AN INVESTIGATION OF SOME ENVIRONMENTAL FACTORS INFLUENCING

THE LOCOMOTOR ACTIVITY OF Cryptolestes ferrugineus

(STEPHENS) (COLEOPTERA : CUCUJIDAE),

A PEST OF STORED GRAIN

A Thesis

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ABSTRACT

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Experiments were designed to evaluate the effects of
various physical and biological factors on the locomotor activ-
ity and behaviour of C. ferrugineus, an important insect pest
of stored grain in the Prairie Provinces. The experiments
were done in the laboratory with adults. Insects emigrated at
a more rapid rate from dry than from damp wheat; from wheat at
28° C. than from wheat at 15° C.; and from wheat exposed to
light than from wheat in darkened containers. Insects were
positively geotactic in columns and boxes of wheat, and nega-
tively geotactic on vertical plane surfaces above dry wheat.
In general, more insects emigrated from mouldy, damp wheat
than from "fresh", damp wheat. Emigration from mouldy or
"fresh" wheat was related to preconditioning. Fewer insects
emigrated from mouldy or "fresh" wheat when they were pre-
conditioned in dry wheat than when preconditioned in damp
wheat.

Insects showed a diurnal periodicity at the bottom of a box of dry wheat, more being trapped per hour during the day than during the night. Locomotor activity was depressed in moist grain and diurnal activity was less apparent.

In a temperature gradient between 12.5° and 43.0° C., more insects became motionless at 28.6° to 34.0° C. than at any other temperature range. Aggregations were formed only in the range 28.6° to 34.0° C.; insects moved more or less continuously between 16.0° and 28.6° C., and became "cold-trapped" at 12.5° to 16.0° C. Insects that were preconditioned for 24 hours at 30° C. tended to discontinue walking and aggregated in the 28.6° to 34.0° zone; those preconditioned at 25° C., tended to continue walking, between 16.0° and 28.6° C.; and those preconditioned at 35° C., tended to continue walking or to be "cold-trapped."

The tendency of insects to discontinue walking and to aggregate in the range 28.6° to 34.0° C., which corresponds closely to the temperatures at which maximum oviposition and most rapid growth occur, suggests an explanation for the rapid development of infestations in warm patches of stored grain.

The humidity reactions were determined by the distribution of insects on small circular screens placed over semi-circular compartments containing $KOH-H_2O$ solutions. Insects that had been preconditioned at 50 per cent relative humidity for 24 hours, aggregated in the moist region of a humidity

gradient provided by the following pairs of relative humidities: 50 and 85 per cent; 50 and 75 per cent; and 50 and 65 per cent. When the insects were preconditioned for 24 hours at the higher of each pair of humidities tested, they came to rest in the low humidity region, with little or no aggregation. A layer of glass beads placed in the circular humidity chamber to provide for a uniform contact stimulus, inhibited insect aggregation but not the humidity reaction.

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CHAPTER I

INTRODUCTION

The rusty grain beetle, *Cryptolestes ferrugineus* (Stephens), is the most important stored grain pest in the Prairie Provinces. The adult is reddish brown and is 1/16 of an inch long. Although it infests all types of stored cereal grains, most infestations occur in wheat, the main cereal crop in this region. The insect feeds on kernels and grain dust. However, it causes most damage in stored grain by the metabolic heat produced by concentrated populations of adults and larvae.

C. ferrugineus became prominent as a storage pest in Canada during World War II when large quantities of grain were stored in emergency buildings. Shortly after the war when grain moved steadily to overseas markets, reports of infestations of *C. ferrugineus* became infrequent. However, with the harvesting of two crops in 1950 (most of the crop left over from the fall of 1949, in addition to the 1950 crop), grain was again stored in large quantities and infestations of *C. ferrugineus* became prevalent.

In the Prairie Provinces, stored grain does not usually provide a favourable environment for the development and spread of insect infestations. Throughout most of the winter months, the temperature of grain stored in granaries of 1,000

bushels capacity, or less, may range from -12.8° C. (9° F.) to -2.2° C. (28° F.); in bulks of about 25,000 bushels, or higher, the range is -12.8° C. to 10.0° C. (50° F.) (Watters, 1959). Owing to the low thermal conductivity of grain $\underline{/}36$ to 40×10^{-5} c.g.s. units, for wheat (Oxley, 1944$\underline{)}7$, there is a considerable time lag before stored grain bulks of about 1,000 bushels reach midsummer temperatures of about 20° C. Such temperatures are lower than those required for the high oviposition and rapid developmental rates that characterize heavy infestations of C. ferrugineus.

Insects can create conditions that approach their developmental and reproductive maxima by aggregating in certain zones within the grain bulk and causing grain to heat. Often, insects aggregate at zones that become damp during storage. However, aggregations may also occur in dry grain that contains a high proportion of grain dust.

Most research on insect control in stored grain has involved the use of insecticides. Less emphasis has been placed on studies of the physical and biological factors that promote or limit the spread of infestations. The present work was initiated to expand our knowledge of stored grain as an insect habitat.

The problem

This investigation was developed to determine the effect of grain moisture content, temperature and other en-

vironmental factors on the locomotor activity of C. ferrugineus
in wheat and on plane surfaces. Insect activity and the direc-
tion and velocity of insect movement in stored grain is in-
fluenced by (1), physical factors, such as grain temperature
and moisture content, light, gravity, density of packing, and
intergranular air movements; and (2), biological factors such
as insect density, fungi, prior conditioning and cyclic be-
haviour. Certain of these factors, individually or in combina-
tion, may affect insect biology and behaviour in stored grain.
Experimental evidence on how these factors influence insect
activity will be of value in predicting the course of an in-
festation under known environmental conditions.

Importance of the study

C. ferrugineus comprises the main threat to the safe
storage of grain in the Prairie Provinces. Infestations may
be effectively controlled by the application of fumigants.
However, these control measures are usually applied only after
the grain has been extensively damaged.

It is a cliché to say that prevention is better than
cure. Yet, preventing infestations is certainly more economi-
cal and effective than applying corrective control measures.
However, before we prevent something we should know what to
prevent and how to prevent it. The temperature and moisture
content of a grain bulk may be readily measured. But in order

to utilize this information we must know what effects tempera-
ture and grain moisture content have on insect activity. For
insects become dispersed in grain chiefly by their locomotor
movements; and they can only cause economic damage by feeding
on the grain, forming aggregations, and causing grain to heat.
Thus, information on the behavioural responses of insects to
temperature and grain moisture content should enable us to
delineate the regions in a grain bulk where infestations may
develop. Specific preventive measures may then be applied.

<u>Organization of the thesis</u>

The literature on the biology of <u>C. ferrugineus</u> is re-
viewed in Chapter II. The experimental work on which the
thesis is based, is presented in Chapters III to VI. Chapter
III deals with the influence of grain temperature, moisture
content, and certain biological and physical factors, on the
locomotor activity of <u>C. ferrugineus</u>. The experiments re-
ported in Chapter IV describe the effect of grain moisture
content on the spatial distribution of insects in a box of
wheat. A temperature gradient with control of relative humid-
ity was devised to measure the temperature reactions of
<u>C. ferrugineus</u>; this work is described in Chapter V. Some
humidity reactions of <u>C. ferrugineus</u> are reported in Chapter
VI. Finally, the experimental results presented in Chapters
III to VI are summarized in Chapter VII.

CHAPTER II

REVIEW OF THE LITERATURE

The rusty grain beetle, _Cryptolestes ferrugineus_ (Stephens), was described in 1845. Although Casey (1916) regarded _Cryptolestes_ as a distinct genus, Leng (1920), in his catalogue of the Coleoptera of America, listed the insect as _Laemophloeus ferrugineus_ (Stephens) because he considered that _Cryptolestes_ was a subgenus of _Laemophloeus_. The insect was generally known in the literature as _L. ferrugineus_ until Steel and Howe (1955) made the following statement: "_Laemophloeus_, as known at present, consists of a number of distinct genera, some previously described and now regarded as subgenera or synonyms and some new. The species recorded as occurring in stored products, with the exception of _janeti_ Grouvelle, that is: _spartii_ (Curtis) (= _ater_ /Olivier/), _turcicus_ Grouvelle, _ferrugineus_ Stephens and _pusilloides_ Steel and Howe, should be placed in _Cryptolestes_ Ganglbauer. _janeti_ Grouv. (which is apparently predaceous on other pests) belongs to _Leptophloeus_ Casey which has, besides other distinguishing features, short, clubbed antennae and five-segmented posterior tarsi, in both sexes." Lefkovitch (1959) further clarified the position of _Cryptolestes_ as a genus in his revision of the family Laemophloeinae. _Cryptolestes ferrugineus_ is now the accepted name in North America and Europe.

C. ferrugineus has a world-wide distribution, being found in temperate and tropical regions and in humid and dry zones. In Great Britain, it has been found in flour mills, farm storages, warehouses and maltings. In Canada, it occurs mostly in grain stored on farms and in country elevators in the Prairie Provinces. The first established infestation in Canada was reported in Ontario in 1932 (Stirret and Arnot, 1932). Bishop (1959) reported that _C. ferrugineus_ was taken in 59 out of 89 localities in the State of Washington, during an insect survey. It was more common than _C. minutus_ or _C. turcicus_, two other species that infest stored products. In a survey of grain storages in the Prairie Provinces, in 1958, _C. ferrugineus_ was found in 36 per cent of the empty granaries (Liscombe and Watters, 1962). Rilett (1949) stated that, in the United States, infestations of stored grain by primary storage pests such as the granary weevil, _Sitophilus granarius_ (L.), is often so severe that infestations by minor pests such as _C. ferrugineus_ may remain unnoticed. Howe and Lefkovitch (1957) have listed a wide range of foods on which it has been imported to Great Britain from various countries. These foods included wheat, sorghum, maize, rice, barley, ground nuts, palm kernels, cocoa beans, cottonseed products. In addition, Lefkovitch (1959) has reported its occurrence under bark, in an aphid gall and in soil.

The damage to wheat is done mainly by the larva, which penetrates the germ region of the kernel through minute perforations of the pericarp. Although the larva feeds mostly on the germ, Rilett (1949) has observed that the entire endosperm portion of the kernel may be consumed. Compared to feeding on and lowering the nutritive value of kernels, the insect probably causes more damage to stored grain by the metabolic heat produced by the larva during growth. Grain heating, a familiar phenomenon to farmers and commercial grain handlers in Canada and in other countries, is often initiated by stored grain insects. Such heating, if allowed to go uncontrolled, encourages the growth of destructive moulds, which continue the heating process beyond the thermal tolerance of the insects that are present. Thus, an infestation of C. ferrugineus in stored grain, in addition to causing a decrease in nutritive value, also causes lower germination, loss in vitamins and baking quality, and lower market values because of the presence of insect-damaged and heat-damaged kernels.

The infestation problems created by C. ferrugineus in bulk grain in Canada during World War II emphasized the role of this insect as a primary pest of stored grain. Prior to this period, C. ferrugineus had always been regarded as a secondary pest, unable to damage apparently sound grain. Smallman (1943) was among the first to report the significance of C. ferrugineus as a primary pest of stored grain, capable of feeding on whole

kernels. Rilett (1949) reported that, although the adults fed only on dockage and grain dust, larvae could penetrate the germ of wheat kernels through very small breaks in the pericarp. He found that 50 per cent of the apparently undamaged wheat kernels used in his experiments contained small breaks in the seed coat over the germ region. Butler and Mickel (1955) reported that 52.8 per cent of 1,000 apparently sound kernels of No. 1 Northern spring wheat had fissures over the germ large enough to hold eggs of Cryptolestes spp. Bishop (1959) estimated that in Washington State, 30 to 60 per cent of all kernels examined had slight breaks in the germ covering through which small larvae could penetrate the kernel and feed.

The eggs of C. ferrugineus are laid in farinaceous material such as flour or grain dockage, on cereal grains, or in holes in kernels (Rilett, 1949). Smith (1962) has indicated that on wheat, oviposition rates are dependent on the number of cracks and crevices available. On wheat kernels, at 30° C. and 70 per cent relative humidity, he obtained an oviposition rate of 5.6 eggs per female-day; in flour, the rate was 7.5. The higher rate in flour was attributed, in part, to the larger number of oviposition sites. Rilett (1949) reported that the optimum environmental conditions for the development of C. ferrugineus was 90° F. (32.2° C.) and 75 per cent relative humidity. At these conditions, the life cycle was completed in about 20 days. At 80° F. (26.7° C.) and 75 per cent

relative humidity, it took 31 days. Ashby (1961) estimated the pre-adult development period in grain at 70+ per cent, to be 130 days at 21° C., and about 850 days at 17° C.

CHAPTER III

FACTORS EFFECTING THE LOCOMOTOR ACTIVITY

OF C. ferrugineus IN WHEAT

Introduction

Spontaneous movements of insects are modulated by environmental stimuli. The physical and biological conditions of the grain will determine the extent to which insects disperse or form aggregations. Among the factors that influence the locomotor movements of insects, and hence their dispersal in bulk grain, are grain temperature and moisture content. Grain is seldom homogeneous with respect to temperature and moisture content (Oxley, 1948) so we may expect that insects will react to gradients that develop in the grain during storage. This chapter reports on laboratory experiments devised to investigate the influence of grain temperature, moisture content and other environmental factors on the locomotor activity of C. ferrugineus in wheat.

Review of the Literature

Many of the devices that have been used to measure insect activity were developed to study diurnal rhythms. Gunn (1940) recorded the daily activity of Blatta orientalis L., by placing it in a box that tilted when the insect walked. The movements of the box were registered on a revolv-

ing smoked drum. Cloudsley-Thompson (1957) used similar apparatus to measure the locomotor activity of cribellate spiders. Activity was assessed by counting the number of times in each 3-hr. period that the spider crossed an axis and caused the arena to rock. An aktograph for small insects was developed by Hammond (1954).

Insect activity has also been measured by the periodic observation of their movements at various temperatures and relative humidities. Bentley, Gunn and Ewer (1941) in this way determined the locomotor activity of the spider beetle Ptinus tectus (Boie.). Gunn and Pielou (1940) measured the activity of the yellow mealworm, Tenebrio molitor (L.), by tracing its path on squared paper corresponding to a grid marked off on the floor of the exposure chamber. Bursell (1957) determined the effect of humidity on the activity of the tsetse fly, Glossina morsitans Westwood. The positions of flies in glass dishes, relative to a grid were recorded every 10 minutes on alternate hours for 9 hours.

Brown (1959) reported a simple activity recorder using transistor circuits and infra-red light. The device had the advantage that it disturbed the animals as little as possible during the long periods of observation.

Edwards (1959) devised photographic equipment to monitor the amount of movement in a group of adult Drosophila melanogaster Meig. over relatively long periods of time. A

slow shutter speed was used to determine the numbers of in-
active insects in the group. The insects that moved left a
blur on the photograph, whereas the ones at rest appeared as
black dots.

Materials and Methods

The locomotor activity of C. ferrugineus adults was
determined by their emigration from wheat during certain time
intervals. The wheat and insects were placed in 100-ml.
glass beakers without pouring spouts, or in plastic tubes,
3.8 cm. in diameter. Each container was filled with wheat,
levelled at the top, and then placed at the center of a glass
Petri dish, 8.9 cm. in diameter and 2.2 cm. high. The adults
that emigrated from the wheat fell into the Petri dishes and
could readily be counted. The insects could not escape or
reinfest the wheat since they were unable to walk on vertical
surfaces of glass or plastic.

The moisture content of wheat was adjusted by mixing
it with the required volume of distilled water and then stor-
ing it at 21° C. in closed containers for 3 or 4 days for the
kernels to equilibrate with the intergranular water vapour.
Wheat moisture content was measured with a Halross dielectric
moisture meter (Canadian Aviation Electronics Ltd., Winnipeg,
Manitoba). Anderson (1956) reported that the standard error
of estimate of this meter was 0.27 per cent on 554 samples

of winter wheat ranging from 12.2 to 17.6 per cent moisture content. The over-all precision and accuracy of the data given by the Halross meter were in the range of those obtained by the standard Brown-Duvel method.

The wheat moisture contents selected for these experiments represented the extremes and averages of grain stored in Canada. According to the Canada Grain Act (1957), spring wheat below 14.6 per cent moisture content is graded "dry"; wheat between 14.6 and 17.0 per cent is "tough"; and wheat above 17.0 per cent is "damp."

The Petri dishes, containing the beakers or tubes of wheat, were placed in clear glass desiccators containing $KOH-H_2O$ solutions to regulate relative humidity (Solomon, 1951). The density of each solution was adjusted to give a relative humidity that was in equilibrium with the moisture content of the wheat. The following equilibrium relationships between relative humidity and wheat moisture content were used, based on the work of Babbit (1949):

Wheat moisture content, per cent	Relative humidity, per cent
9.8	35
13.3	60
14.8	76
17.8	85

In most experiments, the desiccators were enclosed in light-proof, cylindrical cardboard containers, lined with black paper to separate the effect of light from other factors influencing insect locomotor activity in wheat.

The experiments were conducted in rooms maintained at temperatures of $15.0 \pm 1.5^\circ$ C., $22.0 \pm 1.5^\circ$ C., and $28.0 \pm 2.0^\circ$ C.

The insects used in the experiments were taken from laboratory cultures contained in 1-gallon (3600-ml.) glass jars. The culture medium was a mixture of 1200 gm. of wheat and 120 gm. of wheat germ. The cultures were stored in rearing cabinets maintained at $28.2 \pm 0.5^\circ$ C. and 75 per cent relative humidity. The insects were of mixed sexes and were between 2 and 6 weeks old. The insects were placed at the bottoms of the empty beakers or tubes 30 minutes before the wheat was introduced.

Results

Effect of wheat moisture content and temperature, and insect density on the emigration of C. ferrugineus from wheat. Experiments were conducted, to compare the emigration of C. ferrugineus from beakers of wheat at moisture contents of 9.8, 13.3, 14.9 and 17.8 per cent, and at temperatures of 15°, 22° and 28° C. To evaluate the influence of insect density on emigration, densities of 5, 10, 25 and 50 insects per 100 gm.

of wheat were used at each combination of wheat moisture content and temperature. There were four replicates for each determination.

Insect counts were made at intervals of 1, 2, 4 and 8 days after the start of the experiment.

The results are given in Tables I, II and III. At each temperature, wheat moisture content was the dominant factor influencing insect locomotor activity, as expressed by the numbers of insects that emigrated from beakers of wheat. At 15° C., more insects emigrated from wheat at 9.8 per cent moisture content at each of the four assessments than from wheat at 13.3, 14.9 and 17.8 per cent moisture content (Table I). It was thought that mutual stimulation at the highest densities, would result in a higher percentage of emigration than at the low densities. However, such was not the case as in most instances, the percentage emigration at the four densities corresponded closely.

There was little difference between the percentages of insects emigrating at 15° C. and 22° C., after 8 days, when the wheat moisture content was 9.8 per cent. However, there was a tendency for more insects to emigrate at 22° C., than at 15° C., at wheat moisture contents of 13.3 and 14.9 per cent. This was particularly marked at the 4-day assessment.

TABLE I

MEAN CUMULATIVE PERCENTAGES OF C. ferrugineus ADULTS
EMIGRATING AFTER VARIOUS TIMES FROM 100-ML. BEAKERS
OF WHEAT AT DIFFERENT MOISTURE CONTENTS
STORED AT 15.0 ± 1.5° C.

Moisture content, per cent	Initial insect density	Percentage emigration after			
		1 day	2 days	4 days	8 days
9.8	5	5	20.0	35.0	60.0 ± 10.0[a]
	10	5	17.5	35.0	52.5 ± 16.0
	25	19	33.0	44.0	70.0 ± 7.7
	50	15.5	25.5	35.5	61.0 ± 10.9
13.3	5	0	0	0	5.0 ± 5.0
	10	2.5	5.0	15.0	35.0 ± 8.7
	25	0	2.0	8.0	13.0 ± 2.2
	50	0	3.5	8.0	17.0 ± 3.4
14.9	5	0	0	5.0	13.0 ± 13.0
	10	0	2.5	2.5	10.0 ± 5.9
	25	0	1.0	6.0	11.0 ± 5.5
	50	0.5	3.0	8.0	16.0 ± 7.7
17.8	5	0	0	0	10.0 ± 10.0
	10	0	0	5.0	10.0 ± 4.1
	25	0	0	3.0	14.0 ± 3.8
	50	0	0	1.0	5.5 ± 1.2

[a]Standard error

TABLE II

MEAN CUMULATIVE PERCENTAGES OF C. ferrugineus ADULTS
EMIGRATING AFTER VARIOUS TIMES FROM 100-ML. BEAKERS
OF WHEAT AT DIFFERENT MOISTURE CONTENTS
STORED AT 22.0 ± 1.5° C.

Moisture content, per cent	Initial insect density	Percentage emigration after			
		1 day	2 days	4 days	8 days
9.8	5	10.0	20.0	30.0	60.0 ± 21.6[a]
	10	20.0	45.0	45.0	50.0 ± 9.1
	25	47.0	65.0	70.0	77.0 ± 3.4
	50	37.5	50.0	57.5	62.5 ± 9.2
13.3	5	0	0	0	25.0 ± 12.9
	10	0	2.5	12.5	35.0 ± 17.0
	25	3.0	7.0	20.0	42.0 ± 6.6
	50	1.5	6.5	18.0	31.0 ± 1.7
14.9	5	13.3	20.0	20.0	20.0 ± 13.8
	10	3.3	3.3	16.6	23.3 ± 3.3
	25	6.6	6.6	9.3	14.0 ± 3.1
	50	13.3	14.6	20.6	27.0 ± 4.1
17.8	5	0	0	10.0	25.0 ± 9.0
	10	0	0	0	0
	25	0	2.0	4.0	8.0 ± 0
	50	0.5	0.5	1.0	9.5 ± 2.0

[a]Standard error

TABLE III

MEAN CUMULATIVE PERCENTAGES OF C. ferrugineus ADULTS
EMIGRATING AFTER VARIOUS TIMES FROM 100-ML. BEAKERS
OF WHEAT AT DIFFERENT MOISTURE CONTENTS
STORED AT 28.0 ± 1.5° C.

Moisture content, per cent	Initial insect density	Percentage emigration after			
		1 day	2 days	4 days	8 days
9.8	5	30.0	40.0	70.0	80.0 ± 14.1[a]
	10	47.5	57.5	75.0	85.0 ± 9.5
	25	30.0	51.0	67.0	87.0 ± 3.7
	50	26.0	44.5	66.0	87.5 ± 2.2
13.3	5	5.0	10.0	25.0	35.0 ± 17.0
	10	27.5	32.5	55.0	60.0 ± 15.6
	25	10.0	16.5	29.5	49.5 ± 2.8
	50	3.0	15.5	34.0	50.0 ± 3.6
14.9	5	0	5.0	15.0	20.0 ± 11.5
	10	5.0	7.5	10.0	20.0 ± 4.1
	25	3.0	5.0	12.0	30.0 ± 6.6
	50	5.5	9.0	13.5	23.0 ± 3.8
17.8	5	0	0	5.0	35.0 ± 5.0
	10	0	2.5	5.0	25.0 ± 8.6
	25	0	3.0	10.0	39.0 ± 7.5
	50	0.5	3.0	5.0	40.0 ± 7.5

[a]Standard error

At 22° C., more insects emigrated from wheat at 14.9 per cent moisture content after one day than from wheat at 13.3 or 17.8 per cent moisture content. These high initial emigration rates were not maintained, however, during subsequent observations; after 8 days, the emigration of insects was slightly less than that at 13.3 per cent moisture content but higher than that at 17.8 per cent moisture content.

The results in Tables I and II indicated that at 15° C. and 22° C., respectively, insects tended to disperse more slowly in moist wheat than in dry wheat. At 28° C., similar results were obtained for the first four days of observations. However, after 8 days, emigration of insects from wheat at 17.8 per cent moisture content increased sharply and exceeded the emigration from wheat at 14.9 per cent moisture content. The increased emigration was attributed to the growth of moulds which is discussed separately in this chapter.

The wheat used in the emigration experiments was sifted after 8 days and the siftings examined for the presence of eggs and larvae. Although oviposition occurred in wheat at 14.9 and 17.8 per cent moisture content, no eggs were found in wheat at 13.3 or 9.3 per cent moisture content.

Figure 1 summarizes the effects of wheat moisture content, temperature, and initial insect density on the percentage emigration of C. ferrugineus after 8 days. The data show that generally the levels of emigration decreased with
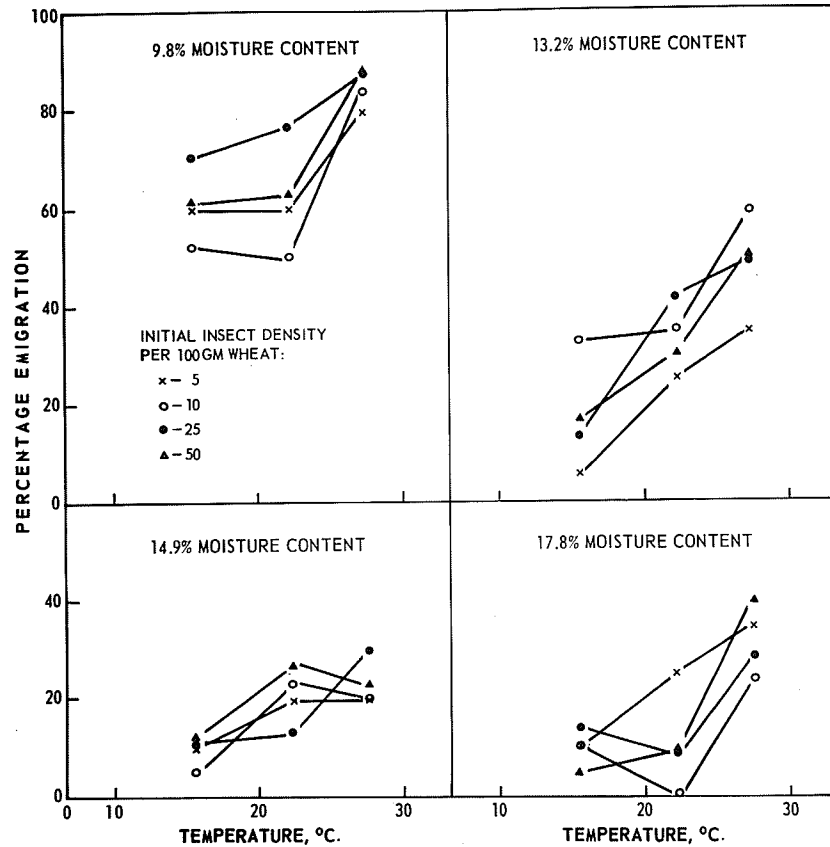
FIGURE 1

INFLUENCE OF MOISTURE CONTENT, TEMPERATURE AND
POPULATION DENSITY ON THE EMIGRATION OF
C. ferrugineus FROM BEAKERS OF
WHEAT AFTER 8 DAYS

an increase in wheat moisture content. At 28° C., more in-
sects emigrated at all moisture levels than at 22° C., except
at 14.9 per cent moisture content. Chi-square tests indicated
that the percentage emigration did not differ significantly
($P < 0.05$) from that expected at the four initial insect den-
sities.

Effect of light on emigration of C. ferrugineus.
An experiment was carried out to determine whether the emigra-
tion of C. ferrugineus from beakers of wheat, was influenced
by exposure to light. Twenty adults of C. ferrugineus were
counted into each of 12 beakers. After 30 minutes, 100 gm.
of wheat of 9.1 per cent moisture content were added slowly
to each beaker. The beakers were set in Petri dishes and
placed in desiccators containing $KOH-H_2O$ solutions, prepared
to give a relative humidity of 35 per cent. There were
four beakers in each desiccator.

One desiccator was enclosed in a light-proof cylin-
drical cover. Two other desiccators remained uncovered.
One of these was illuminated during the time of the experi-
ment with a fluorescent lamp placed 30 cm. above the glass
cover. A household fan provided air circulation to reduce
heat transfer from the light. The other uncovered desic-
cator was in darkness for about 12 hours overnight. The room
temperature was 27° C.

An analysis of variance of insect counts in the Petri dishes, 1 hour after the start of the experiment, showed that there was no significant difference between the numbers of insects emigrating from wheat in darkened containers and numbers emigrating from illuminated containers (Table IV). At 24 hours, however, the analysis showed that significantly more insects (P < 0.05) had emigrated from wheat exposed to continuous illumination than from wheat kept in darkened containers.

There was no significant difference between the numbers of insects emigrating from wheat that was continuously illuminated, and the numbers from wheat exposed to about 12 hours of daylight and 12 hours of darkness.

