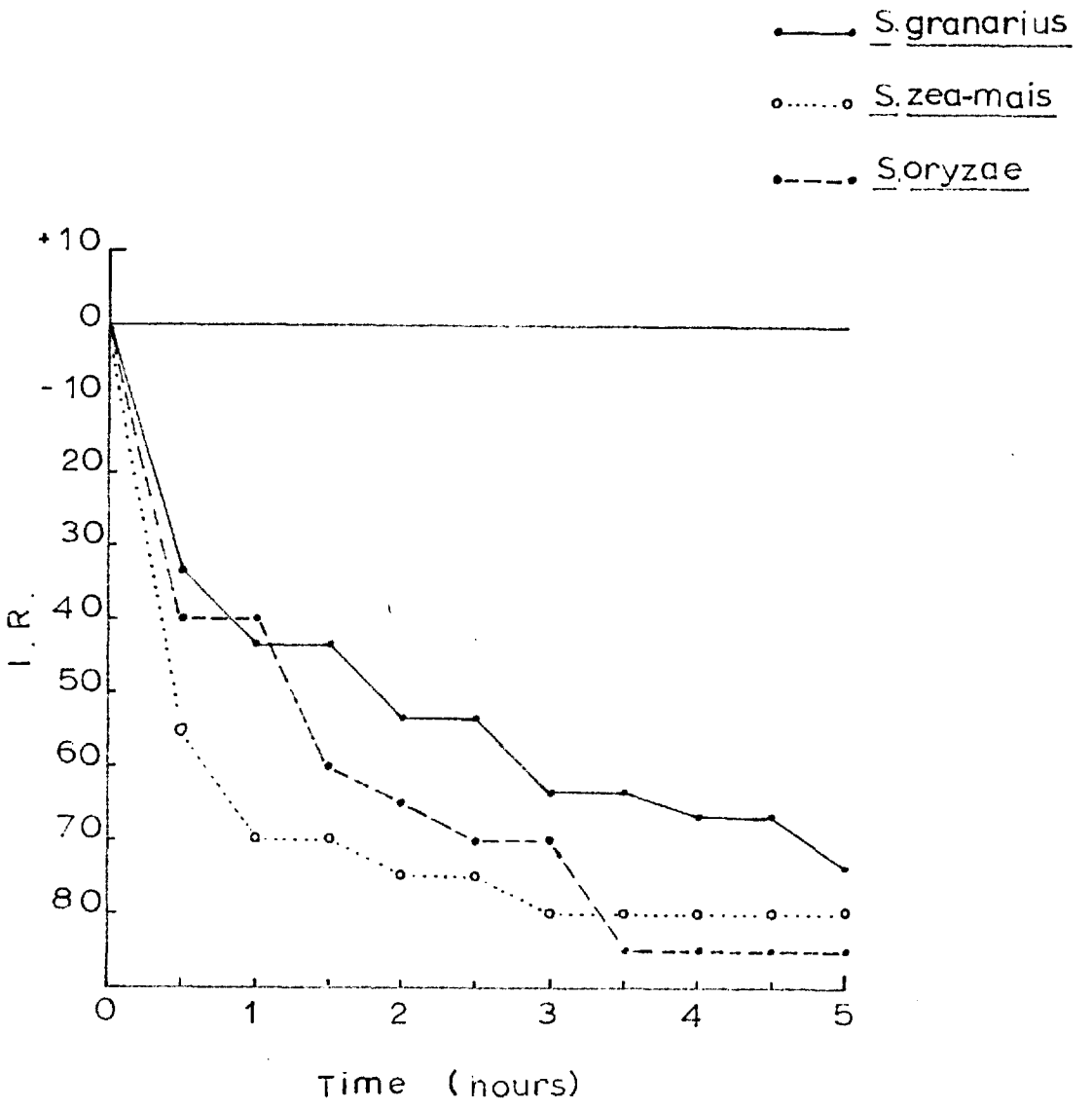


Fig. 84 : Index of reaction of fourth instar larvae previously kept at 70 % R.H., 25°C., when placed in the humidity gradient 0 - 100 % R.H.

The strongest reaction exhibited by the larvae near the end of the experiments was in S.oryzae, followed by that in S. zea-mais and then S.granarius. However, the total mean I.R. values were - 74.5 , - 69.0 and - 56.0 in the decreasing order of S.zea-mais, S.oryzae and S.granarius.

2) Reactions of the larvae to a horizontal beam of light:

The fourth instar larvae when placed, in groups of 10, in the centre of the arena (see Fig. 76 in Section VIII in Text, concerning the light reactions of the weevils), they exhibited a strong photonegative reaction to the horizontal beam of light. The position of each larva to the nearest radius in the arena was recorded after two hours. The radii were drawn at intervals of $22\frac{1}{2}^{o}$. The data for the three species are summarized in TABLE 68. The distribution of the larvae at the different positions from the light source, did not vary significantly in the three species at the upper 5 % level of probability (P= 0.05).

