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Temperature and humidity as they affect the life cycle of the lesser grain borer, Rhizopertha dominica Fab

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C O N T E N T S

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INTRODUCTION

An understanding of the life cycle of an injurious insect is of paramount importance not only for its essential value in the control of the pest, but in its value in biological research. The influence of certain ecological factors, as temperature and moisture, must be understood and appreciated to account for the many changes in the behavior of the organism concerned.

The lesser grain borer is one of the most serious pests of stored grain in all parts of the world, especially in the tropical and warmer regions. Stored grain is most often destroyed, though the insect's habits are somewhat omnivorous. Grain serves as food and shelter for the insect, permitting a world-wide distribution from the tropical to the cooler regions in shipments of grain.

Previous work on this beetle has been limited largely to reports of its occurrence with other grain pests, such as Sitophilus oryzae L., Sitophilus granaria L., and others, with only a superficial treatment of the beetle from the standpoint of life history and habits. However, much work has been done upon the control of the pest by means of poisonous gases, such as H_2S and HCN. It was with this in mind that the following research was planned to determine the duration and the important characteristics of the insect's

life cycle under controlled conditions of temperature and humidity. The facts considered essential were food requirements, activities and habits, reproduction and development, and variations in behavior due to differences in the environment.

DESCRIPTION

The lesser grain borer has no common name, except for local appellations such as the "wood bug" and the "Australian grain borer," this last because of its food habits. From the fact that the head is covered by the thorax it was called "Capuchin" by MacDougall (1925), and "Getreide-Kapuciner" as cited by Chittenden (1911) from Taschenberg.

It is one of the smallest of the injurious grain beetles, being 2.5 to 3 mm. long and only half as wide as long. The body is cylindrical and reddish-brown. The prothorax is sub-quadrate, convex and somewhat rounded at the four corners, covered with fine granulations and becoming hood-like over the head, which is small and deeply inserted in the thorax, with the vertex smooth and shiny. The antennae are clavate, ten-segmented with the first two segments sub-equal and with a terminal triarticulate club, the second segment being angular along the inside edge. Elytra elongate, glabrous,

punctate; straight along the sides, bristled with short incurved hairs behind, and reddish-brown in color.

It is distinguished from the larger grain borer, Dinoderus truncatus Horn, by several minute, but some quite noticeable, differences. The larger grain borer is 3 to 4.3 mm. long, and two-fifths as wide as long; the elytra are more truncate behind and the legs paler in color.

TAXONOMY

Order - Coleoptera
Suborder - Polyphaga
Series - Clavicornia
Super-family - Bostrychoidea
Family - Bostrychidae
Tribe - Dinoderinae
Genus - Rhizopertha
Species - dominica

SYNONOMY

The lesser grain borer has now the established name, Rhizopertha dominica Fab. Many synonyms were used previous to 1897 when Lesne revised the family Bostrychidae and fixed the scientific name of the species as now accepted.

The species was described by Fabricius in 1792 under the name Synodendron dominicum. The original description is as follows:

> "S. (ynodendron) laeve nigrum obscurum elytris striatis, pedibus piceis.
> Habitat in America meridonali Dom. Pflug."

In 1798 Fabricius redescribed the species under the name Synodendron pusillum, not recognizing the duplication created. The description is as follows:

> "S.(ynodendron ferrugineum elytris punctato striatis integris. Habitat in India orientali Dom. Daldroff. Corpus parnum, cylindricum, totum ferrugineum immaculatum. Antennae omnino lamellate huius generis. Thorax gibbus, punctatus. Elytra striato punctata, integra."

This error in assigning two different names to the same species was caused, apparently, by the difference in color of the adults, which varies with age from rust-red to black; and by the difference in habitat from which the species were described. Synodendron dominicum from South America was described as black, and Synodendron pusillum from India as rust-red. Lesne (1897) pointed out that only one species was concerned.

The name, Rhyzopertha pusillum, was applied to the species by Stephens (1830) from what he thought to be the original citation. Consequently, later workers applied the species name pusillum until Lesne (1897) pointed out the antedating species name, dominicum, which now stands corrected to dominica to correspond in gender to Rhizopertha, which is the corrected spelling for the Rhyzopertha of Stephens.

The synonyms of Rhizopertha dominica Fab. according to Lesne (1897) and others are as follows:

Synodendron dominicum Fab. Ent.Syst.1; pt.2:359, 1792.

Synodendron pusillum Fab. Ent.Syst.Suppl.5:156, 1798.

Sinodendron dominicum Fab. Syst.Eleut.2:378, 1801.

Sinodendron pusillum Fab. Syst.Eleut.2:378, 1801.

Ptinus piceus Marsham. Ent.Brit.1:88, 1802.

Rhyzopertha pusilla Stephens. Illus.Brit.Ent.3:354, 1830.

Apate rufa Hope. Trans.Ent.Soc.London 4:17, 1845;
Waterhouse, Ann.Nat.Hist.1:49, 1888.

Apate pusilla Fairmaire. Rev.et Mag.Zool.(2) 2:50, 1850.

Rhizopertha pusilla Wollaston. Ins.Mader:287, 1854;
Duval and Fairmaire, Gen.Col.III,pl.51: 281, 1863;
Redtenbacher, Faun.Austr.(3) II:67, 1872;
Kiesenwetter, Nat.Ins.Deutschl.Col.V:41, 1877.

Rhizopertha pusillus Hamilton. Trans.Amer.Ent.Soc.2:393, 1894.

Rhizopertha dominica Lesne. Ann.de la Soc.Ent.de France 66: 332, 1898.

In a recent communication, Mr. A. J. Mutchler points out that Rhizopertha dominica Fab. and Rhizopertha dominicana Fab. are different species, the first being a grain pest and the latter a museum pest. This notation is included to preclude a possible mistake in the synonomy of the species which might be made from the literature on the species.

DISTRIBUTION

The lesser grain borer is known to be cosmopolitan in habitat being found in many of the seaports of the world. No definite establishment of its original home can be made, but it seems likely that it may have been India or Central Asia, where the damage is the most serious today.

The pest is widely distributed in the United States, being found in New York, Washington, D.C., Iowa, South Carolina, New Jersey, Pennsylvania, Massachusetts, Arizona, Texas, Kansas, Oklahoma, Louisiana, Florida, and California (Chittenden, 1911; Back and Cotton, 1922).

Hamilton (1894) reports Canada within its distribution.

Its southern limit extends to Cuba, Mexico, Honduras, and South America (Lesne, 1897; Fabricius, 1792).

Its European distribution is largely restricted to seaport cities such as London, Trieste, and Stuttgart, to which grain from India, Egypt, Australia, and the United States is imported (Chittenden, 1911; Redtenbacher, 1872; Durrant, 1921).

The distribution within the British Isles is restricted to London, Hull, Manchester, Liverpool, Glasgow, Dublin, New Forest, and Windsor, most of which are ports of entry for grain from Australia and India, as noted by Durrant (1920); Chittenden (1911); and Stephens (1830).

Algeria, Egypt, and Madeira are listed as habitats by Chittenden (1911); India and China by Durrant (1921), and Hope (1845).

ECONOMIC IMPORTANCE

The literature concerning the economic importance of the species is not very extensive, being, for the most part, found among the notes on grain pests in general.

Its diversity of food material makes it a pest of major importance not only in stored grain and flour mills, but in many stored vegetable products and allied substances. Damage is done to stored cereals and grains, manufactured products of grains, and other foods having a starch content.

Fabricius made the first mention of its food habits in 1798, namely, in seeds and roots from India. Fwoggatt (1919) found it of major importance in stacks of wheat in New South Wales.