Gravity response of C. ferrugineus. Studies were made, on a small scale, to determine the extent to which insects moved upwards or downwards in a column of wheat. For these experiments two plastic tubes, 3.8 cm. in diameter and 5.0 cm. high, were joined together with masking tape. The bottom tube had wire screen, containing 3.2 meshes per cm., fused to the bottom to retain the wheat and yet allow the insects to drop into a 30 ml. beaker placed beneath. Wheat of 9.3 per cent moisture content was poured into the bottom half of the two tubes. Twenty-five adults of C. ferrugineus, 4 to 5 weeks old, were placed in the wheat. The top tubes were then filled with wheat of the same moisture content and the surfaces levelled. The tubes were then placed vertically

TABLE IV

MEAN[a] NUMBER OF C. ferrugineus ADULTS THAT EMIGRATED
AFTER 1 HOUR AND 24 HOURS FROM BEAKERS OF WHEAT
AT 9.1 PER CENT MOISTURE CONTENT STORED IN
DARKENED AND ILLUMINATED CONTAINERS
AT $28.0 \pm 1.5^{\circ}$ C.

Experimental conditions	Number emigrating after	
	1 hour	24 hours
Under light-proof cover	1.8	9.8
Day illumination	2.3	17.8
Continuous illumination	2.3	18.3
L.S.D. at 5% level		5.3

[a]Four replicates

in Petri dishes and enclosed in a light-proof cover. There were four replicates.

After 22 hours, the numbers of insects in the Petri dishes, and in the beakers were counted. The masking tape was removed and the wheat in the two tubes was separated by sliding a thin piece of cardboard through the center. The wheat was then sifted to determine the number of insects remaining in each tube.

The results showed that more insects emigrated from the bottom of each tube than from the top ($P < 0.01$) (Table V). Also, more insects were found in the siftings from the bottom half than from the top half ($P < 0.05$). This experiment showed, therefore, that C. ferrugineus was positively geotactic in a column of wheat. Not only did significantly more insects emigrate from the bottom than from the top, but, also, more insects were found in the wheat in the bottom half of the tube than in the top half. These results were confirmed in other experiments reported in this Chapter and in Chapter IV.

Effect of insect conditioned wheat on emigration. In stored grain, certain parts of the bulk may become heavily infested and form centers from which insects may emigrate to other parts of the grain. Experiments were carried out to compare the emigration of insects from insect-conditioned wheat and from "fresh" wheat.

TABLE V

MEAN[a] NUMBER OF <u>C</u>. <u>ferrugineus</u> EMIGRATING FROM, OR
REMAINING IN, THE TOP AND BOTTOM HALVES OF A
VERTICAL TUBE OF WHEAT AFTER 22 HOURS

Location	Number emigrating from wheat	Number remaining in wheat
Top half	0.5	4.0
Bottom half	10.0	10.5
L.S.D. at 1% level	7.7	
L.S.D. at 5% level	5.5	

[a]Four replicates

The insect-conditioned wheat was taken from a two-month culture of C. ferrugineus. The wheat was sifted to remove all stages, except those inside the kernels, and then dried to 11.3 per cent moisture content at room temperature and 30 per cent relative humidity. The "fresh" wheat had not been exposed to insects previously; and it was also dried to 11.3 per cent moisture content. Two plastic tubes, 3.8 cm. in diameter and 5.0 cm. high, were fastened together with masking tape to form a tube, 10 cm. long. The bottom halves of four such 10 cm. tubes were filled with "fresh" wheat. Twenty-five adults of C. ferrugineus were introduced on the surface of the wheat; the top halves of the tubes were then filled with "fresh" wheat. The bottom and top halves of an additional four, 10-cm. tubes were filled with insect-conditioned wheat, the insects being introduced in the same manner as in the tubes containing the "fresh" wheat. All tubes were placed vertically in separate Petri dishes and enclosed in light-proof containers. After 24 hours, the numbers of insects that had emigrated from the tops of the tubes were counted. A divider was then inserted between the top and bottom tubes, and the wheat from each section was sifted.

The results showed that more insects remained in the bottom halves of the tubes than in the top halves (Table VI). Although more insects emigrated from the tubes containing the insect-conditioned wheat than from "fresh" wheat, student's t-test indicated that the difference was not significant $(P>0.05)$.

TABLE VI

MEAN[a] NUMBER OF C. ferrugineus ADULTS EMIGRATING FROM,
OR REMAINING IN, VERTICAL TUBES OF FRESH OR
INSECT-CONDITIONED WHEAT AFTER 24 HOURS

Type of wheat in tubes	Number of insects in		Number emigrating
	Top half	Bottom half	
Fresh	1.5	19.8	3.5
Insect conditioned	3.0	15.0	8.7

[a]Four replicates

Another experiment was carried out to compare the emigration of insects from tubes that contained "fresh" wheat in the bottom half and insect-conditioned wheat in the top half, and _vice versa_. The insects were placed at the center of each tube as in the previous experiment.

The results showed that when "fresh" wheat was in the bottom half of the tube, most of the insects remained there (Table VII). However, when insect-conditioned wheat was in the bottom half, there was no significant difference between the numbers of insects found in each half. There was no significant difference in the emigration of insects from the two sets of tubes (Table VII).

The results indicate that the distribution of insects in stored grain may be influenced by the presence of patches of grain that has been previously infested. Table VI shows how the insects became distributed in a column of wheat of the same quality; Table VII shows how this distribution was altered when the top and bottom halves of a tube contained "fresh" and insect-conditioned wheat, respectively. Thus, when patches or layers of previously infested wheat occur below the surface of stored grain we may expect insects to avoid these regions and infest other areas in the bulk.

Effect of starvation on the emigration of C. ferrugineus from wheat. The insects that were used in the previous experiments were taken from laboratory cultures maintained at

TABLE VII

MEAN[a] NUMBER OF C. ferrugineus ADULTS EMIGRATING FROM,
OR REMAINING IN, ADJOINING VERTICAL TUBES OF FRESH AND
INSECT-CONDITIONED WHEAT AFTER 24 HOURS

Type of wheat at bottom of tube	No. of insects remaining in		Number emigrating from top
	fresh wheat	insect conditioned wheat	
Fresh	17.3	1.5	6.8
Insect-conditioned	8.8	10.0	7.5
L.S.D. at 1% level		10.4	
L.S.D. at 5% level		7.4	

[a]Four replicates

$28.2 \pm 0.5^{\circ}$ C., and 75 per cent relative humidity. The pre-
conditioning of insects on food may influence the extent of
locomotor activity. An experiment was, therefore, devised to
determine the effect of food availability and moisture con-
tent on the subsequent emigration of insects from dry or damp
wheat.

Insects were kept for three days at each of the
following conditions: (1) on 150 gm. of wheat at 17.8 per
cent moisture content that had been crushed in a Waring
Blendor; (2) on 150 gm. of wheat at 9.6 per cent moisture
content, crushed in a Waring Blendor; (3) in Petri dishes
without food, in a desiccator at 85 per cent relative humi-
dity; (4) in Petri dishes without food, in a desiccator at
50 per cent relative humidity. Two hundred adults were used
for each lot.

The wheat at 17.8 per cent moisture content was stored
in a desiccator containing a $KOH-H_2O$ solution to give a rela-
tive humidity of 85 per cent; similarly, wheat at 9.6 per
cent moisture content was stored at 35 per cent relative
humidity. These measures were taken to prevent moisture
loss or uptake from the food during the 3-day preconditioning
period.

Each of the four groups of preconditioned insects was
exposed to wheat at 9.6 or 17.8 per cent moisture content in
100-ml. beakers. There were three replicates for each mois-
ture content. Insect counts were made after 24 hours.

There was appreciable emigration of insects (6.7 to
16.0) from wheat at 9.6 per cent moisture content but few
(0 to 2.7) emigrated from wheat at 17.8 per cent moisture con-
tent (Table VIII). The only insects that emigrated from
wheat at 17.8 per cent moisture content were those that had
been preconditioned on crushed wheat at 17.8 per cent mois-
ture content and those that had been preconditioned without
food at 85 per cent relative humidity. None of those that
had been kept under dry conditions, with or without food,
emigrated.

On the other hand, food availability was more import-
ant than moisture content in the preconditioning of insects
prior to their being exposed to wheat at 9.6 per cent mois-
ture content. Significantly more insects ($P < 0.01$) that had
been preconditioned for 3 days on crushed wheat at 17.8 or
9.6 per cent moisture content emigrated from dry wheat than
did insects that had been starved at 85 and 50 per cent
relative humidity.

Preconditioning of insects on crushed wheat at 17.8
or 9.6 per cent moisture content resulted in no significant
difference in their emigration from wheat at 9.6 per cent
moisture content; nor did preconditioning at 85 or 50 per
cent relative humidity result in different rates of emigra-
tion.

The results indicated that starved insects may be
more tolerant of dry foods than insects that had previously

TABLE VIII

MEAN[a] NUMBER OF C. ferrugineus ADULTS EMIGRATING AFTER
24 HOURS FROM 100-ML. BEAKERS OF WHEAT[b]

Type of preconditioning	Wheat moisture content, per cent	
	9.6	17.8
On crushed wheat at 17.8% M.C.	16.0	2.7
On crushed wheat at 9.6% M.C.	14.0	0
No food at 85% R.H.	7.0	2.3
No food at 50% R.H.	6.7	0
L.S.D. at 1% level	6.8	-
L.S.D. at 5% level	4.7	1.7

[a]Three replicates

[b]The insects were preconditioned for 3 days before the
experiment

been exposed to food since fewer starved insects emigrated.
Few insects from all four groups emigrated from wheat at
17.8 per cent moisture content, as has been shown previous-
ly (Tables I, II and III).

Effect of preconditioning on emigration from mouldy
and "fresh" wheat. The experiments on the influence of wheat
moisture content and temperature on insect locomotor activity
(Table III) indicated that in wheat at 17.8 per cent moisture
content and 28° C., emigration of insects at all population
levels more than doubled after 8 days when compared to the
rate after 4 days. In contrast, the emigration rates in
drier wheats showed progressive increases throughout the
period of observations. Since moulds flourish in damp wheat
at about 28° C., it seemed possible that the increase in
locomotor activity leading to high emigration of insects from
the beakers, was related to the presence of moulds themselves
or to the deteriorative changes in wheat caused by moulds.
Accordingly, experiments were devised to study the locomotor
activity of C. ferrugineus in mouldy and "fresh" wheat hav-
ing similar moisture contents.

About 5 pounds of wheat were tempered with water to
give a moisture content of 17.8 per cent. The wheat was then
stored in a closed container for four weeks at 28° C. An
additional 5 pounds of "fresh" wheat was tempered with water
to give a moisture content of 17.8 per cent. It was stored

in a closed container for 3 days to allow time for the kernels
to equilibrate to the desired moisture content. However, upon
measurement, it contained only 17.3 per cent moisture content.

C. ferrugineus adults, 4 weeks old, were preconditioned
for 3 days on dry wheat at 9.3 per cent moisture content, and
on damp wheat at 17.6 per cent moisture content. Twenty-five
adults were placed at the bottoms of 100-ml. beakers for 30
minutes before the wheat was added. There were three repli-
cates for each determination. The number of insects that had
emigrated were counted after 48 hours.

The results showed that there was no significant dif-
ference between the numbers of insects emigrating from "fresh"
or mouldy wheat when the insects had been preconditioned on
dry wheat at 9.3 per cent moisture content for 3 days before
the experiment (Table IX). Neither was there a difference in
numbers of insects emigrating from "fresh" or mouldy wheats
when they had been preconditioned for 3 days on wheat at 17.6
per cent moisture content. However, when the insects were
preconditioned for 3 days on wheat at 17.6 per cent moisture
content, significantly more insects ($P < 0.05$) emigrated from
beakers of mouldy wheat than did insects that were precon-
ditioned for 3 days on wheat at 9.3 per cent moisture content.

The study showed, therefore, that insects that had
been exposed for 3 days to damp wheat appeared to be more
sensitive to moulds, and thus tended to emigrate to a greater

TABLE IX

MEAN[a] NUMBER OF C. ferrugineus ADULTS EMIGRATING FROM FRESHLY
MOISTENED WHEAT AT 17.3 PER CENT MOISTURE CONTENT AND
MOULDY WHEAT AT 17.8 PER CENT MOISTURE CONTENT
AFTER 2 DAYS AT 28.0 ± 1.5° C.[b]

Type of preconditioning	Type of wheat exposed to insects	Number of insects emigrating
On dry wheat (9.3% M.C.)	Fresh (17.3% M.C.)	4.0
	Mouldy (17.8% M.C.)	4.7
On damp wheat (17.6% M.C.)	Fresh (17.3% M.C.)	6.4
	Mouldy (17.8% M.C.)	10.7
L.S.D. at 5% level		4.4

[a]Three replicates

[b]The insects were exposed to dry or damp grain for 3 days
before the experiment

extent from mouldy wheat, than insects that had been previous-
ly exposed to dry wheat for 3 days.

Emigration of C. ferrugineus from mouldy and "fresh"
wheat at different densities. The effect of moulds on the
locomotor activity of C. ferrugineus was sufficiently marked
to prompt further studies. Experiments were done to deter-
mine the emigration of adults from mouldy and "fresh" wheat
at 17.8 per cent moisture content. Insect densities of 5,
10, 25 and 50 insects per 100 gm. of wheat were used. The
insects were taken from laboratory cultures maintained at
28.0° C. The mouldy wheat was tempered with water to give
a moisture content of 17.8 per cent, and stored for 4 weeks
in a closed container at 28° C., for development of storage
moulds. "Fresh" wheat at 9.3 per cent moisture content was
tempered with water to give 17.8 per cent moisture content,
and stored for two days to allow the kernels to equilibrate
to the desired moisture content. Insect counts were made at
24, 48, 96, 139, 163 and 187 hours to determine their emi-
gration from wheat contained in 100-ml. beakers.

Counts of insects that had emigrated from beakers of
mouldy and "fresh" wheat after 24 hr. indicated that differ-
ences between them were small (Table X). However, after 187
hours, the results showed that the emigration of insects from
mouldy wheat was higher than that from "fresh" wheat, thus
confirming earlier observations (Tables III and VIII). There

TABLE X

MEAN[a] CUMULATIVE PERCENTAGES OF $\underline{C.}$ $\underline{ferrugineus}$ ADULTS
EMIGRATING FROM MOULDY OR "FRESH" WHEAT, EACH AT 17.8
PER CENT MOISTURE CONTENT, AT 28.0 $\pm$ 1.5° C.

Type of wheat	Initial insect density per 100 gm. wheat	Percentage emigration after					
		24 hr.	48 hr.	96 hr.	139 hr.	163 hr.	187 hr.
Mouldy	5	0	6.6	13.3	86.6	86.6	93.3$\pm$6.8[b]
	10	3.3	16.6	30.0	56.6	80.0	90.0$\pm$5.9
	25	2.6	16.0	38.6	58.6	78.6	84.4$\pm$6.2
	50	3.3	15.3	34.6	61.3	78.0	83.3$\pm$9.2
"Fresh"	5	6.6	13.3	46.6	53.3	60.0	66.6$\pm$6.8
	10	6.6	6.6	20.0	43.3	56.6	63.3$\pm$6.8
	25	2.6	8.0	24.0	38.6	48.0	74.6$\pm$2.7
	50	2.6	12.0	21.3	33.3	42.6	62.6$\pm$5.3

[a]Three replicates

[b]Standard error

were no apparent differences in emigration between beakers of wheat charged at different densities.

The fungal flora was determined from a 100-seed sample selected at random from each lot of experimental wheat. The sample was divided into four sub-samples of 25-seeds. The method followed was reported by Wallace and Sinha (1962). Each sub-sample was placed on a No. 3 Whatman filter paper disc fitted in a Petri dish and moistened to saturation with sterile water. The seeds were spaced uniformly around the periphery of the filter paper. The plates were stored for one week at 17° to 24° C. The fungal flora on each seed was then examined and identified using a stereo microscope at magnifications of 50 x and 100 x.

Table XI gives the percentage of seeds that were infected with fungi. The results showed that there was little difference in the total infections between mouldy and "fresh" wheat infested at all insect densities. It appears that the "fresh" wheat became mouldy after the introduction of the insects since "fresh" wheat of 17.8 per cent moisture content, without insects, had a total spore count of 78, the same as dry wheat of 13.1 per cent moisture content. On the other hand, mouldy wheat, without insects, had a high spore count, of the same order as mouldy wheat with insects.

The spore counts of the mouldy and "fresh" wheats infested with insects indicated that the presence of moulds

TABLE XI

PERCENTAGE OF SEEDS FROM MOULDY AND "FRESH" WHEAT SHOWING BACTERIAL AND FUNGAL INFECTIONS AFTER BEING INFESTED WITH C. ferrugineus AT DIFFERENT DENSITIES

Analysis	Mouldy (17.8% M.C.) Insect density/100 gm.					Fresh (17.8% M.C.) Insect density/100 gm.					Dry (13.1% M.C.) Check
	5	10	25	50	0	5	10	25	50	0	Check
Germination	68	71	71	76	76	86	91	87	90	97	95
Bacteria	2		1		3						
Fungi											
Alternaria tenuis sensu Wiltshire	13	10	4	8	1	6	1	2	3	4	12
Ascomycetes		3		2	3	8	1		1		
Aspergillus candidus Link	1	23	18	21	31	16	20	27	29	4	
Aspergillus flavus Link	6	5	3	5	5	29	40	30	14	6	
Aspergillus fumigatus Fresenius	4	3			1	1					
Aspergillus glaucus group			3	6	17	28	34	36	24	10	2
Aspergillus ustus (Bainier) Thom and Church		4	35	8	1		1				
Aspergillus versicolor (Vuillemin) Tiraboschi	73	40	34	51	27	2	6	4	3	4	5
Cladosporidium herbarum (Pers.) Link					1						1
Helminthosporium sativum P. K. & B.	1										1
Mucor spp.	2	6	3	5	4	3	1	2	3	2	3
Penicillium spp.	43	34	31	35	41	33	16	31	28	40	48
Rhizopus nigricans Ehren-burg		1	1							3	
Streptomyces griseus (Krainsky) Waxsman	7	6	13	19	28	5	6	7	3	2	1
Trichothecium roseum Link		1			1	4				3	5
Total	152	136	146	160	164	135	126	139	108	78	78

alone provided no basis for explaining the differences in emigration rates. The results showed that the germination of mouldy wheat was lower than that of "fresh" wheat. Since C. ferrugineus feeds primarily on the germ of kernels, it is possible that mouldy wheat would have a lower food value for this species than fresh wheat. Lack of food, or other deteriorative changes associated with mould growth may, therefore, have been a contributing factor in the higher emigration of insects from mouldy wheat compared with "fresh" wheat. However, additional studies are needed to clarify these observations.

It is worth noting that the percentage of seeds infected with Aspergillus versicolor was much higher in mouldy grain than in "fresh" grain. Sinha et al (1962) have found that this species was present in grain with a germination of 5 per cent, that had been stored for 7 years. Aspergillus glaucus was present on more seeds in the "fresh" than the mouldy grain. Agrawal et al (1957) have reported that this species is able to invade the germs of wheat at moisture contents below 15 per cent. They also found that granary weevils were capable of inoculating grain with storage fungi, thus promoting the spread of fungi within a bulk of grain.

Emigration of C. ferrugineus from wheat in closed containers. The preceding experiments described in this chapter have dealt largely with the locomotor activity of

<u>C</u>. <u>ferrugineus</u> as expressed by the emigration of adults from glass or plastic cylinders of wheat. To emigrate, the insects had to move to the surface of the wheat and fall off the edge of the container. The basic assumption employed in this technique was that insects showing locomotor activity in the restricted, semi-open environment provided in a beaker would eventually move to the surface and emigrate; inactive insects would remain in the wheat. Possibly, one of the factors that might militate against an insect emigrating is the fact that when an insect emerges from a three-dimensional medium such as grain it immediately is exposed to an unrestricted two-dimensional environment as long as it remains on the wheat surface. The environment was unrestricted in that the insect was not confined to the surface. To be classed as an emigrant the insect had to move outwards to the edge of the cylinder and fall off. Since this type of behaviour on a surface, in contact with both air and wheat, might be different from emigration behaviour in wheat alone, a technique was devised to measure emigration from one container of wheat to another.

The experiments were done with round bottom flasks, having a capacity of 41 gm., of wheat, whose necks were inserted in gallon jugs with a capacity of 3600 ml. The neck of each flask had an inside diameter of 1.0 cm. and was 5.0 cm. long. The flasks were filled with wheat to which adults of <u>C</u>. <u>ferrugineus</u> were added. Densities of 25, 50 and 100 adults

per flask were used. The wheat moisture content was 11.8 per cent. There were three replicates for each density. The flasks containing the wheat and the insects were placed in an upright position for 24 hours. The necks were then inserted into the tops of gallon jugs containing wheat of 11.8 per cent moisture content and then placed horizontally. The necks were fitted into rubber stoppers to prevent insects from escaping. Insects were thus able to pass from the wheat in the flask to the wheat in the gallon jug. Since the opening of the flask was small in relation to the volume of wheat in the gallon jug, there was a bias in favour of movement in one direction, from the flask to the jug. The flasks were disconnected from the gallon jugs at various times and the jugs sifted to determine the number of insects that had emigrated from the flasks. At each assessment, the flasks were disturbed as little as possible to eliminate possible emigration effects due to handling. The gallon jugs and flasks were not enclosed in light-proof containers, but were kept in a darkened corner of a room. The room temperature during these experiments was 27.8 ± 2.0° C.

The results showed that after 221 hours, all of the insects, at an initial density of 25 per flask, had emigrated to the wheat in the gallon jug (Table XII). At initial densities of 50 and 100 insects per flask, the final emigrations were 82.6 and 92.3 per cent, respectively. The lower emigra-

TABLE XII

MEAN[a] CUMULATIVE PERCENTAGES OF C. ferrugineus ADULTS
EMIGRATING FROM 50-ML. ROUND BOTTOM FLASKS OF WHEAT
OF 11.8 PER CENT MOISTURE CONTENT

Insect density per 41 gm. wheat	Percentages of insects emigrating after					
	4 hr.	7 hr.	25 hr.	28 hr.	49 hr.	221 hr.
25	38.4	52.0	76.0	80.0	92.0	100.0
50	41.2	48.6	68.6	68.6	76.6	82.6
100	45.6	65.3	79.6	80.6	88.0	92.3

[a]Three replicates

tion from the flasks at a density of 50 insects per flask may be partly accounted for by dead insects remaining in the flasks. The mortalities were 12 per cent at 50 insects per flask and 7 per cent at 100 insects per flask. The mortalities at these densities may have been due to crowding; there was no mortality at a density of 25 insects per flask. The chi-square test showed that there was no significant deviation in percentage emigration from that expected at the four insect densities.

Discussion

The role of wheat moisture content on the locomotor activity of C. ferrugineus has been amply demonstrated in these experiments. Few insects emigrated from wheat of 17.8 per cent moisture content. Although high wheat moisture content tended to depress insect locomotor activity as expressed by emigration from wheat, low moisture contents stimulated locomotor activity. The greater emigration of insects, at 15° C., from wheat at 9.8 per cent moisture content, compared with emigration from wheat at higher moisture contents was apparent at each of the four assessment periods.

Throughout the eight days of the experiment, there was a gradual increase in the emigration of insects at each of the four moisture contents, irrespective of temperature. This was particularly evident with wheat of 9.8 per cent moisture content, at 28° C., when 80 to 87.5 per cent of the insects

had emigrated after eight days.

Surtees (1963 c) found that at 15° C. to 35° C., more of C. ferrugineus occurred at the surface of wheat at 9 per cent moisture content than at 13 or 17 per cent moisture content. His results were based on the numbers of insects at the surface of 500-gm. quantities of wheat in glass jars. These results correspond closely with those of the emigration experiments reported in this chapter, which showed that emigration of insects from the surface of wheat in beakers was higher at a wheat moisture content of 9.8 per cent than at 13.3, 14.9 and 17.8 per cent at temperatures of 15° C., 22° C. and 28° C. (Tables I, II and III). It was considered that the high emigration from dry grain was an expression of locomotor activity.

In a separate experiment in which the behaviour of isolated individuals was measured, Surtees (1963 c) found that locomotor activity of C. ferrugineus was much lower in wheat of 9 per cent moisture content than in wheat of 14 per cent moisture content. The experiments were done by noting the change of positions of single insects in a layer of wheat two grains thick, held between two vertical glass plates. Surtees postulated that the inactivity of insects in dry grain was due to the need to conserve water.

Initially, dry conditions, in grain of 9 per cent moisture content, appear to stimulate locomotor activity, as indicated by the presence of more insects at the surface of

dry grain than moist grain. However, Surtees found that when single insects were exposed to dry conditions, insect activity was depressed. The data given in Table VIII of this chapter have shown that insects that have been without food for three days were much less active, as indicated by the low emigration rates from dry wheat, than insects that had been preconditioned for three days on crushed wheat. The inactivity may be attributed to lack of water as Surtees has suggested for an explanation in his experiments. Cotton (1954) has reported that in dry grain, the survival of bran bugs, which include Cryptolestes spp., depends mainly on the availability of grain dust which can readily be broken down to supply food and water. Thus, inactivity in dry grain may result from desiccation not only from the dry conditions in the grain but also from the lack of grain dust or other food that the insect can metabolize to form water. It is possible that Surtees' conclusions on the inactivity of insects in dry grain, which were based on the behaviour of single insects, may not be applicable to groups of insects where mutual mechanical stimulation is a factor in causing movement.

There was no evidence that high insect density itself stimulated or depressed emigration. There were isolated instances where emigration was low at low population densities, especially during the first two days of observations. However, chi-square tests indicated that there was no consistent depar-

ture from the expected emigration at each insect density.

Other workers have shown that certain stored grain pests emigrate as a result of high densities. Crombie (1944) found that emigration of larvae of the lesser grain borer, Rhyzopertha dominica (Fabricius), in stored grain, was related to density. Voûte (1938) showed that the emigration of rice weevils was influenced by high densities. Surtees (1963 a) has studied the dispersion behaviour of Sitophilus granarius (L.) in the laboratory and found that the numbers of insects that appeared on the surface of 500 gm. of wheat at regular intervals was proportional to the density. He noted that the proportion of insects appearing at the surface was higher in dry grain than in damp grain. In studies with C. ferrugineus, Surtees (1963 c) found that the adults generally were evenly distributed in a vertical "sandwich" of wheat at densities of 2, 10, 20, 30 and 40 insects per 200 gm. of wheat. At the lowest density, however, nearly half the individuals remained near the center at the point where they were first introduced.

The emigration of C. ferrugineus from wheat was influenced by exposure to light (Table IV). Since emigration was measured by the insects that ascended to the wheat surface and moved to the outer edges of the beakers, the light would affect only those individuals that were so exposed. The higher emigration, at the 24-hour assessment, from beakers exposed to the light, compared to emigration from beakers enclosed in darkened containers suggests that a photokinetic

effect may have operated to increase locomotor activity of insects at the wheat surface. These experiments provided the basis for conducting studies on insect emigration in darkness thus eliminating photokinetic influences on insect locomotor activity.

The tendency of C. ferrugineus to move downwards in grain (Table V) is a similar type of behaviour to that reported by Howe (1951) for granary weevils, Cloudsley-Thompson (1953) for Tenebrio moliter L., and Sharangapani and Pingale (1957) for Tribolium castaneum (Herbst) and Rhyzopertha dominica (Fab.). However, the tendency to move downwards in grain may be checked by the presence of grain that has been previously infested (Table VII) and, consequently, nutritionally depleted. Insects may "condition" their environment when they form aggregations. The rate and amount of flour conditioned by Tribolium is proportional to population density. Allee et al (1949) have reported that flour that has been occupied by Tribolium cultures for long periods has certain qualities that were not observed with fresh flour. Adults placed on "conditioned" flour laid fewer eggs as well as more variable numbers than when they were placed on fresh flour. Thus, conditioning of flour contributes significantly to the decline of Tribolium cultures largely through reduced reproduction. It is possible that decreased nutritive value and accumulation of toxic wastes in "insect-conditioned" flour

are mainly responsible for population decrease. Naylor (1959) in reporting results on the dispersal of Tribolium adults in a preferendum apparatus showed that more females and males were found in "insect-conditioned" flour to fresh flour. The conditioned flour had been inhabited by a reproducing laboratory stock for 3 months. These results are surprising since Park and Woolcott (1937) found that Tribolium populations caused energy depletion and biochemical and physical changes in flour. In the laboratory, such flour is unsuitable for the establishment of thriving cultures of Tribolium.