D. The Possible Role Played by some Sensory Organs in the Behaviour of the Larvae

Whole mounts of the head appendages, reveal the presence of some minute thin-walled hairs, which are most probably sensory in function. Basiconic sensilla are located at the apical tips of the 2-segmented palps. On each maxillary palp one large and 9 small pegs are found, while in the

TABLE 68

The angle of track made by the fourth instar larvae of the three species after 2 hours, when placed in a horizontal beam of light.(The angles more than 90° are directly away of the light source).

Angle of track	180°	157°	135°	112°	90°	Total
S. granarius						
Number of larvae	7	10	7	5	1	30
Percentage	23.3%	33.3 %	23.3%	16.7%	3.3%	
S. zea-mais						
Number of larvae	5	7	4	3	1	20
Percentage	25%	35%	20%	15%	5%	
S. oryzae						
Number of larvae	5	8	4	3	0	20
Percentage	25%	40%	20%	15%	0%	

labial palp there are one large and six small pegs (Fig. 85,a and b). These organs are possibly olfactory receptors that mediate differences in R.H. Similar sensilla were found on the palps of Rhizopertha dominica larvae, in addition to the basiconic and trichoid sensilla located on the antennae (Crombie,1944 ,b).

On the ventral surface of the labrum epipharynx , groups of sensory hairs are found between the so called epipharyngeal rods by van Emden (1938) in some coleopterous larvae. In S.granarius, the arrangement of these hairs is as follows : 2 large pegs near the anterior end of the epipharynx, followed posteriorly by a group of 4 small pegs, then 2 large pegs, and finally by another group of 4 small ones (Fig. 86,a) . In S.zea-mais and S.oryzae the arrangement of these pegs are in the following order starting from the distal end of the epipharynx : 2 large + 6 small + 2 large + 4 small pegs (Fig. 86, b and c). These sensory hairs are most likely gustatory in function due to their presence in the mouth cavity.

As in other Rhynchophora larvae (van Emden,1938) the antenna is reduced to a single sensorial cone, and a basal membrane bearing some bristles and smaller sensorial cones (Fig. 86,d). These are possibly olfactory organs, though their actual role, as well as that of the other sensory hairs need further investigation.

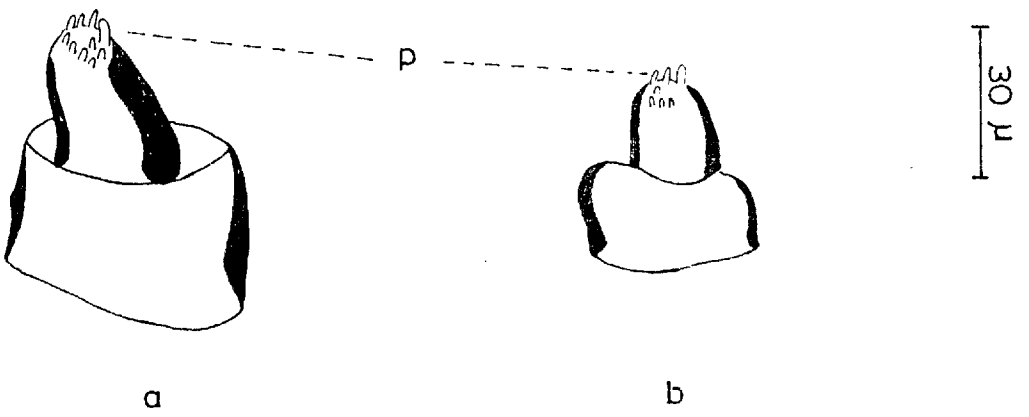


Fig. 85 : a) Maxillary palp, b) Labial palp of 4th. instar larva of S.granarius; p, peg organs.