Materials eaten by Rhizopertha dominica Fab.:

Food Material	Authority
Wheat (stored and fresh)	Leconte (1861), Froggatt (1919), Motschulsky (1857), Chittenden (1911), Back and Cotton (1922).
Rice (Indian and Japanese)	Motschulsky (1857).
Oats	Original
Beans	MacDougall (1925).
Lentils	Chittenden (1911).
Pearl millet	Chittenden (1911).
Powdered roots used as drugs	Kirby and Spence (1822), Lesne (1897), Chittenden (1911).
Edible bulbs	Chittenden (1911).
Manufactured cereal products	Gorham (1883), Cotes (1889), Chittenden (1911).
Wood (for construction, etc.)	Riley (1882), Gorham (1883), Lesne (1897), Lucas (1894).
Bark (Quercus, Cysticus)	Lucas (1849).
Sorghum, white lotus, etc.	Chittenden (1911).

REVIEW OF BIOLOGICAL LITERATURE

Studies of the biology of the lesser grain borer have been limited largely to experiments upon the effects of developmental temperatures, with little consideration of the humidity requirements.

Chittenden (1911) and Back and Cotton (1922) state that it does damage to grains in tropical climates, but is seldom injurious in the cooler ones.

The life cycle required 35 days from May to June, and 183 days from October to April, according to Dendy and Elkington (1920). From data collected on the life cycle Chittenden (1911) states that from eggs deposited April 27 adults were observed August 12. Back and Cotton (1922) give the life cycle as once a month during the summer in the United States; while Froggatt gives it as three months during the summer in Australia.

The optimum temperature for the species was found to be 30° to 31° C. with the lower limit of active metabolism at 21° C., according to Froggatt (1919).[1] MacDougall (1925) found that maximum development occurred at 38° and the minimum amount of development at 22.5° in Scotland, thus assuring that that country would not be greatly subject to the ravages of the pest.

Froggatt (1919) found that the insect became motionless when subjected to a temperature of 10° for 7 days; the same effect taking place at 52° and 58° with survivals the next day.

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[1] All temperatures hereafter will be expressed in degrees Centigrade, and all humidities in per cent of relative humidity.

In a research with lethal temperatures Doane (1919) states that most of the beetles die at temperatures of 50° to 52°, and all die before a temperature of 60° is reached. Under storehouse conditions the beetles in the grain die in twelve hours from an exposure of 60°, or at temperatures of 90° when the grain sacks and grain prevent the approach to lethal temperatures at the center of the sacks. Tucker (1912), from experiments with the beetles in rice, found that 49° was fatal.

Hermetically sealing the beetles in flour containers for three days at 31° was fatal, due to the increased pressure of carbon dioxide and to the moisture content of the grain (Dendy and Elkington 1920). Dendy (1920) gives the effects of the gases under sealed conditions at 31° as follows:

ACTIVITY	TIME	PER CENT OF GASES PRESENT		
		CO_2	O_2	N
Motionless	48-96 hours	16.7	0.04	83.24
Motionless	44-68 hours	16.62	0.02	83.31

Experiments with the moisture content of wheat and its influence upon the insect's metabolism showed that a moisture content of less than 5.35 per cent was fatal to sixty per cent of the insects at temperatures from 17° to 22° in 55 days (Froggatt, 1919).

TEMPERATURE AND RELATIVE HUMIDITY EFFECTS UPON INSECT ACTIVITY

The effects of temperature are much better known than are the effects of moisture upon insect metabolism. Each insect species has a definite range of favorable temperatures and moisture conditions within which it can live and maintain its metabolism. The optimum is not a definite point, but a zone, according to Pierce (1916), who described the experimental method of approximating it. By varying the temperature from the absolute fatal minimum at a given humidity until the time for the fatal exposure increases to one of indefinite duration, one arrives at the zone of optimum metabolism. The effects upon the insect are as follows. The temperature when rising from the absolute fatal minimum temperature of the species passes through the zone of ineffective temperatures in which dormancy is the rule. An increase above dormancy produces a sensibility characterized by (1) an active metabolism; (2) movement; and (3) the necessity for feeding. This activity continues to increase until the optimum is reached, falling off above this until a coma is produced, which may be broken by a return to lower temperatures. A further increase causes instantaneous death at the absolute fatal maximum temperature. The effects of heat and cold seem to give the same visible effects upon the metabolism of the organism, according to physiologists.

Some of the effects of varying humidity are stated by Pierce (1916) from various compilations. Dryness causes stupor and death. A rising humidity goes through the zones of increasingly effective humidity, decreasingly effective humidity, excessive humidity causing stupor, and fatal humidity.

Chapman (1931) after Hill (1908) summarizes the combined effects of moisture and temperature as follows: (1) a moist cold atmosphere causes a rapid conduction of heat away from the body, producing cooling; poikilothermic organisms, such as insects, undergo a decrease in metabolism; (2) a cold dry atmosphere causes a slower heat loss, due to the less rapid conduction; (3) a dry warm atmosphere causes a rapid evaporation on the surface of the body producing cooling; and (4) a moist warm atmosphere causes a rapid conduction of heat to the body, but the low evaporation prevents the conduction of heat from the body quickly bringing the organism into an equilibrium with the surrounding atmosphere. Temperature and humidity when working together are interdependent in most cases, although the effect of humidity may be so slight, in some cases, that temperature may be the controlling factor. Some of the preceding effects will be discussed in the division on experimental results.

PROCEDURE AND TECHNIQUE

Controlled conditions of temperature and relative humidity were used in which all stages of the insect were reared in all stages of the life cycle. Cabinets having a capacity of 18 cubic feet were used. A two inch cork insulation lined the sides and bottom, and a double glass insulation covered the top and the door.

Heat was furnished by electric light bulbs, one burning constantly and another bulb of a smaller rating (10 to 15 watts) being under thermostatic control. Temperature variations were within $\pm 1^{\circ}$ C. Temperatures maintained in different cabinets were 22, 27, 32, 34, 37, 39, and 40° C.

Humidities ranging from 10 to 100 per cent relative humidity were obtained by means of aqueous salt solutions in closed pint jars placed in the temperature chambers. Humidity regulation was quite satisfactory under the conditions encountered after the salt was added in excess over the saturation point. Variations were small as evidenced by the humidity readings which were taken after the salts had been used for about seven months.

Chemically pure salts were used in distilled water with the following precautions: (1) extraneous matter, such as dirt and insects, was removed when present; (2) a change of solutions was made when signs of chemical breakdown were evident; (3) an excess of salt was maintained; and (4) the

jars were kept closed as much as possible while making observations.

An explanation of the action of the salt in maintaining the humidity is explained by the vapor pressure relationships of the air and the water. The vapor pressure of water produces a movement of the water molecules. Some of these escape into the air above the liquid to set up a partial pressure there. Some of them return to the liquid but not as fast as those escaping therefrom, until an equilibrium is set up and the air becomes saturated. The action of the salt, which has practically no vapor pressure of its own, reduces the vapor pressure of the water, likewise reducing the relative humidity of the atmosphere in the container (Wood, 1929).

The hydroscopic action of a dry soluble salt absorbs moisture to form a saturated solution, only if the vapor pressure of the solution is lower than the vapor pressure of the water vapor in the atmosphere. On the other hand, a moist solid loses water in an atmosphere of lowered partial pressures of the water vapor thereby raising the humidity. Factors influencing this action, according to Graham and Swan (1921), are: (1) the partial pressure of the air differing from the vapor pressure of the solution; (2) the temperature of the air and of the solution; (3) the extent of the solid surface exposed to the air; (4) the velocity of the

air movement; and (5) the "reaction constant" of the solid used.

Wood (1929), who was working with manufactured products, points out the disadvantages of salt solutions in humidity control in contrast to sulfuric acid solutions. Each salt's stability curve must be known in order to insure freedom from gaseous impurities arising from the breakdown of the salt at high temperatures. Numerous advantages are cited also by the same worker: (1) inexpensiveness; (2) facility and safety of handling; and (3) maintenance not very exacting over long periods of time.

