BIOLOGY OF THE CORN BILLBUG,

CALENDRA CALLOSUS OLIVAR,

IN SOUTH CAROLINA

A Thesis Presented for the
Degree of Master of Science

by

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The Ohio State University
1934

Approved by:

[Signature: Dwight M. DeLong]
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INTRODUCTION

History - Among the early records of "billbugs" there has been some confusion of the two closely allied species Calandra callosus and C. maidis. Although both species are frequently referred to as corn billbugs, the term refers properly only to the former.

The earliest record of the corn billbug in the Carolinas was likely that of Oliver (8)* who first described the species as Calandra callosa in 1807. The first record to be published on billbugs in South Carolina was probably that of Townsend Glover (5) in the Agricultural Report of the Patent Office for 1854. His report, in the opinion of Dr. Chittendon, referred only to Calandra (Sphenophorus) maidis.

In 1881 billbugs were again reported from South Carolina, and L. O. Howard was sent, by the U.S. Department of Agriculture, to Columbia, S.C., to investigate the situation. Howard found C. maidis causing much damage to corn along "the bottom lands of the Congaree River".

Every few years since 1881 serious damage by both species has been reported in various parts of South Carolina. Injury by C. callosus has occurred principally in the eastern part of the state. In 1929 the South Carolina experi-

*Numbers in parenthesis refer to bibliography.
ment Station undertook an investigation of this pest.

**Time and Place of Study** - The study was made in Florence County, S.C. at the Pee Dee Branch of the South Carolina Experiment Station. The work was carried on under the direction of Mr. O. L. Cartwright, Associate Entomologist, with the cooperation of Mr. E. E. Hall, Superintendent of the station. These studies were in progress from 1929 to 1934. This report, however, covers only the years 1932, 1933 and 1934.
CLASSIFICATION AND SYNONYMY

Various common names, such as corn weevil, curlew bug, kloo bug, and elephant bug are used locally to designate any and all billbugs found in corn. Generally, however, Calendra callosus and C. maidis are known as corn billbugs or merely as "billbugs" (2).

The corn billbug Calendra callosus Oliver is one of fifteen or more members of the genus Calendra (Clairville and Schellenberg 1798) (9) which possibly may be found in South Carolina. The closely related species Calendra maidis Chittn. is the only other billbug causing severe injury to corn in this state.

As has been previously mentioned, the insect was first described by Oliver in 1807, from "Carolina" as Calendra callosa. Since then it has also been known as Sphenophorus callosus. Dr. F. H. Chittendon (3), in his paper relating to this and other species of the genus, came to the conclusion that S. sculpticis Horn is a synonym of S. callosus and that S. sculpticis Uhler is a synonym of S. cariosus Oliver; also that in many cases specimens received by him showed that references to either of these three species related properly to S. callosus. In recent years, however, Calendra callosus seems to have become the more commonly accepted name for the species (9).
DISTRIBUTION

_Calendra callosus_ covers a wider range in the United States than _C. maidis_. It seems to center in point of abundance in eastern North Carolina. A series of locality records as compiled by Webster (13) shows the following distribution in North America: N.C., S.C., Fla., Va., Md., Ohio, Ill., Ind., Ky., Tenn., Mo., Kan., Okla., Texas, Miss., La., New Mexico, Ariz., and Mexico. It has also been reported from Georgia.

In South Carolina the species occurs in Florence, Marion, Dillon, Darlington and probably most of the other counties in the eastern part of the state.

DISPERSAL

The usual method of dispersal is by crawling from field to field. The adults have very little tendency to travel as long as they have ready access to an abundance of food, but when crop rotation is practiced, they will migrate to the newly located fields. Movement on foot is very slow.

It is possible that an occasional individual is capable of flight, but it is believed that migration never occurs on the wing.

During heavy rains the adults may be carried for some distances by running water. Since they float readily
and are extremely resistant to drowning, it is likely that they are sometimes carried long distances down streams.

FOOD PLANTS

The corn billbug will feed on most all of the coarser grasses.

Smith (12) lists the following food plants for this species in North Carolina: Corn, Rice, *Cyperus flavicomus* (elegant nut-grass), *C. strigosus* (a nut-grass), *C. cylindricus*, *C. overlaris* and *C. esculentus* (yellow nut-grass or chufa).

Webster (13) has compiled a list of plants, in which immature stages of the species have been reported developing as follows: *Cyperus strigosus* in Ill., *Cyperus esculentus* in Okla. and the Carolinas, *Cyperus rotundatus* in Fla., *Cyperus exaltatus* in Va., *Carex frankii* (Frank's sedge) in Va., *Panicum capillare* in Md. and *Tripsacum dactyloides* in Texas.

Condit, working at the Arlington Farms, Va., reported that Frank's sedge was the natural food of the billbug in that locality. Dr. Forbes gives *Cyperus strigosus* as the natural food plant, in the roots of which it develops, in Illinois.

Due to the relation of the two species, *C.*
callosus and C. maidis, it seems entirely possible that some of the earlier records referred to above might have been for either species.

In South Carolina the preferred food of C. callosus, so far as known, is the corn plant. The adult beetles have been observed in the field feeding on corn, oats, crab-grass (Digitaria sanguinalis Soop.), joint-grass, nut-grass and other undetermined grasses. No evidence was obtained which might indicate that any of these, other than corn, were host plants in which the larvae would develop to maturity, though eggs were found deposited in the stems of one of the unidentified grasses.

In addition to the above listed plants, billbugs in the insectary have fed on napier-grass, large water-grass and sorghum. In the insectary eggs were laid in all of them with the exceptions of nut-grass and joint-grass. The adults would neither feed nor oviposit on the vegetative parts of peanuts.
The corn billbug has four stages in its development, - egg, larva, pupa and adult. The eggs are laid in the corn plants in spring and summer by the adult, and the footless grub feeds and develops to maturity within the root. The mature larva may pupate either in its old cell in the tap root or immediately outside among the masses of feed roots. After a few days the adult emerges from the pupa and usually remains in the cell to spend the winter.

Methods and Materials

Each spring a number of adults were collected from the field and kept in the insectary for obtaining oviposition records. Jelly glasses filled half full of soil served as oviposition cages. Fresh sections of small corn plants were added daily to each cage for food and oviposition.

The eggs were removed from the cages each day and placed in quarter-ounce tin boxes for incubation. Moist plaster of paris in the bottom of the boxes aided in maintaining a desirable degree of humidity.

The larvae, upon hatching, were transferred to sections of fresh corn plants. The section of plant was first split longitudinally, and a hole cut in one piece large enough to accommodate one larva. The pieces were
then bound together, with the larva inside, by a rubber band. It was necessary to transfer the developing larvae to fresh sections of corn every few days. Four-ounce tin boxes were used as larval cages.

Description of Stages

Egg - The egg of the corn billbug is cylindrical, elongate, slightly curved, about three millimeters in length and about one millimeter in diameter. It is pearly white, without markings when laid, but gradually turns creamy white before hatching.

Larva - The newly hatched larva is a small white footless grub. At first the head capsule is white, but turns brown after a few hours. The mandibles are darker than the other parts of the head. When first hatched the larva is of uniform diameter, but it grows rapidly and soon assumes a characteristic curved pear shape, the posterior end becoming much larger than the anterior end. The full-grown larva is about one-half inch in length.

Pupa - The pupa is creamy white at first, but later becomes pale yellow, and finally, at the end of the prepupal period takes on the red coloration characteristic of the newly emerged adult. The pupa varies in size from one-half to about five-eights of an inch in length. The legs, wing-pads, snout, and antennae are free and folded
over the under side of the body.

Figure 1. Adult of the corn billbug.
Left: female
Right: male

Adult - The adult is light red in color when it first emerges from the pupal skin, but gradually changes to dark brown. Beetles taken from the field are often caked with mud or soil particles, which may make it rather difficult to locate them on the ground. They average about one-half inch in length and are two-fifths as wide. The chitinous body wall is very hard and cannot be crushed between the fingers without difficulty. The males are usually smaller in size than the females and are distinguished by the truncate posterior end and conceave hollow on the first segment of the abdomen. The female abdomen is convex on the first segment and ends in a sharply rounded tip.
Number of Generations - Each year in which studies were made there was a second generation in the insectary. However, there was no evidence that a second generation occurred under field conditions. A few of the newly transformed adults in the field emerged and fed on the coarser grasses during the late summer, but it did not seem likely that the insect was capable of producing a second generation in these plants. At this season the corn was well matured and did not furnish succulent food for larval development.