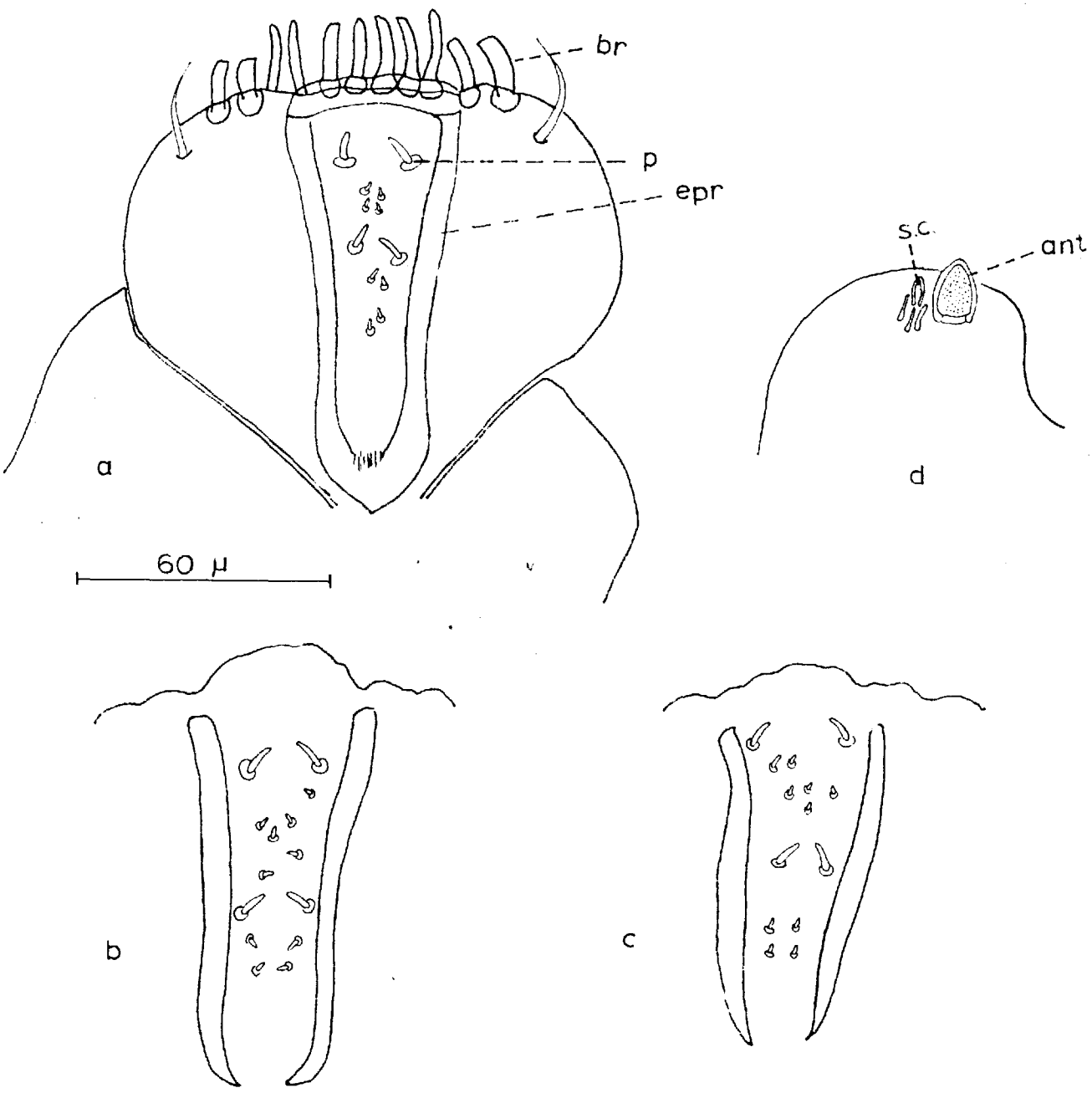


Fig. 86 : Labrum epipharynx; a) S.granarius; b) S. zea-mais ; c) S.oryzae; d) antenna (ant) and sensorial cones (s.c.) ; br: bristles ; p : peg organs ; epr : epipharyngeal rods.

As regards the response of the larva, which has no eyes or ocelli, to light stimuli, it can be suggested that the general body surface may be sensitive to light as is the case of several other insects cited by Wigglesworth (1953) , for instance , Blatella (Graber,1883) and Periplaneta (Brecher,1929) which still settle for preference in the dark after complete blinding. Caterpillars will go towards the source of light after the eyes are blackened (Lammert,1925). The bug Neides in a state of partial hypnosis turns over when the eyes are blackened much more readily in the light than in the dark as though activated by a dermal light sense (Godgluck,1935). In the case of Chironomus larvae the responses to light after blackening the eyes are due to light entering the translucent head capsule and reaching the eyes from below (Oehring,1934) . But this cannot be a general explanation of the results, for Tenebrio larvae avoid the light even after decapitation (Tucolesco,1933) . With the exception of the case of the house-fly larvae in which, as Bolwig (1946) has shown, small groups of vacuolated retinulae-like cells are pocketed among the hypodermal cells of the cephalic region, the light sensitive end-organs in the skin have not been identified. The reactions of the eyeless sheep-tick Ixodes ricinus to light are due to a dermal sense as concluded by Lees (1948).

X. GENERAL DISCUSSION

Ideally, all species should be separated not only on the basis of differences in their morphological characters but also on the basis of difference in their cytology , physiology, ethology and distribution. The study of ethology of closely related species may reveal behaviour patterns which tend to ' isolate ' the species from one another e.g. in many groups of singing insects where several closely related species live together in one habitat, it has been described by Haskell (1961) that reproductive isolation based on differences in song of species certainly occurs. Fulton (1952) and Alexander (1957) found song variations to be the best clue to differentiation of species of the field crickets of the genus Acheta. Perdeck (1957) has shown that the sole barrier to interspecific mating between the two closely related sympatric species Chorthippus brunneus and C. biguttulus, resides in their stridulation behaviour. Haskell (1957) comments on the striking song differences between the closely related bugs Keidocerys ericae and K. nesadae, which are almost impossible to separate morphologically. Adriaanse (1947) studying the behaviour of the hymenopteron Ammophila campestris discovered that two sibling species differed in methods of

constructing and provisioning their nests. Tinbergen (1951) has emphasized the need for studying the behavioural aspects of speciation, i.e. to study the behaviour differences between subspecies belonging to one species, and between closely related species that might have evolved originally from one species. A high degree of adaptiveness is found in numerous behavioural characteristics in such phenomena as , for example, habitat selection, host selection, food preferences, and reactions to predators.