Determinations of the relative humidities encountered when using the different salts and temperatures were obtained by means of a Dew Point Hygrometer, Alluard's form, composed of a nickled box with a highly polished surface, with two contrasting surfaces on both sides. An aspirator bulb was used to evaporate the ether or the alcohol inside the box to bring about temperature lowering. (Ether was used at low humidities, and alcohol at the high humidities.) The cooling by the aspiration of the liquids in the box lowered the temperatures to the dew point which was evidenced by the formation of a mist on theoutside of the box, whereas none formed on the two side pieces which gave a contrast and greater accuracy in perceiving the dew point when first formed.

The temperatures at the dew point and in the air were recorded and the relative humidity computed from a table of vapor pressures corresponding to the two temperatures recorded.

Table I shows the relative humidities as computed by the above method. An average of two or more readings grouped within one or two degrees of each other were used. The recorded values of the relative humidity as given by Spender (1926) in the International Critical Tables were used as indicators of the humidities expected, but not taken as final under the conditions of the research. Variations in the individual salts in different containers had to be tested in order to find the true relative humidity in the atmosphere in each brood container.

Table I

The Chemical Compounds Used and the Relative Humidities Obtained in the Various Chambers

Crit. - International Critical Tables; Test - actual measurement.

Salt	22°		27°		32°		34°		37°	
	Rel. Hum. Crit. Per Cent	Test Per Cent	Rel. Hum. Crit. Per Cent	Test Per Cent	Rel. Hum. Crit. Per Cent	Test Per Cent	Rel. Hum. Crit. Per Cent	Test Per Cent	Rel. Hum. Crit. Per Cent	Test Per Cent
NaCl	76	76.5			75	71.9		73.8		73.2
KCl			85	83.7						85.6
$NaNO_2$	65	60.4						62.7		64.2
NH_4NO_3						60.2				60.1
NaBr	57	53.4		57.2						
$MgCl_2$	32	37.1	32	33.5		31.7				
$CaCl_2$	31.5	40.6								
LiCl								10.6		

A preliminary part of the work was undertaken to find the best means of rearing the insect in all of its stages. One ounce tin boxes were suspended in the humidity jars by means of wires. Eleven different variations were tried before the best means of running the oviposition period was settled. The most important of these were:

1. The adults were placed among fresh wheat grains in an open tin. The beetles crawled or flew out of the tin, did not eat into the grain readily, and could not gain a footing readily upon the smooth tin bottom of the box.

2. The adults were placed among fresh grains in a box with a perforated cover, and blotting paper on the paper bottom. No escape was possible, a footing could be gained on the paper, the eggs could be observed readily, but the beetles crawled beneath the paper and did not enter the grain readily.

3. Ground flour was used for food, but it was extremely difficult to find the white eggs in the white flour.

4. Beetles were introduced which had already entered a kernel, the paper was shellacked down, and the perforated cover was used. This final method will be described later, and produced the best results of any tried.

Various methods were used in the larval stage. Of the fourteen variations tried the following are the most outstanding:

1. Larvae placed in the loose grain died quickly and did not enter the grain for feeding.

2. Larvae placed in pastry flour in a vial died quickly because the flour had not been conditioned for moisture; they were hard to find in the white flour because of their smallness and white color.

3. Larvae placed in whole wheat flour in the tin pupated, but were hard to find, and did not thrive well if more than one was present.

4. One larva placed in conditioned flour in a No. 3 gelatin capsule supported by a cardboard disc could be easily counted without damage due to handling, which was necessary in the other methods. This method seemed to be the most satisfactory, and will be discussed later.

The pupae were raised in empty capsules, presenting no great problem in technique of handling or observation.

The final procedure and technique used for the various stages was varied to conform to peculiarities in the life cycle and habits. All stages of the insect were raised in half-ounce tin boxes with perforated covers suspended in the jars above the salt solution by means of wire baskets. Number 20 copper wire was fastened to each box through holes in the sides, and secured to a wire ring at the top of the jar secured under the jar cover.

The bottoms of the tins used in the oviposition and egg stages were covered with rough black paper. The white eggs could be easily observed, and the paper provided a rough surface on which the adults could gain an easy footing.

Oviposition Stage. Adult beetles were transferred to the tins from stock cultures in the grains which they had entered in order to prevent direct and perhaps injurious contact with the tweezers, and to shorten the time necessary to gain entrance to the grains which delays oviposition. A perforated cover was used to prevent escape by flying or crawling under certain conditions. The eggs were laid on the paper and among the debris created by the beetles and could be easily counted and inspected.

Egg Stage. As soon as the eggs were observed the adults and the grains were removed to prevent mechanical injury and possible cannibalism of the eggs. The young larvae were removed as they hatched and transferred to the larval containers by means of a small wet camel's hair brush.

Larval Stage. The larvae were transferred from the egg chambers to open No. 3 gelatin capsules containing whole wheat flour. The flour was conditioned for six to eight days in the environment to be used, to insure a moisture equilibrium becoming established. Barley (1920) states that flour takes

on hygroscopic moisture to the extent of 5.18 per cent at 29.4 per cent relative humidity and 15 per cent at 80 per cent relative humidity, and tends to become unsound through the activity of its own enzymes or the development of fungi in this latter condition. While some fungous growth occurred in the 85 per cent humidity conditions, larval development appeared normal; however, in the 96 per cent humidity environment the larvae were destroyed.

The larvae were observed in the capsule or after being removed from the capsule by pouring out the flour and observing therein. Transference back into the capsule was accomplished by means of a small damp camel's hair brush.

Pupal Stage. Most of the pupae were kept in empty capsules, though some were allowed to develop free in the flour and others in the grains split for observation purposes. No perforated cover was used in this and the larval stages as the activity in either case was not great enough to permit escape. Pupae of different ages were placed singly in capsules, as some factor or factors operated to make a group development unsatisfactory.

EXPERIMENTAL RESULTS

Oviposition. Adults of unknown ages were transferred from stock cultures to the oviposition tins, and exposed to the various environments only until eggs were produced. The minimum amount of time required for oviposition in any condition was 3 days, and the maximum 29 days; most of the oviposition took place from the fourth to the seventh day after exposure. Egg laying did not occur in many conditions even after exposure over long periods (two to four weeks). The adults died in many cases before eggs were laid. The time elapsing before oviposition was not significant as the beetles may have mated in the stock cultures before introduction to the oviposition container. The results of the egg counts are shown in Figure 1.

Low humidities produced a small oviposition at all temperatures at and above 22° where a few eggs were laid at 32 per cent relative humidity. The zone of optimum oviposition occurred at temperatures of 27° to 37° and humidities of 56 to 85 per cent. The exact limits of the zone cannot be definitely demarked due to the limitations of the data available. A smaller number of eggs was deposited in the Intermediate zone at 22° in 32 and 72 per cent humidities; at 27° in the 28, 32, 56, and 60 per cent humidities, and at 39° in the 56 and 60 per cent humidities. Outside this zone little or no oviposition occurred.

At 22° and 75 per cent relative humidity, and 40° and 60 per cent relative humidity, the beetles were exposed until they died, very little oviposition occurring at these points.