The presence of ubiquitous storage moulds throughout stored wheat and their concentration in regions that encourage mould growth, may influence insect activity and distribution. The results showed that fewer insects emigrated from damp, mouldy wheat after being preconditioned on dry wheat than when they had been preconditioned on damp wheat (Table IX). These results may be accounted for partly on the basis of humidity responses since the data in Chapter VI indicated that C. ferrugineus formed aggregations in the moist region of a humidity gradient after being preconditioned at 50 per cent relative humidity for 24-hr.; insects that had been preconditioned at 85 per cent relative humidity showed less tendency to form aggregations. It is possible, also, to account for the results in Table IX on the basis of feeding thresholds. Insects kept on dry, vitreous wheat kernels for 3 days would have less food

available than those placed on soft, damp wheat. The data in Table VIII showed that starved insects were less likely to emigrate from wheat than insects that had been preconditioned on crushed wheat. Kennedy (1961) has shown that in migrating aphids, feeding responses and locomotor activity may be antagonistic reflexes.

Mellanby (1939) suggested that the rate of movement of insects appeared to be correlated with their rate of metabolism. Within the temperature range of normal activity, Mellanby found that whenever an insect was transferred from one temperature to another its rate of movement changes to that characteristic of the new temperature. He also pointed out that insects which feed often are difficult to work with as their state of hunger changes rapidly and induces further variables. Thus, in laboratory experiments designed to measure the activity of insects both the exogenous conditions, such as environmental stimuli, as well as the endogenous conditions, such as "hunger", should be kept constant. For instance, Browne and Evans (1960) have shown that blowflies were less active immediately after they were fed on glucose, fucose or mannose than they were 24 hours after feeding.

Although more insects emigrated from beakers of mouldy wheat than from "fresh" wheat the difference was not statistically significant (P > 0.05) (Table IX). Emigration from mouldy wheat has generally been higher than that from "fresh"

wheat (Table X). Although no fungal analysis was made of wheat stored for 8 days in beakers at 17.8 per cent moisture content and 28° C. (Table III), the sharp increase in emigration between the 4- and 8-day assessments may be attributed to moulds, since heavy mould growth was found on freshly moistened grain (Table XI) after a similar period at the same temperature.

The lack of evidence that high insect density itself caused a higher percentage emigration than that at low densities calls for comment in view of field observations by Crombie (1944) and Voûte (1938) with other stored grain insects. It is often assumed that heavily populated regions in a grain bulk are foci from which insects spread throughout the bulk, and that high densities may stimulate emigration. Although heavy, localized populations may supply a large proportion of migrants the data resulting from the present studies do not indicate that high density itself stimulates emigration and resultant dispersal. The percentage of emigrations from wheat at various densities were approximately the same. This was confirmed using a flask technique to measure emigration (Table XII).

Summary

Wheat moisture content was the most important factor affecting locomotor activity of C. ferrugineus in wheat at 15°, 22° and 28° C.; more insects emigrated from dry than from damp wheat. Light also influenced locomotory activity; more in-

sects emigrated from beakers of wheat exposed in a lighted room than from beakers enclosed in darkened containers. C. ferrugineus was positively geotactic. When given a choice, more insects emigrated from the bottom of a tube of wheat than from the top. Also, when the top and bottom halves of a cylinder of wheat were sifted, more insects were found in the wheat in the bottom than in the top. When downward movement was restricted in short cylinders that contained small volumes of dry wheat, insects moved upwards and emigrated.

Lack of food influenced locomotor activity in dry wheat. Few insects that had been without food for 3 days emigrated from dry wheat. On the other hand, significantly more of the insects ($P < 0.01$), that had been preconditioned on food, emigrated.

Preconditioning also influenced locomotor activity in "fresh" or mouldy wheat. Insects that had been kept for 3 days on dry wheat showed no difference in their emigration rates from "fresh" or mouldy wheat. But when insects were kept on damp wheat for 3 days, more emigrated from mouldy wheat than from "fresh" wheat.

The higher emigration rates from mouldy, compared to "fresh", wheat could not be accounted for on the basis of total mould counts which were similar for each type of wheat.

For each temperature and moisture content investigated, the percentage of emigration was approximately the same at each density.

CHAPTER IV

THE SPATIAL DISTRIBUTION OF C. ferrugineus
IN STORED WHEAT

Introduction

Insect pests are seldom, if ever, distributed evenly
in stored grain. Infestations have been reported at all
depths and locations in grain bulks. The non-uniform distri-
bution of insects in stored grain is due largely to gradients
of temperature and moisture content that are formed during
storage. Such physical factors have an influence on the
velocity and direction of insect movement in grain and, con-
sequently, on insect distribution.

The distribution and abundance of insects has an im-
portant bearing on the application of control measures. The
decision on whether to control insects in stored grain is
based largely on their abundance; but the type of control that
is to be applied will depend on where they occur.

The initial distribution of insects in a bulk of grain
will depend on the source of infestation. For example, if in-
sects invade grain from an adjoining bin, they will tend to
be concentrated along one wall. Surveys of granaries in the
Prairie Provinces have shown that insects and mites live and
breed in cereal dust and kernels in floor and wall cracks of
empty granaries (Liscombe and Watters, 1962). It is likely

that such locations serve as primary sources for the infesta-
tions of newly stored grain.

The purpose of the studies described in this chapter
was to follow, by trapping, the movement and distribution of
C. ferrugineus in wheat at different moisture contents, at
regular time intervals and to relate these results to previous
work on this insect.

Review of the literature

One of the difficulties of determining the locomotory
activity and location of insects in a bulk of grain is that
most of the insects are not visible. The grain and the in-
sects must, therefore, be sampled or otherwise disturbed to
determine their position. Cox and Smith (1957) in studying
the distribution of Tribolium confusum J. du V. in a box of
flour divided the flour into cubes and sifted them. Pimentel
(1958) in measuring temperature changes in vials of flour
populated with Tribolium spp., obtained a measure of vertical
distribution from the numbers appearing on the surface at
various times. Naylor (1959) used two flat circular arenas
containing 10 or 48 tubes, 0.3 in. in diameter, equally spaced
near the periphery to measure dispersal of T. confusum from
the center of the arena. The tubes, containing flour, could
be sifted at various times to determine insect distribution.

Howe (1951) devised equipment to determine the prob-
able movement of granary weevils in stored grain. The appara-

tus consisted of a metal tube, 4-in. in diameter and 26 or
52-in. long. The column was sampled from the bottom to measure
the vertical distribution of insects throughout the grain. The
weevils tended to move towards the bottom.

Materials and methods

The experiments were devised to determine by means of
tube traps, the spatial distribution of insects in boxes of
wheat at different moisture contents (Figure 2). Three boxes
were made from 3/4-in., 5-ply, fir plywood. They were 50 cm.
long, 30.6 cm. wide and 30.6 cm. high. The traps consisted
of pyrex tubes with an internal diameter of 1 cm. The tubes
were inserted in No. 5 rubber stoppers fitted in holes, 2.5
cm. in diameter, drilled in the bottom of each box. The tops
of four tubes were even with the inside bottom surface of each
box to trap insects at the bottom of the wheat; four tubes
extended 9 cm. into the box to trap insects at the center; and
four extended 20 cm. into the box to trap insects at the grain
surface (Figure 3). Tubes at the grain surface protruded
slightly above the grain. A layer of masking tape at the top
enabled the insects to climb up the sides.

To prevent the escape of insects from each box, cracks
and joins on inner surfaces were sealed with melted paraffin,
and the top was covered with a sheet of clear plastic, 0.05
cm. thick, fastened in position with masking tape. An opening,
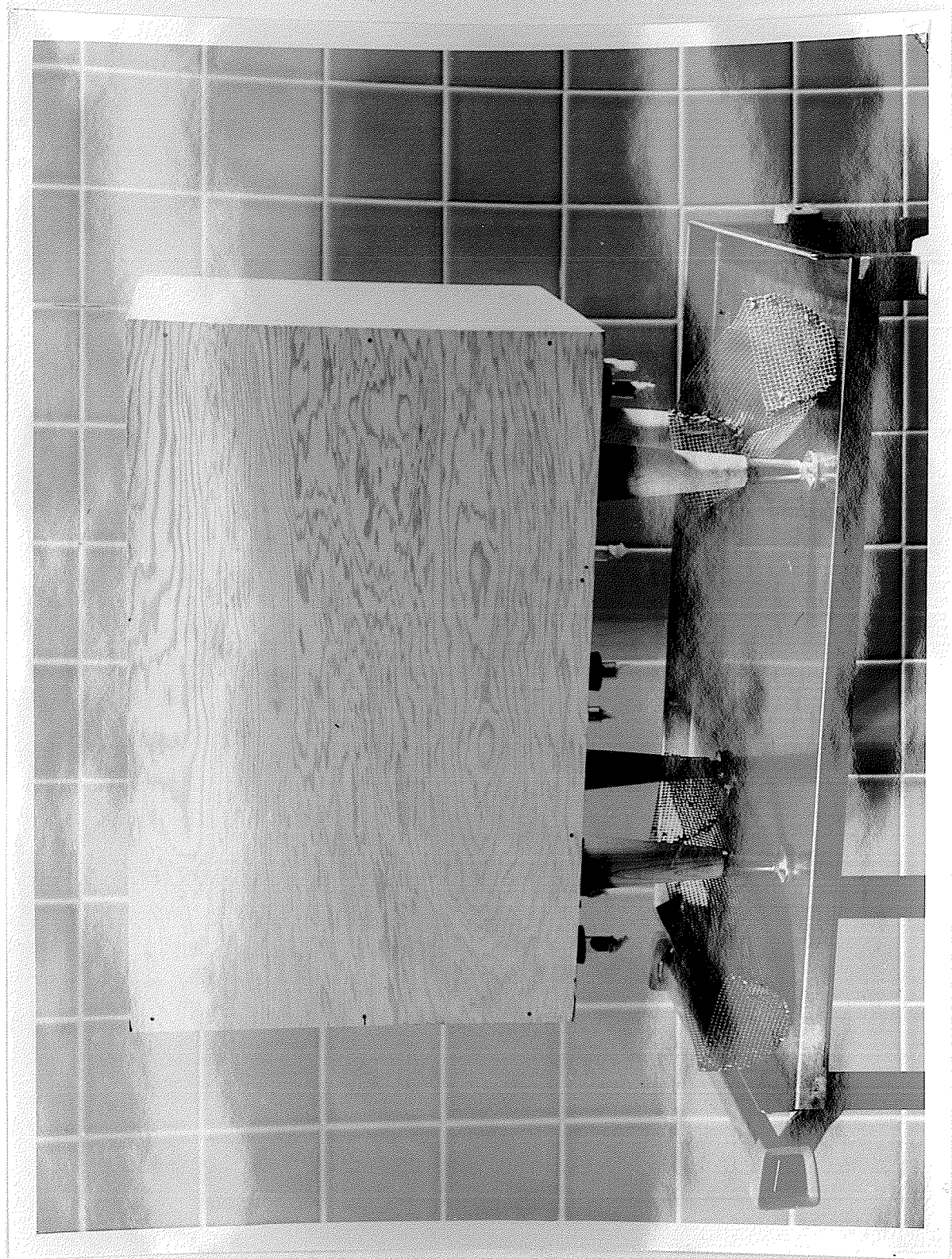
FIGURE 2

BOX USED TO INVESTIGATE SPATIAL DISTRIBUTION OF C. ferrugineus IN WHEAT

FIGURE 3

INTERIOR VIEW OF BOX SHOWS SAMPLING TUBES AT THE SURFACE, CENTER AND BOTTOM.
THOSE AT THE CENTER AND BOTTOM ARE COVERED WITH WIRE SCREEN TO
ALLOW INSECTS TO DROP INTO THE TUBES

13 cm. x 11.5 cm., at the center of each plastic sheet provided access to the wheat. A tight-fitting plywood cover excluded light.

The boxes were mounted on wooden legs, 16 cm. high, to provide access to the bottoms of the tubes. A "skirt" made from two layers of heavy brown paper was fastened to the bottom of each box to exclude light from the tubes.

Each box was filled to a depth of 18 cm. with No. 2 Northern wheat conditioned to the moisture content required for each experiment. A fresh lot of No. 2 Northern wheat was used for each experiment. As the boxes were being filled with wheat, the tops of tubes extending into each box were covered with wire screen having 3.2 meshes per cm. This size of mesh prevented wheat from falling into the tube but allowed insects to drop through. The bottom of each tube was plugged with a wad of cotton wool extending one cm. into the tube.

The experiments were done in a room at $25 \pm 3^\circ$ C. The insects for each experiment were taken from cultures maintained at $25 \pm 3^\circ$ C. and 75 per cent relative humidity. The age of the adults was 4 to 6 weeks; 500 were sprinkled evenly over the surface of the wheat in each box. Assessments were made at 9:00 a.m. and 5:00 p.m. each day by removing the cotton plug from each tube and counting the insects. Dead insects were discarded and were not replaced with live ones; live insects taken from traps were returned to the grain surface.

Results

Effect of wheat moisture content on the distribution
of C. ferrugineus in wheat. The experiments reported in
Chapter III indicated that C. ferrugineus was positively geo-
tactic and was more active in dry wheat than in damp wheat.
The experiments described in Chapter IV were carried out to
determine whether the insects showed a similar type of be-
haviour in larger quantities of wheat.

The first experiment was done with wheat at 9.7 per
cent moisture content. Assessments were discontinued after
four days when insect counts decreased and high mortalities
of trapped insects were observed. The mean numbers of in-
sects per tube trap at 9:00 a.m. each day are shown in Figure
4. The larger numbers trapped at the bottom compared to the
numbers obtained in surface tubes gave an indication of how
insects were distributed vertically. The low numbers of in-
sects in tubes at the center of the box indicated the small
amount of locomotor activity that occurred at this level.

The distribution of insects in wheat at 11.0 per cent
moisture content is shown in Figure 5. The trend is similar
to that observed in Figure 4. However, a longer time elapsed
before high mortalities and decreased locomotor activity
resulted in low trap counts which led to the termination of the
experiments. It would appear that the higher moisture content
had the effect of prolonging locomotor activity beyond the
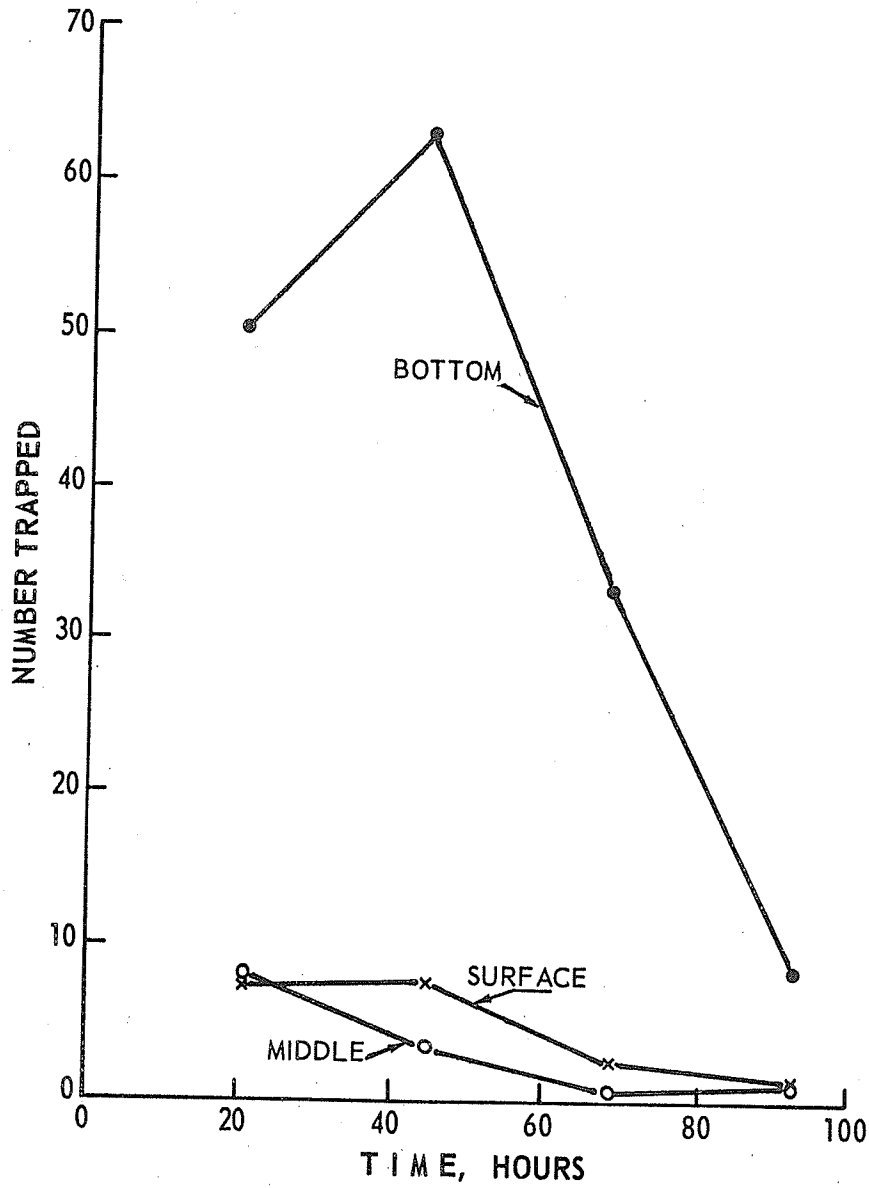
FIGURE 4

MEAN NUMBERS OF INSECTS TRAPPED AT THE SURFACE,
CENTER AND BOTTOM OF THREE BOXES OF WHEAT
AT 9.7 PER CENT MOISTURE CONTENT
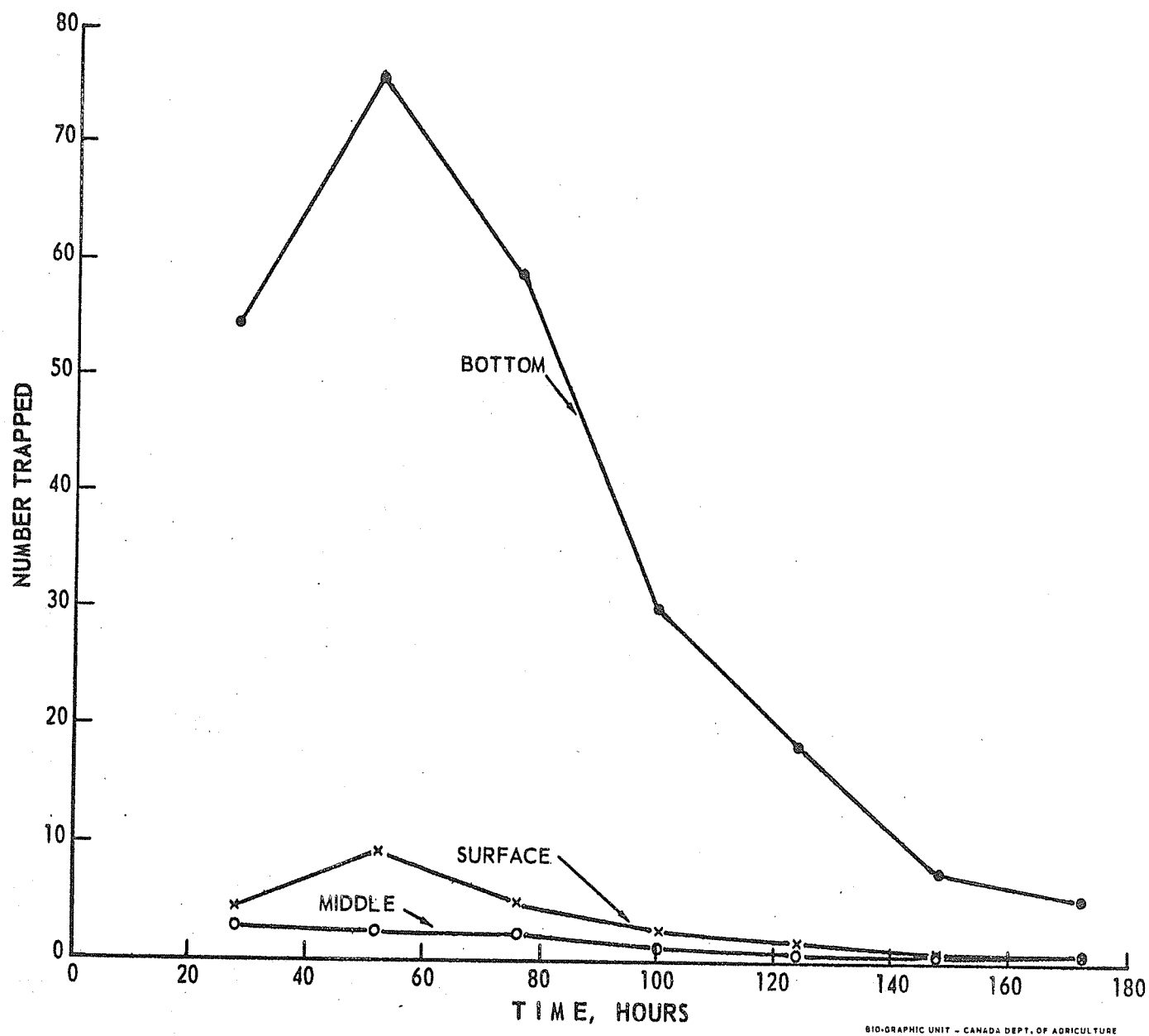
FIGURE 5

MEAN NUMBERS OF INSECTS TRAPPED AT THE SURFACE,
CENTER AND BOTTOM OF THREE BOXES OF WHEAT
CONTAINING WHEAT AT 11.0 PER CENT
MOISTURE CONTENT

period observed at 9.7 per cent moisture content.

Few insects were trapped at the surface of wheat at
17.0 per cent moisture content (Table XIII). During the
first 24 hr., the mean number obtained from the tubes at the
bottoms of the boxes was 26.0. However, 24 hr. later, the
mean was 8.8, thus reflecting a considerable decrease in
locomotor activity with time. This trend continued until the
termination of the experiment after 168 hr. Again, as was
shown with the data with wheat at 15.5 per cent moisture con-
tent (Figure 6), the decrease in numbers trapped was not due
to high mortalities as was mainly the case with dry wheat,
but due, rather, to low locomotor activity at high moisture
content. Similar results were obtained in Chapter III
except where moulds developed and locomotor activity in-
creased.

Effect of moist "pockets" on insect distribution in
dry grain. Patches of moist grain often form near the sur-
face of stored grain due to translocation of water (Anderson
et al., 1943), condensation, and leaking roofs. An experi-
ment was set up to determine how a patch of moist grain in-
fluenced insect distribution. The three boxes were filled
to a depth of 19 cm. with wheat at 11 per cent moisture con-
tent. Two U-shaped troughs (Figure 2), 2.5 cm. long, 7.5 cm.
wide and 5.5 cm. high, were placed at each end. The screen
forming the wall of the trough contained 3.2 meshes per cm.
One trough contained wheat at 11.0 per cent moisture content;

TABLE XIII

MEAN NUMBERS OF INSECTS TAKEN IN TUBE TRAPS AT
DIFFERENT DEPTHS IN WHEAT AT 17.0
PER CENT MOISTURE CONTENT

Elapsed time (hours)	Location of tube traps		
	Surface	Center	Bottom
24	0.1	0.0	26.0
48	0.2	0.0	8.8
72	0.5	0.2	3.8
96	0.0	0.0	3.3
120	0.1	0.0	2.4
144	0.4	0.0	2.8
168	0.3	0.2	1.8
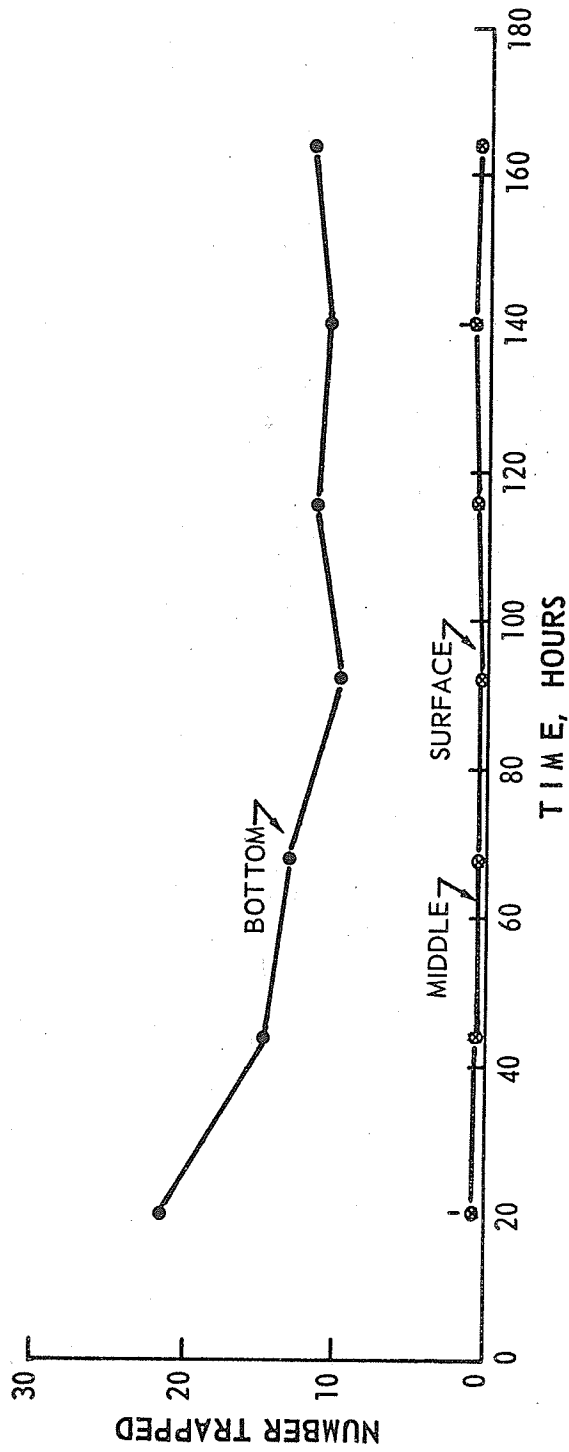
FIGURE 6

MEAN NUMBERS OF INSECTS TRAPPED AT THE SURFACE,
CENTER AND BOTTOM OF THREE BOXES OF WHEAT
AT 15.5 PER CENT MOISTURE CONTENT

the other contained wheat at 15.3 per cent moisture content.
The wheat surface in both troughs was levelled with the rest
of the wheat. Two shell vials were inserted in each trough
to act as pitfall traps. The wheat was uniformly infested
with insects at the surface. The troughs were sifted for in-
sects at the end of each experiment.

The results are shown in Figure 7. The presence of
a trough of moist grain did not appear to influence insect
distribution as indicated by counts of insects in tube traps
at different depths. However, fewer insects were taken from
the bottom tubes than was the case with grain at a uniform
moisture content of 11 per cent (Figure 5); also, the counts
tapered off less abruptly. Few insects were taken in the
shell vials throughout the experiment thus indicating low
activity of insects at the grain surface in the vicinity of
the troughs.