As Brown (1959) mentions in his review of taxonomic problems, there is abundant evidence of sibling species in Coleoptera especially in Rhynchophora and Chrysomelidae . Buchanan (1934) was able to discover the feeble morphological characters that distinguish the two adults of Hylobius radicis and H. pales, from the difference in the feeding behaviour of their larvae. The American forms identified commonly as Chrysomela interrupta Fab. are a complex of siblings (Brown, 1956). Morphologically they appear identical, but vary greatly both within populations and geographically ; their host plants are also different. The identification of different species in other chrysomelid genera based primarily on the variations in their host plants are Chalmisus (Brown, 1943, 1952) and Calligrapha (Brown, 1945).

Differentiation of dipterous species on the basis of host selection has been demonstrated by Stokes (1955) in two species of Dasyneura which were apparently identical morphologically. Mayr (1950) concluded that sexual isolation between Drosophila pseudoobscura and D. persimilis seemed to depend upon scent among other factors, for females of each species attempt to mate indiscriminately with males of either after their antennae have been removed. Spieth's study (1947) of Drosophila courtship showed differences in the posturing movement of the male, particularly of the wings. In D. fumipennis it is ' wing-waving ' , in D. nebulosa it is ' scissoring ' and in D. capricornis, D. sucinea , D. willistoni and D. equinoxial is it is ' wing-vibration '. There are also other clear genetic differences in the different reactions of closely allied species. Thus three species of the fly Dacus are attracted by different compounds of eugenol (Howlett,1912).

In Diptera, cytology has been a very useful taxonomic tool, for instance it has been used in separating species of Drosophila (Patterson and Stone,1952; Carson,1953), Eusimulium (Dunbar,1958), of Anopheles and Culex (Bates , 1949 ; Rozeboom and Kitzmiller,1958).

The taxonomic position of the two species of the rice weevils namely of S.zea-mais Motsch. and of S.oryzae (L.),

was a matter of dispute for several years until recently when Kuschel (1961) satisfactorily settled the question by describing two convincing morphological differences between the two species. Richards (1944) and Birch (1944) described them as two strains of the same species on the basis of differences in their body size and in some biological and ecological aspects. Both authors found that the two species were inter-sterile, although in very few cases the two " strains " were able to cross but with considerable difficulty and the few fertilised eggs did not produce any offspring. By 1954 Birch considered them as sibling species.

The present work was aimed at finding differences in ethology i.e. different patterns of behaviour which can be used as subsidiary characters in distinguishing the two closely allied species S.zea-mais and S.oryzae . A third species S.granarius was included in the experimental analysis since it frequently occurs in the same habitats as the first two mentioned species of Sitophilus.

A number of reactions to external stimuli, and several behaviour patterns have been analysed. Commonly in observations of this nature (i.e. attempts to distinguish closely allied species by differences in ethology), premating behaviour is analysed, but this aspect has not been considered here and remains to be studied. Since it was already known

that the two species of the rice weevils are capable of mating, but are inter-sterile, it was considered that it would be interesting to find other differences in their reactions to external stimuli.

It has been found in this comparative study, that differences in behaviour exist in all the three species, and that the only major similarity between the two species of the rice weevils was in their ability to fly compared with S. granarius which is unable to do so.

Considering the behaviour patterns and reactions to external stimuli one at a time, it may be said that one of the most striking differences between S. zea-mais and S. oryzae was in their preference for different 'host grains'. The latter species, in common with S. granarius preferred to lay on wheat rather than on rice, maize or sorghum, whereas S. zea-mais laid on maize in preference to the other cereals offered. On the other hand, all the three species showed common patterns of behaviour in the choice of the part of the grain in which they laid. It is considered that the choice of the part of the grain may be partly determined by 'mechanical' considerations, but chemoreceptors on the maxillary and labial palps and on the ovipositor may also be involved. The presumed chemoreceptors are, as far as is known, similar in the three species.

The factors that govern the host selection in insects whether they are the nutritional requirements or the presence or absence of chemical attractants or repellents, have been discussed by many authors (e.g. Kennedy, 1951 ; Lipke and Fraenkel,1956 ; Friend, 1958). The difficulty in investigating the major factor lies in the fact that two kinds of stimuli (those activated by chemical feeding factors and by nutrients) are provided by the same host plant.

Again, S.zea-mais differed from both S.oryzae and S.granarius in its reactions to light of its newly emerged individuals. The weevils of S.zea-mais were predominantly photopositive, in contrast to the other two species which are predominantly photonegative.

Both S.zea-mais and S.oryzae differed greatly from S.granarius in their climbing ability on a smooth glass surface. In fact not all the tested weevils of the latter species could climb the height of the experimental glass tubes. On the other hand, S.zea-mais was more efficient than S.oryzae. This ability is related to the development and the number of tenent hairs forming the climbing organs. It was found that the number of these hairs differed significantly in the three species, and was greater in the most efficient climber i.e. S.zea-mais. Thus this

ability is related to a morphological character, which on a statistical basis distinguishes the two closely allied species, S.zea-mais and S.oryzae.