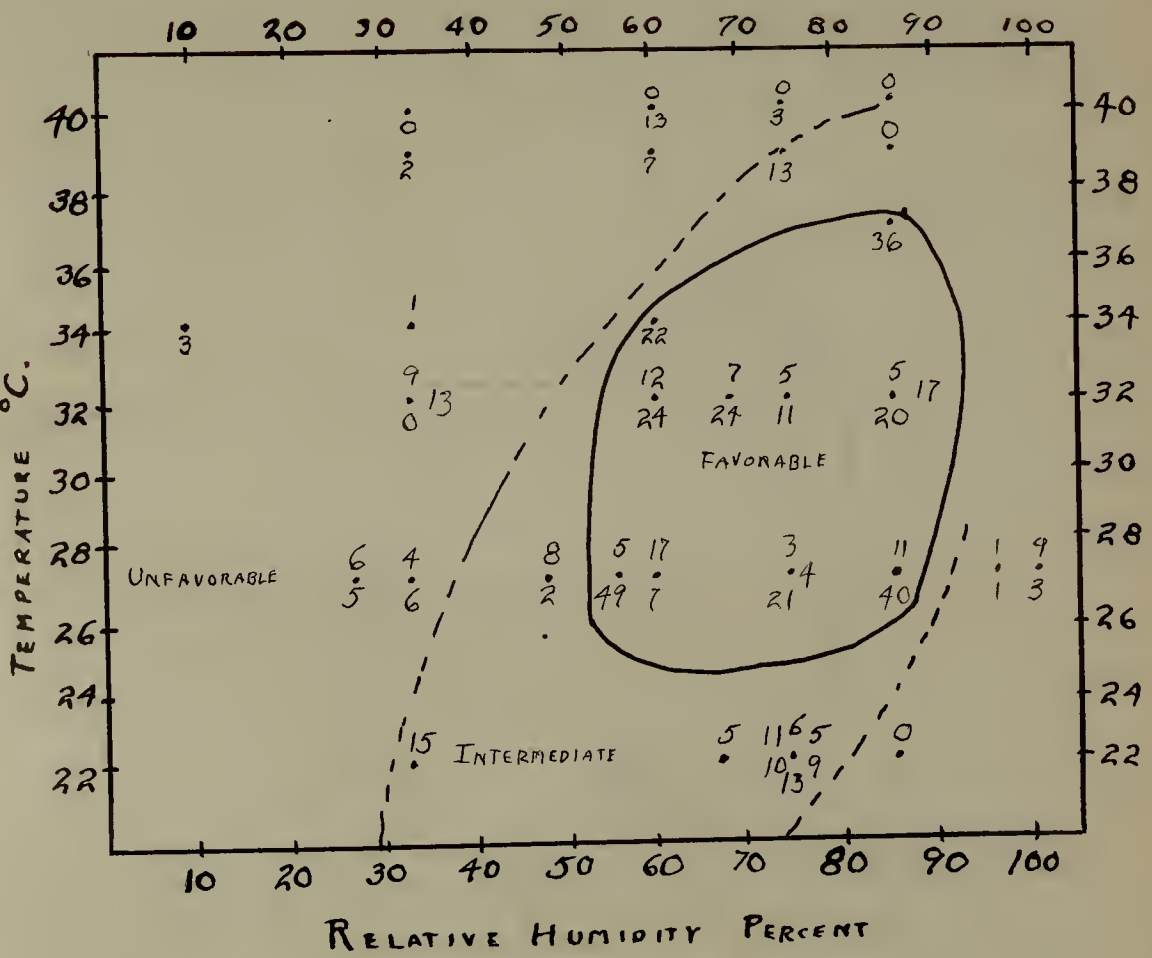
When the beetles were placed in a few loose and sound wheat grains the time elapsing before their entrance into the grain materially delayed oviposition. This was rectified by introducing only the beetles already in a kernel. More than one beetle was observed in a single kernel where mating may have taken place. The total length of the oviposition period was not determined as the adults were removed from the culture after the eggs were laid, to prevent damage to them through mechanical injury or by cannibalism.

Egg Stage. When freshly laid, the egg is white, 0.51 mm. long and 0.18 mm. wide at its widest part and 0.15 mm. wide at its narrowest part. It is elongate, pear-shaped, and slightly curved, tapering toward one end and with both ends slightly rounded. A constriction occurs at the tapered end which forms a small stalk turning brown previous to hatching, the remainder of the egg turning a lighter brown. The chorion is translucent, smooth and polished, becoming rougher after hatching and turning a chalky white in color. The embryo can be seen through the chorion previous to hatching; the dark mandibles are quite apparent at this time.

The eggs are laid loosely in a mass of 9 to 10, in the debris among the grains, and rarely upon the grains themselves under normal conditions. This contradicts Froggatt (1919) who maintains that the eggs are never laid upon the wheat grains. In the oviposition containers the eggs are generally laid vertically with the stalked ends up and adhere to any object in which they come in contact by adhesive substance secreted around the eggs during oviposition. In one case observed the eggs were laid in a crescent-shaped chain with the eggs stuck together end to end. Sometimes the eggs are laid horizontally, but adhering together as mentioned above. The larvae escape by chewing through the chorion from a point slightly to the side of the base of the tapered end of the egg.

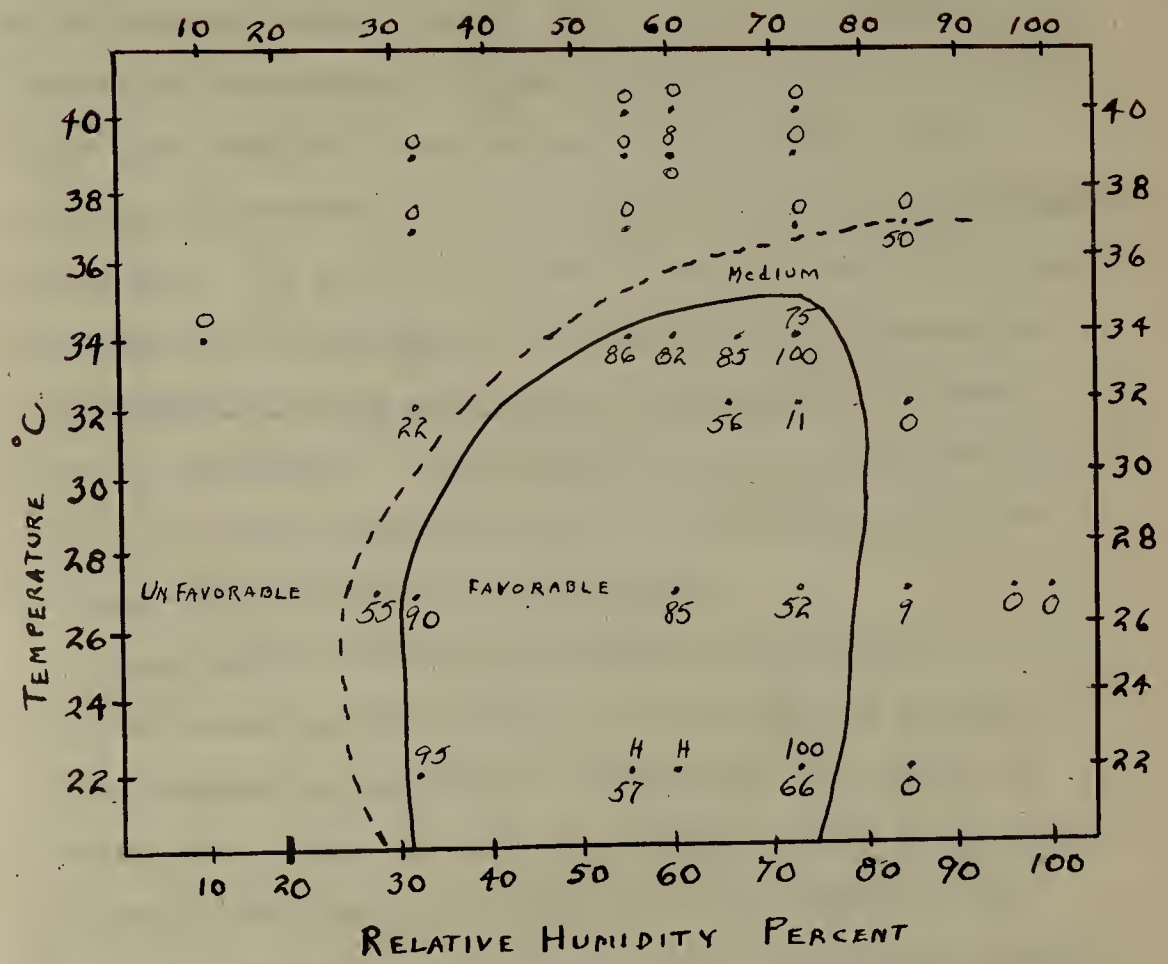
The percentage of eggs hatching and the optimum zoneis given in Figure 2. The optimum (High) zone for the percentage of hatch is rather definite. Good hatches occurred at temperatures ranging from 22° to 34°, and humidities of 32 to 75 per cent at the low temperatures of 22° and 27°, and 60 to 75 per cent at the higher temperatures. The medium hatch zone indicates the possible limits of an intermediate region of hatching, whereas the third region occurring outside this zone indicates little or no hatch in any condition.