There are several factors which probably influence the development of a second generation in the insectary. First, the development of the first generation is speeded up somewhat, and may be completed from one to two weeks earlier than in the field. Second, young succulent corn plants are kept growing all during the summer for insectary work. Third, the somewhat abnormal humidity and temperature conditions in the oviposition cages may stimulate the activities of the insect.

First generation adults from both field and insectary have been placed in field cages (4'x4'x4' screen wire) over late corn, but no oviposition has occurred under these conditions.
The First Generation

The first generation, as here referred to, includes those individuals developing from eggs laid by overwintering adults.

**Incubation** - The length of the incubation period was recorded (table 1) for each of 7040 eggs in 1932, for 4497 in 1933, and 896 in 1934. This period varied from 16 days in the cool spring days in 1933 to only 3 days in mid-summer. The majority hatched in 4 days. The average was 5.56, 5.27, and 4.67 days respectively for the three years.

Table 1. - Summary of incubation data for three years.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Year</th>
<th>Number Laid</th>
<th>Number Hatched</th>
<th>Number failed to Hatch</th>
<th>Per-cent failed to Hatch</th>
<th>Incubation Period in Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>1932</td>
<td>7040</td>
<td>6597</td>
<td>443</td>
<td>6.3</td>
<td>4 11 5.6</td>
</tr>
<tr>
<td>First</td>
<td>1933</td>
<td>4497</td>
<td>3929</td>
<td>563</td>
<td>12.6</td>
<td>4 16 5.3</td>
</tr>
<tr>
<td>First</td>
<td>1934</td>
<td>896</td>
<td>447</td>
<td>449</td>
<td>50.1</td>
<td>3 10 4.9</td>
</tr>
<tr>
<td>Total or av.-</td>
<td>12433</td>
<td>10973</td>
<td>1460</td>
<td></td>
<td></td>
<td>3 16 5.4</td>
</tr>
<tr>
<td>Second</td>
<td>1932</td>
<td>429</td>
<td>390</td>
<td>39</td>
<td>9.1</td>
<td>4 8 4.9</td>
</tr>
<tr>
<td>Second</td>
<td>1933</td>
<td>605</td>
<td>537</td>
<td>68</td>
<td>11.2</td>
<td>4 7 5.0</td>
</tr>
<tr>
<td>Second</td>
<td>1934</td>
<td>25</td>
<td>18</td>
<td>7</td>
<td>28.0</td>
<td>4 4 4.0</td>
</tr>
<tr>
<td>Total or av.-</td>
<td>1059</td>
<td>945</td>
<td>114</td>
<td></td>
<td></td>
<td>4 8 5.0</td>
</tr>
</tbody>
</table>
The percent of eggs which failed to hatch was 6.29, 12.63, and 50.11 respectively for 1932, 1933, and 1934. Incubation is given by months for 1932 and 1933 in tables 2 and 3.

Table 2. - Incubation by months for first generation eggs of 1932.

<table>
<thead>
<tr>
<th>Month</th>
<th>Number</th>
<th>Number hatched</th>
<th>Number failed to hatch</th>
<th>Percent failed to hatch</th>
<th>Incubation Period in Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>6</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>8  9  8.3</td>
</tr>
<tr>
<td>May</td>
<td>1553</td>
<td>1500</td>
<td>53</td>
<td>3.4</td>
<td>6  10  7.7</td>
</tr>
<tr>
<td>June</td>
<td>2574</td>
<td>2465</td>
<td>109</td>
<td>4.2</td>
<td>4  7  5.1</td>
</tr>
<tr>
<td>July</td>
<td>1878</td>
<td>1734</td>
<td>144</td>
<td>7.7</td>
<td>4  6  4.4</td>
</tr>
<tr>
<td>Aug.</td>
<td>807</td>
<td>700</td>
<td>107</td>
<td>13.3</td>
<td>4  7  5.1</td>
</tr>
<tr>
<td>Sept.</td>
<td>221</td>
<td>192</td>
<td>29</td>
<td>13.1</td>
<td>4  11 7.1</td>
</tr>
<tr>
<td>Oct.</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>100.0</td>
<td>-  -  -</td>
</tr>
<tr>
<td>Total</td>
<td>or Av.</td>
<td>7040</td>
<td>6597</td>
<td>443</td>
<td>6.29 4 11 5.6</td>
</tr>
</tbody>
</table>

Table 3. - Incubation by months for first generation eggs of 1933.

<table>
<thead>
<tr>
<th>Month</th>
<th>Number</th>
<th>Number hatched</th>
<th>Number failed to hatch</th>
<th>Percent failed to hatch</th>
<th>Incubation Period in Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>April</td>
<td>23</td>
<td>20</td>
<td>3</td>
<td>13.0</td>
<td>8  16 11.1</td>
</tr>
<tr>
<td>May</td>
<td>1319</td>
<td>1173</td>
<td>146</td>
<td>11.1</td>
<td>4  8  5.7</td>
</tr>
<tr>
<td>June</td>
<td>1713</td>
<td>1527</td>
<td>186</td>
<td>10.9</td>
<td>4  7  5.1</td>
</tr>
<tr>
<td>July</td>
<td>1127</td>
<td>975</td>
<td>152</td>
<td>13.5</td>
<td>4  8  5.0</td>
</tr>
<tr>
<td>Aug.</td>
<td>298</td>
<td>225</td>
<td>73</td>
<td>24.5</td>
<td>4  7  4.9</td>
</tr>
<tr>
<td>Sept.</td>
<td>17</td>
<td>9</td>
<td>8</td>
<td>47.1</td>
<td>4  6  4.7</td>
</tr>
<tr>
<td>Total</td>
<td>or Av.</td>
<td>4497</td>
<td>3929</td>
<td>568</td>
<td>12.6 4 16 5.3</td>
</tr>
</tbody>
</table>
Larval Stage - The duration of the larval stage varied considerably (table 4). The maximum number of days required was 72 (1934) and the minimum was 23 (1932). The average time for 115 individuals in 1932 was 36.99 days, for 87 in 1933, 34.37 days and for 28 in 1934, 40.64 days.

Molting - The first visible evidence of molting of the larva was the splitting of the head capsules vertically along the middle. The old skin with half of the head capsule on either side, was worked slowly toward the posterior end of the body. Several minutes were required for the larva to become completely rid of the old skin. The new head capsule was at first white but gradually turned darker until it was dark brown.

Number of Larval Instars - The number of larval instars varied from 3 to 6. The usual number was 4.

Food of the Larva - Under field conditions the larvae fed principally on the underground parts of the corn plant, but in the insectary it was often necessary to make use of the above ground parts. It was evident that larvae developing on the roots required a somewhat longer time to reach maturity than those fed on the more succulent, above-ground parts of the plant. In order to compare the duration of development for each type of food, one series of 29 larvae (tables 5 & 6) were fed only on the above
Table 4. - Summary of life history stages for Individuals of the first and second generations for 1932, 1933, and 1934.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number of Individuals</th>
<th>Duration of various stages in days</th>
<th>Number of each sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932 First</td>
<td>115</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933 First</td>
<td>87</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934 First</td>
<td>28</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>230</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932 Second</td>
<td>60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933 Second</td>
<td>51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934 Second</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>112</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
ground parts from the time of hatching to maturity, while 22 others were fed only on the roots of the corn.

Larvae used for obtaining these data were of the first generation of 1933.

Table 5. - Comparison of duration of instars for larvae fed only on the root of the corn plant and those fed only on the above ground parts.

<table>
<thead>
<tr>
<th>Fed only on above-ground parts of the corn plant</th>
<th>Number of Larvae</th>
<th>Average length of instar in days</th>
<th>Total Larval Period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1* 2 3 4 5 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>4.5 3.5 5.5</td>
<td></td>
<td>13.5</td>
</tr>
<tr>
<td>20</td>
<td>4.8 3.7 4.6 5.6</td>
<td></td>
<td>18.7</td>
</tr>
<tr>
<td>6</td>
<td>4.7 3.5 4.5 5.8 6.5</td>
<td></td>
<td>25.0</td>
</tr>
<tr>
<td>1</td>
<td>6.0 4.0 3.0 4.0 5.0 4.0</td>
<td></td>
<td>25.0</td>
</tr>
<tr>
<td>29</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fed only on the roots of the corn plant</th>
<th>Number of Larvae</th>
<th>Average length of instar in days</th>
<th>Total Larval Period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 2 3 4 5 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>5.7 3.7 7.3</td>
<td></td>
<td>16.7</td>
</tr>
<tr>
<td>15</td>
<td>5.2 4.5 5.7 7.8</td>
<td></td>
<td>23.1</td>
</tr>
<tr>
<td>2</td>
<td>5.5 3.5 7.0 8.0 7.0</td>
<td></td>
<td>31.0</td>
</tr>
<tr>
<td>2</td>
<td>6.0 4.5 5.5 4.5 8.0 7.0</td>
<td></td>
<td>35.5</td>
</tr>
<tr>
<td>22</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* First instar
Table 6. - Comparison of growth in diameter of head capsules for various instars of larvae fed only on the root of the corn plant and those fed only on the above ground parts.