S.granarius is unable to fly, since the hind wings are vestigial . Differences in flight behaviour of the two species of the rice weevils, however, were noted, the most interesting one being the inability of S.oryzae to fly when they were 2 weeks old. S.zea-mais, on the other hand, flew at that age, although not as efficiently as at 4 weeks . When 4 weeks old weevils were compared, it was found that S.zea-mais were more efficient than S. oryzae, although the latter were more easily activated by increase in light intensity and temperature than S. zea-mais. This was true of freely moving weevils, but when the weevils were suspended from the pronotum S.oryzae weevils were more active than S.zea-mais at the low light intensity, but the latter was significantly more efficient than S.oryzae at the high light intensity used. The criterion of efficiency used was the time taken to initiate flight.

In their humidity reactions, the weevils of all the three species tended to move to the dry side (i.e. to the region of lower humidities) when they were previously kept (i.e. preconditioned) in high humidities of 70 %

and of 100 % R.H. When the weevils were previously kept at 0 % R.H. for 24 hours, their reactions altered, and they became either indifferent to the humidity gradients or showed a reversal of reaction tending to move to the zones of higher humidity.

The species least effected by preconditioning was S.granarius and the most S.oryzae. This sequence in alteration of behaviour was probably related to the rate of water loss from the body, since it was found that some S.granarius withstood desiccation at 0 % R.H. up to 6 days, some S.zea-mais up to 4 , but S.oryzae only 3 days.

The sense organs connected with humidity reactions are on the antennal club segment. Without the club segment, the weevils of the three species are unable to discriminate between the high and low humidities.

No clear differences in the behaviour of the three species could be detected in temperature gradients. The weevils tended to move towards lower temperatures. This tendency was greater in S.zea-mais than in S.oryzae, and in the latter greater than in S.granarius.

Some observations were also made on the behaviour of the larvae of the three species of weevils. The reactions of the larvae to humidity and to a light gradient were examined, but no differences in behaviour were detected,

except that the larvae of S.granarius tended to move more slowly than the somewhat more active larvae of the other two species. The three species were photonegative to light and preferred the wet side of the humidity gradient.

In conclusion it may be said that the reactions and behaviour of S.zea-mais and S.oryzae were more close to one another than to S.granarius, but many interesting differences were also found between the closely allied species. The difference in ' host ' preference appears to be especially fundamental. It was Thorpe who pointed out that differentiation in behaviour may arise by habituation to different chemicals for instance of Drosophila and Nemeritis to the smell of cedar wood oil and of Drosophila melanogaster to peppermint (Thorpe,1938,1939) This adherence or habituation to a host may gradually be selected and new strains may arise within a species. This isolation due to differences in host preference may eventually lead to further differentiation into species.

Some minor morphological differences, which may be of taxonomic value, were revealed in this study, e.g. 1) the tenent hairs on the third tarsal segments differed greatly in number in the three species, and this number is distinguishable on a statistical basis. The greater

number was in S. zea-mais, followed by that in S. oryzae and the least number was in S. granarius , 2) on the ovipositor and on the last hidden abdominal segment, campaniform sensilla are present which differ in size in the three species, 3) on the labrum epipharynx of the fourth instar larvae sensory hairs are found, which are most probably gustatory organs ; the same number is found in S.zea-mais and S.oryzae , but this differs from that in S.granarius.

Finally the most striking differences in the behaviour of the three species are summarized in TABLE 69 .

TABLE 69

Comparison between the reactions of the weevils of the three species

Reactions studied	Species of weevils			Differences between reactions	Sense organs examined
A. Oviposition Sites	S.granarius	S.zea-mais	S.oryzae		
1) Order of preference of cereals	Wheat rice maize sorghum	maize wheat rice sorghum	wheat rice sorghum maize	Greater preference by S.zea-mais for maize and the other two species for wheat	Probably maxillary and labial gustatory organs; and peg organs on ovipositor- (no difference in the three species) ; campaniform sensilla on ovipositor responsible of touch, which differ in size in the three species.
2) Preferences for parts of grain	Preference for hairy end in wheat Preference for embryo end in rice Preference for tapering end in maize and sorghum.			Similar in all the three species	

B. Flight Activity					
(i Free moving weevils	No flight	Flight		Flight	
1 Effect of age					No flight at all in S.granarius. S.zea-mais is far more active in 4 experimental conditions than S.oryzae
(a) 2-week old	-	able to fly		unable to fly	
(b) 4-week old		both species are able to fly			
2) Number of flights/15 min. per 100 weevils :		♂	♀	♂	♀
a)at low light,low temperature		215	203	84	62
b)at low light,high temperature		369	291	150	149
c)at high light,low temperature		534	387	324	289
d)at high light,high temperature		799	535	493	452
Total		1917	1416	1051	952