FIGURE 1



The numbers of eggs laid in the different environments. Each numeral represents the number of eggs laid the first day of oviposition.

Figure 2



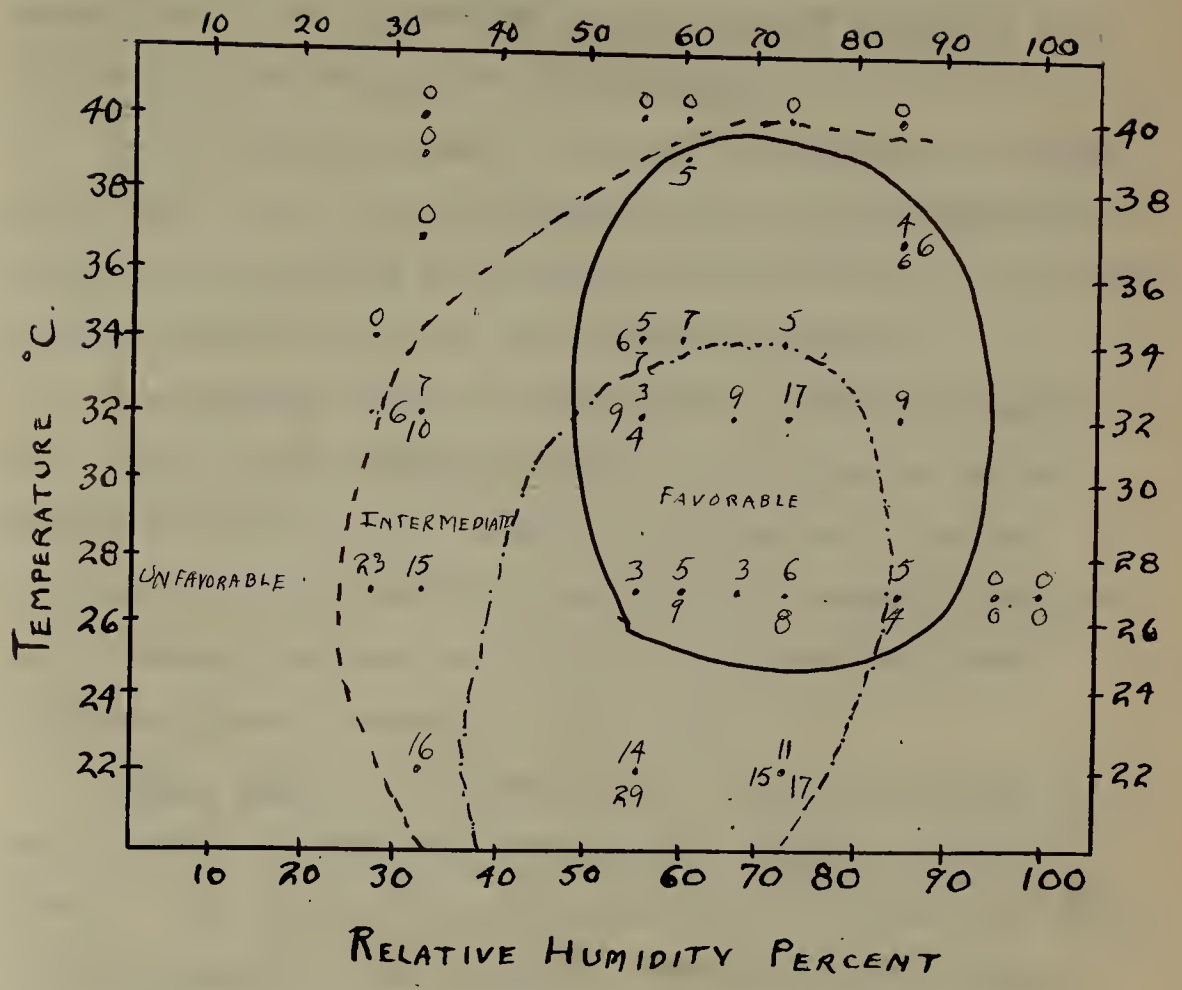
The percentage of eggs hatching in various temperature and moisture conditions. Each numeral represents the percentage of hatch from one lot of eggs.

The data showing the length of the incubation period is shown graphically in Figure 3. One fairly definite zone (Favorable) can be demarked from this data. This region shows the variations ranging from 3 to 9 days duration of embryonic development. This variability seems unusually large from work with the optimum environments of other insects, and cannot be satisfactorily explained with present knowledge. It seems to indicate, however, more favorable conditions of development than the zone of intermediate development, and the zone of poor development in which hatching occurred. The intermediate and unfavorable zones cannot be readily separated with the available data, but the approximate limits are suggested.

One factor which might possibly have operated to give this variation is the retention of the eggs in the uteri of the females in unfavorable conditions, or because of disturbances where the eggs may develop before oviposition. Sweetman (1927) notes this effect in May beetles where dissections of the uteri of dead females showed eggs which were appreciably developed, and which hatched a few days later.

A comparison of the results shown in Figures 2 and 3 should indicate an optimum region for both percentage of hatch and the rate of embryonic development. Both optimum

FIGURE 3



The length of the egg incubation period in days in the various environments. Each numeral represents the number of days necessary for the hatching of a single lot of eggs. The region demarked by the dot and dash line represents the favorable zone of egg hatch from Figure 2.

zones are indicated in Figure 3, the zone limits of Figure 2 being indicated by the dot and dash line. This zone of most favorable development occurs between 27° and 34° and humidities of 56 to about 80 per cent at 27° and 60 to 72 per cent at the 27° and 32° temperatures.

Considering the rate of embryonic development, moisture seems not to be a very important factor at the lower temperatures as indicated by the development at 22° where it is fairly uniform from 32 to 72 per cent relative humidity.

The apparent length of development at 27° in 28 and 32 per cent relative humidities seems to be explained by the faulty technique used in earlier experiments. The one reading of 23 days at 28 per cent relative humidity explains this readily, but the two readings at 32 per cent would indicate greater accuracy at this point.

Larval Stage. The young larvae are 0.3 mm. long; white and slightly transparent; head yellow; mandibles brownish-black. The head and abdomen bear scattered hairs; the three thoracic segments bear prolegs. The older larvae reach a length of 2 - 2.8 mm.; covered with pale brown hairs; the prolegs turn brown.