<table>
<thead>
<tr>
<th>Number of Larvae</th>
<th>Fed only on the above-ground parts of the corn plant</th>
<th>Fed only on the roots of the corn plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average increase in mm. in diameter of head-</td>
<td>Average increase in mm. in diameter of head-</td>
</tr>
<tr>
<td></td>
<td>capsules of various instars</td>
<td>capsules of various instars</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>.335</td>
<td>.465</td>
</tr>
<tr>
<td>20</td>
<td>.279</td>
<td>.327</td>
</tr>
<tr>
<td>6</td>
<td>.255</td>
<td>.253</td>
</tr>
<tr>
<td>22</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* First instar
Duration of Instars - Two series of larvae (table 5) were examined daily and the time of molting determined for each individual. In this way it was possible to compare the duration of each instar as influenced by the type of food consumed, and by the number of instars.

Growth of Larvae as Indicated by the Increase in Diameter of Head Capsules - By means of a vernier caliper the diameters of the head capsules of 51 larvae were measured to the nearest hundredth of a millimeter for each instar (table 6). These data indicated that the total larval growth and also that of any individual instar was influenced by the number of instars. These factors were influenced also by the type of food consumed.

Pupal Stage - The average duration of the pupal stage for 1932, 1933, and 1934 was 11.3, 8.5, and 7.4 days respectively (table 4). The maximum was 24 days and the minimum 5.

Duration of Period from Oviposition to Adult - The duration of the incubation, larval, and pupal stages combined (table 4) gave the time required for the new generation to reach the adult stage. This period varied from 87 to 35 days. The average for the three years was 53.5, 48.3, and 52.9 days for 115, 87, and 28 individuals respectively.
The Second Generation

The second generation includes those individuals developing from eggs laid by first generation females, and has been observed only under insectary conditions.

**Incubation** - The duration of the egg stage for the three years (table 1) varied from 4 to 8 days. The usual time required for hatching was 4 days. The average for the three years was 4.9, 5.0, and 4.0 days for 1932, 1933, and 1934 respectively. The percentage of eggs which failed to hatch varied from 9.1 in 1932 to 28.0 in 1934.

Incubation records by months for 1932 and 1933 are shown in tables 7 and 8 respectively.

Table 7. - Incubation by months for second generation eggs of 1932.

<table>
<thead>
<tr>
<th>Month</th>
<th>Eggs Laid</th>
<th>Number hatched</th>
<th>Number failed to hatch</th>
<th>Percent failed to hatch</th>
<th>Incubation Period in Days</th>
<th>Min.</th>
<th>Max.</th>
<th>Aver.</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>181</td>
<td>157</td>
<td>24</td>
<td>13.3</td>
<td>4</td>
<td>6</td>
<td></td>
<td>4.6</td>
</tr>
<tr>
<td>Aug.</td>
<td>215</td>
<td>202</td>
<td>13</td>
<td>6.1</td>
<td>4</td>
<td>6</td>
<td></td>
<td>4.9</td>
</tr>
<tr>
<td>Sept.</td>
<td>33</td>
<td>31</td>
<td>2</td>
<td>6.1</td>
<td>4</td>
<td>8</td>
<td></td>
<td>5.9</td>
</tr>
<tr>
<td>Total</td>
<td>or Av.</td>
<td>429</td>
<td>390</td>
<td>9.1</td>
<td>4</td>
<td>8</td>
<td></td>
<td>4.9</td>
</tr>
</tbody>
</table>
Table 8. - Incubation by months for second generation eggs of 1933.

<table>
<thead>
<tr>
<th>Month</th>
<th>Eggs Laid</th>
<th>Number hatched</th>
<th>Number failed to hatch</th>
<th>Percentage failed to hatch</th>
<th>Incubation Period in Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>85</td>
<td>58</td>
<td>27</td>
<td>31.8</td>
<td>Min. 4, Max. 7, Aver. 4.6</td>
</tr>
<tr>
<td>Aug.</td>
<td>406</td>
<td>371</td>
<td>35</td>
<td>8.6</td>
<td>Min. 4, Max. 7, Aver. 5.0</td>
</tr>
<tr>
<td>Sept.</td>
<td>114</td>
<td>108</td>
<td>6</td>
<td>5.3</td>
<td>Min. 4, Max. 6, Aver. 4.9</td>
</tr>
<tr>
<td>Total</td>
<td>605</td>
<td>537</td>
<td>68</td>
<td>11.2</td>
<td>Min. 4, Max. 7, Aver. 5.0</td>
</tr>
</tbody>
</table>

Larval Stage - The duration of the larval stage for the second generation (table 4) varied from 89 to 22 days. The average for the three years was 38.1, 33.0, and 27 days for 1932, 1933, and 1934 respectively.

Pupal Stage - The duration of the pupal stage for the second generation (table 4) varied from a maximum of 52 days to a minimum of 6 days. The average for each of three years was 13.0, 14.7 and 8.0 days for 60, 51, and 1 individuals for 1932, 1935 and 1934 respectively.

Duration of Period from Oviposition to Adult - The number of days required for total development (from egg to adult) for second generation individuals (table 4) varied from a maximum of 115 to a minimum of 34. The average dur-
ation for each of the three years was 56.1, 52.7, and 39.0 days for 60, 51, and 1 individuals for 1932, 1933, and 1934 respectively.

Duration of Developmental Stages for Males and Females

A comparison of the duration of the various developmental stages for male and female individuals (table 9) indicated that slightly more time was usually required in all stages of the male sex. However, this was not always the case. For the second generation individuals of 1933 the mean duration for all stages of the females was greater than for males.

Table 9. - Comparative duration of various developmental stages for male and female individuals of 1932 and 1933

<table>
<thead>
<tr>
<th>Year</th>
<th>Generation</th>
<th>Number of Individuals</th>
<th>Sex</th>
<th>Total</th>
<th>Average</th>
<th>No. days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Larval stage</td>
<td>Pupal stage</td>
<td>Egg to adult</td>
</tr>
<tr>
<td>1932</td>
<td>First</td>
<td>52</td>
<td>Male</td>
<td>36.6</td>
<td>11.9</td>
<td>53.7</td>
</tr>
<tr>
<td></td>
<td>First</td>
<td>63</td>
<td>Female</td>
<td>37.4</td>
<td>10.7</td>
<td>53.4</td>
</tr>
<tr>
<td>1933</td>
<td>First</td>
<td>54</td>
<td>Male</td>
<td>34.6</td>
<td>8.5</td>
<td>43.6</td>
</tr>
<tr>
<td></td>
<td>First</td>
<td>33</td>
<td>Female</td>
<td>34.0</td>
<td>8.4</td>
<td>47.8</td>
</tr>
<tr>
<td>1932</td>
<td>Second</td>
<td>31</td>
<td>Male</td>
<td>39.9</td>
<td>15.5</td>
<td>58.4</td>
</tr>
<tr>
<td></td>
<td>Second</td>
<td>26</td>
<td>Female</td>
<td>36.3</td>
<td>12.0</td>
<td>52.9</td>
</tr>
<tr>
<td>1933</td>
<td>Second</td>
<td>25</td>
<td>Male</td>
<td>31.2</td>
<td>12.9</td>
<td>43.6</td>
</tr>
<tr>
<td></td>
<td>Second</td>
<td>26</td>
<td>Female</td>
<td>34.9</td>
<td>16.8</td>
<td>56.6</td>
</tr>
</tbody>
</table>
Ratio of Sexes

First Generation - Of 230 first generation adults, for which developmental records were kept, during the three years, 124 were males and 106 females. The ratio for different years varied slightly (table 4).

Second Generation - Of 112 second generation individuals, for which developmental data was kept, during the three years (table 4), 57 were males and 52 females.