Reactions studied		Species of weevils				Difference between reactions	organs involved in the reaction
		S.granarius	S.zea-mais		S.oryzae		
(ii) Suspended weevils							
1) Time taken to initiate flight(sec.)			♂	♀	♂ ♀	S.zea-mais responds more readily at high light intensity. S.oryzae responds more readily at low light intensity. In S.zea-mais significant difference exists at two light intensities; but no such behaviour in S.oryzae	
a) At high light intensity	-		10.1	13.9	35.7 30.4		
b) At loe light intensity	-		48.4	49.1	35.6 29.5		
2) Wingbeat frequency R.P.S.	-		74.1	73.7	85.6 87.0	No significant difference between the two species	
(iii) Relation of area of hind wing to body weight	-		3.481 2.79	3.351 2.92	1.787 1.808 1.61 1.71	No significant difference between the two species	
(iv) Ratio of length of hind wing to elytron	-		2.065	2.052	1.990 1.975	No significant difference between the two species.	

C. Climbing on smooth vertical glass surface									
1) Average distance climbed by about 100 weevils of each species (maximum=150 cm.)	♂ 126.6	♀ 123.1	♂ 150	♀ 150	♂ 150	♀ 150	Decreasing Order of efficiency in climbing: S.zea-mais, S.oryzae and S. granarius , as regards the speed of climbing.	Tenent hairs on the third tarsomeres which differ in number and in length in the three species.
2) Speed (cm./min.) at 25 C., 70 % R.H.	12.81	12.73	30.49	28.39	19.79	20.68		
3) Tarsal width (u)	98.12	97.68	114.64	114.1	95.8	95.7	Significant difference between the three species	
4) Number of tenent hairs on third tarsomere	35.0	35.5	63.5	64.9	40.7	41.3		
	35.2		64.2		41.0		Significant difference between the three species.	

Reactions Studied	Species of weevils			Difference between reactions	organs involved in the reactions
	S.granarius	S.zea-mais	S.oryzae		
Climbing ability (cont.) 5) Relation between body weight and speed ; and between tarsal width and speed	Significant in males , [illegible]s and not in females		Significan in both sexes		
D.Humidity Reactions 1)Preconditioning for 24 hours at 100 % and 70 % R.H.	Positive reactions to lower humidities. Reactions of S.zea-mais to lower humidities were stronger than those of S.oryzae and S.granarius			The three species differed from each other , but all preferred the dry side.	Trichoid sensilla on the antennal club segment. No difference between the three species. In the rice weevils pit organs present on the club, not found in S.granarius
When R.H. gradient did not exceed 20% in any part of the humidity range	indifferent	both species prefer the dry side			
2) Preconditioned at 0% R.H. retained low	both species showed preference for strong reactions to lower R.H.			The strongest reaction to the wet side was shown by S.oryzae, followed by S.zea-mais. S. granarius became indifferent.	
3) Loss of water at 0 % R.H.	Most resistant, survived 6 days	survived 4 days	survived 3 days	S.granarius most resistant to desiccation, followed by S.zea-mais, them S.oryzae	
E. Temperature preference	20-22.5 C	10-12.5 C.	10-12.5 C.	S.granarius preferred the warmest region of the gradient(20-22.5 C.); S.oryzae and S.zea-mais,the coldest, (10-12.5 C.). The three species preferred the coldest region of a wide-range gradient.	
Ranges presented 10-22.5 C.					

Reaction studied	Species of weevils			Differences between reactions	Sense organs
F. Light	S.granarius	S.zea-mais	S.oryzae		
1)Reactions to a horizontal beam of light	76.75 % photonegative	72.60 % photopositive	61.00 % photonegative	Majority of S.granarius and S.oryzae photonegative ; majority of S.zea-mais photopositive.	
2)Unilateral blinding circus movements	towards blinded eye	towards seeing side	towards blind side		
track turnings	zigzaging	not not frequent	not frequent		
G. Larvae					
1) Humidity reactions: (0-100% R.H. gradient)				The three species prefer the wet side of the gradient. The order of preference : S.zea-mais S. oryzae S.granarius	Basiconic sensilla on maxillary and labial palps possibly olfactory ; peg organs on epipharynx possibly gustatory. Number of pegs same in S.zea-mais and S. oryzae, and differs in S.granarius.
Mean I.R.	- 56.0	-74.5	- 69.0		
2) Light reactions (to a horizontal beam of light)	p h o t o n e g a t i v e			No significant difference between the three species.	

XI. SUMMARY

The behaviour of two closely related species of rice weevils Sitophilus zea-mais Motschulsky and Sitophilus oryzae(Linnaeus) and of a third species of the genus namely Sitophilus granarius (Linnaeus) commonly associated with them in the same habitats was studied. The weevils were subjected to a number of experimental conditions and then reactions to them were compared . The following behaviour patterns were analysed :-

1) Selection of Oviposition Sites by the three Species :

The female weevils showed a decided preference for certain parts of the grains of four cereals, namely of wheat, rice , maize and sorghum. The three species differed significantly in selecting their oviposition sites on the four cereals. Mechanical, tactile and chemical senses are suggested to be involved in these mechanisms. The basiconic sensilla on the apices of the maxillary palps and the sensory hairs on each stylus of the ovipositor are probably chemoreceptors, and campaniform sensilla on the coxites of the ovipositor and on the last hidden abdominal segment are probably mechanoreceptors.