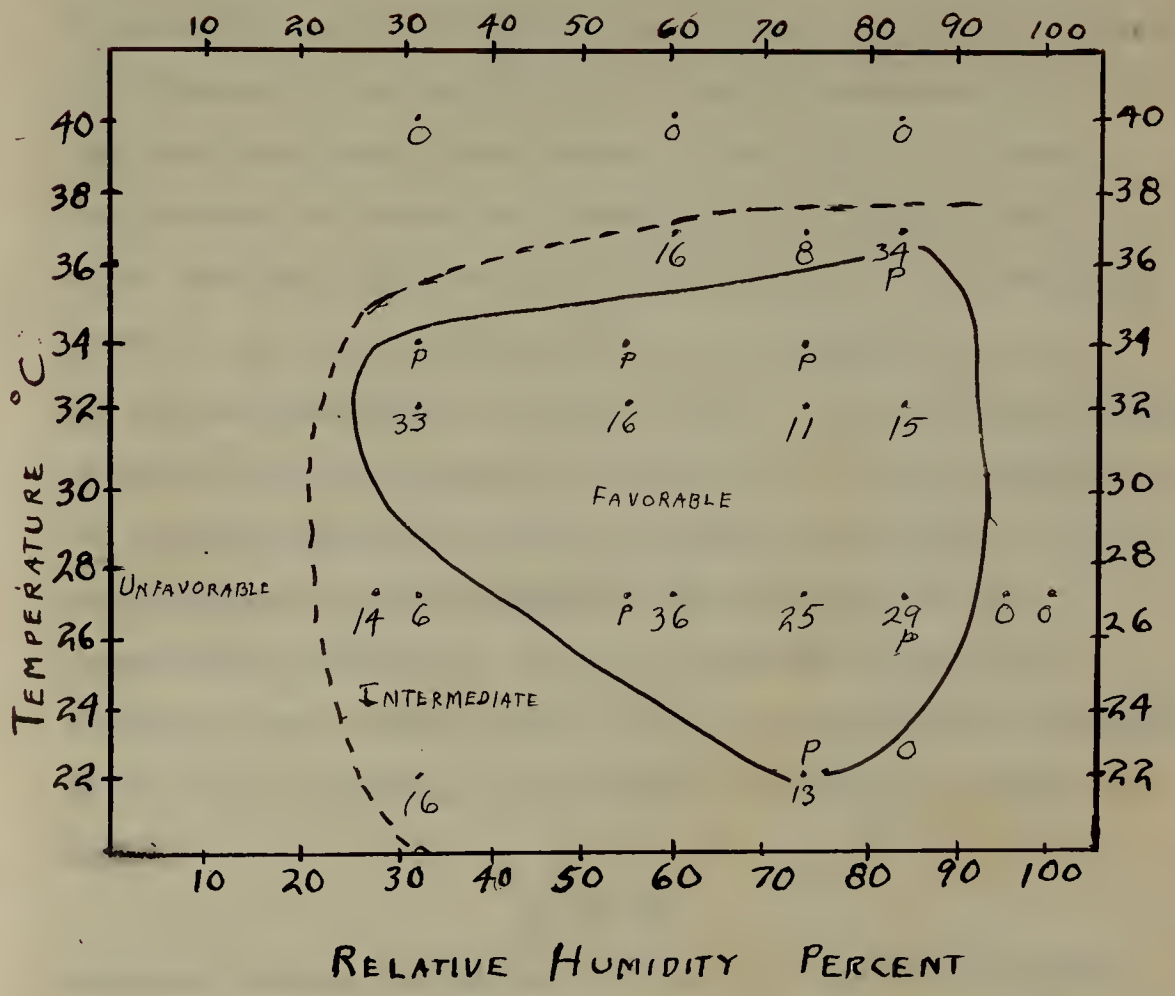
The larva upon emerging from the egg searches for suitable food. The debris among the grains, consisting of fecal pellets and "milled" flour, provides a food which tides

the young larva over for a time until it can become large enough to bore into the grains. Young larvae cannot enter a kernel unless it has been softened by moisture or has been scarred or abraded by the adults. Some larvae were observed entering unscarred kernels at the embryo end where the pericarp is softer.

Larval survival culminating in the pupal stage was low. In some cases only one out of many larvae was able to pass through complete larval development (See Table II and Figure 4). A higher mortality occurred among the larvae when more than one was placed in any container, possibly because of biting or cannibalism. Consequently, in later rearings only one larva per capsule was used. However, with one larva the mortality was still high, especially during early development.

Death in the later stages may be explained from the standpoint of the varying rates of development of the organs of the body. Various systems or groups of organs develop at different rates in different environments. Some organs may develop at a normal rate while others may develop at a decreased rate, depending upon the temperature and humidity complex obtaining. A point may be reached, after a certain time, in which the development of one organ may be the limiting factor in the further development of the organism, thus causing death.

FIGURE 4



The length of the larval period of survival before death in days. The letter P represents pupation.

Another factor which may influence mortality is the amount of metabolic water produced. The products of animal metabolism are water and carbon dioxide. To some extent, the production of metabolic water by the organism may offset the effects of low humidity or a high temperature by replacing the water lost through evaporation. A high temperature and fairly low humidities may cause a loss of water from the organism which is irreplaceable by metabolic water. Low temperatures decrease the evaporation rate, but not sufficiently to prevent death. The principal means of water loss in an organism are (1) by surface evaporation, (2) through excretion, and (3) through evaporation. A low temperature and a high humidity may, through the low evaporation concurring, cause an increase in the water content of the insect which cannot be expelled from the body, by the above methods, fast enough to prevent an excess and death.

Table II

Length of larval development in days, the number starting larval development, and the number pupating in different environments.

Temp. °C.	Rel. Humidity Percent	Number Starting	Number Pupae	Days
37	86	19	1	34
27	85	2	1	29
27	56	18	2	28
22	76	3	2	24

The rate of the larval development was not very variable as seen from Table II, from 22° to 27° and humidities from 56 to 85 per cent. The greater length of development at the high temperature of 37° and the high humidity of 86 per cent seems to indicate that the approach to unfavorable conditions was being reached, as an increase in temperature usually means an increase in the rate of development. The high mortality of the larvae is indicated, and discussed previously in the discussion of the larval stage.

The larval periods and the days of survival in the case of death before pupation are shown in Figure 4. The zone of most favorable development seems fairly well demarked. Pupation occurred in many conditions, though in many cases larval development was almost completed in this zone. The range of optimum conditions occurs between 22° and 72 per cent relative humidity and 37° and 85 per cent relative humidity. The range widens at 27° between the humidities of 56 to 85 per cent. Development at 32° did not culminate in pupation at any humidity. At 34° well-developed larvae, when introduced, pupated at humidities of 32, 60, and 72 per cent. At 37° pupation occurred in 85 per cent humidity, but the larval development was extremely slow (34 days). This apparently indicates a less favorable condition. Outside this optimum zone development lasted from 6 to 16 days. No development occurred at the high temperature of

39° in any humidities or in the extremely high humidities of 96 to 100 per cent at 27°. In the latter case, fungous growths prevented larval development by destroying the food, and possibly proving detrimental to the larvae themselves.

No evident acceleration of development due to moisture was evident at any temperature. This indicated that temperature is the chief limiting factor in the rate of development, the humidity merely limiting the range of development.

Pupal Stage. The color of the developing pupa changes from white to yellow, as the wing-pads and the adult-like head appear. In the later stages a reddish cast is assumed. The pupa remains motionless until after the full adult form is assumed, and remains motionless in this condition for a few days before feeding.

The pupae were raised from well-developed pupae taken from stock cultures in most cases and placed in capsules in the same sort of tin box and jar arrangement as in the other stages.

The length of the pupal period is shown in Table III.

Table III

The number of pupae transforming to adults and the length of the pupal period in days.

Temperature °C.	Relative Humidity	Number to Adults	Days
37	86	1	25
34	60	1	8
34	56	1	6
27	56	2	11
22	76	1	9

Pupal development was most rapid between humidities of 56 and 60 per cent at 34°. The length of the developmental period decreased from 11 days at 27° and 56 per cent humidity to 9 days at 22° and 76 per cent humidity. The slow rate of development at 37° in 85 per cent humidity might be explained from the facts concerning body surface evaporation discussed previously. It would appear from the data that the high temperature and humidity placed a burden upon the water eliminating functions of the organism. Young pupae seemed sensitive to external stimuli during the first day of development, becoming quiescent toward the end of the period.