The boxes were also set up with wheat at 9 per cent
moisture content that contained two troughs of wheat at 15.5
per cent moisture content. The results are shown in Figure
8. Here, again, fewer insects were trapped at the bottom,
initially, than was the case with wheat at 9.7 per cent
moisture content (Figure 4). Also, moderate counts of in-
sects were obtained over a longer period. Although no esti-
mate of insect mortality was made beyond that of the insects
taken in the tubes, it is likely that the presence of moist
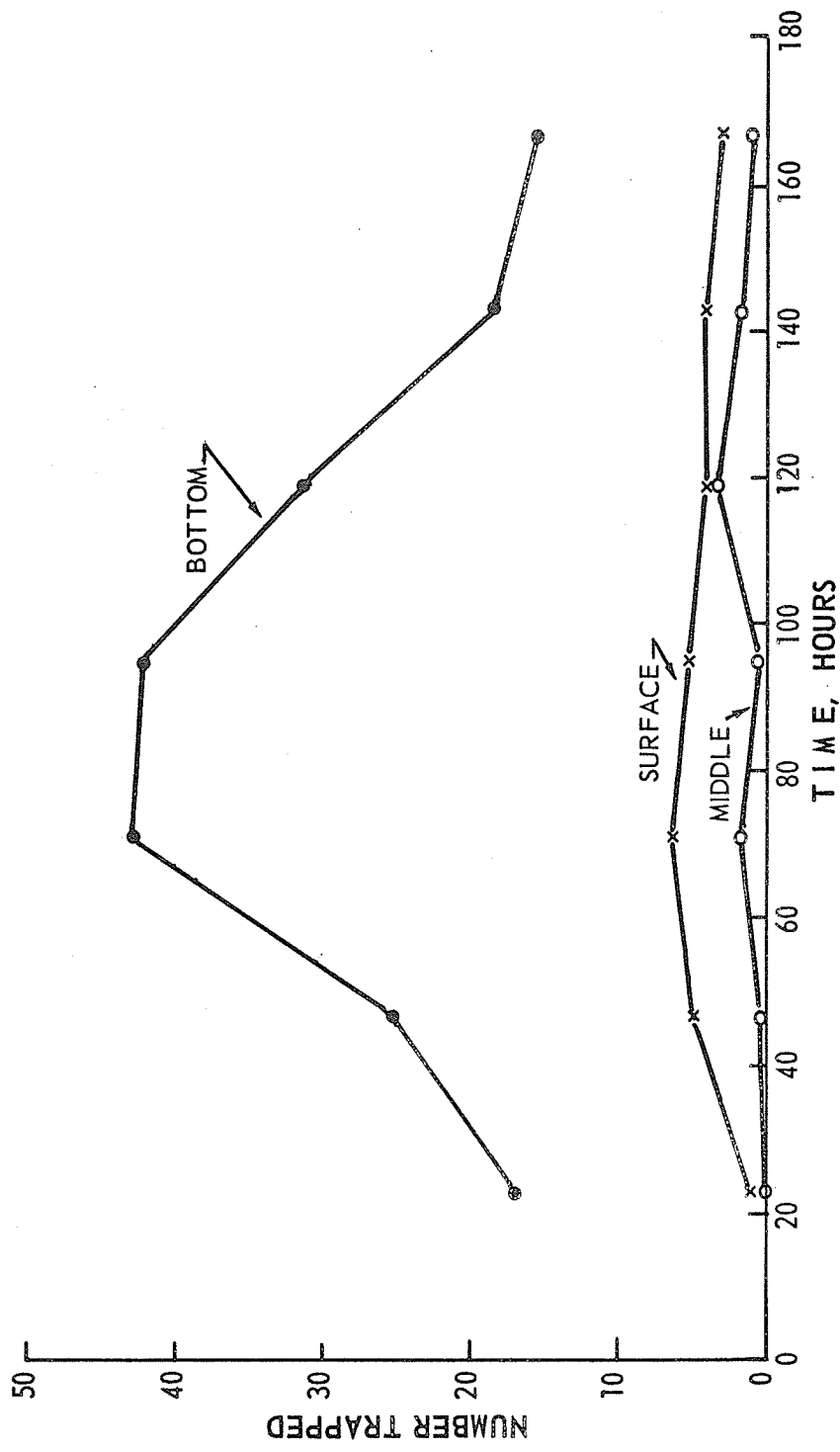
FIGURE 7

MEAN NUMBERS OF INSECTS TRAPPED AT THE SURFACE, CENTER AND BOTTOM OF A BOX OF WHEAT AT 11.0 PER CENT MOISTURE CONTENT, CONTAINING ONE TROUGH OF WHEAT AT 15.3 PER CENT MOISTURE CONTENT
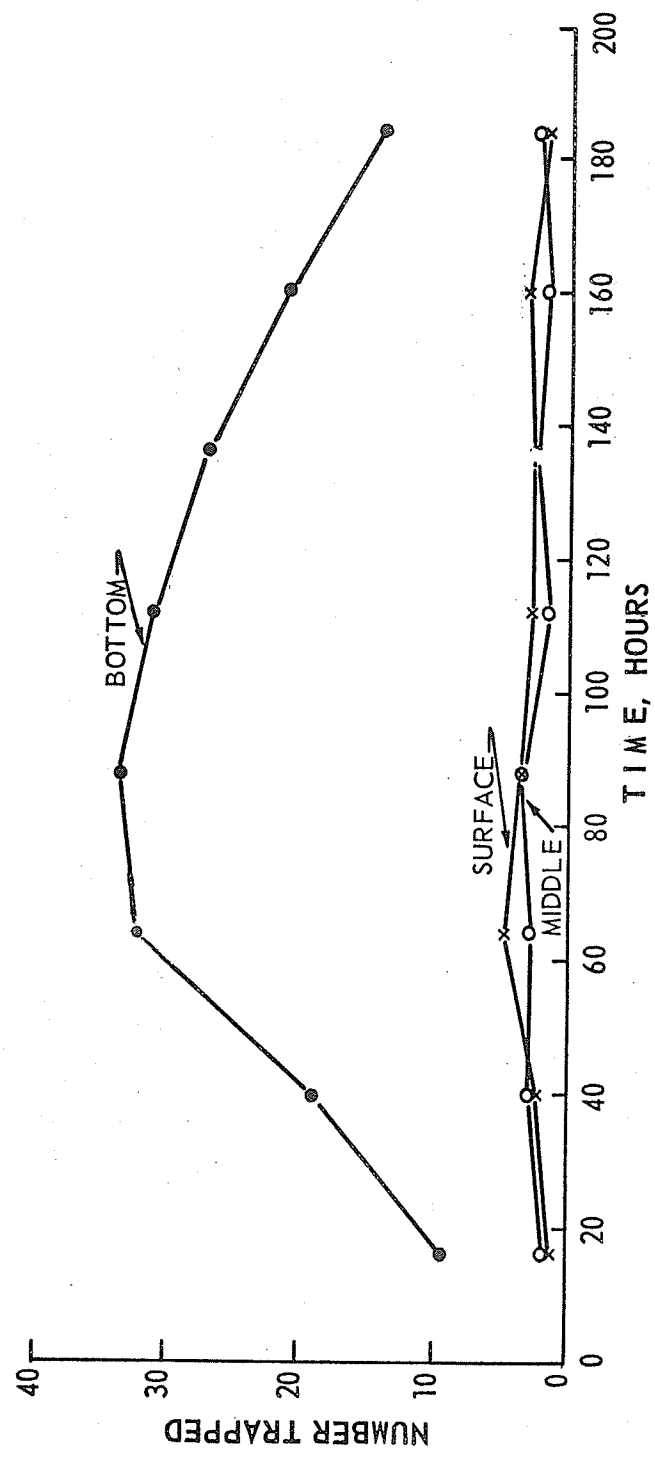
FIGURE 8

MEAN NUMBERS OF INSECTS TRAPPED AT THE SURFACE, CENTER AND BOTTOM
OF THREE BOXES OF WHEAT AT 9.0 PER CENT MOISTURE CONTENT, CON-
TAINING TWO TROUGHS OF WHEAT AT 15.5 PER CENT MOISTURE CONTENT

grain in the box enabled more insects to survive than in uniformly dry wheat. This was shown by the larger numbers of live insects sifted from the boxes of dry wheat containing the troughs of moist wheat than from the wheat that was uniformly dry.

At the end of each experiment, the troughs in the boxes were sifted to determine the numbers of insects that were present. The results are shown in Table XIV. Student's t-test showed that there was no significant difference between the numbers of insects in troughs in wheat at 11.0 per cent moisture content, or in the insects in troughs at 15.7 per cent moisture content. However, significantly more insects were found in the trough that contained 15.3 per cent moisture content than in the trough at 11.0 per cent moisture content ($P < 0.05$). The larger number of insects found in troughs in wheat that had a uniform moisture content of 15.7 per cent indicates that in moist grain, more insects may occur in the sub-surface layers than in dry grain. The data in Figure 6 suggest, however, that few were trapped on the surface of wheat at 15.5 per cent moisture content. This indicates that the absence of insects in pitfall traps on the surface of wheat does not necessarily imply that insects are absent in sub-surface layers.

Periodism in insects taken in bottom tube traps. It was observed that the daily insect counts taken at 9:00 a.m.

TABLE XIV

MEAN[a] NUMBERS OF INSECTS TAKEN IN VIAL TRAPS IN
TROUGHS, AND SIFTED FROM TROUGHS OF WHEAT,
AT DIFFERENT MOISTURE CONTENTS

Moisture content of surrounding wheat, per cent	Moisture content of wheat in troughs, per cent	Mean number of insects in	
		vial traps	in troughs
11.0	11.0	1.1	2
	11.0	1.0	4
11.0	11.0	1.5	16 |[b]
	15.3	1.1	90
15.7	15.7	0.7	40
	15.7	0.7	50

[a]Mean of 3 boxes

[b]Significant at the 5 per cent level

and 5:00 p.m. showed a pronounced periodicity, especially in dry wheat. An analysis of variance was carried out to determine the statistical significance of the differences at various times.

The counts in tube traps in wheat at 9.7 per cent moisture content are given in Table XV. The results show that the mean number of insects trapped per hour was generally higher from 9:00 a.m. to 5:00 p.m. than from 5:00 p.m. to 9:00 a.m., except towards the end of the experiment when low counts were obtained during both sampling periods. Maximum and minimum temperature readings, taken at each assessment period, indicated that there was a temperature span of about 2.8° C. between daytime and evening readings. The higher temperature was attained about noon each day, and the low, about midnight.

Table XVI gives the counts of insects in bottom tubes of boxes of wheat at 11 per cent moisture content. Again, the mean numbers of insects per hour were significantly higher during the day than during the night ($P < 0.05$), from the beginning of the experiment until near the end, when few insects were trapped.

The periodism shown by the insects in wheat at 15.7 per cent moisture content is not as striking as in the dry wheats (Table XVII). Only the counts taken at 5:00 p.m., 4 hours after the start of the experiment, were significantly

TABLE XV

MEAN NUMBERS OF INSECTS TRAPPED PER HOUR FROM 5:00 P.M.
TO 9:00 A.M., AND FROM 9:00 A.M. TO 5:00 P.M., AT THE
BOTTOM OF THREE BOXES CONTAINING WHEAT AT
9.7 PER CENT MOISTURE CONTENT

Elapsed time, (hours)	Time of day		Temp. (°C.)	
	9:00 a.m. to 5:00 p.m.	5:00 p.m. to 9:00 a.m.	Minimum	Maximum
5	12.1[a]			26.7
21		8.8	24.4	27.8
29	17.7		24.4	27.8
45		8.8	23.9	26.7
53	11.0		24.4	27.8
69		3.5	25.0	27.8
77	2.0		25.0	28.9
93		0.8	23.9	26.7

L.S.D. at 5 per cent level = 4.9

[a]Mean calculated on basis of 5 hr. after start

TABLE XVI

MEAN NUMBERS OF INSECTS TRAPPED PER HOUR FROM 5:00 P.M.
TO 9:00 A.M., AND FROM 9:00 A.M. TO 5:00 P.M., AT THE
BOTTOM OF THREE BOXES CONTAINING WHEAT AT
11.0 PER CENT MOISTURE CONTENT

| Elapsed time, (hour) | Time of day | | Temp. ($^\circ$ C.) | |
	9:00 a.m. to 5:00 p.m.	5:00 p.m. to 9:00 a.m.	Minimum	Maximum
4	14.8[a]			23.9
20		9.9	21.1	23.3
28	14.9		22.8	25.0
44		11.4	21.7	25.0
52	13.2		23.3	26.1
68		8.1	23.3	25.0
76	6.2		23.9	25.6
92		4.4	22.2	23.9
100	4.0		22.8	23.3
116		2.1	22.2	23.9
124	1.9		22.8	25.0
140		0.9	-	-
148	1.2		22.2	25.6
164		0.7	22.2	25.0

L.S.D. at 5 per cent level = 1.05

[a]Mean calculated on basis of 4 hr. after start

TABLE XVII

MEAN NUMBERS OF INSECTS TRAPPED PER HOUR FROM 5:00 P.M.
TO 9:00 A.M., AND FROM 9:00 A.M. TO 5:00 P.M., AT THE
BOTTOM OF THREE BOXES CONTAINING WHEAT AT
15.7 PER CENT MOISTURE CONTENT

| Elapsed time, (hour) | Time of day | | Temp. (° C.) | |
	9:00 a.m. to 5:00 p.m.	5:00 p.m. to 9:00 a.m.	Minimum	Maximum
4	7.8[a]		21.7	24.4
20		2.5	22.2	25.0
28	2.7		22.8	26.1
44		2.3	23.9	26.7
52	2.8		24.4	26.7
68		1.7	22.8	26.7
76	2.1		23.9	26.7
92		1.3	22.8	26.7
100	1.9		23.3	25.0
116		1.8	21.7	25.0
124	2.3		21.7	23.9
140		1.5	22.8	24.4
148	2.2		22.8	24.4
164		1.3	22.2	24.4

L.S.D. at 5 per cent level = 2.3

[a]Mean calculated on basis of 4 hr. after start

higher ($P < 0.05$) than those during the following 16-hour
period. The lower locomotor activity of the insects in this
wheat compared to that of insects in dry wheat may well
account for these low counts.

The periodism of insects in dry wheat was not affect-
ed appreciably by the presence of two troughs of wheat at 15.5
per cent moisture content (Table XVIII), with certain excep-
tions. There was no significant difference in the mean
number of insects trapped per hour at the 31- and 47-hour
assessments. Neither was there a significant difference
between the 9:00 a.m. to 5:00 p.m., and the 5:00 p.m. to
9:00 a.m. assessments after 119 hours, when insect counts
became significantly lower.

Periodism of insects was less evident in wheat at 11
per cent moisture content, that contained one trough of
wheat at 15.3 per cent moisture content (Table XIX). The
only two instances noted may be attributed to low room tem-
peratures during the night at the 80-hour and 104-hour
assessments. Low average counts per hour were obtained
during both of these nights, which resulted in significant
differences ($P < 0.05$) when compared to the corresponding day-
time counts.

"End" and "Side" effects in tube traps at the center
of a box. The center tube traps extended vertically through
the bottom of each box to the center of the wheat. The tubes
were placed 2 cm. out from the center of each side and 8 cm.

TABLE XVIII

MEAN NUMBERS OF INSECTS TRAPPED PER HOUR FROM 5:00 P.M.
TO 9:00 A.M., AND FROM 9:00 A.M. TO 5:00 P.M. AT THE
BOTTOM OF THREE BOXES CONTAINING WHEAT AT 9.0 PER
CENT MOISTURE CONTENT WITH TWO TROUGHS EACH
CONTAINING 350 GM. OF WHEAT AT 15.5 PER
CENT MOISTURE CONTENT

| | Time of day | | Temp. ($^\circ$ C.) | |
Elapsed time, (hour)	9:00 a.m. to 5:00 p.m.	5:00 p.m. to 9:00 a.m.	Minimum	Maximum
7	4.7[a]			23.9
23		2.1	22.2	24.4
31	3.9		22.2	26.7
47		4.3	21.1	24.4
55	9.2		21.1	25.6
71		6.5	20.0	25.6
79	9.7		21.1	24.4
95		5.7	19.4	24.4
103	7.2		21.1	24.4
119		4.0	22.2	25.6
127	4.1		21.1	24.4
143		2.3	21.1	22.8
151	3.7		21.1	23.3
167		1.9	21.1	23.3

L.S.D. at 5 per cent level = 1.8

[a]Mean calculated on basis of 7 hr. after start

TABLE XIX

MEAN NUMBERS OF INSECTS TRAPPED PER HOUR FROM 5:00 P.M.
TO 9:00 A.M., AND FROM 9:00 A.M. TO 5:00 P.M., AT THE
BOTTOM OF THREE BOXES CONTAINING WHEAT OF 11.0
PER CENT MOISTURE CONTENT WITH ONE TROUGH
CONTAINING 350 GM. OF WHEAT AT 15.3
PER CENT MOISTURE CONTENT

Elapsed time, (hour)	Time of day		Temp. (° C.)	
	9:00 a.m. to 5:00 p.m.	5:00 p.m. to 9:00 a.m.	Minimum	Maximum
16		3.5	22.8	25.0
24	2.9		23.9	26.7
40		3.2	22.2	26.7
48	4.9		22.8	26.1
56		5.3	22.2	25.6
72	7.1		22.8	23.9
80		4.8	18.9	24.4
96	6.4		22.2	23.9
104		4.6	19.4	23.3
120	5.5		21.7	23.9
128		4.0	21.7	23.9
144	5.5		21.7	23.9
152		3.0	22.2	23.9
168	-		-	-
176		2.1	20.6	23.3

L.S.D. at 5 per cent level = 1.7

from each end (Figure 3). Comparisons were made to determine
whether insect locomotor movements were directed towards the
ends or the sides of the boxes. An analysis of variance
carried out on the data obtained in wheat at 9.7 per cent
moisture content indicated that within the first 21 hours,
significantly more insects were taken in traps near the ends
of the boxes than in traps near the sides (P < 0.01) (Table
XX). There was no significant difference between the sides
and ends at subsequent assessment periods when most of the in-
sects trapped were taken in the bottom tubes (Figure 4).
Similar results were obtained with wheat at 11.0 per cent
moisture content (Table XXI). Significant differences be-
tween the numbers of insects taken in traps at the ends and
sides (P < 0.01) were obtained throughout the observation
period.

Since the insects were distributed uniformly over the
wheat surface at the start of each experiment, there was no
initial bias for a particular section of the box. Thus it
seems possible that the insects that became concentrated at
the ends did so as a result of collisions and reflections
with the ends and sides of the boxes. However, there is no
experimental evidence indicating in what manner the collisions
and reflections took place. The tendency for insects to be-
come concentrated at the ends of containers was noted by
Howe (1951). He used horizontal cylinders, 26 inches long

TABLE XX

MEAN[a] NUMBER OF INSECTS TRAPPED IN TUBES EXTENDING TO
THE CENTER OF A BOX OF WHEAT AT 9.7 PER
CENT MOISTURE CONTENT

Elapsed time, (hour)	Tube location			
	N. side	E. end	S. side	W. end
21	1.7	17.0	1.0	13.3
45	1.3	5.3	0.6	5.6
69	0	2.3	0	0.3
93	2.3	0.3	0.6	0.6

L.S.D. at 1 per cent level = 7.1

L.S.D. at 5 per cent level = 5.2

[a]Mean of three boxes

TABLE XXI

MEAN[a] NUMBER OF INSECTS TRAPPED IN TUBES EXTENDING TO
THE CENTER OF A BOX OF WHEAT AT 11.0 PER
CENT MOISTURE CONTENT

Elapsed time, (hour)	Tube location			
	N. side	E. end	S. side	W. end
20	0.7	4.7	0	6.3
44	0.3	3.7	0	5.0
68	0	4.0	1.0	3.0
92	0.7	1.0	0.3	1.7
116	0	0	0	1.3
140	0.3	0.3	0	0.3
164	0	1.3	0.3	0

L.S.D. at 1% level = 3.3

L.S.D. at 5% level = 2.4

[a]Mean of three boxes

and 4 inches in diameter. When granary weevils were intro-
duced at the center of the cylinder the insects moved rapidly
to the ends.

The presence of two troughs of wheat at 15.5 per cent
moisture content in wheat at 9.0 per cent moisture content
resulted in fewer insects being trapped in the center tubes
(Table XXII) than was the case when wheat was uniformly dry
(Table XX). Only at the 71-hour and 119-hour assessments,
was there any significant difference between the numbers of
insects taken in the end and side tubes. In these two in-
stances, however, the same trend was evident as in the two
previous examples (Tables XX and XXI). The data in Table
XXII show that no insects were taken from the center tubes
during the first 23 hours, suggesting that the predominantly
downward movement of insects observed in uniformly dry grain
may have been arrested temporarily by the presence of moist
wheat in the two troughs. The counts in the bottom tubes,
as shown in Figure 7, at the 23-hour assessment, were also
noticeably less than in uniformly dry grain (Figure 4).

When one trough of wheat was at 15.3 per cent mois-
ture content, in wheat at 11 per cent moisture content, the
results, given in Table XXIII, were similar to those obtained
with wheat at 11 per cent moisture content throughout (Table
XXI). Although significantly more insects were taken in the
center tube traps at the end positions than at the side posi-

TABLE XXII

MEAN[a] NUMBER OF INSECTS TRAPPED IN TUBES EXTENDING TO
THE CENTER OF A BOX OF WHEAT AT 9.0 PER CENT
MOISTURE CONTENT THAT INCLUDED TWO TROUGHS,
EACH CONTAINING 350 GM. OF WHEAT AT 15.5
PER CENT MOISTURE CONTENT

Elapsed time, (hour)	Tube location			
	N. side	E. end	S. side	W. end
23	0	0	0	0
47	0.3	0	0	0.7
71	0.3	2.3	0.3	4.7
95	0	0.3	0	2.0
119	0.3	8.0	0	4.3
143	1.0	2.0	1.3	2.7
167	0.3	0	0	2.7

L.S.D. at 5 per cent level = 3.7

[a]Mean of three boxes

TABLE XXIII

MEAN[a] NUMBER OF INSECTS TRAPPED IN TUBES EXTENDING TO THE CENTER OF A BOX OF WHEAT AT 11.0 PER CENT MOISTURE CON- TENT THAT INCLUDED ONE WIRE TROUGH CONTAINING 350 GM. OF WHEAT AT 15.3 PER CENT MOISTURE CONTENT

Elapsed time, (hour)	Tube location			
	N. side	E. end	S. side	W. end
16	0.7	4.3	0.3	4.3
40	1.7	2.7	2.0	6.7
64	0.7	5.7	1.3	3.3
88	0.3	5.0	1.0	7.0
112	1.0	3.7	0.3	1.7
136	1.7	5.0	2.0	1.3
160	1.7	3.3	0.7	1.7
180	0.7	4.7	1.0	2.7

L.S.D. at 1 per cent level = 3.4

L.S.D. at 5 per cent level = 2.6

[a]Mean of three boxes

tions in 2 of the 7 assessments (P <0.05), there was no evidence that a particular end was preferable to the other.

Occurrence of insects on the sides of boxes. Many of the insects that were introduced at the surface of the wheat crawled up the sides of the boxes above the wheat surface. Some of these insects became trapped on the masking tape adhesive. It was found that the numbers on the sides were related to the moisture content of the wheat. Few insects occurred on the sides of boxes containing wheat at 15.7 per cent moisture content during the first four days (Figure 9). However, more were observed during subsequent assessments; the diurnal fluctuations of insects, characteristic of the insect counts in the bottom tubes, in dry wheat (Tables XV and XVI), were evident from 4 to 7 days after the insects were introduced. This might have been due to the drying of the surface grain which, in previous experiments, has been accompanied by an increase in locomotor activity. At the start of the experiments, more insects were counted on the sides of the boxes containing wheat at 11 per cent moisture content than at the other moisture contents. However, fewer were noticed on the sides as the experiments continued. Except for the first 40 hours, the numbers of insects on the sides of boxes containing wheat at 11 per cent moisture content, with a trough of wheat at 15.5 per cent moisture content, was higher than with other wheats, throughout the experiment. Thus, the trough of moist
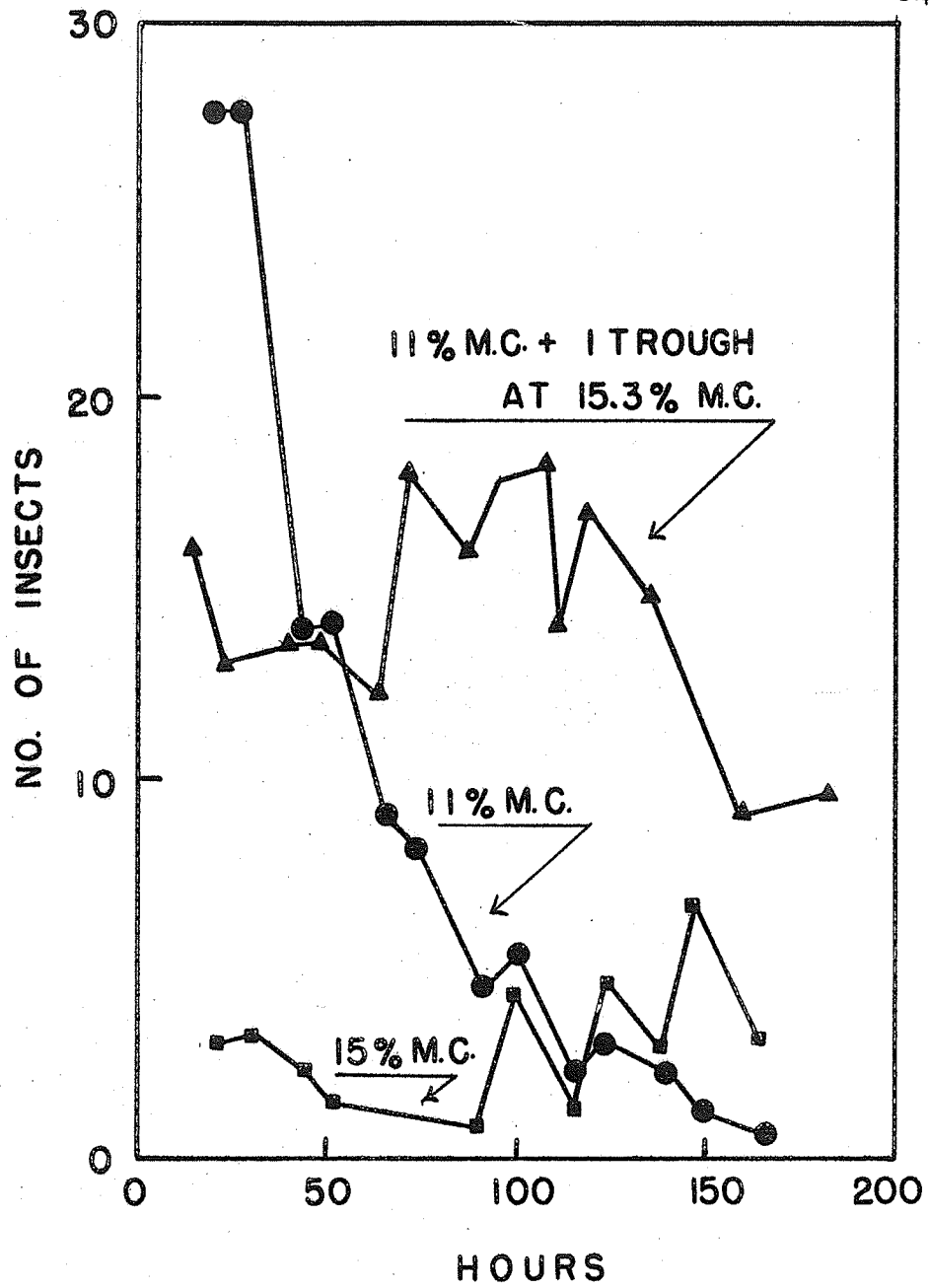
FIGURE 9

MEAN NUMBERS OF INSECTS OBSERVED ON THE SIDES
OF THE BOXES ABOVE THE GRAIN SURFACE

wheat apparently acted as a reservoir from which insects moved along the sides above the wheat.

The component of gravity was probably a factor in the position and movement of the insects on the sides of the boxes. The insects just above the grain surface were usually oriented vertically, facing upwards, while many of those at the top edge were usually in a horizontal position. Crozier and Stier (1929), working with Tetraopes, concluded that the "geo-tropic" progression of the insect on an inclined plane was a function of body weight. The torque on the legs of C. ferrugineus may have provided sufficient stimulus for the insects on the sides of the boxes to move upwards. But when they reached the top most of them assumed horizontal positions. Few insects were observed moving downwards.

Discussion

One of the most striking results in these experiments was the consistent occurrence of large numbers of C. ferrugineus in tube traps at the bottom of wheat, irrespective of wheat moisture content; fewer insects were taken in the traps at the center and surface of wheat at all moisture levels used (Figures 4 to 8). The results confirm the conclusion reached in Chapter III that C. ferrugineus is positively geo-tactic in grain.

Locomotor activity in wheat at all moisture contents, as expressed by insect counts in the bottom tube traps, was

high at first but decreased with time (Figures 4 to 8). In dry wheats (9.7 and 11 per cent moisture content), this decline in activity was attributed to high mortalities and, possibly, to decreased movement due to prolonged exposure in dry conditions, which was reported in Chapter III. In moist wheats (15.5 and 17.8 per cent moisture contents), also, locomotor activity decreased with time, but to a less extent. The high mortalities encountered in the dry wheats were not evident in moist wheats. In moist wheat, the decreased numbers of insects in traps was considered to be partly due to the low locomotor activity generally observed at high relative humidities and moisture contents. The decrease in level of activity with time in moist grain, may be due to an ortho-kinetic adaptation such as that reported by Ewer and Bursell (1950) in reference to studies of the humidity reactions of Tenebrio molitor L., carried out by Gunn and Pielou (1940). Although locomotor activity was high when the beetle moved from dry to moist conditions, prolonged exposure to high humidities resulted in a rapid decline of activity with time. Waloff (1941), in studying the humidity reactions of Porcellio, also, reported that activity was low at high humidity.

The observation that certain stored product insects are more active at low than at high relative humidities has been reported by others. Bentley (1944) noted that Ptinus tectus adults that had been kept at zero per cent relative

humidity for several days, became more active than insects
kept at 80 per cent relative humidity. The red flour beetle,
Tribolium castaneum (Herbst), remained in the dry region of a
humidity gradient as long as it was non-desiccated (Willis and
Roth, 1950). Bursell (1957) reported that the activity of
hungry tsetse flies was greater in dry air than in wet.
Smereka and Hodson (1959) found that the granary weevil, Sito-
philus granarius (L.), was more active at low than at high
humidities.