2) Observations on Flight Activity : S.granarius weevils were unable to fly, but the two species of the rice weevils were able to do so. The 2-week old S.oryzae were unable to fly,when released or suspended, while the 4-week old ones flew, but were less efficient than S.zea-mais of the same age. The latter species also showed a marked ability to fly at the age of 2 weeks. The readiness to fly increased with temperature and light intensity.

3) Ability to Climb Smooth Surfaces : The three species differed in their speed of climbing on smooth glass surfaces. S.zea-mais was a more efficient climber than S.oryzae and the latter more than S.granarius. The tenent hairs on the third tarsomeres which grip on to the substratum during climbing differed significantly in number in the three species, in the same order as did their

efficiency in climbing. The mean body weight and the mean tarsal width differed significantly in the three species. The relation between the body weight and speed or the tarsal width and the speed of climbing was significant in the males of the three species and in the females of S.oryzae.

4) Humidity Reactions : The three species when preconditioned in humid atmospheres of 70 % R.H. and 100 % R.H. showed a marked preference for the dry side of all the humidity gradients offered . S.granarius were unable to disriminate between any two humidities when the range of the gradient was 20%. When the weevils were desiccated at 0%R.H. for 24 hours, S.granarius lost ability to discriminate between high and low humidities,and the other two species showed a preference for higher humidities. S.oryzae reacted to the wet side more strongly than S.zea-mais. This was attributed to the difference in their resistance to desiccation at 0%R.H.;all S.oryzae died after three days,S.zea-mais after four days,while some S.granarius survived up to six days. Trichoid sensilla located on the antennal club segment are the hygroreceptors.

5) Reactions in a Temperature Gradient : In a temperature gradient ranging between 13 and 37 C., the three species aggregated in the cold end. In a gradient ranging between 10 and 22.5 C.,S.granarius preferred the warmest region,while S.oryzae and S.zea-mais aggregated in the coldest. More S.zea-mais than S.oryzae aggregated in the coldest compartment.

6) Reactions to Light : In a horizontal beam of light, the majority of the newly emerged weevils of S.granarius and S.oryzae were photonegative,while in S.zea-mais the majority ewere photopositive.

7) Fourth instar larvae of the three species were also photonegative in a horizontal beam of light. Larvae preconditioned in 70% R.H. strongly preferred the wet side of a humidity gradient of 0-100 % R.H. Basiconic sensilla on the maxillary and labial palps are possibly hygroreceptors. Sensory hairs on the epipharynx are probably gustatory. The number of these in S.granarius differed from that in the two species of the rice weevils, in which it was identical.

This work has indicated that S.granarius differed appreciably in its ethology from the other two species studied. However, a number of differences in behaviour of the two closely allied species S. zea-mais and S. oryzae were also found.

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XIII. APPENDIX

TABLE 70

Number of eggs laid by S.granarius weevils on wheat grains

(Combinations of different positions)

Entire side		Sutured side		Hairy end		Embryo end	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
121	122	96	21	49	76	30	56
97	26						
		87	11				
				39	52		
						47	61
141	33	111	29				
165	33			41	58		
126	39					36	73
		104	13	62	95		
		102	25			66	91
				75	104	51	54
139	20	134	29	59	99		
178	46			71	112	54	72
		165	42	88	124	63	77
99	23	79	13			25	46
Total 1066	242	878	183	484	720	372	530

(360 females offered 1280 grains)

TABLE 71

Number of eggs laid by S.zea-mais weevils on wheat grains
(Combinations of different positions)

(360 females offered 1280 grains)

Entire side		Sutured side		Hairy end		Embryo end	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
89	61	38	14	61	46	43	37
75	50						
		69	32				
				47	50		
						38	40
92	65	43	8				
90	47			54	66		
81	47					22	38
		65	18	62	73		
		61	27			20	54
				53	36	26	38
99	60	57	21	49	59		
113	58			75	77	21	48
106	51	60	23			40	45
		89	36	97	99	43	80
Total 745	439	482	179	498	500	253	380

TABLE 72.

Number of eggs laid by 360 females of S.oryzae on 1280 grains of wheat. (Different combinations)

Entire side		Sutured side		Hairy end		Embryo end	
HAR	EMB	HAR	EMB	ENT	STD	ENT	STD
64	53	54	26	39	55	26	35
54	25						
		60	15				
				37	43		
						30	42
59	45	59	24				
43	35			30	33		
53	82					54	42
		53	32	35	51		
		81	22			35	29
				24	55	22	35
77	65	82	33	45	60		
72	49			23	75	35	61
88	53	77	28			48	35
		74	18	39	64	40	55
Total 510	407	540	198	272	436	290	334

TABLE 73

Number of eggs laid by 360 female weevils of S.granarius on 1280 grains of rice (Combinations of different positions).