Adult Stage. The adults upon emergence from the pupal stage are a reddish-brown color which darkens with age to a brown and later to a darker hue approaching black. Under normal conditions they remain within the larval burrow in the

kernel for pupation, emerging a few days later. The adults also eat into the kernels, consume the endosperm, leaving the pericarp riddled with large irregular holes. The grain serves secondarily as a shelter until the entire endosperm is consumed, many beetles, however, crawling over the grain. A debris is created by the feeding adults and larvae which is composed of fecal pellets and "milled" flour and portions of the pericarp and the underlying bran layer. An excess over that necessary for food is "milled" which is in agreement with the findings of Dendy and Elkington (1920). This material served as larval food and place of oviposition for the adults in both the stock and the experimental cultures.

Observations of the food habits showed that the most suitable foods, or those producing the highest development (in order) are: wheat grain, whole wheat flour, pastry flour, spaghetti, and oats. Cannibalism took place among the adults when food was scarce, but only the dead adults, larvae, or pupae were eaten. The head and abdomen were the most frequently consumed portions of the body. The larvae were observed feeding upon the pupae in the grains when more than one was present therein. The egg counts immediately after oviposition, and after the eggs hatched, were identical showing that the eggs were not eaten.

Upon exposure to light the adults would try to crawl beneath the paper and under the grain, indicating a negative phototropism, or perhaps a reaction to the disturbance of opening the container. When feeding upon spaghetti in the dark conditions in the container, the bottom portions of the spaghetti were consumed and never the top portions, indicating, perhaps, a positive thigmotropism or a response to gravity. This may have been a factor in producing the high mortality in the small cultures as the beetles thrived well in the stock cultures where the grain was tightly packed furnishing a uniform medium in which to feed. The need for a rough surface for locomotion was evident, the adults being quite helpless on smooth surfaces, but quite at home inside grains or in the debris among the grains where the footing was satisfactory.

A group of adults of unknown ages were subjected to temperatures above the optimum for a period of 5 minutes in vials submerged in hot water of the proper temperatures. Temperature readings were obtained by the thermometer projecting through a cork stopper into the vial with the bulb reaching almost to the bottom in the close vicinity of the beetles.

Table IV gives the results of the subjection of the adults to lethal and sublethal temperatures.

Table IV

Time Exposure	Temperature °C.	Number Adults	Activity	Time Survival	Percent Survival
5 min.	46	5	death		0
5 "	45	5	death		0
5 "	43	5	death		0
5 "	42	5	inactive	2 hrs.	50
5 "	41	5	death		0
5 "	40	8	death		0
2 days	39 (60 r.h.)	8	inactive	10 min.	100
2 "	39 (85 " ")	8	death		0
2 "	39 (56 " ")	8	death		0
2 "	39 (32 " ")	8	death		0
2 "	37 (all" ")		active		100

Temperatures above 39° seemed to be lethal to the insects except in the case of the exposure to 42° for 5 min. This one case may have produced such results because of insufficient exposure or differences in the conditions of the adults used in that particular test. Mortality was high at 37° after a few days exposure, but the adults lived long enough to oviposit under these conditions, although mating may have taken place previously in the stock culture from which the adults were taken. Death occurred at 39° in all humidities tried except 60 per cent, which indicates that this temperature approaches closely to lethal temperatures. These results are much lower than those expressed by previous workers. Froggatt (1919) states that temperatures of 52° and 58° produced inactivity with survivals the next day. Doane (1919) finds 50° to 52° fatal. The age of the beetles may have made them more susceptible to high temperature

exposures under the conditions of this experiment, or the beetles used by the other workers may have been in the grain when exposed, which is not indicated in the literature reviewed.

The length of the life cycle was determined by recording the time elapsing from the oviposition of the eggs until the adults emerged. The length of the life cycle from the egg to the adult stages varied over a range of 50 to 63 days between temperatures of 22° and 37°. The duration was 50 days at 22° in 76 per cent relative humidity, 50 days at 27° in 56 per cent relative humidity, and 63 days at 37° in 85 per cent relative humidity. The upper range of development was quite definite at the 37° level, but the minimum range of development was not determined as the conditions of the experiment did include temperatures below 22°. At this temperature development was possible, and it would be expected that temperatures a few degrees lower might produce development.

DELIMITATION OF OPTIMUM REGIONS

Many of the conclusions of the research could not, from their nature and the numbers of factors operating, be very conclusive. In defining the zones of optimum development it will be noticed that each stage of the life cycle has its range of optimum conditions in which it will develop at its optimum rate. Much of the data are variable and somewhat

contradictory within each zone. The definiteness of the zone of no development, however, is fairly clear in most of the stages. Much of the data of the negative character should have as great a value as the positive data obtained. When there is a great variation in one environmental condition it would seem to indicate that the approach to unfavorable condition is being made very closely. One particular condition bears this out in the egg, larval, and pupal stages very definitely. Referring to Figure 2 it is seen that 37° and 85 per cent relative humidity gives an area of high viability, not supported by data at closely related points at the same temperature. Above this point there is no hatch. It would appear that this environment is at the extreme edge of egg development, above which a small variation in temperature and humidity is unfavorable. Referring to Figure 4, the same condition seems to hold true. Pupation occurs at 37° and 85 per cent humidity, but with a very long larval developmental period. Observing that within the optimum region in larval development from 32° to 34° and moderate humidities the speed of development is greater, the contradictory length of the developmental period at 37° and 85 per cent humidity seems to be an indication that the limits of development are being approached. Referring to the pupal period (Table III) it is

seen that the period is greatly lengthened at 37° and 85 per cent humidity although pupation took place only at this point and at no other humidity environments at this temperature. These cases seem to indicate that a close approach to the limits of the zone occurred, or that conditions may have varied due to other factors not recognized. Tests of the moisture and temperature showed that the correct humidity and temperature were being maintained at 37°.

The data suggest that unknown factors may have been operating to cause some variations which could not be determined by the methods used. In order to verify the data many more conditions of temperature and humidity should be tested for comparison and substantiation of the results recorded already.

CONCLUSIONS

An improvement in the general technique of observation and recording makes the later observations more accurate than some of the earlier ones. With these things in mind, the following general conclusions were formulated concerning the life cycle and habits of Rhizopertha dominica Fab.

1. Rhizopertha dominica completes development from the egg to the adult stage at temperatures ranging from 22° to 37° in humidities of 75 per cent at 22°, 56 per cent and

85 per cent at 27°, 32 to 75 per cent at 34°, and 85 per cent at 37°.

2. The duration of the life cycle was 50 days at 22° in 76 per cent humidity and 63 days at 37° in 85 per cent humidity.

3. The duration of the egg stage was fairly uniform (3 to 9 days) at 27° and above, with a rapid development of 3 to 5 days at humidities of 56 to 85 per cent humidity, 4 days at 39° and 65 per cent humidity, and averaging 5 days at 34° in humidities of 56 to 75 per cent.

4. Egg viability was high (82 to 100 percent) within a range of 22 to 32 per cent humidities at 34°, 90 per cent at 27° and 32 per cent humidity, 95 per cent at 22° in 32 per cent humidity, and 66 to 100 per cent at 32° in 75 per cent humidity, with moderate hatches occurring at humidities of 28 per cent at 27°, 32 per cent at 32° and 85 per cent humidity at 37°, little hatch occurring outside this zone.

5. The numbers of eggs laid was greatest between 27° in 75 to 85 per cent humidity and 37° in 85 per cent humidity widening in range between 27° and 34°, narrowing at both extremes.