Oviposition Studies

Method of Oviposition - Under field conditions the female assumes a position at the base of the corn plant and with the snout downward. By means of the chewing mouthparts on the tip of the snout, she feeds, moving slowly downward so as to produce an elongate cavity. When the plants are very small, this cavity may reach the heart or center, but in larger plants it only reaches through the outer sheath. The female then reverses her position, so that the abdomen is downward, and deposits her egg in the cavity, the edges of which later converge so that the only evidence that oviposition has occurred is an inconspicuous slit on the plant. After the ovipositing process has been completed the female seeks a new plant on which to feed or oviposit, or she may conceal herself under a clod of soil or debris for a period of time before repeating the ovi-
position process.

Sometimes in the insectary as many as two or three eggs have been deposited in the same cavity but this has not been observed in the field.

**Oviposition by Females Emerged from Field Hibernation.** - The adults began emerging from hibernation, usually, early in April and began ovipositing in the field as early as the size of the corn plants permitted. The average number of eggs laid (table 10) by 48 females, taken from the field in the spring of 1932, was 151.5. The average for 23 females in 1933 was 112. The maximum number laid by one female in one season was 370. The average number per day per female was slightly more than 1.5. The average postoviposition period was about 7.2 days.

**Oviposition by First Generation Females** - The duration of the preoviposition period for first generation females varied from 10 to 46 days. The average for each year (table 10) was 15.8, 24.7, and 14.5 days for 1932, 1933, and 1934 respectively. The average number of eggs laid per female during the season was 45.5, 54.8, and 13.5 for 10, 11, and 2 individuals for 1932, 1933, and 1934 respectively. The average number laid per day per female during the oviposition period was about 1.5. The average postoviposition period was about 8 days.
<table>
<thead>
<tr>
<th>Oviposition for Year Group</th>
<th>Number of females</th>
<th>Average number of eggs per female</th>
<th>Av. egg laying period in days</th>
<th>Av. eggs per female per day</th>
<th>No. days aver. Precvip. Postovip. period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932 F.C.S.*-1932</td>
<td>48</td>
<td>151.5</td>
<td>86.2</td>
<td>1.8</td>
<td>7.3</td>
</tr>
<tr>
<td>1933 F.C.S. -1933</td>
<td>23</td>
<td>112.0</td>
<td>74.5</td>
<td>1.5</td>
<td>7.2</td>
</tr>
<tr>
<td>1932 1st gen-1932</td>
<td>10</td>
<td>45.5</td>
<td>28.0</td>
<td>1.6</td>
<td>15.8</td>
</tr>
<tr>
<td>1933 1st gen-1933</td>
<td>11</td>
<td>54.8</td>
<td>36.9</td>
<td>1.5</td>
<td>24.7</td>
</tr>
<tr>
<td>1934 1st gen-1934</td>
<td>2</td>
<td>13.5</td>
<td>12.5</td>
<td>1.1</td>
<td>14.5</td>
</tr>
<tr>
<td>1933 1st gen-1932</td>
<td>12</td>
<td>77.0</td>
<td>61.2</td>
<td>1.3</td>
<td>8.0</td>
</tr>
<tr>
<td>1933 2nd gen-1932</td>
<td>4</td>
<td>77.0</td>
<td>59.3</td>
<td>1.3</td>
<td>8.5</td>
</tr>
<tr>
<td>1934 Misc. O.W.I.**</td>
<td>13</td>
<td>69.3</td>
<td>58.6</td>
<td>1.3</td>
<td>8.3</td>
</tr>
</tbody>
</table>

* F.C.S. = Field collected in the spring of 1932
** O.W.I. = Overwintered in the insectary.
Oviposition Recorded by Months - Oviposition for overwintered and first generation adults of 1932 and 1933 has been tabulated (table 11) by months. Groups A and B include overwintered individuals taken from the field in the springs of 1932 and 1933 respectively. Group C includes first generation insectary-reared individuals of 1932 which survived the winter 1932-33 in the insectary. Group D is composed of second generation insectary-reared individuals of 1932 which survived the winter 1932-33 in the insectary. Groups E and F include the first generation insectary-reared individuals of 1932 and 1933.
Table 11. - Oviposition recorded by months for field collected and insectary-reared adults of 1932 and 1933.

<table>
<thead>
<tr>
<th>Group No.</th>
<th>Ovip. record for</th>
<th>Number of females</th>
<th>Eggs of</th>
<th>Month</th>
<th>Total no. eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1932</td>
<td>48</td>
<td>1st.gen. 4</td>
<td>1580</td>
<td>2689</td>
</tr>
<tr>
<td>B</td>
<td>1933</td>
<td>23</td>
<td>1st.gen. 25</td>
<td>668</td>
<td>1086</td>
</tr>
<tr>
<td>C</td>
<td>1933</td>
<td>12</td>
<td>1st.gen.</td>
<td>350</td>
<td>356</td>
</tr>
<tr>
<td>D</td>
<td>1933</td>
<td>4</td>
<td>1st.gen.</td>
<td>143</td>
<td>130</td>
</tr>
<tr>
<td>E</td>
<td>1932</td>
<td>10</td>
<td>2nd.gen.</td>
<td>197</td>
<td>234</td>
</tr>
<tr>
<td>F</td>
<td>1933</td>
<td>11</td>
<td>2nd.gen.</td>
<td>95</td>
<td>385</td>
</tr>
<tr>
<td>Total</td>
<td>108</td>
<td>29</td>
<td>2741</td>
<td>4261</td>
<td>3134</td>
</tr>
</tbody>
</table>
Effect of Age and Hibernating Conditions on Fecundity of Females. - During the season 1933 oviposition records (table 12) were kept for three series of overwintered adults to determine the effect of age and hibernating conditions on fecundity. Females of group 1 were field collected in the early spring of 1933 as they emerged from hibernation. Females of group 2 were taken from an outdoor hibernation cage containing individuals which had survived two winters. Individuals of group 3 were carried over from the preceding season in their individual oviposition cages in the insectary. Most of the latter series were first and second generation adults reared in the insectary in 1932. A few of them had been field collected late in 1932.

The average number of eggs laid per female for groups 1, 2, and 3 was 112.0, 32.3, and 36.5 respectively.

Nearly 100 percent of all eggs laid by each group of females hatched.

Oviposition by Two-year Old Individuals - Twenty-five females which had survived two winters (1931-32 and 1932-33) were placed in cages early in 1933 for individual oviposition records. Fourteen of them died without ovipositing, and the remaining 11 laid an average of 32.3 eggs each. The average duration of the oviposition period was 22.6 days, the maximum 54, and the minimum 2. The average postoviposition period was 3.7 days. The earliest oviposition record was May 3 and the latest August 12.
Table 12. - Oviposition by three series of females which overwintered under various conditions.

<table>
<thead>
<tr>
<th>Ser No.</th>
<th>Year</th>
<th>Number</th>
<th>Total</th>
<th>Av. No.</th>
<th>Av. ovipos.</th>
<th>Av. eggs</th>
<th>Av. Post oviposition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1933</td>
<td>23</td>
<td>23</td>
<td>112.0</td>
<td>74.5</td>
<td>1.5</td>
<td>7.2</td>
</tr>
<tr>
<td>2</td>
<td>1933</td>
<td>11</td>
<td>14</td>
<td>32.3**</td>
<td>22.0**</td>
<td>0.5**</td>
<td>3.7**</td>
</tr>
<tr>
<td>3</td>
<td>1933</td>
<td>23</td>
<td>0</td>
<td>86.5</td>
<td>59.9</td>
<td>1.4</td>
<td>11.6</td>
</tr>
</tbody>
</table>

*1. - Field collected in the spring 1933

2. - Two-year old individuals taken from outdoor hib. cage. 1933.

3. - Overwintered in insectary 1932-33

** - Includes only 11 females which oviposited.
Comparison of Oviposition in Field and Insectary

In the insectary all eggs were laid in sections of corn plants which were about one-quarter inch in diameter, fresh sections being used each day. It was desired to compare the rate of oviposition under insectary conditions with that of field conditions, where the eggs are deposited directly in the growing plant. On July 18, 1933 I selected from the insectary 4 females, each of which had been ovipositing at about the same rate. Two of them were removed to the field where they were caged with a new plant each day, and the other two continued to oviposit in the insectary. During 11 days the females in the field laid an average of 2.2 eggs per day each, and those in the insectary averaged 1.9 eggs per day each.