Embryo side		Sutured side		Embryo end		Tapering end	
EMB	TAP	EMB	TAP	KLD	STD	KLD	STD
34	25	12	15	36	24	26	27
37	20						
		19	7				
				38	29		
						24	11
45	31	14	21				
18	19			36	25		
30	22					22	27
		16	21	32	22		
		21	18			31	21
				49	14	23	22
44	37	29	39	44	36		
36	25	23	33			25	33
46	30			33	38	41	28
		36	31	31	41	28	36
Total 290	209	170	185	299	229	220	205

TABLE 74

Number of eggs laid by 360 weevils of S.zea-mais on 1280 grains of rice (Combinations of different positions)

Keeled side		Sutured side		Embryo end		Tapering end	
EMB	TAP	EMB	TAP	KLD	STD	KLD	STD
57	15	14	8	15	6	12	3
31	5						
		19	7				
				27	11		
						29	12
66	28	11	14				
58	14			22	12		
48	10					12	9
		28	18	33	12		
		36	21			12	8
				24	22	22	14
38	15	21	9	19	4		
57	16	31	9			6	6
50	18			20	19	17	10
		23	16	31	22	22	16
Total 405	121	183	102	191	108	132	78

TABLE 75

Number of eggs laid by 360 weevils of S.oryzae on 1280 grains of rice (Combinations of different positions).

Keeled side		Sutured side		Embryo end		Tapering end	
TAP	EMB	TAP	EMB	KLD	STD	KLD	STD
52	17	30	14	25	13	10	12
39	8						
		17	14				
				30	11		
						12	24
31	24	34	14				
28	24			24	13		
46	22					27	13
		20	14	18	12		
		31	32			34	24
				28	33	28	12
37	39	33	24	19	19		
50	24	26	22			10	18
47	23			39	23	32	23
		26	22	36	24	22	11
Total 330	181	217	156	219	148	175	137

TABLE 76

Number of eggs laid by 360 weevils of S.granarius on 640 grains of maize (in different positions)

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
14	1	21	5	30	27	3	2
25	2						
		24	..				
				22	21		
						3	5
33	2			20	41		
26	2	44	3				
23	1					..	8
		19	1	22	31		
		27	2			1	6
				16	47	5	8
26	..	21	1	17	30		
31	..	25	1			1	4
13	...			18	38	..	..
		29	..	21	33	1	3
Total 191	8	210	13	166	268	14	36

TABLE 77

Number of eggs laid by 360 weevils of S.zea-mais on 640 grains of maize (offered in different positions)

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
16	..	12	5	22	19	..	10
18	1						
		27	..				
				21	25		
						1	13
12	..	16	..				
12	..			22	13		
24	..					..	13
		21	10	20	14		
		20	7			8	8
				22	34	1	7
28	..	33	1	23	16		
32	..	26	1			..	12
38	4			23	22	7	5
		26	1	18	6	..	15
Total 180	5	181	25	171	149	17	83

TABLE 78

Number of eggs laid by 360 weevils of S.oryzae on 640 grains of maize (offered in different positions)

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
14	..	20	2	14	11	..	9
14	..						
		13	4				
				14	15		
						2	9
12	..	13	1				
11	1			17	20		
14	..					2	2
		15	3	18	20		
		22	2			..	..
				16	21	1	1
15	..	19	4	16	21		
18	..	28	1			..	8
15	..			19	24	1	5
		18	4	19	27	..	4
Total 113	1	148	21	133	159	6	38

TABLE 79

Number of eggs la-id by 360 weevils of S.granarius on 1280 grains of sorghum (in different combinations)

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
10	7	26	2	15	10	9	4
27	5						
		36	1				
				20	14		
						13	16
14	5	30	2				
27	7			17	11		
26	10					3	5
		31	2	12	7		
		55	..			5	7
				34	21	23	13
35	24	50	2	22	14		
72	40	85	8			24	25
77	50			51	43	36	25
		66	1	28	20	10	12
Total 288	148	379	18	199	140	123	107

TABLE 80

Number of eggs laid by 360 weevils of S.zea-mais on 1280 grains of sorghum (offered in different positions).

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
40	18	50	7	10	13	7	6
30	25						
		43	..				
				22	20		
						22	9
27	6	39	2				
30	7			16	7		
40	18					10	3
		74	12	5	6		
		53	10			7	3
				19	13	12	6
42	14	44	7	5	9		
28	19	43	8			7	10
42	32			37	15	19	14
		104	24	29	24	27	16
Total 279	139	450	70	143	107	111	67

TABLE 81

Number of eggs laid by 360 weevils of S.oryzae on 1280 grains of sorghum (offered in combinations of different positions).

Entire side		Embryo side		Tapering end		Broad end	
TAP	BRD	TAP	BRD	ENT	EMB	ENT	EMB
22	13	42	1	27	27	13	7
24	16						
		43	3				
				24	17		
						11	11
27	11	36	..				
17	15			21	10		
33	9					15	11
		27	1	10	14		
		37	2			3	..
				20	29	18	6
12	11	11	2	14	3		
71	25			39	36	10	31
56	19	93	1			12	18
		87	7	34	18	33	18
262	119	376	17	189	154	115	102