6. The larval stage varied within a narrow range of 24 to 34 days duration, varying from 29 days at 27° and 85 per cent humidity to 34 days at 37° in 85 per cent humidity, indicating that the 37° condition was approaching the zone of unfavorable conditions very closely.

7. Larval development was completed from 22° in 75 per cent humidity to 37° in 85 per cent humidity, widening in range at 27° to 56 to 85 per cent humidities and 34° to 32 to 75 per cent humidities. Deaths outside this range may have been due to combinations of high variations in metabolic water or the varying rates of development of the organs of the body at different conditions of temperature and moisture.

8. Temperatures of over 43° are fatal after a duration of five minutes. Development throughout the entire life cycle took place at 37° and one humidity (85 per cent), the range of development was recorded at 22° and 75 per cent humidity with a possible development at lower temperatures, as indicated by the data at 22°.

9. Temperatures of over 39° were fatal to the adults when exposed 5 minutes or longer.

BIBLIOGRAPHY

(Including the more important literature of Rhizopertha dominica Fab. and ecological literature)

Back, E. A. and Cotton, R. T.

1922 Stored Grain Pests.
U.S.D.A. Farmers Bull. 1260:7-11.

1924 Effective use of hydrocyanic gas in the protection of chickpeas.
Jour. Agr. Res. 28:649-660.

Barley, C. H.

1920 The hygroscopic moisture of flour exposed to atmospheres of different relative humidity.
Jour. Ind. and Eng. Chem. 12:1102.

Barnes, J. H. and Grove, A. J.

1916 The insects attacking stored grain in the Punjab and methods of combating them.
Mem. Dept. Agr. India, Chem. Ser. 4:165-284.
Abstract in Exp. Sta. Rec. 37:356, 1917.

Baumberger, J. P.

1914 Studies in the longevity of insects.
Ann. Ent. Soc. Amer. 7:323-353.

Bodine, J. H.

1921 Factors influencing the water content of certain Orthoptera.
Jour. Exp. Zool. 32:137-164.

Buxton, P. A.

1924 Measurements of animal environment.
Nature 125:158-159.

Carmichael, E. B. and Rivers, T. D.

1932 The effects of dehydration upon the hatchability of Limax flavus' eggs.
Ecology 17:375-380.

Chapman, R. N.

1931 Animal ecology.
McGraw Hill Book Co. N. Y.

Chittenden, F. H.

1911 Papers on insects affecting stored products.
U.S.D.A. Bur. Ent. Bull. 96 (3):29-52.

Coleman, D. A. and Fellows, H. C.

1925 Hygroscopic moisture of cereal grains and flax seed exposed to atmospheres of different relative humidity.
Cereal Chem. 5:75-287.

Cotes, E. C.

1889 Indian Mus. Notes:60. (Title and publication not seen)

1891 Indian Mus. Notes 2:150. " " " " "

Dendy, A.

1919 Report on the effect of air-tight storage upon grain pests Pt. II.
Rpt. of Grain Pests (War) Com. (Trans. Roy. Soc. London) 1:6-23.

1920 Report on the effect of air-tight storage upon grain pests Pt. III.
Rpt. of Grain Pests (War) Com. (Trans. Roy. Soc. London) 6:1-26.

Dency, A. and Elkington, H. D.

1918 Report on the effects of air-tight storage upon grain insects.
Rpt. of Grain Pests (War) Com. (Trans. Roy. Soc. London) 3:3-14.

Doane, R. W.

1919 Weevils in Australian wheat in California.
Jour. Ec. Ent. 12 (4):308-312.

Durrant, J. H.

1921 Insects associated with grain.
Rpt. of Grain Pests (War) Com. (Trans. Roy. Soc. London) 9:33-51.

Fabricius, J. C.

1792 Entomolgia Syst. 1 (2):359.

1798 Entomologia Syst. Suppl. 5:156.

Fitch, E. A.

1879 Granary Weevils: Sitophilus granarius and S. oryzae. The Entomologist 12:45 (not seen).

Froggatt, W. W.

1919 A serious pest of stored grain, the lesser grain borer. Agr. Gaz. N. S. W. Sydney 24, pt. 10:726-728.

Gemminger, M. and Harold, B.

1869 Catalogus Coleopterorum 2:1792.

Gorham, H. S.

1883 Biologia Centrali Americana, Col. 3 (2):217. (not seen)

Graham, E. and Swan, W. O.

1921 The factors determining the hygroscopic properties of soluble substances. I. The vapor pressures of saturated solutions.
Jour. Amer. Chem. Soc. 44:570-577.

Hamilton, J.

1894 Distribution of Coleoptera.
Jour. Trans. Amer. Ent. Soc. 21:393.

Hatfield, J.

1931 Control of moisture content of air in fresh air chambers.
Jour. Agr. Res. 42:301-305.

Headlee, J.

1913 Some facts regarding temperature and moisture changes on the rates of insect metabolism.
Science N. S. 37:310.

Holdaway, F. G.

1932 An experimental study of the populations of the "flour beetle," Tribolium confuscum Duval as affected by atmospheric moisture.
Ecol. Mon. 2:263-304.

Hope, F. W.

1845 On the entomology of China with descriptions of the new species sent to England by Dr. Cantor from Chusan and Canton.
Trans. Ent. Soc. London 4:17.

Horn, M. A.

1878 Revision of the Bostrychidae of the United States (notes).
Trans. Amer. Phil.Soc. 17:550 (not seen).

Husain, M. A. and Bhasin, H. O.

1921 Preliminary observations on lethal temperatures for the larvae of Trogoderma kharpa a pest of stored wheat. (Also R. dominica).
Rpt. Proc. 4th Ent. Meeting Pusa: 240-248.

Kirby and Spence

1822 Introd. to Ent. 1:232 (not seen).

Leconte, J. L.

1861 Classification of North American Coleoptera (Smithsonian Institution).
Pt. 1:208 (not seen).

Lesne, P.

1897 Revision des Coleopteres de la famille des Bostrychides.
Ann. de la Soc. Ent. de France 66:332-333.

Loeb, J. and Northrop, J. N.

1917 On the influences of food and temperature on the duration of life.
Jour. Biol. Chem. 32:103-121.

Lucas, H.

1849 L'Histoire Naturelle des animaux articules de l'Algerie.
I Coleopteres: 468 (not seen).

MacDougall, R. S.

1925 Insects and other invertebrate pests of 1925.
Highland Agr. Soc. Scotland Trans. (5) 38:151-194.

McCarthy, T.

1922 Insects infesting stored grain in New South Wales.
Agr. Gaz. N. S. W. Sydney 33:253-259.

Motschulsky, T. V.

1857 Etudes Entomologuiques 6:78 (not seen).

Pierce, W. D.

1916 A new interpretation of the relationships of temperature and humidity to insect development.
Jour. Agr. Res. 5:1183-1191.

Redtenbacker, L.

1872 Faun. Austr. (3) II: 67, (not seen).

Robinson, W.

1926 Low temperature and moisture as factors in the ecology of the rice weevil, Sitophilus oryzae L. and the granary weevil, Sitophilus granarius L.

Saunders, S. S.

1874 Ent. Soc. London Trans. Feb. 16 (notes).
In Entomologist's Monthly Mag. 10:259.

Spencerl H. M.

1926 Laboratory methods of maintaining constant humidity.
Inter. Crit. Tables 1:67-68.

Sweetman, H. L.

1927 A preliminary report of the factors controlling the oviposition of the May beetles in Minnesota. Jour. Ec. Ent. 20:783-794.

Tucker, E. S.

1912 Department of Entomology (notes). La. Rpts. for 1912:18.

1908 Principal injurious insects of 1908. U. S. Year Book :579.

Wood, E. B.

1929 Humidity test equipment. Tycos Rochester Jan. 14-16.

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