Time of Day at which Oviposition Occurred

On May 29 and 30, 1933, 4 female billbugs in the insectary were under observation (for 24 hours) in order to determine the relative percentage of eggs laid at night and in daylight. At intervals of two hours, examinations for oviposition were made and a fresh piece of corn added for oviposition during the next two hours. During the 24 hours the 4 individuals laid a total of 14 eggs, 7 of which were laid between 4:00 P.M. and 4:00 A.M., and 7 between 4:00 A.M. and 4:00 P.M. Those laid during the night period were oviposited as follows: 6:00 P.M. - 1, 10:00 P.M. - 3, 12:00
Midnight - 1, 2:00 A.M. - 1, 4:00 A.M. - 1.

Similar records for 2 females June 6 to 8, 1932 show that a total of 25 eggs were laid as follows: 11 between 6:00 P.M. and 8:00 A.M.; 14 between 8:00 A.M. and 6:00 P.M.

From these observations it seems that oviposition occurs about equally during the day and night.

_Earliest Seasonal Records for the Various Stages in Field and Insectary_

The dates on which the first adults, eggs, larvae and pupae were observed in the field and insectary were recorded (table 13) for each year. First generation eggs as recorded here were oviposited by adults collected from the field for that season.
Table 13. - Comparison of earliest seasonal records for the various stages of billbug in field and insectary

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1932</td>
<td>Field</td>
<td>April 27</td>
<td>July 20</td>
<td>*</td>
<td>May 15</td>
<td>May 16</td>
<td>-</td>
<td>July 19</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Insectary</td>
<td>-</td>
<td>June 25</td>
<td>Aug. 15</td>
<td>Apr. 29</td>
<td>July 9</td>
<td>May 8</td>
<td>July 13</td>
<td>June 20</td>
<td>Aug. 8</td>
</tr>
<tr>
<td>1933</td>
<td>Field</td>
<td>April 3</td>
<td>July 7</td>
<td>-</td>
<td>Apr. 14</td>
<td>No</td>
<td>-</td>
<td>July 1</td>
<td>record</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Insectary</td>
<td>-</td>
<td>June 11</td>
<td>Aug. 27</td>
<td>Apr. 15</td>
<td>July 8</td>
<td>Apr. 30</td>
<td>July 14</td>
<td>May 31</td>
<td>Aug. 21</td>
</tr>
<tr>
<td>1934</td>
<td>Field</td>
<td>April 9</td>
<td>July 20</td>
<td>-</td>
<td>No</td>
<td>-</td>
<td>No</td>
<td>-</td>
<td>July 12</td>
<td>record</td>
</tr>
<tr>
<td></td>
<td>Insectary</td>
<td>-</td>
<td>July 14</td>
<td>Sept. 10</td>
<td>May 4</td>
<td>Aug. 2</td>
<td>May 19</td>
<td>Aug. 6</td>
<td>July 5</td>
<td>Sept. 2</td>
</tr>
</tbody>
</table>

* No second generation has been recorded in the field.
These records indicate that the life history in the insectary was usually slightly more advanced than that in the field.

The field records are somewhat less accurate than those for the insectary, since it was not possible to make daily examinations of large quantities of material in the field. However, such examinations were made each week.
Overwintering Habits

The billbug was found overwintering only in the adult stage in South Carolina. When the adults emerge from the pupae in the field they usually remain in their cells, which may be in the tap root, just outside among the lateral roots, or in the soil just under the roots, where they pass the winter. A few newly developed individuals which emerge and feed late in the summer, and those old spring emerged adults which are still living at hibernation time, probably work their way into a depression or crevice in the soil or under masses of debris where they pass the winter. When the soil is not extremely packed and hard, the beetles will burrough downward for several inches.

Winter Survival and Spring Emergence

Winter Survival of Adults in the Insectary 1932-33—All billbugs in the insectary (used for oviposition records for 1932) which were alive the last of October, were left in their individual oviposition cages to overwinter. Some of them were individuals which had been collected from the field in the spring of 1932, and some were first and second generation individuals of 1932. The numbers of males and females of each group which successfully survived the winter in the insectary are recorded in table 14.

The total average percentage of survival for the
three groups was 35.3.

Table 14. - Winter survival of adults in the insectary - 1932-33.

<table>
<thead>
<tr>
<th>Group</th>
<th>Number of Adults living Oct. 29, 1932</th>
<th>Number of Adults living Apr. 4, 1933</th>
<th>Percent of total surviving adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males Fem. Total</td>
<td>Males Fem. Total Total</td>
<td></td>
</tr>
<tr>
<td>Field coll. in spring-1932</td>
<td>21 25 56</td>
<td>4 9 13</td>
<td>23.2</td>
</tr>
<tr>
<td>First generation -1932</td>
<td>34 47 81</td>
<td>15 19 34</td>
<td>42.0</td>
</tr>
<tr>
<td>Second generation -1932</td>
<td>8 8 16</td>
<td>4 5 9</td>
<td>56.3</td>
</tr>
<tr>
<td>Total or mean</td>
<td>63 80 153</td>
<td>23 33 54</td>
<td>35.3</td>
</tr>
</tbody>
</table>

Comparison of Winter Survival in Insectary and Field - In November 1933 there were 38 adults of the first generation and 34 of the second generation (of 1933) alive in the insectary. It was desired to keep these individuals until the following season when their oviposition records could be continued. The males and females of each generation were divided approximately into two equal groups. One group of each generation was left in the insectary to overwinter in their respective oviposition cages. The other groups were placed (by pairs) in cylindrical screen cages (3"x5") which were filled with soil and placed just below the soil surface in the field. The cages were fitted closely together,
resting upon a large piece of screen wire in the bottom of the hole, and covered by another piece of wire. In this type of cage the beetles could hibernate at a depth of 1 to 5 inches below the surface of the soil, which condition closely approximated natural field hibernating conditions.

The percentage of winter survival (table 15) was appreciably higher for the field cages than for the insectary cages.

Table 15. - Comparison of winter survival in the insectary and field.

<table>
<thead>
<tr>
<th></th>
<th>Number of Adults</th>
<th></th>
<th></th>
<th>Percent of total adults surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1933</td>
<td>Placed in hibernation cages</td>
<td>Emerged from hibernation in November 1933</td>
<td>in 1934</td>
</tr>
<tr>
<td>Overwintered</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insectary First</td>
<td>9 9 18 3 4 7</td>
<td>39.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field First</td>
<td>10 10 20 6 7 13</td>
<td>65.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insectary Second</td>
<td>11 11 22 5 3 8</td>
<td>36.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field Second</td>
<td>5 7 12 3 6 9</td>
<td>75.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Spring Emergence of Two-Year Old Individuals - In the spring of 1932, 730 adults were collected from the field at the time they were emerging from winter quarters. They were kept and fed all during the active season in a large screen field cage. They were kept in this cage during the winter 1932-33. The time and percentage of emergence was determined the following spring (1933).

The earliest emergence was April 6. The percentage of the total emergence by months was as follows: April - 52.85%; May - 47.15%. The last emergence was May 18. The total number emerging was 125, or 16.84% of the total number placed in the cage the preceding spring.

In the spring of 1933, 484 overwintered individuals were taken from the field and kept in the hibernation cage until the following spring (1934). Only one individual (male) survived and emerged in 1934. This one emerged May 23.

Longevity of Second Year Adults

The duration of life for 25 females in 1933, after emerging from their second winter of hibernation, varied from 5 to 73 days. The average was 29.8 days. For 15 males the duration of life varied from 9 to 57 days, with an average of 26.8.
Longevity of Beetles Without Food in the Spring -
To determine the longevity of adult billbugs without food, an experiment was conducted as follows: Two cages were prepared by placing two lantern globes (10 inches in diameter and 12 inches in height) over pans of soil. Sixteen beetles (8 males and 8 females) were taken from an outdoor hibernation cage April 28, 1933 and placed in cage 1. These individuals had survived two winters (first in the field and second in the hibernation cage) and had not fed since October 1932. In cage 2 were placed 8 males and 8 females collected directly from the field (where they were feeding on corn) April 28, 1933.

The beetles in each cage were confined without food until their death, the date of which was recorded.

Water, on a piece of absorbent cotton, was furnished for the insects to drink. The soil in the cages was also kept in a moist condition.

The average, maximum, and minimum durations of life, after being placed in cages 1 and 2, were recorded (table 16) for both sexes of each group.

For the two-year old individuals (cage 1) the duration was 18.9 days for males and 15.6 days for females. For those collected from the field the average was 36.5 days for males and 52.0 for females.
Table 16. - Longevity of beetles with and without food in the spring.