The response of insects to a trough of wheat at 15.3
per cent moisture content placed near the surface of wheat at
11 per cent moisture content was quite marked (Table XIV).
The presence of insects in the trough of moist wheat was not
reflected by their presence in pitfall traps at the wheat sur-
face. Likewise, in the boxes that contained wheat at 15.7 per
cent moisture content throughout, average counts of 40 and 50
insects were obtained in the two troughs, whereas few were
taken in pitfall traps at the surface of the troughs. In
wheat at 11 per cent moisture content that contained troughs
at the surface, few insects were taken in pitfall traps and few
were sifted from the troughs. These results indicated that in
a large volume of wheat fewer insects occurred in sub-surface
layers of dry wheat than in moist wheat.

An important observation in these experiments was that
of periodism exhibited by insects that were trapped at the

bottom of dry wheat. At almost every assessment, significantly more insects were trapped per hour during the day than during the evening. However, in wheat of 15.7 per cent moisture content, the only time significantly more insects were taken during the day than during the night was at the start of the experiment when there was a marked movement of insects towards the bottom. The low counts subsequently recorded at the bottom of the boxes were due to the low amount of locomotor activity observed in moist grain, previously reported in Chapter III. Temperature measurements taken at each assessment showed that the minimum and maximum readings were not greatly different for each period. However, the change from low to high temperature occurred during the day when the room warmed as a result of heat from the sun. Although the temperature of the box itself was not measured during the experiments, subsequent measurements indicated that the temperature at the bottom of a box of wheat corresponded closely with the room temperature. The slight increase of about 3° C. from night to day temperature which occurred at noon each day may have been sufficient to cause increased locomotor activity of insects in contact with the bottom. This was reflected in the increased counts recorded from 9:00 a.m. to 5:00 p.m., each day in dry wheat. From 5:00 p.m. to 9:00 a.m. the room temperature decreased. Low, night temperatures prevailed for a longer period than the high temperatures that were recorded during the day.

Others have noted diurnal rhythms of behaviour in stored product insects. Bentley, Gunn and Ewer (1941) reported that the spider beetle, Ptinus tectus Boie., an important pest of stored cereals in Great Britain, showed greater locomotor activity in darkness than in light, at a constant temperature. A fluctuating temperature of 10° C. to 20° C., with the low temperature phase coinciding with darkness, resulted in more locomotor activity than when the dark and light periods were at 25° C. Ewer (1943) made hourly observations of P. tectus, Ephestia (Anagasta) kühniella (Zeller), and Calandra (Sitophilus) granaria, for 24 hours on bags of spaghetti stored in a flour mill. He found that more of P. tectus and S. granarius were visible and active on specified areas of the sacks during the night than during the day; A. kühniella was more active during the daytime than at night. Howe (1951) observed that P. tectus was normally more active at dusk than during darkness. Watters (1963) has reported that more adults of the hairy spider beetle, Ptinus villiger (Reit), were trapped in jars of water at the surface of wheat during the late morning, in a darkened granary, than at any other time during 45 hours of observations. Cloudsley-Thompson (1953) reported that the yellow mealworm, Tenebrio molitor L., showed diurnal periodicity in bran when exposed to alternating light and darkness; more appeared on the surface in darkness than in light. The rhythm persisted in continuous darkness. A tem-

perature determined rhythm has been shown to persist in the cockroach, _Periplaneta americana_ (L.) (Cloudsley-Thompson, 1953) and in the spider, _Ciniflo ferox_ (Walckenaer) (Cloudsley-Thompson, 1957).

Few insects were taken in tube traps at the center of the wheat compared with those at the bottom, thus indicating that little locomotor activity occurred at this level. The counts from each of the four center positions near the two sides and two ends, showed that more insects occurred in tube traps near the ends of the boxes than near the sides. This "end effect" was more pronounced in dry than in moist wheat. At the center depth, the presence of more insects at the ends of the box than at the sides, suggests that the majority of the insects continued to move until they reached a boundary where they became concentrated. Howe (1951) found that _Calandra_ (_Sitophilus_) spp. became concentrated at the ends of a horizontal cylinder, 4 inches in diameter and 26 inches long. Cox and Smith (1957) reported that the density of _Tribolium confusum_ gradually increased towards the sides of a rectangular-shaped container of flour, with the densities being highest in the corners.

At the bottoms of the boxes, there was no significant difference between the numbers of insects trapped at the ends and near the centers of the boxes. No bottom tubes were inserted near the two sides so no direct comparisons between the

distribution of the insects at the centers and at the bottoms
of the boxes were possible.

Although C. ferrugineus was considered to be positive-
ly geotactic in wheat, many insects were observed on the sides
of boxes above the wheat surface (Figure 9). An average of
26 insects per box was observed 28 hours after introduction
on wheat of 11 per cent moisture content. On the other hand,
in wheat of 15.7 per cent moisture content, an average of 3
insects per box was noted. Higher locomotor activity in dry
compared with moist wheat may partly account for these dif-
ferences; this was established in Chapter III. However, nega-
tive geotaxis may also be involved.

Fraenkel and Gunn (1961) have listed two kinds of
orientation responses caused by gravitational force:
(1) geotaxis, in which the animal moves towards or away from
the center of the earth; and (2) a transverse orientation
which may not involve movement but enables the insect to main-
tain a position of equilibrium with respect to gravity. Thus,
both kinds of gravity reactions may be involved in the orien-
tation and position of insects on vertical surfaces and in
grain.

The large numbers of insects found in tube traps at
the bottoms of the boxes in both dry and damp wheat indicate
that, in wheat, the insects are positively geotactic. But
insects at the edge of the wheat surface are expressing nega-

tive geotaxis when they climb up the sides of the box. It is possible, therefore, that wheat kernels may supply a contact stimulus to induce positive geotaxis, which, according to the large numbers trapped at the bottoms of the boxes, was the predominant reaction. On the other hand, such a contact stimulus, if operative, would have less effect on the insects that moved to the edge of the wheat surface where they came into contact with the sides.

These studies have provided information on the behaviour and spatial distribution of C. ferrugineus in a small bulk of wheat. Although the results of the laboratory studies may not be directly applicable to large bulks of wheat, the studies indicate how insects may react to moisture gradients and localized conditions in wheat. For instance, the finding that more insects penetrated to the bottom of dry wheat than moist wheat may partly explain why infestations develop deep in a pile of apparently dry wheat. The counts of insects obtained in screen troughs indicated that more were present in sub-surface layers of moist wheat than dry wheat. Insects were attracted to a trough of moist wheat surrounded by dry wheat. The low numbers of insects in pitfall traps at the wheat surface indicate that heavy infestations of C. ferrugineus in wheat would be difficult to detect at the surface.

The fact that C. ferrugineus was positively geotactic in both dry and moist wheat indicates that surface in-

festations may result in the establishment of insects at various depths in a bulk of wheat. However, wheat pressure may limit the penetration of insects at depths in a bin of wheat. Jones (1943) has reported that the intergranular air space of compacted wheat of 12.6 per cent moisture content is 36.2 per cent compared with 40.8 per cent for loosely piled wheat.

The diurnal activity of C. ferrugineus in wheat was associated with the mid-day temperature rise. Activity was more marked in dry than in moist wheat. A knowledge of the times of day during which insects show maximum activity in grain or warehouses would be useful in timing the application of control measures.

Summary

Experiments conducted with boxes, each containing 18 kgm. of wheat, showed that when C. ferrugineus adults were released on the wheat surface of each box, more were trapped at the bottom than at the center and surface levels. These results indicate that in wheat, C. ferrugineus is positively geotactic. Although fewer insects were trapped at the bottom of wheat at 15.8 and 17.8 per cent moisture content than in dry wheat, positive geotaxis was still evident. The distribution of insects in dry wheat was altered by the presence of troughs of moist wheat at the surface; fewer insects were trapped at the bottom of dry wheat that contained troughs of

moist wheat than when the wheat was uniformly dry. Also, more insects were found in troughs containing moist wheat than in troughs containing dry wheat, indicating that insects tend to become concentrated in pockets of moist grain.

In dry wheat, significantly more insects were trapped per hour at the bottoms of boxes, between 9:00 a.m. and 5:00 p.m. than between 5:00 p.m. and 9:00 a.m. This diurnal periodicity coincided with an increase in room temperature at noon and a decrease during evening. Locomotor activity was depressed in moist grain and diurnal activity, as expressed by trapping, was less apparent.

There was evidence that insects tended to collect near the ends of boxes to a greater extent than near the sides. This was particularly noticeable in dry wheat at the center level.

In dry wheat, more insects were observed on the sides of boxes, above the wheat surface, than in moist wheat. This indicates that in dry wheat, insects near the edges may be negatively geotactic; but insects within the wheat were positively geotactic.

Locomotor activity in wheat at all moisture contents decreased with time. In dry grain, the fewer numbers trapped as observations continued past the time of the maximum trap counts were attributed mainly to increased mortality due to desiccation. In moist wheat, insect mortality was low and the fewer numbers trapped, compared with dry wheat, were attributed

to decreased locomotor activity, and, possibly, an ortho-
kinetic adaptation.

CHAPTER V

TEMPERATURE REACTIONS OF C. ferrugineus

Introduction

Insects move, feed, grow and reproduce between certain temperature limits. For most animals, this range is not more than about 40° C. (Bĕlehrádek, 1935). The temperature range within which stored product insects move is usually wider than that at which they feed, grow and reproduce. Beyond the limits of the range for movement, sub-lethal and lethal effects begin (Fraenkel and Gunn, 1961).

In stored grain, there often exists a patchwork of temperatures which influences insect movement. Teleologically, one would expect the behaviour of insects to provide for a tendency to reduce locomotor activity whenever they encounter a region favourable for development. The responses of insects to certain zones in a temperature gradient may enable us to account for the manner in which they become distributed in stored grain and on plane surfaces.

Insects may regulate their body temperature by locomotor movements towards or away from a warm or cold source. If an insect moves into a cold area, it sometimes changes its direction of travel and moves into a warm area. Some insects may move too far into the cold zone and become "cold-trapped" for several hours (Deal, 1941).

The region in which insects aggregate or become stationary has been termed the "preferred temperature" (Bodenheimer and Schenkin, 1928). Deal (1941) reported that the term "temperature preferendum" was first proposed by C. B. Williams in Egypt in 1922. Fraenkel and Gunn (1961) have objected to the use of the term "optimum temperature", which implies a condition that may not be implicit in the experiment. Gunn and Cosway (1938) have suggested that the term "eccritic temperature" may be used by those who object to the use of preferred temperature on anthropomorphic grounds.

It is important to stipulate what type of behaviour is evinced at a so-called "preferred" temperature. For instance, at one particular temperature zone insects may aggregate; at another they may walk. Thus, when speaking of a "preferred" temperature it is necessary to state what the insects "prefer" to do at that temperature: walk or stay still. This difficulty has been circumvented in the present investigation by describing the type of behaviour observed in the insect at each temperature zone rather than by attributing to the insect "likes and dislikes."

Temperature is probably the most important physical factor affecting the biology of insects in stored grain. During winter, grain cools slowly because of its low thermal conductivity. As a result, large temperature differentials may be established, especially in bulks of over 10,000 bushels.

The relatively few living insects that have been found in grain samples taken near the periphery of wheat bulks during winter indicate that insect activity at these locations is severely restricted. In fact, as has been stated in practical recommendations, as long as stored grain remains uniformly cool and dry, insect infestations are unlikely to develop (Watters, 1959).

In addition to the temperature differences that occur in stored grain during winter due to cooling, biological heating may cause other differences. Heating may be initiated by the growth of fungi, the respiration of the grain itself or by insects (Milner and Geddes, 1954). The heat produced at these localized regions may result in insects orienting themselves towards the source of heat. If the temperature and moisture content of the heating grain fall within the range for feeding and breeding, insects might establish dense populations.

A knowledge of the temperature reactions of insects is important in accounting for insect movement and distribution in grain. Insect temperature reactions will be related to the previous temperature history of the insect. The present studies were undertaken to determine the effects of population density and thermal conditioning on the temperature reactions of C. ferrugineus in a gradient of 12.5 to 43.0° C.

Review of the literature

Much of the work on the temperature preferences of insects has been done with rectangular bars or plates of copper,

brass or aluminum, heated at one end and cooled at the other.
Bodenheimer and Schenkin (1928), using an aluminum bar, heated
at one end with a flame and cooled at the other with ice, re-
ported that the confused flour beetle, _Tribolium confusum_,
J. du V., aggregated at 24.760° to 26.568° C., if kept at 15°
to 18° C. before the experiment. However, when the insects
were kept at 25° C., they aggregated at 9.118° to 10.740° C.
The three decimal places reported are possibly due to the
calculation of mean temperatures rather than to the accuracy
of the thermometer.

Fulton (1928) exposed adult click beetles, _Melanotus_
communis Gyll in a glass tube imbedded in a trough of sand
heated at one end and cooled at the other. The sand formed a
temperature gradient from one end to the other. He found that
57 per cent remained stationary at 26° to 29° C.

Gunn (1934) in his experiments with the oriental cock-
roach, _Blatta orientalis_ L., used an insulated copper trough,
heated electrically at one end and cooled by ice at the other.
He found that adult males became immobilized at 20° to 29° C.;
the temperature range of this insect was not affected by
changes in air humidity.

Deal (1941) used an insulated copper trough, 1 inch
deep, 2 inches wide, and 4 feet long. The effective length
was 37-1/2 inches. A false floor of muslin was inserted half-
way between the brass floor and the cover so that all parts

of the insect could be exposed to the same temperature. The
temperature gradient was approximately a straight line allow-
ing the insect a choice of about 1° C. every 4 cm. The range
extended from 5 to 10° C., at the cold end, to 35° C. The
relative humidity varied from 45 per cent at the cold end to
10 per cent at the warm end. The temperature behaviour of
several species of stored product insects was determined with
and without food.

Most of the adults of T. confusum that were reared at
18° and 21° C., collected at 25° to 30° C., the remainder
occurring at temperatures as low as 10° C.; most of those kept
at 27° C. for a month prior to testing in the gradient became
stationary at 14° C., the balance of the insects distributing
themselves from 16° to 30° C. Deal (1941) has pointed out
that the metabolic activities of insects at the low tempera-
ture region of the gradient were slowed down to such an ex-
tent that many were trapped there. In view of this statement,
reports of insects occurring in the low temperature region of
a temperature gradient is not necessarily an indication of
thermal "preference." The presence of a layer of bran in the
gradient did not alter the temperature behaviour of this
species.

Graham (1958) determined the temperature behaviour of
T. confusum and T. castaneum, with a rectangular, cast alumi-
num trough with wall and floor about 1 cm. thick, and with

internal dimensions of 8.4 cm. x 3.8 cm. x 1.6 cm. deep. It had an inner perspex and outer wooden cover, through which five thermometers were inserted through corks into the air space of the trough. A temperature gradient of 30.5° to 13.5° C. was obtained with two lamps at one end and ice at the other. To avoid the inverse relative humidity gradient coexistent with the temperature gradient, Graham used a layer of flour, 1 cm. deep, in the trough. Flour of various moisture contents from 10 to 13 per cent, were distributed along the trough to give a uniform relative humidity. At the end of the 4-hour exposure period, partitions were inserted in the trough and the insects in each section were counted. The results indicated that both species of Tribolium collected at 26.3° to 30.5° C. when they were preconditioned at 20° C.; when both species were preconditioned at 27° C., most of the T. confusum collected at 13.5° to 16.5° C., but most of T. castaneum were found at 26.3° to 30.5° C.

Totze (1933) was the first to use a circular gradient. It was heated at the center and cooled at the edge. Using the black-legged tick, Ixodes ricinus scapularis Say, he showed that it gave a series of avoiding reactions at both high and low temperatures. This was interpreted as an indication of klino-kinetic behaviour. Totze also found that its temperature behaviour was dependent on the temperature at which it was kept for 2 hours prior to exposure.

Henson (1958) described a circular temperature gradient made from a disc of electrolytic copper, 1/4-inch thick and 6 inches in diameter. Copper tubing, 1/4-inch outside diameter, was soldered to the outside for circulation of iced water; a 1/2-inch copper tube containing a 1/4-inch tube was soldered into an opening at the center for circulation of hot water. The temperature of the gradient was monitored by copper-constantan thermocouples in conjunction with a potentiometer. Relative humidity was controlled by air from a compressed air line fed through a porous stone into water in a Dewar flask.

Hans and Thorsteinson (1961) used an aluminum plate, 60 cm. long and 30 cm. wide, as a heat gradient. One end was cooled with frozen gelatine in plastic bags; the other end was heated by a bar adjusted with a rheostat. Adults of the sweet-clover weevil, Sitona cylindricollis Fahr., were confined on the metal surface by strips of cardboard. Humidity was regulated with filter paper moistened with water.

<u>Materials and methods</u>

The initial studies of the temperature reactions of C. ferrugineus were done with a rectangular heat gradient. A fine-mesh bronze screen was used as the platform and heat conductor. Acetate strips, 1 cm. high were used to confine the insects. Control of relative humidity was achieved with water under the warm end and a desiccant under the cool end. The rectangular gradient was abandoned for the following reasons:

(1) It was not known whether the insects that came to rest along the sides did so because of a contact stimulus or because of a temperature response; (2) a temperature gradient was established from one side of the platform to the other as well as from the heat source to the cold source; this was particularly marked at the cold and warm ends of the gradient; and (3) it was felt that the insects did not have sufficient "running room" at each temperature because of the restricted space.

To overcome some of these disadvantages, a circular heat gradient was constructed. Bronze mesh having 24 squares per cm. was used as the platform. The mesh was soldered to an outer brass ring, 0.3 cm. high, 0.8 cm. wide, with an inside diameter of 24 cm. A brass disc, 0.3 cm. high and 9.0 cm. in diameter, was clamped to the center of the bronze mesh with a brass ring on the other side. Copper tubing (1/4-inch outside diameter) was soldered to the upper edge of the disc to provide for circulation of warm water from a water bath. Cold water was circulated in 1/4-inch copper tubing soldered to the outer brass ring. The details are shown in Figure 10.

The temperature gradient platform was placed on a porcelain dinner plate, 25.5 cm. in diameter. A saucer, 14.5 cm. in diameter, containing water, was placed at the center of the plate so that the edge almost touched the bottom of the bronze screen. This provided humidity control at the center

COLD SOURCE

HOT SOURCE

BRONZE SCREEN

25.5 CM.

HOT SOURCE

BRONZE SCREEN

PLEXIGLASS COVER

COLD SOURCE

DRIERITE CRYSTALS
TYGON TUBING

WATER
PORCELAIN PLATE
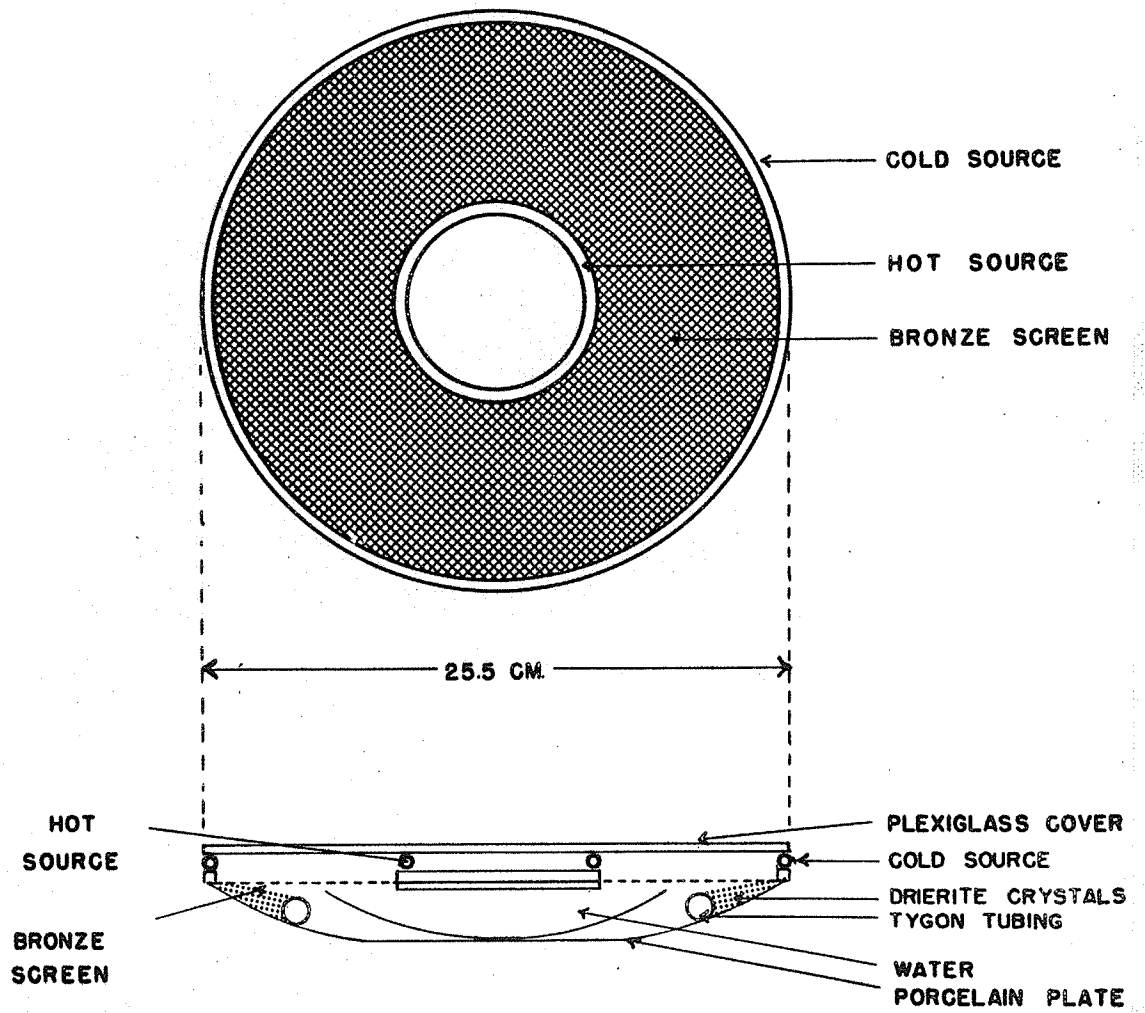
FIGURE 10

DIAGRAM OF THE CIRCULAR
TEMPERATURE GRADIENT

of the gradient beneath the heat source. A layer of Drierite
(anhydrous calcium sulphate) crystals was distributed at the
periphery of the porcelain plate. A ring of Tygon tubing,
18 cm. in diameter formed a retaining wall on the bottom of
the plate to keep the Drierite crystals close to the cold
source. The crystals absorbed the water that condensed on
the bronze screening. Asbestos tape was used to enclose
partially the copper tubing at the periphery and at the center
of the gradient. These precautions prevented condensation on
the copper tube carrying the cold water at the periphery, and
insulated the warm and cold sources of the gradient.

Water at $60.0 \pm 0.5^\circ$ C. from a constant temperature
water bath, was circulated by an electric pump through the
copper tubing at the center of the gradient. Cold water was
circulated by a compressed air pump through copper tubing at
the periphery. The cold water was supplied from a one-gallon
thermos flask which was kept filled with water and ice cubes
during each experiment. The gradient, together with ancillary
equipment is shown in Figures 11 a and 11 b.

The top of the gradient was covered with a sheet of
Plexiglass 0.3 cm. thick. Concentric circles, 1 cm. apart,
were enscribed on the surface to designate isotherm boundaries
and to map insect distribution. A hole was drilled in each
concentric circle in the plastic cover for the insertion of a
thermistor thermometer probe. The temperatures of the gradient
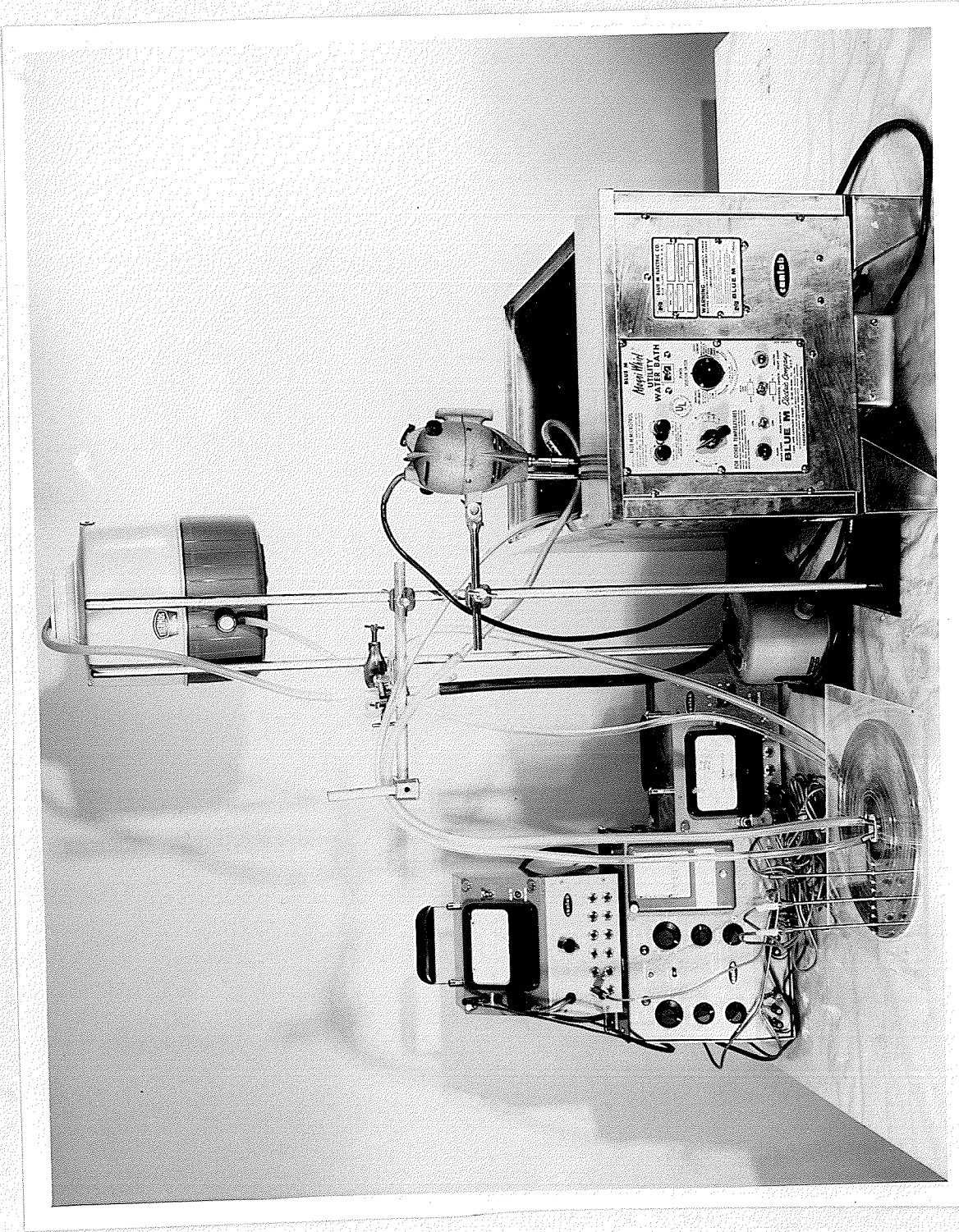
FIGURE 11 a

TEMPERATURE GRADIENT AND ANCILLARY EQUIPMENT

107
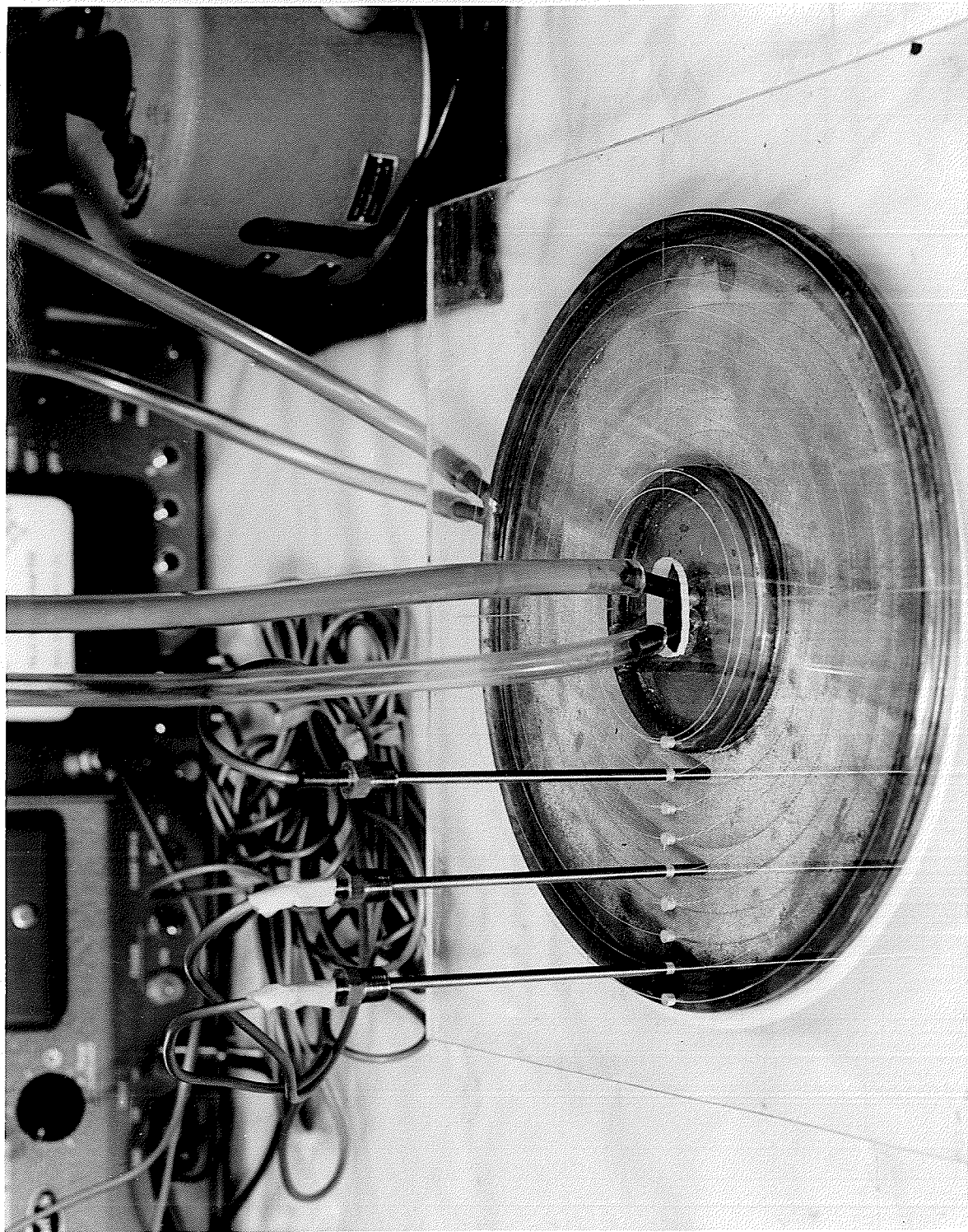
FIGURE 11 b

TEMPERATURE GRADIENT AND THERMISTOR PROBES FOR MONITORING TEMPERATURES

were monitored with thermistor probes in conjunction with a telethermometer.[1] The stability of the hot and cold ends of the temperature gradient was checked with a dual temperature recorder that was in operation during each experiment. In practice, the temperature of the cold periphery was 12.5 $\pm$ 0.8° C.; that of the center plate was 43.0 $\pm$ 0.5° C. The temperature was approximately linear throughout most of the range in which the insects moved (Figure 12).