<table>
<thead>
<tr>
<th>Cage Treatment</th>
<th>Males</th>
<th></th>
<th></th>
<th>Females</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of</td>
<td>Duration of life</td>
<td></td>
<td>No. of</td>
<td>Duration of life</td>
<td></td>
</tr>
<tr>
<td></td>
<td>uals</td>
<td></td>
<td></td>
<td>uals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>* Fed on corn</td>
<td>15</td>
<td>57 9 26.8</td>
<td>25 73 5 29.8</td>
<td>8</td>
<td>23 7 18.9</td>
<td>8 31 8 15.6</td>
</tr>
<tr>
<td>1 No food</td>
<td>8</td>
<td>23 7 18.9</td>
<td>8 31 8 15.6</td>
<td>23</td>
<td>- - -</td>
<td>23 - - 81.7</td>
</tr>
<tr>
<td>** Fed on corn</td>
<td>-</td>
<td>- - -</td>
<td>23 - - 81.7</td>
<td>8</td>
<td>61 16 36.5</td>
<td>8 104 31 52.0</td>
</tr>
<tr>
<td>2 No food</td>
<td>8</td>
<td>61 16 36.5</td>
<td>8 104 31 52.0</td>
<td>-</td>
<td>- - -</td>
<td>- - -</td>
</tr>
</tbody>
</table>

* Beetles having survived two winters, included here for comparison with cage 1.

** Beetles collected from the field in the spring of 1933 and kept in oviposition cages (see table 10); included here for comparison with cage 2.

For the sake of comparison, I have included in table 17 the duration of life (after emergence from hibernation) for individuals which had the same history (same as for cages 1 and 2) previous to the time of this experiment, but which were not subjected to starvation. See notes accompanying table 16.
MISCELLANEOUS STUDIES OF THE ADULT

Seasonal Increase in Field Population

The relative field population during the period of spring emergence was determined in two ways as follows: first (1932), by collecting beetles in a particular section of a field for a definite period of time, and second (1933), by counting (not collecting) all beetles found active on a definite area at a definite hour of the day.

In 1932 a severely infested field was selected for making population studies. Beginning May 3, counts were made at intervals of 5 or 7 days on approximately the same area. For each count, one hour was spent in collecting all the beetles which were active. The counts were as follows: May 3-17, May 10-40, May 17-84, May 24-140, June 2-65, and June 7-60.

The marked decrease in population for the last two counts was due, partially at least, to the number of beetles picked off on the preceding dates.

In 1933 four rows were selected in an infested field for determining the range in seasonal population. At intervals of several days the beetles observed on these four rows were counted but were not removed from the plants. Three counts made during the week of April 28 to May 5 revealed a total of 12 adults. Two counts in the week of May 5 to 11 revealed a total of 90 individuals, and one count May 18 revealed 126 active beetles.
Activity of Beetles in the Field at Various Hours During the Days - When making field collections of beetles it was noted that in a given field many more individuals could be found active at certain times during the day than at others. To determine the periods of greatest activity during the day, one row was selected in an infested field, for making observations.

Beginning at 6:00 A.M. May 29, 1933 and continuing until 6:00 A.M. May 30, the number of beetles found active on this row every two hours was recorded (table 17). A flashlight was used for making counts during the night.

Table 17 - Activity of beetles in the field at various hours during the day.

<table>
<thead>
<tr>
<th>1933 Date</th>
<th>Time of day</th>
<th>Number of billbugs active</th>
<th>No. under slats</th>
<th>Temperature: degrees Fahrenheit</th>
<th>Light conditions</th>
<th>Weather conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 29</td>
<td>6 A.M.</td>
<td>6</td>
<td>-</td>
<td>70</td>
<td>Just after sunrise</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>8 A.M.</td>
<td>2</td>
<td>0</td>
<td>78</td>
<td>Bright</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>10 A.M.</td>
<td>38</td>
<td>0</td>
<td>85</td>
<td>Bright slightly cloudy</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>12 Noon</td>
<td>17</td>
<td>4</td>
<td>78</td>
<td></td>
<td>slightly cloudy</td>
</tr>
<tr>
<td></td>
<td>2 P.M.</td>
<td>11</td>
<td>6</td>
<td>88</td>
<td>Bright</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>4 P.M.</td>
<td>9</td>
<td>1</td>
<td>88</td>
<td>Bright</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>6 P.M.</td>
<td>7</td>
<td>3</td>
<td>84</td>
<td>Bright</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>8 P.M.</td>
<td>16</td>
<td>4</td>
<td>79</td>
<td>Dusk</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>10 P.M.</td>
<td>5</td>
<td>7</td>
<td>75</td>
<td>Half-Moon shining</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>12 M.N.</td>
<td>0</td>
<td>8</td>
<td>73</td>
<td>Half-Moon shining</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>2 A.M.</td>
<td>3</td>
<td>9</td>
<td>71</td>
<td>Moon going down Day</td>
<td>Fair</td>
</tr>
<tr>
<td></td>
<td>4 A.M.</td>
<td>7</td>
<td>4</td>
<td>70</td>
<td>breaking</td>
<td>Heavy fog</td>
</tr>
</tbody>
</table>
The maximum number of individuals active at any one time was 38 at 10:00 A.M. The second and third largest active populations were 17 and 16 individuals at 12:00 Noon and 8:00 P.M. respectively. At least 2 or more beetles were active at the time of every examination with the exception of 12:00 Midnight, at which time none were found.

The following notes were made on conditions occurring at the time the above observations were made: The row of corn on which counts were made was 130 yards long and consisted of 338 plants, many of which had been injured by billbugs prior to this time. Rain had fallen about 36 hours previous. The temperature range (table 16) during the 24 hours was 70 to 80 degrees Fahrenheit. The weather was fair with the exception of a few clouds in the sky at noon May 30. There was a half-moon which set at 2:30 A.M.
**Flying Ability** - The corn billbug has practically lost the use of its wings as organs of flight. It has never been observed in flight in the field during the several years of study at Florence.

In June 1932 an experiment was conducted to determine whether or not the billbug was capable of flying. Six adults were placed in a glass dish 5 inches in diameter and 1 inch deep, the side being nearly vertical. At mid-day they were placed in direct sunlight. After two hours, two of the beetles were dead, and none had succeeded in escaping. The four individuals surviving this treatment were again placed in the sun a few days later. After a few hours all four beetles had died in the dish.

June 22 at 11:00 A.M. six normal beetles were placed in the same dish and exposed to the direct sun rays. The temperature in the insectary at this time was 89 degrees fahrenheit. During the first two or three minutes of exposure the insects were extremely active, crawling rapidly about in an attempt to escape from the hot dish, but none of them succeeded. All six of the beetles were dead after five minutes.

Several other groups of individuals subjected to similar treatment during the season showed the same results.

June 22, 1932 at 11:20 A.M. one billbug which was confined in the insectary in a glass lantern-globe cage 8 inches in diameter, was observed to spread its wings and
fly the distance across the cage. A few days later I observed two other individuals fly the distance across a similar cage. One of these beetles was removed to the glass dish in direct sunlight. It spread its wings on two occasions in an attempt to fly but failed to clear the sides of the dish. Death occurred after five minutes. On this occasion a piece of paper was placed in the bottom of the dish to prevent burning of the insect by contact with the hot glass. The paper also furnished a firmer footing for the beetle in its attempts to fly.

On several other occasions beetles were observed to fly 5 or 6 inches across their cages.

The corn billbug was never taken on insect flight screens, which were maintained for insect records during the three years. Occasionally specimens of other billbug species were taken.

**Drowning Experiments** - In 1933, three drowning experiments, beginning May 8, June 9, and July 24 respectively, were conducted for adult billbugs. Since the beetles hibernate in soils which frequently are covered by water for prolonged periods during hibernation, it was deemed desirable to study their resistance to total submersion in water. The author appreciates the fact that the reactions of the insects to such treatment will doubtless vary considerably with the season of year, nevertheless,
the experiments show some interesting data.

For the first experiment (began May 8) 50 beetles were completely submerged in plain tap water. This was accomplished by inverting a jelly glass over the beetles in a battery jar filled with water. Five individuals were removed from the water each day (beginning the day after the experiment began) until all had been removed. In all cases the insects appeared dead when first removed from the water, but they usually showed signs of life within a few hours after being removed, unless they were really lifeless. All those removed within 4 days after submergence became active again within 24 hours after removal. Of those removed on the fifth day, 4 survived; on the sixth day, 3 survived; on the seventh day and afterward, none survived. Those females taken from the water before and through the fifth day after submergence, began ovipositing after reviving.

For the second experiment, two series of 25 beetles each were used. Series number 1 was submerged in a battery jar of plain tap water as in the first experiment, and series number 2 was submerged, 5 each, in 25 x 70 millimeter glass vials filled with water which had been boiled in order to expell the oxygen. The vials were kept airtight by means of rubber stoppers so as to prevent the entrance of fresh air. The beetles were removed (5 each day) from the water just as in experiment No. 1, except that none were removed until after 3 days submergence (table 18). After 3 days, all 5 beetles of series 1 survived, while 4
of series 2 survived; after 4 days, 5 of series 1 survived; while only 2 of series 2 survived; after 5 days, 4 of series 1 survived, while only 1 of series 2 survived; after 6 and 7 days respectively, 3 of series 1 survived, while none of series 2 survived. Those females of series 1 which survived 7 days submergence began ovipositing within 24 hours after being removed from the water.

The third drowning experiment (begun July 24) included two series of 40 billbugs each. Series 1 was submerged in a jar of plain tap water, and series 2 was buried under 1 inch of soil in a dish and covered with tap water. A piece of screen wire was weighted down over the soil to prevent the insects' rising to the surface for air. Beginning the second day after submergence, 5 or 10 beetles were removed from the water in each series either every day or every two days (table 18). After 2 days submergence 4 out of 5 in series 1 survived, also 4 out of 5 in series 2 survived; after 3 days, 2 out of 5 of series 1 survived, and 4 out of 5 of series 2 survived; after 5 days, none of series 1 survived, and only 1 of series 2 survived. All those in both series removed after the fifth day were dead.
Table 13. - Drowning experiments 2 and 3.

<table>
<thead>
<tr>
<th>Experiment number</th>
<th>Date submerged</th>
<th>Removed from each series</th>
<th>No. surviving Series No.</th>
<th>Duration of submergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Date</td>
<td>No.</td>
<td>1</td>
</tr>
<tr>
<td>2*</td>
<td>June 9</td>
<td>June 12</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>&quot; 9</td>
<td>&quot; 13</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>&quot; 9</td>
<td>&quot; 14</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>&quot; 9</td>
<td>&quot; 15</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>&quot; 9</td>
<td>&quot; 16</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>July 24</td>
<td>July 25</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>&quot; 24</td>
<td>&quot; 27</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>&quot; 24</td>
<td>&quot; 29</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>&quot; 24</td>
<td>&quot; 30</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>&quot; 24</td>
<td>&quot; 31</td>
<td>10</td>
<td>0</td>
</tr>
</tbody>
</table>

* Series 1 - Submerged in tap-water
Series 2 - " " air-free water (boiled)

** Series 1 - Submerged in tap-water
Series 2 - " " soil (covered by water)

In June 1932 a drowning experiment similar to those just described was conducted. Sixty adults were submerged in a jar of plain tap water June 9. Beginning June 16, several individuals were removed from the water each day for a period of 14 days. Only one beetle out of 60 completely revived. This one had survived after being submerged for 7 days. It was apparently dead at the time of removal from water, but revived within 24 hours. One beetle taken from water on the 12th day of submergence, and another on the 14th day showed slight involuntary movement of the appendages within 24 hours after removal from water but they never completely revived.
Sense of Direction Exercised by Adults in Locating Corn. - (Experiment 1). - The purpose of this experiment was to learn whether or not beetles emerging from hibernation show any marked ability to locate their host plants.

The observation took place in a shaded area at about 2:00 P.M. May 25, 1933. The temperature was about normal for that season of the year. One male and one female were taken from an outdoor hibernation cage, where they had passed the winter. They had not fed since the previous October. The two beetles were apparently of normal vigor at this time. They were now placed at the extreme edge of a metal cylinder (3 inches in height and 18 inches in diameter) in the center of which was a vigorous corn plant (12 inches in height). The actions of the insects were observer and recorded for 72 minutes.

The male, after remaining inactive for 5 minutes, began crawling toward the corn plant. It crawled for a short distance and stopped for a moment, but within 1 minute after starting, the insect reached the plant and began an attempt to feed. The beetle was immediately removed to the extreme east edge of the cylinder, from which it again began moving toward the corn. Its journey was characterized by short periods of forward movement alternated frequently with several minute periods of inactivity. The route this time was not direct, the beetle sometimes turning to the right or left for about half an inch and then turning back toward the plant. This time the beetle required 16
minutes to reach the corn. Two other similar journeys were made in succession from the north and south edges of the cylinder. These trips required 13 and 32 minutes respectively.

The female, almost immediately after being released at the west edge of the cylinder, crawled about 3 inches in the direction of the corn. From this point the beetle turned and wandered back to the side of the cylinder, where it traveled back and forth (occasionally pausing for a few minutes), never leaving the edge more than 2 or 3 inches, for 72 minutes. During that time the female did not travel completely around the plant but spent most of the time pacing back and forth along the north and east sides. Not once did the insect appear to have sensed the presence of the plant.

**Experiment 2** - On June 29, 1932 a different type of experiment was conducted to learn whether or not billbugs are attracted to the corn plant.

A circular hole one-half inch in diameter was cut in each end of a shallow cardboard box (8 inches by 10 inches). Two dark paper tubes 15 inches in length were inserted in the holes at the ends of the box. Two shell vials (25 x 70 mm.) were fitted over the outer ends of the tubes. One vial contained a fresh section of corn plant while the other was empty. Four adult beetles (which had not fed for 7 days) were placed in the center of the box, which was covered tightly to exclude sunlight. Five
minutes later 3 of the beetles had entered the vial containing the corn. The other one had entered the empty vial. The procedure was then repeated in the same manner (with the same beetles) except that the vial with the corn was located on the opposite side of the box. Within 5 minutes 3 of the beetles had again entered the vial with the corn, while the fourth one entered the empty vial. Later in the same day 10 other adults, which had not been previously starved, were placed in the dark box. During the next half hour none of them entered either vial, but after an hour, 4 beetles were observed in the vial containing corn, while only one was in the empty vial.
INJURY TO CORN

Injury by the Adult. - The beetles fed and deposited their eggs in corn, usually at the base of the plants, from the time it came up until it was practically mature. The most serious injury was incurred from the time the plants came up until they were about pencil-size in diameter. During this time the mouthparts of the adult, when feeding, reached the heart or center of the small plants, thus causing the growing point to wither and die. Plants thus injured became stunted and gave rise to suckers, which gave the plant a bunchy, ragged appearance. When eggs were deposited in the plants, the adult feeding-injury was followed by injury of the larva, which tunneled its way through the main root. In some cases the injured plant grew lop-sided and was left lying on the ground where it was likely to be broken-off in cultivation. Such plants never produced ears.

Soon after the plants were about pencil-size in diameter the adult beetle could no longer reach the heart of the plant with its mouthparts, and the feeding injury was not serious. At this stage the plants usually out-grew the injury, which was evidenced only by several rows of characteristic oblong holes in the leaves. These plants, when no eggs had been laid, usually grew normally throughout the season and produced ears.

Injury by the Larva. - Upon hatching the small legless grub was completely surrounded by its food and
began feeding almost immediately. Since the larva does not go from plant to plant, each individual developing to maturity obtained all of its food in the root of one plant. Quite a large cavity was eaten in the base of the plant by the time the larva reached maturity. The larva frequently tunneled several inches up and down the plant, near the surface of the ground, thus decreasing its vitality to such an extent that the plant became discolored and stunted and often failed to produce an ear.

**Comparison of Male and Female Injury** - Both the male and female incurred considerable injury to seedling corn. Injury by the male was incurred only when feeding, while that of the female was done at the time of feeding and also oviposition. Plants injured by the male only, recovered much more readily than those in which the female deposited her egg (and larval injury followed). The female not only incurred more fatal injury, but she also attacked a much greater number of plants in a given time. This was shown by caging 5 individuals of each sex separately in two outdoor screen cages, each of which covered 50 growing seedlings. Several examinations made from day to day showed that the females injured about twice as many plants per day as the males. At the end of 11 days, 14 plants had been injured in the male cage and 32 in the female cage. A few weeks later the difference in injury in the two cages was even more pronounced (figure 2).
Figure 2. Comparison of corn exposed to attack by male and female beetles - 1933.

Left: Five males caged with 50 Plants when 3 inches high.