The relative humidity at the surface of the gradient was measured by colour changes of cobalt-thiocyanate papers (Solomon, 1957). The following readings were obtained:

Temperature (degrees Centigrade)	Relative humidity (per cent)	
	Controlled	Uncontrolled
34.0-28.2	35	5
26.0-23.0	35	15
17.8-14.0	40	70

The experiments were carried out in a dimly lighted room at 27.0 $\pm$ 1.5° C. and 40 $\pm$ 5 per cent relative humidity. It was found that in the absence of any direct light, some insects collected in shadows cast by the surrounding equipment. To eliminate this, the gradient was illuminated throughout each experiment with 3 six-inch fluorescent tubes

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[1]Model 41 TS, Yellow Springs Instrument Co., Yellow Springs, Ohio.
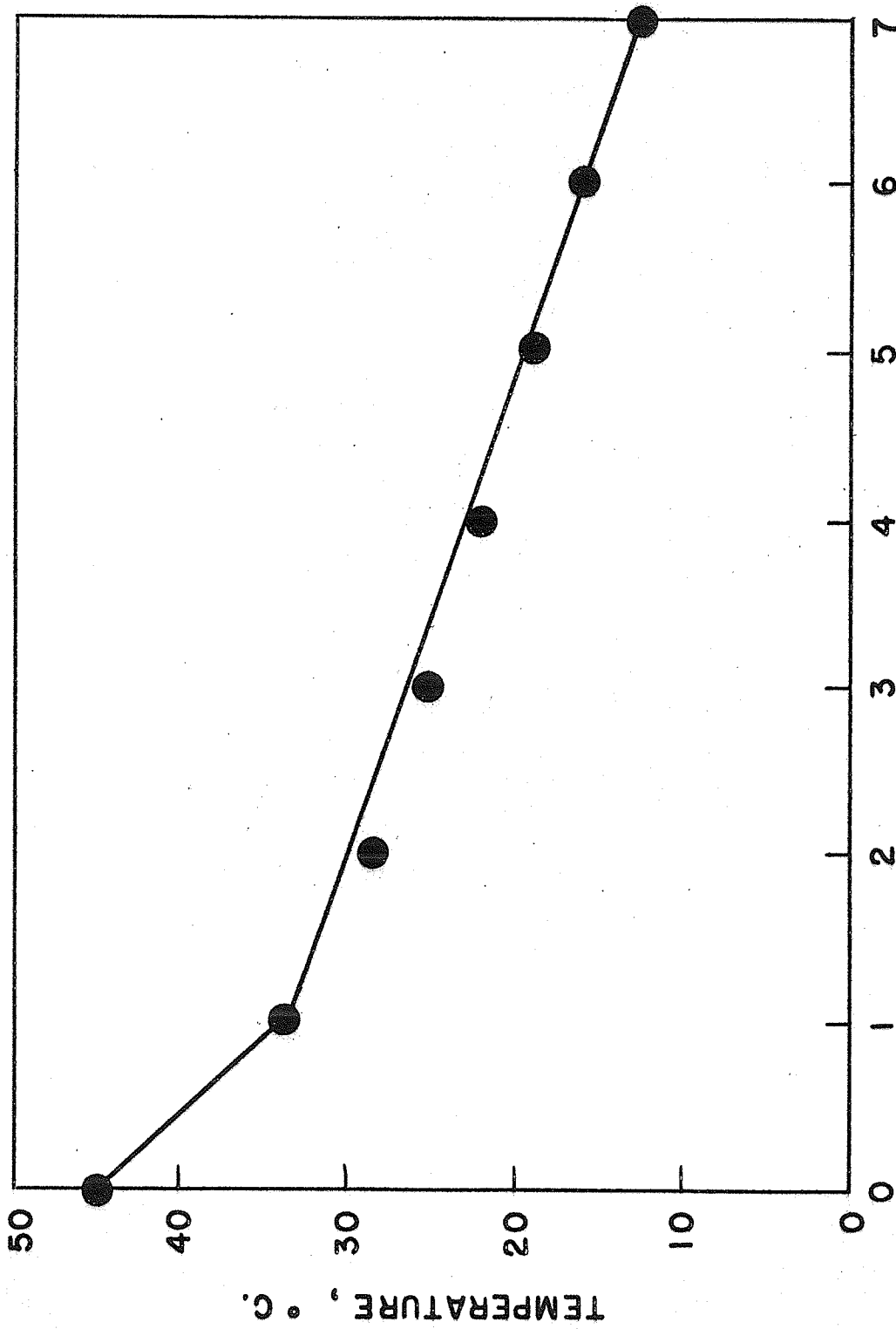
FIGURE 12

RELATIONSHIP BETWEEN TEMPERATURE AND THE DISTANCE FROM THE HOT
SOURCE OF A CIRCULAR TEMPERATURE GRADIENT

placed 60 cm. above the center. Temperature measurements at this distance indicated that no appreciable transfer of heat occurred from the light to the gradient. The temperature gradient was established and allowed to stabilize for about 30 minutes before the start of each experiment.

Adults of C. ferrugineus, 4 to 8 weeks old, were sifted from laboratory cultures maintained at 28.2 ± 0.2° C. and exposed to appropriate preconditioning temperatures before being released on the gradient. The insects were introduced at the central area of each gradient, which was 23° to 26° C. The positions and number of stationary and moving insects were recorded at hourly intervals, for 3 or 7 hours, depending on the nature of the experiment. Each experiment was repeated five times.

Occasionally, one or two insects flew to the top of the plastic cover and landed on the hot source where they were killed by the heat. The dead insects were not replaced.

C. ferrugineus has a tendency to form aggregations when exposed on flat surfaces. The aggregations in the temperature gradient varied in number from 2 to 70, depending on the initial numbers introduced on the gradient platform. The form of the aggregation varied. Two insects or more were considered to have formed an aggregation if they were not more than one body length (0.2 cm.) apart, while remaining stationary during a three-minute assessment period. In practice, aggregations consisting of 10 or more insects were usually

in close physical contact; aggregations of less than 10 were often loosely formed.

Results

The effect of population density on insect distribution in a temperature gradient. The first series of experiments were carried out at densities of 10, 25, 50 and 100 adults per test. The insects were introduced on the gradient at about 10:00 a.m., and counts of stationary insects were made at hourly intervals for three hours. Insect counts were made on the basis of insects that were walking or were stationary in each zone. Insects were classed as stationary if they remained at one position for longer than 10 seconds. They rarely remained stationary for more than 10 seconds, at temperatures between 16.0° and 28.6° C. From 12.5° to 16.0° C., some individuals were "cold-trapped." Some of these insects remained in this region for the duration of the experiment; others moved to higher temperatures after various times. Insects tended to remain stationary and to form aggregations at 28.6° to 34.0° C. (the warm zone). Some aggregations, especially those formed at a density of 100 insects per gradient, measured 0.8 cm. in diameter. Most aggregations were irregular in shape; they varied in number from 2 to 70.

The numbers of insects at 28.6° to 34° C., at each assessment were expressed as a percentage of the total number. The results are summarized in Table XXIV.

TABLE XXIV

MEAN[a] PERCENTAGE OF INSECTS AT 28.6° TO 34.0° C., AT
HOURLY INTERVALS AFTER INTRODUCTION IN A TEMPERA-
TURE GRADIENT AT 12.5° TO 43.0° C.

Time	Number of insects in gradient			
(hours)	10	25	50	100
1	16.0±4.0[b]	44.0±8.7	18.8±3.7	31.6±4.3
2	38.0±4.5	65.6±5.9	57.2±3.7	65.8±8.6
3	50.0±7.1	64.0±8.1	65.2±4.1	80.5±4.9

[a]Mean of 5 experiments

[b]Standard error

An analysis of variance carried out on the data showed that there was a significant difference ($P < 0.01$) between the percentages of insects observed at each hourly assessment. There was also a significant difference ($P < 0.01$) between insect densities. There was no significant difference between experiments at each density.

When the insects were first introduced, they moved in a path, approximately equidistant from the center, some approaching the warm region and then veering away, while others maintained a zig-zag movement between 20° and 28° C. The results showed that after the first hour, at densities of 10, 50 and 100 per test, few insects were stationary at 28.6° to 34.0° C. Most individuals were actively moving around the central zone in either a clockwise or counterclockwise direction. At the 2- and 3-hour assessments, progressively more insects had become stationary in the 28.6° to 34.0° zone; most of these were in the center of the zone at 30° to 32° C. After 3 hours, proportionately more insects, at a density of 100, had gathered at the warm part of the gradient than those at other densities. There were no significant differences between densities of 10, 25 and 50 per test, in their selection of the warm zone, after 3 hours (Table XXIV). No insects remained stationary in the zone between 34° and 44° C. Occasionally, a fast-moving insect would stray into this zone but when this occurred, it quickly reversed its path and moved into the 20° to 28.6° C. zone

where it usually pursued a circular path equidistant from the center.

Insects formed aggregations readily at a density of 100 insects per test (Table XXV). After 1 hour at this density, the only insects that had collected in the 28.6° to 34.0° C. zone were those that had formed aggregations. At densities of 10, 25 and 50 insects per test, there were more single insects that remained stationary at 28° to 34° C., than at a density of 100. At a density of 10 insects, none had formed aggregations at the 1-hour assessment; only 20 per cent of the insects had formed aggregations even after 1 hour. At a density of 25 insects per test, at the 1-hour assessment, more single insects were noted than at the 2- and 3-hour assessments. However, the percentage of insects aggregating at densities of 25 and 50 were similar (Table XXV). The results showed that the temperature reactions of insects in a temperature gradient may be intensified by high insect densities. There was not a direct relationship, however, between insect density and the percentage of insects aggregating at 28.6° to 34.0° C. At densities of 10, 25 and 50 per test, the percentages of insects immobilized at 28.6° to 34.0° C., were 50, 64 and 65.2, respectively; at the highest density of 100 insects, 80.5 per cent became immobilized (Table XXIV).

Table XXVI gives the percentages of insects that were walking between 16.0° and 28.6° C., at each of the three hourly assessments. Few insects in this temperature range remained

TABLE XXV

MEAN[a] PERCENTAGE OF INSECTS AGGREGATED AT 28.6° TO
34.0° C., AT HOURLY INTERVALS AFTER INTRODUCTION
IN A TEMPERATURE GRADIENT AT 12.5° TO 43.0° C.

Time (hours)	Number of insects in gradient			
	10	25	50	100
1	0	16.8±6.4	15.6±3.7	31.6±4.3
2	20.0±3.2[b]	53.6±3.7	50.8±4.0	63.0±7.8
3	16.0±6.8	60.0±4.9	60.4±4.9	80.0±3.5

[a]Mean of 5 experiments

[b]Standard error

TABLE XXVI

MEAN[a] PERCENTAGE OF INSECTS WALKING BETWEEN 16.0°
AND 28.6° C., IN A TEMPERATURE GRADIENT

Time (hours)	Number of insects in gradient			
	10	25	50	100
1	60.0±7.1[b]	40.0±9.2	63.6±8.7	58.4±5.8
2	42.0±5.8	16.8±4.2	28.8±2.4	24.6±10.5
3	15.6±5.1	22.4±7.8	24.4±2.9	14.5±5.4

[a]Mean of 5 experiments

[b]Standard error

stationary for more than 5 to 10 seconds. The insects comprising this group were: (1) those that had broken away from aggregations in the 28.6° to 34.0° C. zone; (2) those that had never become immobilized in the warm zone; and (3) those that had moved out of the cold zone. It was difficult to keep track of individuals so it was not possible to say whether there were any insects that were walking, that had not at some time or other remained for a period in either the warm or cold zone. Therefore, whether or not there were any insects in category (2) is questionable.

The results showed that after 1 hour, a large proportion of insects at each density were walking. At the 1- and 2-hour assessments, progressively fewer were walking. The high standard error of some percentages indicates the rather high variability in the numbers walking during each repeated experiment. Thus, significant differences are apparent only between the 1- and 3-hour assessments, at most densities.

Few insects became cold-trapped at all densities. However, there was a tendency for more insects to become cold-trapped at a density of 10 than at the other densities (Table XXVII). This might have been due to less mutual interference at the low density. Certain insects were able to extricate themselves from the cold zone after a period of 5 minutes or so. Others remained at the same location for the duration of the experiment. The ability of an insect to resume activity after being cold-trapped might be due to acclimatization.

TABLE XXVII

MEAN[a] PERCENTAGE OF INSECTS INACTIVE AT 12.5° TO
16.0° C., IN A TEMPERATURE GRADIENT

Time (hours)	Number of insects in gradient			
	10	25	50	100
1	24.0±4.0[b]	14.4±2.7	17.2±5.8	11.8±3.1
2	20.0±3.2	13.6±3.5	13.6±2.1	9.4±2.6
3	18.0±3.8	11.2±2.9	8.0±2.3	5.6±3.1

[a]Mean of 5 experiments

[b]Standard error

Those insects that could acclimatize readily would be able to move into warm zones. On the other hand, certain insects that regained their ability to move, moved further into the cold zone.

The effect of thermal preconditioning on insect distribution in a temperature gradient. It is well known that the temperature reactions of an insect are often related to the conditions at which the insect was previously exposed (Wigglesworth, 1953). In the patchwork of temperatures that exists in a bulk of grain when parts of it are heating, insects that move from warm grain into cooler zones may have temperature reactions that differ from those expressed by insects in cool regions. Experiments were, therefore, conducted to determine the distribution of insects in the temperature gradient after they had been exposed for one day at various temperatures.

The preconditioning temperatures were 20°, 25°, 30°, 32.5° and 35° C. The insects were removed from laboratory cultures and placed on Petri dishes containing a layer of crushed wheat. The relative humidity at each temperature was 75 per cent. Twenty-five insects were used for each experiment. Hourly counts were made of stationary, aggregated and walking insects in each temperature zone. Each experiment ran for 7 hours. Five experiments were performed with insects taken from each preconditioning temperature.

Table XXVIII shows the numbers of insects that were stationary at 28.6° to 34.0° C. An analysis of variance

TABLE XXVIII

MEAN[a] NUMBERS OF INSECTS AT 28.6° TO 34.0° C., AFTER
BEING PRECONDITIONED FOR 24 HOURS AT
VARIOUS TEMPERATURES

Time (hours)	Preconditioning temperatures (° C.)				
	20	25	30	32.5	35
1	3.4	0	7.6	6.2	0.4
2	9.0	2.6	14.4	6.0	1.4
3	10.4	3.0	14.8	10.6	1.8
4	10.3	4.6	14.6	15.0	4.0
5	8.4	5.6	17.6	10.8	2.6
6	11.6	5.6	16.2	13.2	3.2
7	13.0	4.6	17.0	12.0	3.8

L.S.D. at 5% level = 4.11

[a]Five experiments of 25 insects each

indicated significant differences between temperatures ($P < 0.01$) and between hourly assessments ($P < 0.05$). There was no significant difference between repeated experiments carried out with insects from each of five preconditioning temperatures.

More insects became stationary at 28.6° to 34.0° C., when insects were preconditioned at 30° C., than at any of the other preconditioning temperatures. It is worth noting that the mid-point of this zone corresponds closely with 30° C.

Insects that were preconditioned at 35° C. showed little tendency to collect at 28.6° to 34.0° C. Also, few insects that were preconditioned at 25° C., became stationary in the warm temperature zone. Most of these remained active in the zone between 16.0° and 28.6° C. On the other hand, insects that were preconditioned at 30° C., showed a tendency to collect at 28.6° to 34.0° C.

The results also showed that insects that were preconditioned at 30° C., formed aggregations more readily in the warm temperature zone than insects that had been reared at 32.5° C. (Table XXIX). After 7 hours, many of the insects that had been conditioned at 20° C. and 30° C. had formed aggregations at the 28.6° to 34.0° C. temperature zone.

As has been previously suggested, most of the insects that had not become stationary in the warm temperature zone continued to move, more or less intermittently, between 16.0° and 28.6° C. (Table XXX). This was particularly evident with

TABLE XXIX

MEAN[a] NUMBERS OF INSECTS AGGREGATING AT 28.6° TO
34.0° C., AFTER BEING PRECONDITIONED
FOR 24 HOURS AT VARIOUS TEMPERATURES

Time (hours)	Preconditioning temperatures (° C.)				
	20	25	30	32.5	35
1	1.6	0	5.2	4.4	0
2	4.8	1.4	13.4	4.0	0
3	6.8	1.4	12.8	6.2	0
4	7.0	3.2	14.0	8.6	0
5	5.8	3.6	17.0	8.6	0.8
6	7.6	4.2	15.0	9.0	1.2
7	10.6	2.8	11.6	5.0	2.2

L.S.D. at 5% level = 5.1

L.S.D. at 1% level = 6.9

[a]Five experiments of 25 insects each

TABLE XXX

MEAN[a] NUMBERS OF INSECTS WALKING AT 16.0° TO 28.6° C.,
IN A TEMPERATURE GRADIENT AFTER BEING PRECONDITIONED
FOR 24 HOURS AT VARIOUS TEMPERATURES

Time (hours)	Preconditioning temperatures (° C.)				
	20	25	30	32.5	35
1	18.4	23.0	15.0	16.4	18.4
2	13.6	19.8	7.8	13.4	19.0
3	11.8	18.0	6.8	11.6	15.8
4	11.8	16.2	6.8	9.4	14.0
5	11.4	16.0	5.0	10.6	15.6
6	11.4	17.4	5.0	8.4	15.2
7	8.6	16.2	6.6	7.4	14.6

L.S.D. at 5% level = 3.4

L.S.D. at 1% level = 5.1

[a]Five experiments of 25 insects each

those insects that had been conditioned at 35° C.; also, most
of the insects that had been preconditioned at 25° C., continued
to move at a distance more or less equidistant from the center,
in the range between 16.0° and 28.6° C.

The preconditioning temperature also had an influence
on the numbers of insects that became cold-trapped throughout
the experiments (Table XXXI). An analysis of variance showed
that there was a significant difference between insects that
had been preconditioned at various temperatures ($P < 0.01$).
There was no significant difference between hourly assessment
times. Insects that had been preconditioned at 35° C., showed
a higher tendency to become cold-trapped than insects precon-
ditioned at other temperatures.

Discussion

The technique for measuring the temperature reactions
of C. ferrugineus with a circular temperature gradient provided
an unrestricted path for insect movement at any temperature.
As a result, insects could travel in concentric circles in
various temperature zones until they became quiescent. The
locomotor behaviour in the warm temperature zone was character-
ized by deceleration, turning, intermittent stopping and start-
ing, and finally, a complete stop. Often an insect would stop
near a stationary insect or group of insects without establish-
ing physical contact. At high densities of 100 insects per
test, however, one or two large aggregations were formed where

TABLE XXXI

MEAN[a] NUMBERS OF INSECTS AT 12.5° TO 16.0° C., IN A
TEMPERATURE GRADIENT AFTER BEING PRECONDITIONED
FOR 24 HOURS AT VARIOUS TEMPERATURES

Time	Preconditioning temperatures (° C.)				
(hours)	20	25	30	32.5	35
1	3.2	1.8	1.8	2.4	3.2
2	3.2	2.4	2.4	3.6	4.0
3	2.0	2.0	2.1	2.8	5.4
4	1.4	1.8	2.0	3.4	5.4
5	1.2	1.0	2.0	3.4	5.2
6	0.8	1.6	1.8	3.4	4.2
7	2.0	2.2	1.4	3.2	4.6

L.S.D. at 5% level = 1.8

L.S.D. at 1% level = 2.1

[a]Five experiments of 25 insects each

the insects were piled two-deep at the center. Some of these
aggregations remained relatively stable for two hours. Thus it
would appear that other behavioural mechanisms associated with
the formation and maintenance of aggregations may be involved
that might supplement or even supplant the temperature response,
to keep the insect in the warm temperature zone.

The zone of least movement ranged from 28.6° to 34.0° C.
This range formed a concentric band 1 cm. wide. Although indi-
vidual insects were scattered at the upper and lower limits of
the band, the majority were observed at the center of this
range. The insects did not align themselves at any particular
angle in relation to the heat source. It is worth noting that
between 16.0° and 28.6° C., insects showed more or less contin-
uous locomotor activity. Occasionally, an insect would stop
moving but these stops rarely lasted longer than 5 to 10 seconds.
Therefore, they were not classed as temperature-arresting
responses. The fact that most insects continued to move at
temperatures below the warm temperature band and above the band
at which cold-trapping occurred, might account for the rapid
development of infestations in warm grain. Insects may continue
to disperse in grain at temperatures below the preferenda at
which aggregations are formed. If they continue to move at
these temperatures, their chances of arriving at a warm tempera-
ture zone where aggregations may be formed, are greater than if
they formed aggregations at temperatures lower than 28.6° C.

Factors other than grain temperature are involved, however, in the aggregation of insects in grain. Smallman (1943) has reported that C. ferrugineus infests regions in a grain bulk that contain large quantities of grain dust. In time, biological heating in such regions would serve as sites for the assembly of vagrants from outside the hot zone.

It is important to note that the temperature range at which insect movement was arrested corresponds closely to the temperature of highest oviposition and most rapid development. Smith (1962) reported that C. ferrugineus laid the most eggs (7.5 per day) at 30° C. on wheat flour that contained 5 per cent wheat germ. Rilett (1949) reported that the optimum temperature range for development was 90° to 100° F. (32.2° to 37.8° C.) at a relative humidity of 75 per cent. Thus, population explosions in stored grain, which contribute greatly to biological heating, may be attributed not only to high oviposition rates and rapid development of insects at temperatures between 30.0° and 37.8° C., but also to a behavioural response which inhibits insect mobility and promotes aggregations at temperatures conducive to maximum oviposition and most rapid development.

Deal (1941) has reported on the temperature behaviour of several species of stored product insects, using a rectangular gradient. C. ferrugineus was not used but results were obtained with a closely related insect, Laemophloeus (Crypto-

lestes) turcicus (Grouv.). The highest "preference" recorded
was 28° C., which corresponded closely with the lower limit of
the warm range at which C. ferrugineus became immobile. No
humidity control was attempted with Deal's apparatus. Experi-
ments carried out with the circular gradient without humidity
control indicated that insects tended to become stationary
near the lower limit of the "preferred" temperature band.
Therefore, Deal's temperature "preferences" may have been
lower than if he had used devices to control humidity.

It might be argued that control of humidity introduces
an artificiality into the experiment which would not occur in
practice. However, in grain that is heating, it has not been
my experience that the heating grain is dried to a moisture
content below 9 per cent. This is in equilibrium with grain
of about 35 per cent relative humidity (Babbit, 1945).
According to measurements with cobalt-thiocyanate paper
(Solomon, 1957) in the warm temperature zone, the relative
humidity was 35 to 40 per cent.

At 28.6° to 34.0° C., there appeared to be no differ-
ence in the temperature response of single, stationary insects
compared to those that formed aggregations. Henson (1960)
reported that the average temperature chosen by single adults
of the white cone beetle, Conophthorus coniperda Sz., was
about 3° lower than that of aggregated beetles.

The data showed that the formation of aggregations at the 28.6° to 34.0° C. zone was related to initial insect density (Table XXV). The tendency to form aggregations resulted in higher proportions of insects in the warm temperature zone at high densities than at low densities (Table XXIV).

A large proportion of insects were active between 16.0° and 28.6° C. (Table XXVI). This might be considered an activity zone because of the few insects that stopped moving for longer than 5 to 10 seconds. Most activity was from 20.0° to 28.6° C. Between 20° and 16° C., locomotion decelerated. Although insects protected themselves from high temperatures by ortho-kinesis, there was no indication of a similar protective mechanism against being cold-trapped. Some insects propelled themselves directly towards the cold zone where they became trapped for various periods. Some of these insects became stationary at the extreme limit of the gradient (12.5° C.) where they remained for the duration of the 3-hour experiment, apparently incapable of changing their positions.

Although the experiments on the effects of preconditioning temperatures on temperature reactions lasted for 7 hours, the results showed that in most cases no significant change took place after the first three hours. Probably, the most notable results occurred with insects that were kept at 25°, 30°, and 35° C. for 24 hours prior to their being released in the temperature gradient. It will be recalled that the

temperature range of highest locomotor activity was 20.0° to 28.6° C., which spanned the preconditioning temperature of 25° C. for one group of insects. When insects were preconditioned at this temperature and then released in the gradient, few were observed in the temperature zone between 28.6° and 34.0° C. (Table XXVIII). A large proportion were observed to be walking (Table XXX). When insects were preconditioned at a temperature of 30° C., which was close to the mid-point of the warm temperature zone, significantly more occurred in this zone than when the insects were preconditioned at other temperatures.

When insects were preconditioned at 35° C., before being released in the gradient, few were observed in the warm temperature zone (Table XXVIII); most of them continued to move throughout the 7 hours of the experiment (Table XXX). Significantly higher numbers were found in the cold zone (12.5° to 16.0° C.) than were insects preconditioned at the lower temperatures.

It is apparent that more work is needed on the temperature reactions of this as well as other stored product insects. The effect of preconditioning periods longer than the 24 hours used in these experiments should be investigated. The effects of keeping insects without food prior to exposure should also be tested since certain insects are not able to feed to any extent on grain that is dry and hard. Their temperature reac-

tions under these conditions may help to explain certain behaviour patterns in stored grain.

The data for these experiments were recorded at hourly intervals. However, unrecorded observations were made at various times throughout the experiments to observe the behaviour of individuals and groups. Wellington (1960) has drawn attention to the necessity of direct observations of insects in choice-type experiments in order to obtain satisfactory interpretation of insect behaviour. He advised the use of small numbers of insects to facilitate direct observation. Observations on the behaviour of individual insects for extended periods at regular time intervals should assist in giving a precise picture of insect behaviour in a temperature gradient.

Summary

In a circular temperature gradient of 12.5° to 43.0° C., C. ferrugineus adults demonstrated a marked tendency to become immobilized and to form aggregations at 28.6° to 34.0° C. Chance collisions between two insects occasionally caused them to stop and to form the center of a larger aggregation. Most aggregations remained stable throughout the experiments; others broke up and re-formed at new locations within the warm temperature zone.

No aggregations were observed at temperatures other than 28.6° to 34.0° C. Although insects became immobilized

at 12.5° to 16.0° C., this was due to cold-trapping. Between 16.0° and 28.6° C., insects moved more or less continuously in circular paths around the heat source.

Locomotor activity was accelerated as the insects approached the heat source where they exhibited ortho-kinesis. Deceleration and frequent turning movements in the warm temperature zone usually preceded immobilization. High insect densities promoted aggregations and high proportions of insects at 28.6° to 34.0° C. More insects were observed between 28.6° to 34.0° C., at the 3-hour than at the 1-hour assessment.

Insects that were preconditioned at 30° C. for 24 hours prior to their being released in the gradient, tended to move into the warm temperature zone and to become immobilized; those preconditioned at 25° C., tended to continue walking in a concentric path around the heat source, between 16.0° and 28.6° C. Few of the insects preconditioned at 35° C., moved into the warm temperature zone; most of these continued to walk, and significantly more became cold-trapped ($P < 0.05$) than did those from the other preconditioning temperatures.

Insects tended to become immobilized at 28.6° to 34.0° C., which corresponds closely to the temperatures at which maximum oviposition and most rapid growth occurs.

CHAPTER VI

SOME HUMIDITY REACTIONS OF C. ferrugineus

Introduction

The results in Chapters III and IV showed that the
biology and behaviour of C. ferrugineus in wheat was pro-
foundly influenced by wheat moisture content. The amount of
moisture present in stored wheat is related to the inter-
granular relative humidity. Since stored cereals and cereal
products are hygroscopic, their moisture content tends to
come into equilibrium with the moisture present in the air
surrounding the kernels. The amount of moisture in grain
affects its physical, chemical and biological properties and
thus its susceptibility to insect damage. For example, hard,
dry grain would be more difficult for insects to feed on than
soft, damp grain. Hence, locomotor activity of insects in
grain may be due to (1) food-seeking behaviour, and/or
(2) a kinetic response induced by the desiccating action of
low humidities. Experiments were, therefore, carried out to
investigate the humidity reactions of insects under laboratory
conditions.

Review of the literature

Various devices have been used to study the humidity
reactions of insects. The alternative chamber developed by

Gunn and Kennedy, (1936) for determining the humidity responses
of insects has been used or modified by several workers. Gunn
(1937) used it to study the humidity behaviour of wood-lice;
and Kennedy (1937) used it in studies of the locust, _Locusta
migratoria migratorioides_ (R. and F.). The yellow mealworm,
Tenebrio molitor L., was the first stored product insect to
be studied in the alternative chamber (Pielou and Gunn, 1940).
These authors found that adults tended to collect in the dry
region of a range of humidities. The humidity reaction was
most marked when one of the two humidities being compared
reached 100 per cent relative humidity. Bentley (1944) found
that adults of the spider beetle, _Ptinus tectus_ Boie., also,
collected in the drier region of two alternative humidities.
Desiccated adults were more active than ones that had been
exposed to cotton wool soaked in water. Willis and Roth
(1950) used an olfactometer to study the humidity reactions
of the red flour beetle, _Tribolium castaneum_ (Herbst). They
found that unstarved, nondesiccated beetles could discriminate
between humidities differing by 15 per cent relative humidity
or more over the entire range. The ability to discriminate
between two humidities decreased as the value of the higher
humidity was reduced.

Smereka and Hodson (1959) found that the granary
weevil, _Sitophilus granarius_ (L.), was more active at lower
than at higher humidities. Conditioning the insects at zero

per cent relative humidity caused most insects to collect in
the wet region; conditioning them at 100 per cent relative
humidity at first caused them to collect in the dry region but
after several hours this response was reversed.

Materials and methods

The humidity responses were determined with an alter-
native chamber similar in principle to the one used by Gunn
and Kennedy (1936). Petri dishes, 1.2 cm. high, with an in-
side diameter of 9.6 cm., were divided into two equal compart-
ments by a metal strip fastened at the center with melted
paraffin. The compartments were filled with the humidity-
controlling solutions, consisting of water or graded solutions
of KOH. Extremely dry conditions, approaching zero per cent
relative humidity, were obtained with Drierite crystals (an-
hydrous calcium chloride). The platform on which the insects
were introduced consisted of 60-mesh bronze screening, having
24 meshes per cm., cemented to a plastic ring, 1.0 cm. high
and 9.6 cm. inside diameter. The ring rested on the Petri
dish, the bronze screening being 0.3 cm. above the humidity-
controlling solutions. A glass cover, 10.2 cm. square was
placed over each ring to exclude the effects of air currents
in the room during observations.

Twelve alternative chambers were constructed, one of
which is shown in Figure 13. Each was placed in a plastic
sandwich box, 11.7 cm. square and 2.7 cm. high. The boxes
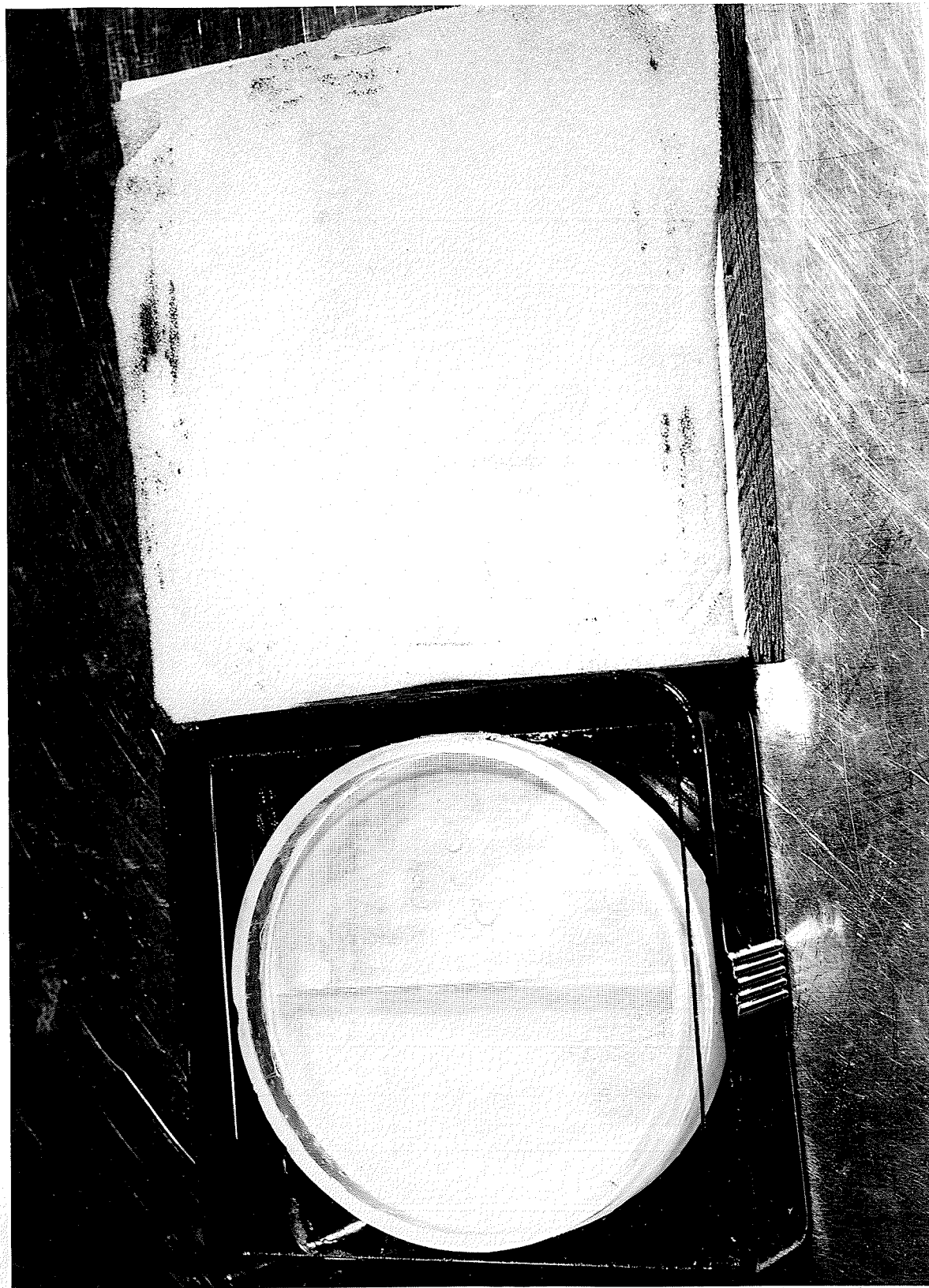
FIGURE 13

ALTERNATIVE CHAMBER USED TO STUDY THE HUMIDITY
REACTIONS OF C. ferrugineus

had previously been made light-proof by spraying the outer surfaces with three coats of black paint. The covers for the boxes consisted of three-quarter inch plywood, 13.2 cm. square. A foam rubber pad was stapled to the inside of the cover to ensure a close fit and to exclude light.

The relative humidities on each side of the bronze platform were checked with cobalt thiocyanate papers (Solomon, 1957).

The insects used in these experiments were taken from standard laboratory cultures of wheat and wheat germ, stored at 27.2° C., and 75 per cent relative humidity. They were 2 to 4 weeks old when used in the experiments. Twelve alternative chambers were used in each experiment. Ten insects were exposed in each chamber, five being introduced at the center of each semicircle. The experiments were carried out in a room at 24° to 26° C. Observations were made every 30 minutes for 5.5 hours. The numbers of insects that were inactive, walking, and aggregating in each half of the container, were recorded at each assessment. A reaction index was calculated from the formula $\frac{D-W}{N}$ x 100 (Gunn and Cosway, 1938). D was the number of insects on the dry side of the chamber, and W, the number on the wet side. N was the total number of insects used in the test. The standard error was calculated for each assessment.

A negative reaction index indicated a wet reaction, with insects gathering on the side at the higher relative

humidity; a positive reaction index indicated a dry reaction. An intermediate or neutral response was indicated when the reaction index fluctuated about zero.

After each experiment the chambers were washed with soap and water, rinsed with water, and dried.

Results

Effects of humidity conditioning on humidity reactions. The literature is well documented with examples showing the influence of prior conditioning on the humidity reactions of insects. Experiments were carried out to determine the effect of humidity conditioning on the humidity reactions of C. ferrugineus at three pairs of humidities.

The test insects were removed from laboratory cultures and exposed without food for 24 hours to one of two humidities used in the alternative chambers. The humidity reactions were studied over the range from 50 to 85 per cent relative humidity. These humidities represent the extremes of intergranular humidities in equilibrium with wheat moisture contents used in Chapter III. Relative humidities of 50 and 85 per cent are in equilibrium with wheat of 11 and 17 per cent moisture content, respectively.

The first experiments were carried out with insects exposed at relative humidities of 50 and 85 per cent in the alternative chambers. Table XXXII shows the results obtained when the insects were exposed to 50 per cent relative humi-

TABLE XXXII

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 85 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 50 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	85% R.H.	50% R.H.	85% R.H.
0.5	-21.7	13.1	35	56	0	0
1.5	-13.3	16.2	39	45	3	6
2.0	-6.7	13.3	36	42	2	4
2.5	-20.0	17.6	16	23	11	20
3.0	-23.3	16.3	11	16	14	24
3.5	-25.0	17.3	7	9	19	37
4.0	-	-	-	-	-	-
4.5	-30.0	17.5	3	4	18	49
5.0	-33.3	14.9	4	3	20	61
5.5	-40.0	10.6	0	2	21	62

[a] $\dfrac{D-W}{N} \times 100$

dity for the preceding 24 hours; Table XXXIII shows results obtained with the same relative humidities when the insects were preconditioned at 85 per cent relative humidity.

In the first experiment, when insects were preconditioned at 50 per cent relative humidity, more insects collected in the region at 85 per cent relative humidity than in the region at 50 per cent relative humidity (Table XXXII). The standard error of estimate was higher than expected throughout these as well as in subsequent experiments of this series, indicating the high variability in the data. However, towards the end of the observations in most experiments, the value for standard error became less.

Table XXXII shows that a high percentage of insects aggregated in the region at 85 per cent relative humidity. Although there was a high percentage of insects walking at each relative humidity, at the first assessment, the percentage decreased near the end of the experiment.

The humidity reaction was opposite in sign when the insects had been exposed to 85 per cent relative humidity for 24 hours prior to their being introduced into the alternative humidity chamber (Table XXXIII). More insects were seen in the region at the lower humidity during the first two hours of observations, but thereafter, they were approximately equally distributed on each side of the chamber. Fewer insects aggregated in either of the alternative humidity zones than when they were preconditioned at 50 per cent relative humidity.

TABLE XXXIII

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 85 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 85 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	85% R.H.	50% R.H.	85% R.H.
0.5	21.7	14.7	58	33	0	6
1.0	25.0	9.9	52	35	3	4
1.5	18.0	14.4	36	25	12	9
2.0	13.3	11.9	15	15	3	9
2.5	0	12.3	18	18	8	5
3.0	21.7	6.7	15	12	7	2
3.5	10.0	11.9	13	11	9	12
4.0	-1.7	12.4	11	8	9	12
4.5	-6.7	13.0	8	11	9	12
5.0	-6.7	15.3	10	6	10	8
5.5	-1.7	14.7	10	6	10	18

[a] $\dfrac{D-W}{N} \times 100$

Insects that were preconditioned at 50 per cent relative humidity for 24 hours prior to their being introduced into alternative humidity chambers at 50 and 75 per cent relative humidity, tended to come to rest in the region of higher humidity where they formed aggregations (Table XXXIV).

When the insects were preconditioned at 75 per cent relative humidity, more were observed at the lower humidity for the first 1.5 hours (Table XXXV). Subsequent observations indicated that, with time, the insects tended to become uniformly divided on each side of the chamber. Few insects aggregated in either zone; the percentage of walking insects remained moderately high throughout the observations.

The humidity responses of C. ferrugineus were next tested at 50 and 65 per cent relative humidity. The humidity reactions of insects preconditioned at 50 per cent relative humidity, are given in Table XXXVI. Although, initially, more insects were found on the higher than on the lower humidity side, the numbers on the high humidity side increased with time. As with the previous two experiments (Tables XXXII and XXXIV), there was a strong tendency for insects to form aggregations at the higher humidity, when they were preconditioned at the lower humidity for 24 hours. There was little tendency for the insects to form aggregations when they were preconditioned at 65 per cent relative humidity (Table XXXVII), although more insects were found in the wet region. Thus, all of the indi-

TABLE XXXIV

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 75 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 50 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	75% R.H.	50% R.H.	75% R.H.
0.5	-5.0	13.1	43	42	0	0
1.0	-35.0	9.3	27	48	0	9
1.5	-35.0	7.4	19	26	2	25
2.0	-35.0	9.3	15	13	3	36
2.5	-31.7	13.4	9	15	8	38
3.0	-31.7	13.8	8	15	8	38
3.5	-	-	-	-	-	-
4.0	-28.3	15.6	8	5	13	46
4.5	-33.3	18.0	3	4	15	46
5.0	-21.7	17.7	3	4	15	45
5.5	-25.0	18.8	4	6	15	44

[a] $\dfrac{D-W}{N} \times 100$

TABLE XXXV

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 75 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 75 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	75% R.H.	50% R.H.	75% R.H.
0.5	33.3	10.3	58	29	0	0
1.0	31.7	9.0	53	28	7	0
1.5	13.3	12.6	41	32	7	0
2.0	-8.3	9.7	30	29	5	5
2.5	-6.7	12.0	28	25	5	13
3.0	8.3	12.4	26	18	4	10
3.5	-3.3	11.8	18	15	5	10
4.0	8.3	12.2	16	13	17	11
4.5	6.7	15.5	10	12	24	9
5.0	13.3	13.7	12	8	21	13
5.5	8.3	15.1	13	8	18	16

[a] $\frac{D-W}{N} \times 100$

TABLE XXXVI

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 65 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 50 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	65% R.H.	50% R.H.	65% R.H.
0.5	-10.0	7.9	43	55	0	0
1.0	-5.0	12.9	29	27	3	7
1.5	-18.3	13.8	18	22	3	14
2.0	-23.3	13.9	17	18	3	17
2.5	-31.7	12.4	13	21	0	22
3.0	-23.3	13.9	10	8	3	33
3.5	-30.0	13.6	9	7	5	28
4.0	-38.3	14.2	4	9	10	33
4.5	-35.0	11.9	5	5	10	38
5.0	-38.3	11.9	3	5	13	43
5.5	-41.7	11.9	3	5	8	53

[a]$\dfrac{D-W}{N} \times 100$

TABLE XXXVII

THE HUMIDITY RESPONSES OF C. ferrugineus AT 50 PER CENT
AND 65 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE
CHAMBER AFTER BEING PRECONDITIONED WITHOUT FOOD
FOR 24 HOURS AT 65 PER CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking at		Per cent aggregating at	
			50% R.H.	65% R.H.	50% R.H.	65% R.H.
0.5	-9.1	13.8	0	3	40	45
1.0	-30.9	18.5	12	20	21	36
1.5	-3.6	18.2	16	18	5	8
2.0	-41.8	19.9	12	22	32	13
2.5	-29.1	20.9	22	29	7	7
3.0	-21.8	20.8	24	32	3	9
3.5	-29.1	20.0	18	38	3	9
4.0	-30.9	21.6	22	39	4	2
4.5	-29.1	20.7	24	49	2	0
5.0	-29.1	22.1	20	42	2	0
5.5	-29.1	20.7	22	43	2	0

[a] $\dfrac{D-W}{N} \times 100$

viduals that were recorded in the zone at 65 per cent relative humidity were either nonaggregated and motionless, or walking. The data showed that a high percentage of insects were walking at each observation. This was particularly marked in the zone of higher humidity.

The distribution of insects and the extent of their activity were recorded when both sides of the alternative chamber were at the same relative humidity. At 50 per cent relative humidity, the insects were evenly distributed on each side of the chamber after 3 hours (Table XXXVIII).

Insects were also evenly distributed on each side of the alternative chamber when both sides were at 85 per cent relative humidity (Table XXXIX). There was a tendency for insects to be more active at 85 per cent relative humidity than at 50 per cent, after 5.5 hours of observations.

Effect of aggregations on reaction index. The data given in Table XXXII suggested that in an alternative chamber at 50 and 85 per cent relative humidity, there was a strong tendency for insects to aggregate at 85 per cent relative humidity following a 24-hour preconditioning period at 50 per cent relative humidity. Since insects often aggregate in regions where movement velocities are low, it appears that at least two mechanisms are involved in the response of insects to two alternative humidities: (1) a humidity response, and (2) an aggregation response. The aggregations were in the

TABLE XXXVIII

THE HUMIDITY RESPONSES OF C. ferrugineus IN ALTERNATIVE
CHAMBERS AT 50 PER CENT RELATIVE HUMIDITY AFTER BEING
PRECONDITIONED WITHOUT FOOD FOR 24 HOURS AT 50 PER
CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking on		Per cent aggregating on	
			left side	right side	left side	right side
0.5	1.7	10.9	27	43	3	3
1.0	3.3	10.7	22	22	3	0
1.5	20.0	7.9	24	15	5	0
2.0	28.3	13.4	17	15	10	0
2.5	16.7	14.9	13	16	10	0
3.0	5.0	11.6	9	14	8	3
3.5	0	14.4	6	13	20	3
4.0	-5.0	13.6	9	13	12	15
4.5	5.4	14.7	12	7	6	16
5.0	-1.8	12.2	6	6	11	17
5.5	1.8	10.3	8	3	11	17

[a] $\dfrac{\text{Left} - \text{Right}}{N} \times 100$

TABLE XXXIX

THE HUMIDITY RESPONSES OF C. ferrugineus IN ALTERNATIVE
CHAMBERS AT 85 PER CENT RELATIVE HUMIDITY AFTER BEING
PRECONDITIONED WITHOUT FOOD FOR 24 HOURS AT 85 PER
CENT RELATIVE HUMIDITY

Time (hours)	Reaction index[a]	Standard error	Per cent walking on		Per cent aggregating on	
			left side	right side	left side	right side
0.5	6.0	14.6	37	43	13	0
1.0	8.0	14.3	25	28	8	3
1.5	10.0	16.8	24	19	12	7
2.0	20.0	16.9	27	17	13	7
2.5	24.0	14.8	27	20	13	6
3.0	0	12.6	21	27	6	9
3.5	-8.0	20.8	14	19	10	23
4.0	-18.0	20.1	14	14	8	33
4.5	2.0	20.3	14	13	19	25
5.0	-2.0	15.9	16	14	9	24
5.5	8.0	18.5	17	10	14	19

[a] $\frac{Left - Right}{N}$ X 100

form of immobile clusters, with insects in close physical contact or proximity. Since it appeared that the aggregation response may have been due to a contact reaction or thigmotropism, an experiment was devised to provide for a uniform contact over the entire area of the alternative chamber. Glass beads, 0.5 cm. in diameter, were used for this purpose. In the first experiment, the insects were preconditioned for 24 hours in a desiccator containing Drierite crystals. The insects were then exposed to ten alternative chambers containing Drierite on one side and distilled water on the other. Tests with cobalt thiocyanate papers indicated that the relative humidities on each side were <5 per cent and >95 per cent. Ten insects were introduced in each chamber.

The results showed that a high percentage of insects were present on the high humidity side throughout the 5.5-hour observation period (Figure 14). The variation among chambers, as indicated by the standard error determination at each observation, was lower than in previous experiments. There was no aggregation of insects at either humidity. Most of the insects on the high relative humidity side continued to walk throughout the observation period; the remainder were motionless and nonaggregated.

When insects were exposed to 100 per cent relative humidity for 24 hours prior to their being released in the alternative humidity chambers, a high proportion of insects were present on the dry side, initially (Figure 15). As the

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FIGURE 14

THE HUMIDITY REACTION OF C. ferrugineus AT ZERO PER CENT AND 100 PER CENT RELATIVE
HUMIDITY IN AN ALTERNATIVE CHAMBER CONTAINING GLASS BEADS. THE INSECTS WERE
PRECONDITIONED WITHOUT FOOD FOR 24 HOURS AT ZERO PER CENT RELATIVE
HUMIDITY. VERTICAL LINES REPRESENT STANDARD ERROR

FIGURE 15

THE HUMIDITY REACTIONS OF C. ferrugineus AT ZERO PER CENT AND 100 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE CHAMBER CONTAINING GLASS BEADS. THE INSECTS WERE PRECONDITIONED WITHOUT FOOD FOR 24 HOURS AT 100 PER CENT RELATIVE HUMIDITY. VERTICAL LINES REPRESENT STANDARD ERROR.

observations were continued, the large numbers of insects on the dry side diminished. As in the previous experiment (Figure 14), no insects aggregated on either side of the alternative chamber. The numbers of insects walking on the dry side were high at first, but, later, decreased considerably. Most of the insects on the dry side were motionless and nonaggregated towards the end of the experiment.

An experiment was carried out to determine the humidity reactions of insects that had been preconditioned for 24 hours on crushed wheat containing 9.2 per cent moisture. The results showed that a high percentage of insects were present on the high humidity side initially but these numbers decreased as the observations were continued (Figure 16). Most of the insects on the high humidity side were active at first, but movement decreased with time. Only 10 per cent of the insects on the high humidity side were aggregated from 2 to 5.5 hours during the experiment; most of them were motionless and nonaggregated after 5.5 hours.

The humidity reactions of insects that had just been removed from cultures were determined. Figure 17 shows that more were on the high than on the low humidity side during the observation period. The standard error determinations indicated low variability among the 10 alternative chambers at each assessment. As in previous experiments, there was no or negligible aggregation on both sides of the chambers. On the dry

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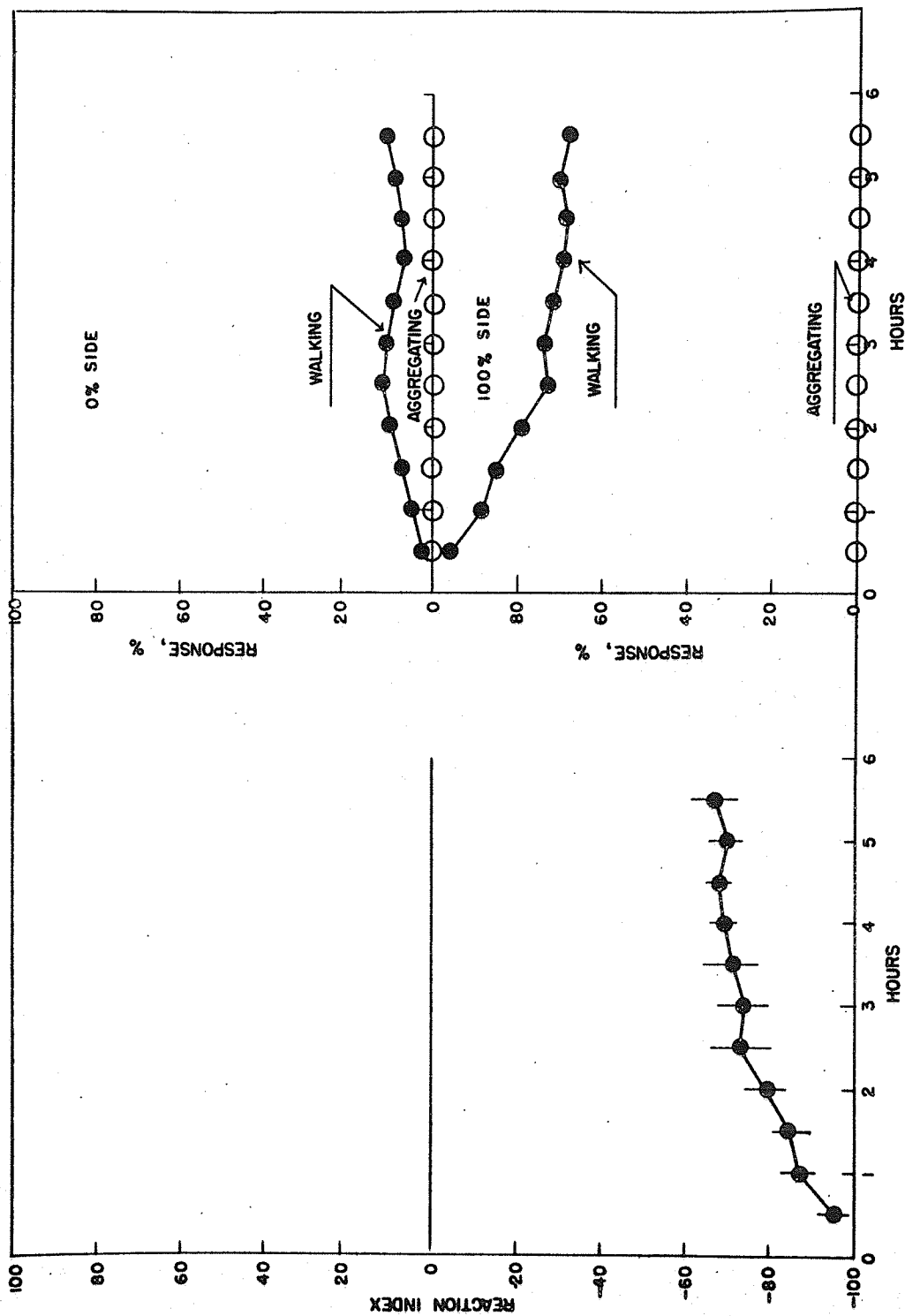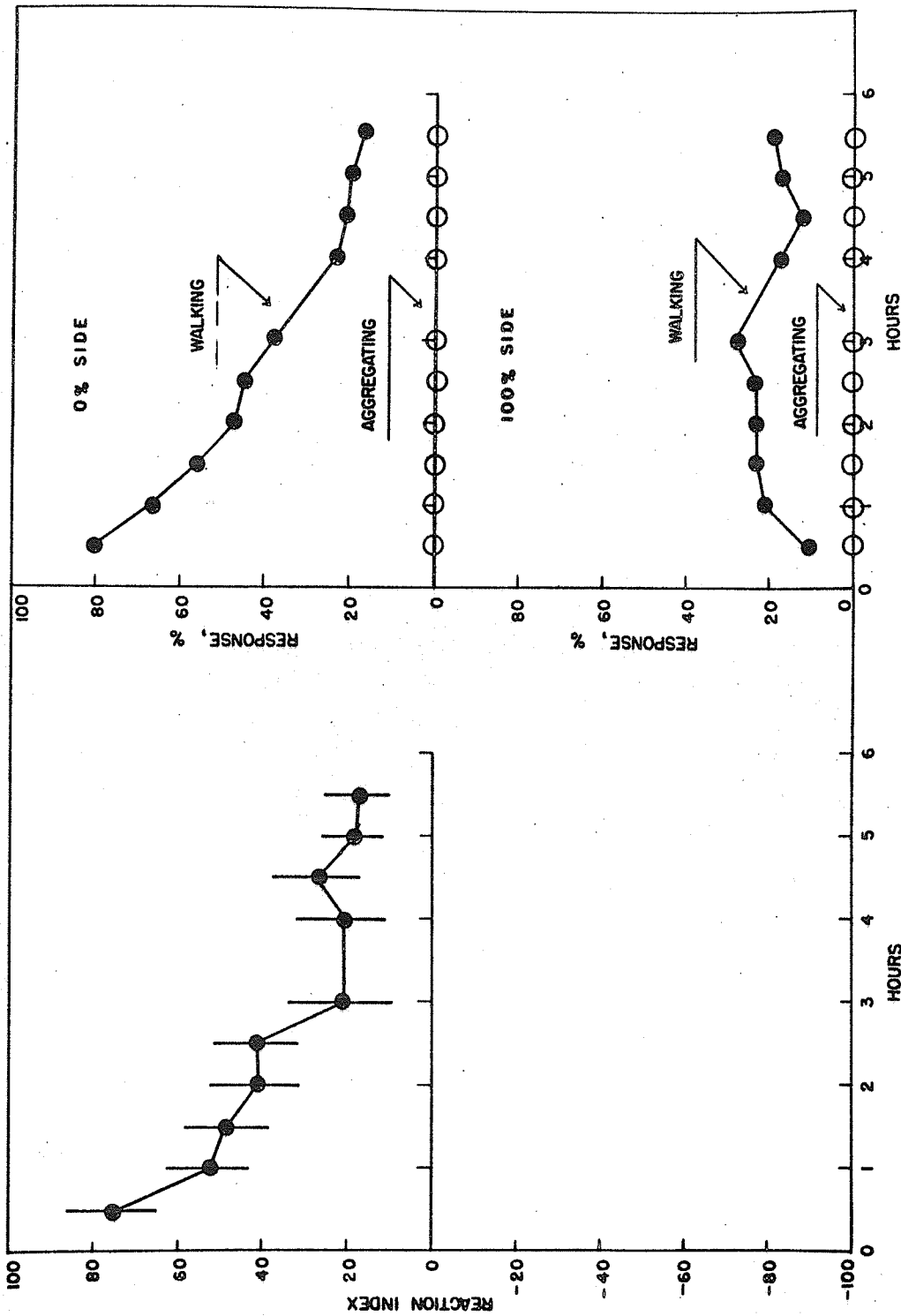
FIGURE 16

THE HUMIDITY REACTIONS OF C. ferrugineus AT ZERO PER CENT AND 100 PER CENT RELATIVE
HUMIDITY IN AN ALTERNATIVE CHAMBER CONTAINING GLASS BEADS. THE INSECTS WERE
PRECONDITIONED ON CRUSHED WHEAT AT 9.2 PER CENT MOISTURE CONTENT FOR
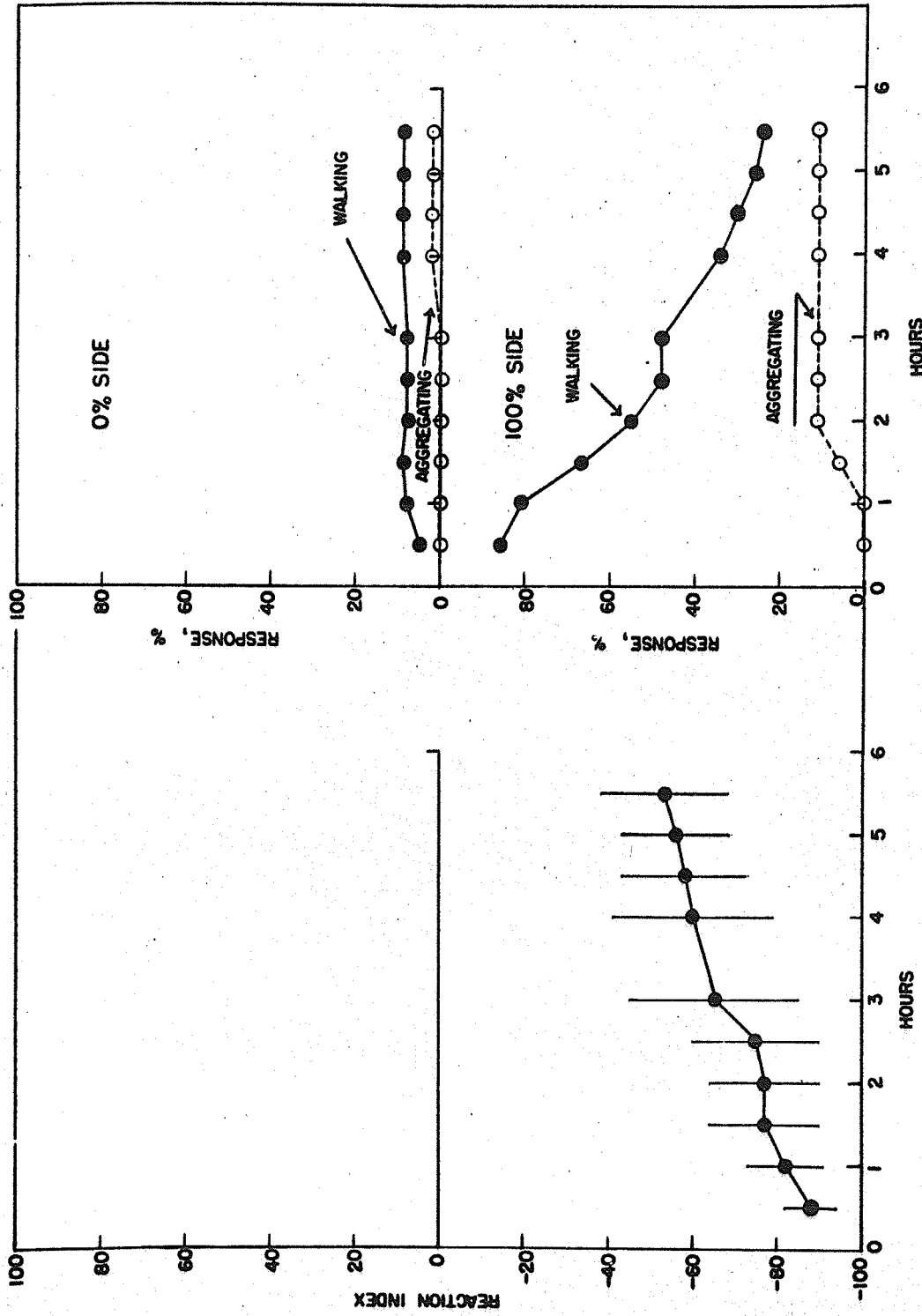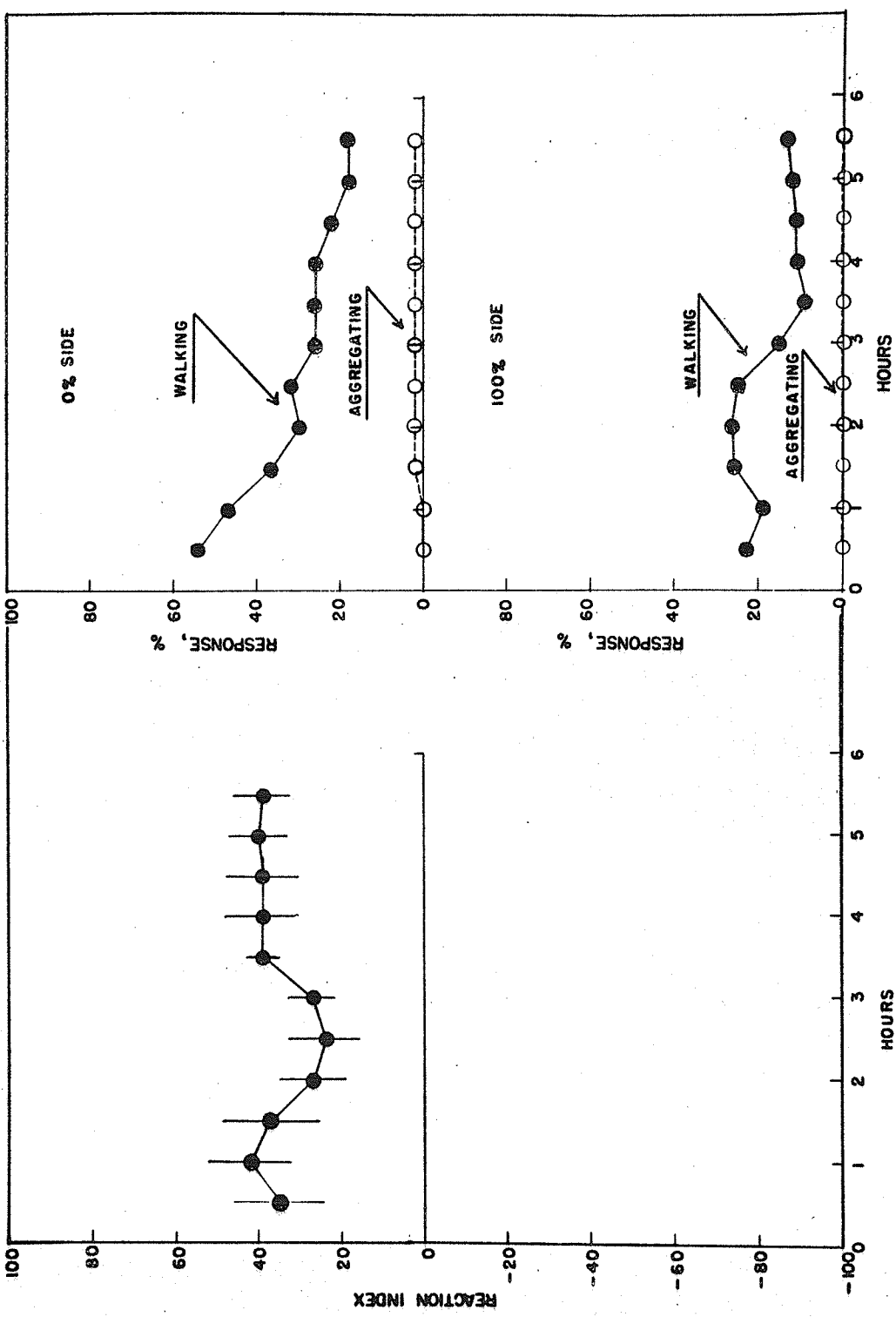24 HOURS. VERTICAL LINES REPRESENT STANDARD ERROR.

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FIGURE 17

THE HUMIDITY REACTIONS OF C. ferrugineus AT ZERO PER CENT AND 100 PER CENT RELATIVE HUMIDITY IN AN ALTERNATIVE CHAMBER CONTAINING GLASS BEADS. THE INSECTS WERE INTRODUCED IMMEDIATELY AFTER BEING REMOVED FROM CULTURES AT 27.2° C. AND 75 PER CENT RELATIVE HUMIDITY. VERTICAL LINES REPRESENT STANDARD ERROR.

side, the numbers of insects that were walking declined with time. Most of the insects were motionless and nonaggregated on each side of the alternative chamber, after 5.5 hours.

Discussion

These experiments have served to clarify to some extent the apparent humidity responses of C. ferrugineus reported in Chapters III and IV. In a humidity gradient between 50 and 85 per cent relative humidity, more insects were found in the high humidity region than in the dry region, when the insects had been preconditioned for 24 hours at 50 per cent. Also, the insects formed aggregations in the high humidity region. When the insects were preconditioned at 85 per cent relative humidity prior to their being released on the 50 to 85 per cent humidity gradient, most of them were found on the low humidity side initially, but these numbers decreased with time. Few aggregations were formed in the dry region. These reactions indicate the important role of water in the biology of C. ferrugineus, one of the smallest stored grain insect pests in the world. With a larger surface area-to-volume ratio than most other stored grain pests, dependence on the availability of water and on water conservation are important factors in its biology. Whereas larger stored grain insects such as the yellow mealworm, Tenebrio molitor L. (Pielou and Gunn, 1940), Ptinus tectus Boie. (Bentley, 1944), and Tribolium spp. (Willis and Roth, 1950), showed a tendency

to collect in the driest region of a gradient when they were
preconditioned at high relative humidities, C. ferrugineus
showed an initial dry reaction, which later decreased in
intensity with time.

The fact that insects, following exposure at 50 per
cent relative humidity, showed a strong tendency to aggregate
at the higher relative humidity, may explain the rapid devel-
opment of insect infestations in stored grain that contains
damp patches. Aggregations of insects at the higher of two
alternative humidities did not occur when the insects were
preconditioned at the higher humidity. Also, the apparent
ability of insects to discriminate between two relative
humidities, viz., 50 to 85, 50 to 75 and 50 to 65, was more
pronounced when the insects were preconditioned at the lower
relative humidity.

The humidity sensing elements of certain stored prod-
uct insects reside in the antennae /Tenebrio molitor L.
(Pielou, 1940) and Tribolium spp. (Willis and Roth, 1950)7.
Carthy (1957) has suggested that the humidity sense receptors
may act as evaporimeters, especially in those insects whose
humidity reactions seem to be related to saturation deficien-
cy rather than to relative humidity. Wigglesworth (1953) has
pointed out that when the water balance of an animal is upset
it is usually caused by desiccation. Therefore, precondition-
ing the insects in a dry environment would have a greater
effect on their water balance than when they were preconditioned

in a damp environment. In terrestrial insects, desiccation is a serious potential hazard because of the large ratio of evaporative surface to water reserve. Teleologically, therefore, insects would need to possess behaviour patterns that would tend to correct a moisture deficiency. The results presented are in harmony with the hypothesis that C. ferrugineus possesses such behaviour mechanisms.

The data in Chapters III and IV indicated that insects were more active in dry grain than in damp grain. It was expected, therefore, that insect activity would be higher on the dry side of the alternative humidity chamber than on the damp side. The data, however, did not show this to occur. The percentage of insects walking was usually high on both sides of the chamber initially, but it decreased with time. An exception to these occurrences was when the insects were preconditioned at 65 per cent relative humidity before being exposed to alternative chambers containing 50 and 65 per cent relative humidity. Initially, few insects were observed to be walking, whereas a high percentage was found to be aggregated (Table XXXVII). Towards the end of the observations, these responses were reversed.

At zero and 100 per cent relative humidity, the humidity reactions paralleled those obtained at 50 to 85, 50 to 75 and 50 to 65 per cent relative humidity. However, aggregation at the higher of two humidities, which was apparent

when insects were preconditioned at 50 per cent relative
humidity, did not occur in alternative chambers containing
glass beads. The absence of aggregation behaviour, however,
did not noticeably influence the humidity reaction: insects
that had been preconditioned at the lower of two humidities
moved to the wet region of a humidity gradient; insects pre-
conditioned at the higher of two humidities moved to the dry
region but this reaction became weaker with time and insects
tended to become evenly distributed on each side of the
gradient.

Insects that had been preconditioned on crushed wheat
at 9.2 per cent moisture content, moved to the high humidity
side of the gradient (Figure 16). The reaction was of the
same intensity as in insects that had been preconditioned with-
out food at zero per cent relative humidity (Figure 14). This
indicated that availability of dry food before exposure to
alternative humidities did not influence the humidity reaction.
Roth and Willis (1951) found that although T. confusum adults,
that had been starved in dry air for 6 days, collected in the
wet region of a humidity gradient, this reaction was reversed
when the insects were allowed to feed for 66 hours on oven-
dried flour. There was no evidence in the present experiments
that C. ferrugineus exhibited a similar preference for dry
conditions. In experiments with water traps in dry wheat,
Watters and Cox (1957) found that while low numbers of

T. confusum were taken in the traps, large numbers of C. ferrugineus were found. Thus, it would appear that the humidity response of C. ferrugineus is quite different to that of T. confusum. This might be related to a less efficient water-conserving mechanism in C. ferrugineus or to its higher surface area-to-volume ratio, which would result in higher rates of evaporation.

Insects that had been removed from a culture maintained at 75 per cent relative humidity, tended to move to the dry region of a gradient. These results are similar to those obtained with beetles that had been starved for 24 hours at 75 per cent relative humidity (Table XXXV); but the number of starved insects in the dry region decreased towards the end of the experiment. Therefore, although C. ferrugineus adults that were recently fed tended to remain in the dry region of a humidity gradient, starvation under moist conditions resulted in a reduced number of insects in the dry region. The results further indicate the dependence of C. ferrugineus on a moist environment. Preconditioning with or without food under dry conditions intensifies the tendency to collect at high humidities.

The experiments were not designed to determine whether C. ferrugineus was capable of orienting itself towards either of two humidities in the alternative chamber. This can most readily be investigated by making continuous observations at

regular intervals on individual insects, and recording the paths of their movements. Gunn and Pielou (1940) noted that yellow mealworm beetles waved their antennae when approaching the higher of two humidities. Roth and Willis (1950) reported that the flour beetles, Tribolium confusum and T. castaneum moved almost directly towards a circular piece of moistened filter paper placed in a Petri dish. C. ferrugineus gave no indication of direct orientation towards either of two humidities in the alternative chamber. At the regular observation periods, those insects that were walking appeared to be moving at random.

There was a tendency for most insects to stop near the walls of the chamber, in contact with it or about 0.2 cm. from it. Some individuals, however, formed immobile aggregations well out from the sides. It was not possible to generalize, therefore, on the locations in the gradient where insects became motionless, nor on the manner in which aggregations were formed.

Summary

Some humidity reactions of C. ferrugineus were determined with an alternative chamber similar in principle to one developed by Gunn and Kennedy (1936). The humidity reactions were determined for three pairs of relative humidities, viz., 50 to 85, 50 to 75 and 50 to 65. These relative humidities were chosen because of their water vapour equilibrium rela-

tionships with wheat; wheat moisture contents of 11, 13, 14.6 and 17 per cent, being in equilibrium with relative humidities of 50, 65, 75 and 85 per cent, respectively. The insects were preconditioned for 24 hours at the higher or lower relative humidity of each pair. The results showed that insects that were preconditioned at 50 per cent relative humidity moved to the wet region of each of the three alternative humidities tested; there was a tendency for insects to form aggregations in the wet region of each gradient. Insects generally showed high locomotor activity, initially, on both sides of the alternative chamber, but activity decreased as observations continued for the 5.5 hours of each experiment.

When insects were preconditioned at the higher of each pair of relative humidities, they moved to the dry region of a humidity gradient, but the reaction was less intense than when insects moved to the wet region after being preconditioned at 50 per cent relative humidity. There was little tendency for the insects to aggregate in the dry region of a gradient. At alternative relative humidities of 50 and 65 per cent, a high percentage of insects were observed to be walking on the platform at 65 per cent relative humidity.

Observations on the distribution and activity of insects on platforms over chambers containing a solution 50 per cent relative humidity showed that the insects were largely inactive towards the end of the experiment; there was little

tendency to aggregate. Similar results were obtained when the insects were exposed to 85 per cent relative humidity on both sides of the alternative chamber. The insects were evenly divided on each side of the container, towards the end of the observations.

The humidity reactions of insects were observed at zero and 100 per cent relative humidity when they were exposed to alternative chambers that contained a single layer of glass beads. The purpose of the beads was to provide for a uniform physical contact on the surface of the platform. The results showed that no aggregations occurred when glass beads were present. There appeared to be higher locomotor activity with glass beads than without them.

C. ferrugineus adults that were taken from cultures moved to the dry region of a humidity gradient. A similar but less intense reaction was evinced by insects starved for 24 hours at high humidities.

Practical Significance of the Investigation

Although the preceeding laboratory experiments were
done on a small scale, the results are in agreement, in many
instances, with field observations of insect distribution and
behaviour in stored grain. For example, the experiments showed
that insects tended to congregate in pockets of moist grain at
the surface of dry grain. Insects tended to be positively geo-
tactic in uniformly dry grain but negatively geotactic on
vertical surfaces above the grain surface. Thus in a bulk of
uniformly dry grain we would expect insects to move downwards
and infest grain at the bottom of a bin. In dry grain, con-
taining damp patches at the surface or at other locations, we
would expect insects to become concentrated in these regions.

The experiments have indicated the role of grain
moisture content and temperature in the dispersal and aggrega-
tion of insects in grain. The information obtained will make
it possible to predict reasonably well the sequence of events
that may occur during the development of an infestation in
stored grain. The data showed that the environmental condi-
tions that cause insects to disperse are different from those
associated with the development of localized infestations.
Locomotor activity, leading to dispersal, occurred in dry grain
at 22° C. and 28° C., but was less apparent in moist grain,
except when moulds developed. The tendency of insects to dis-
continue walking when they encounter moist grain is likely to

be a significant factor in the development of localized infest-
ations. This behaviour appears to be a prerequisite for the
congregation of insects in moist grain and for the subsequent
initiation of biological heating.

The temperature reactions of insects are such as to
contribute to the development of localized heating in bulk
grain. The data showed that the insects became immobilized
only in the temperature range $28.6°$ to $34.0°$ C. Beyond these
limits insects continued to walk except those individuals that
became immobilized in the range $12.5°$ to $16.0°$ C. Thus, it
would appear that the minimum critical temperature for the
rapid development of localized heating in insect-infested grain
is about $28°$ C. It may be postulated, therefore, that below
$28°$ C., C. ferrugineus is unlikely to become immobilized and
thus to contribute significantly to the production of meta-
bolic heat unless the insect encounters moist grain. For in-
sects contribute to the development of a potential hot spot
mainly by concentrating and by breeding in confined areas
where their rates of heat production exceed the rates at which
heat is dissipated to the surrounding grain. Behavioural
mechanisms which arrest insect movement and stimulate oviposi-
tion lead to the development of dense populations in small
pockets of grain and thus contribute significantly to biologi-
cal heating.

Insects are likely to increase the rate of heat production in warm, moist zones of grain, above 28° C. and 15 per cent moisture content, for the following reasons: (1) under these conditions, insects are most likely to become immobilized and to lay large numbers of eggs; (2) dense populations of feeding, growing larvae have high respiration rates and will, therefore, produce heat; (3) above 28° C., the growth of mesophilic and thermophilic fungi will contribute substantially to the rate of heat production which will thereby accelerate insect growth.

The data showed that insects that had been preconditioned at 35° C., for 24 hr., did not become immobilized in warm grain; most individuals continued to walk and significantly more became immobilized in the cool region (12.5° C. to 16.0° C.) of a temperature gradient than insects preconditioned at 30° C. These reactions indicated that insects would tend to emigrate from heating grain after the temperature reached 35° C. It is possible that they would tend to move into cool, moist regions of the grain mass, or, alternatively, would move about at random, outside of the warm zone until they became "ready" to re-enter the zone. Thus, it would appear that C. ferrugineus possesses mechanisms whereby its movements are re-cycled to enable it to enter and emigrate from warm and cool grain.

The evidence that C. ferrugineus was positively geo-tactic indicates that deep infestations may develop readily. Thus it would not be possible to determine the presence or

severity of infestations on the basis of insects found in surface samples or surface traps.

Ecological control of infestations in stored grain can only be perfected through expanding our knowledge of the environmental factors that limit the dispersal, aggregation and abundance of insect pests, and applying this knowledge to improve the management of stored grain stocks.

CHAPTER VII

SUMMARY

The present investigation of the effects of tempera-
ture, grain moisture content and relative humidity on the
locomotor activity and distribution of C. ferrugineus in
wheat, were initiated to expand our knowledge of stored grain
as an insect habitat. Progress in detecting and controlling
infestations in stored grain will depend partly on the avail-
able information concerning the biology and behaviour of insect
pests. Laboratory experiments were developed to determine:
(1) locomotor activity of insects in wheat at different mois-
ture contents and temperatures; (2) the effect of wheat
moisture content on the spatial distribution of insects in a
small bulk of wheat; (3) the temperature reactions of insects
when released in a circular temperature gradient; and (4) the
humidity reactions in a series of alternative humidity
chambers. The results of these studies are summarized briefly
in this chapter.

At 15°, 22° and 28° C., the most important factor
affecting the locomotor activity of C. ferrugineus in wheat
was wheat moisture content. Insect locomotor activity, as
expressed by the emigration of adults from open containers of
wheat, was more pronounced in dry wheat than in damp wheat.
Exposure to light, also, influenced insect locomotor activity

since more insects emigrated from beakers of wheat exposed in a lighted room than in darkness. C. ferrugineus was positively geotactic. When insects were placed in the center of a vertical column of wheat, more emigrated from the bottom than from the top.

Insects that had been kept without food for 3 days were less active in dry wheat than those removed from cultures. Insects that had been kept on dry wheat for 3 days were relatively inactive when placed on "fresh" or mouldy wheat. More insects emigrated from mouldy than from "fresh" wheat when they had been preconditioned on damp wheat for 3 days. Fungal analyses of "fresh" and mouldy wheat infested with C. ferrugineus showed that, in general, the flora of the two wheats were quantitatively and qualitatively similar.

The results of the emigration experiments suggest that insect dispersal in stored grain is related not only to the moisture content and mould flora of the grain, but also to the humidity history of the insects. Insects that have lived in dry grain are more likely to become immobilized when they reach a damp patch of grain than insects that have been in damp grain for several days. It is possible, therefore, that the bulk of migrating insects comprise those that have emigrated from damp regions in a bulk of grain.

Positive geotaxis of C. ferrugineus was confirmed in studies of the spatial distribution of insects in wheat. More

insects were taken in tube traps at the bottom of boxes of
wheat than at the center or surface. Many insects near the
outer edges at the surface of dry wheat tended to climb up the
sides of the boxes, indicating that on vertical plane surfaces,
C. ferrugineus may be negatively geotactic. Moist wheat
placed in screen troughs near the surface of dry grain
resulted in fewer insects occurring at the bottom than when
grain was uniformly dry. There was a diurnal periodicity in
the numbers of insects trapped at the bottom of dry wheat.
More insects were trapped per hour during the day than during
the night. Locomotor activity was depressed in moist grain
and diurnal periodicity was less apparent.

In a circular temperature gradient at 12.5° to 43.0° C.,
more insects became immobilized between 28° and 34° C., than
at any other temperature range. No insects were observed
above 34° C. Below 28° C., most insects continued to walk
except the few that became "cold-trapped" at 12.5° to 16.0° C.
Aggregations were formed only at 28° to 34° C. A larger per-
centage of insects were immobilized at 28° to 34° C., at a
density of 100 insects per test than at 10 insects per test.
This was attributed partly to the tendency to aggregate at the
higher density. The aggregated insects remained immobilized
in the 28° to 34° C. region for longer periods than nonag-
gregated insects.

Insects that were preconditioned at 30° C. for 24 hours, tended to move into the 28° to 34° C. zone and to become immobilized. Few of the insects that were preconditioned at 35° C., moved into the 28° to 34° C. zone; most of these insects continued to walk and significantly more became "cold-trapped" at 12.5° to 16° C. than insects taken from other preconditioning temperatures. Most of the insects preconditioned at 25° C. continued to walk in a concentric circle around the heat source, between 16° and 28° C. Significantly fewer became immobilized at 28° to 34° C. than insects that were preconditioned at 30° C.

The data indicate, therefore, that insects are likely to emigrate from heating grain that has reached 35° C., and that they would be unlikely to re-enter a warm area until they had been conditioned at a lower temperature. It would appear that the most critical stage for the accelerated development of a "hot spot" in stored grain lies in the temperature range between 28° and 34° C. Within this range insects aggregate, become immobilized, and are least likely to emigrate; also, insects lay the most eggs and develop most rapidly between these temperatures.

The humidity reactions of C. ferrugineus were studied in an alternative humidity chamber containing graded $KOH-H_2O$ solutions. The following pairs of relative humidities were tested: 50 and 85 per cent; 50 and 75 per cent; and 50 and

65 per cent. When insects were preconditioned at 50 per cent relative humidity for 24 hours they moved to the wet region of each pair of humidities and tended to form immobile aggregations. When preconditioned for 24 hours at the higher of each pair of humidities tested, they tended to move to the dry region of the gradient but fewer insects were involved than when they moved to the wet region after being preconditioned at 50 per cent relative humidity. Few insects aggregated in the low humidity region.

The humidity reactions were investigated when the floor of the chamber was covered with a single layer of glass beads which were used to provide a uniform contact stimulus for the insects over the entire surface area. The results showed that no aggregations were formed when insects became immobilized in the high humidity region. The data indicate that the humidity reactions were stabilized by the physical contact stimulus supplied by the glass beads.

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