Center: Five females caged with 50 Plants when 3 inches high.

Right: Check - free of injury.

Photographed in July, when plants were about 5 weeks old.
Those plants in which eggs were laid and the larvae began feeding in the roots, usually remained stunted and dwarfed during the growing season. Plants injured by the male only, usually recovered (except when the bud was killed) and developed normally throughout the season.
Destruction of Successive Plantings in an Infested Field - One field under observation in 1933 was severely attacked by the beetles just after the corn began coming up (April 18). By May 11 it was estimated that 72.86 percent of the plants had been injured. The beetle population on one row under observation had increased during May, as shown by actual counts, as follows: May 2-3, May 3-7, May 9-76, May 18-126. By June 6 there was an average of 1 beetle for each 2.36 plants in the field.

At this time the destruction of the crop was so complete (figure 3), the corn was plowed up. A second planting was made June 13. By June 30 billbug injury, supplemented by that of several other pests, was so severe that the corn was again plowed up.

A third planting was made on July 1. For a few days after this planting began coming up it seemed that serious injury would possibly be avoided, but shortly afterward the billbugs, cutworms and other insects attacked the seedlings vigorously. The crop was again plowed up July 27 and the field planted to a cover-crop.

Injury to Plantings of Various Dates - To determine the relative degree of injury to early and late plantings of corn, several plots in an infested field were seeded on April 3, April 18, April 25, May 5, May 25, and June 5 successively. The plantings were designated 1,2,3,4,5 and 6 respectively. Weekly observations were
Figure 3. Almost complete destruction of a field in Florence County by the corn billbug - 1933.
Planted April 2
Photographed June 2, 1933.
made for determining the severity of the injury. Records through July 6 showed that the percentage of plants injured in each planting was 28.6, 73.89, 52.94, 52.33, 53.85, and 80.00 percent for numbers 1, 2, 3, 4, 5 and 6 respectively. The earliest planting received far less injury than the later ones.

**Injury by an Artificial Infestation in a Field of Late Corn** — About July 1, 1933 corn was planted, following small grain, in an area of billbug-free land. On July 25, 15 male and 16 female billbugs were released in a space of 5 yards on one row in the center of the field. There were 35 plants (12 inches in height) on the 5 yards.

On September 21 (7 weeks later), when the corn had completed its development, an examination was made to determine the injury incurred by the artificial infestation. It was very noticeable that within an area of 15 to 20 yards in each direction from the point of original infestation severe injury had been done. The plants which now remained alive on a 25 yard section of rows 1, 2, 3, 4, and 5, of which row 3 was the center and the one receiving the infestation, were counted and recorded as follows: row 1-39; row 2-27; row 3-13; row 4-31; row 5-32. The 25 yard sector of each row extended, on each end, 10 yards beyond the 5 yard area of original infestation. Little injury was evident beyond this limited area.
STUDIES IN CONTROL

Rotation - A crop rotation in which corn is followed by such crops as cotton, tobacco and legumes, which are not attacked by billbugs, is by far the most effective measure in preventing injury.

One field under observation in 1933 presented an excellent example of the value of rotation. Part of the field, which had been planted in corn for the past several years, was severely injured by the pest. The remainder of the field (adjoining the former), which had been planted in cotton the preceding year, was practically free of injury. On May 23, when the corn was about 15 inches in height, a count of 1757 plants in the heavily infested area revealed 37.7 percent injury, while a count of 2024 plants in the adjoining section revealed only 1.3 percent injury.

Time of Planting - In South Carolina early planting was usually a very important factor in control. Corn planted the latter part of March or the first of April, under favorable seasonal conditions, usually attained sufficient growth before large numbers of hibernated beetles emerged, that it received appreciably less injury than corn planted later.

Whenever possible the time of planting factor should be combined with crop rotation.
Trap-rows - Beetles emerging from hibernation in the spring, tended to congregate and remain indefinitely on the first corn with which they came in contact. This habit made it possible to check their migration from infested to uninfested fields by sowing a strip of land (2 or 3 feet wide) in corn early in the season, between the two areas. Whenever this trap-row was used, the migration of beetles was almost invariably checked for a sufficient period of time for the corn thus protected to attain sufficient growth to insure a minimum degree of injury.

In 1933 an uninfested area, which was devoted to corn variety studies, was very efficiently protected from billbug migration (from an adjoining infested field) by a trap-row. A strip of land (about 2 feet in width) between the two fields was sowed thickly with corn. It was sowed at the time the variety plantings were made (March 30). The rows in the variety field ran perpendicular to the trap-row. The adjoining infested field had been planted to corn for several preceding years and was a potential source of infestation. This year it was planted to corn April 13.

Observations revealed that by the latter part of April, the trap-row and the infested field were being severely injured by the beetles, while the variety field was almost free of injury. On May 11, 66.7 percent of 828 plants examined in the infested field were injured, while only 4.8 percent of 525 plants on the proximal sec-
tions of the variety rows were injured. By this time the corn was advanced sufficiently that very little further injury was incurred.

**Handpicking** - During the season 1933, the beetles were handpicked from part of a check-row (between two fields of corn) to determine the value of handpicking as a supplement to the trap-row. The results revealed that handpicking did not appreciably increase the efficiency of the trap-row.

In small areas, such as garden plots, handpicking may be found an effective measure of control, but this method would be impractical on large areas.
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Figure 4. Trap-row planted between an uninfested area (left) and an infested area (right) to check migration of beetles - 1933. Photographed June 2.
Collecting Beetles from an Artificially Supplied Concealment - When the adults were not feeding or ovipositing they usually remained concealed under clods of soil or some kind of debris in the field. It was observed that at certain periods during the day a large percentage of the population in the field could be collected from under wooden slats or boards laid along the rows of corn.

In a heavily infested field, on May 29, 1933, a series of wooden slats, four inches in width and five feet in length, were placed along a 25 yard section of one row. The slats were arranged alternately on each side of the row so that one was near each plant. Every two hours during the day and night the slats were turned over and the number of beetles found concealed under them was recorded (table 17).

It was estimated that there were a total of 14 beetles present along this 25-yard section of the row. The greatest number found under the slats at one time was 9 at 2:00 A.M., e.g. 64.3 percent of the total number estimated to be present on that area.

The field in which the above observations were made was somewhat freer of clods and miscellaneous debris than the average billbug infested field, thus providing less natural concealment for the beetles. This condition doubtless increased the effectiveness of the slats to some extent.


A Ditch as a Barrier to Migration - In 1933 a ditch, 12 feet deep and 6 feet wide separated two fields of corn. One field, at the time of planting (first week in April), was uninfested with billbugs, while the other was heavily infested with hibernating beetles. A wooden bridge 15 feet wide spanned the ditch at the extreme south edge of the two fields.

Frequent observations were made during the season to determine whether or not the beetles would succeed in migrating across the ditch into the uninfested field. Previous to May 10, there was no evidence of billbugs in this field, but after that time a few beetles and injured plants were found on the ends of several rows nearest the bridge. At other points along the ditch there was practically no injury. About the middle of May 11, 2 percent of 322 plants observed in an area nearest the bridge revealed injury, while only 1.4 percent of 370 observed a short distance from the bridge were injured.

Toxicity of Lead Arsenate to the Adult. - On two occasions during the summer 1933 arsenate of lead and lime dust (1-2) was thoroughly dusted on several small corn plants while wet with dew. Several male and female beetles, which were confined with the plants, proceeded to feed and oviposit normally. Examinations during several succeeding days revealed no fatal effects to the beetles.
Toxicity of Sulfuric Acid Fumes to the Adult. - On June 2, 1933 sulfuric acid fumes were being blown by an electrical fan, through a 12 inch pipe, from a hood in the chemical laboratory, where nitrogen determinations were being made. The fumes proved exceedingly offensive to men working in the insectary 40 yards away. To determine the toxicity of the fumes to billbugs, 5 individuals were placed in each of two small screen-wire cages. One was suspended directly over the mouth of the exit through which the gases were escaping, while the other was suspended 5 yards distant (in a tree) but directly in the draft of fumes. After 45 minutes exposure the cages were removed and examined. All of the beetles were quite active and apparently in normal condition. On the following day they were all apparently still normal.

Natural Enemies - In the field several beetles were found with all six legs tightly bound by a web, which was evidently that of a spider. However, no spiders were observed in the process of tying, nor taken near the victims.

On several occasions, in the insectary, mites were found crawling over the billbug eggs which were being incubated in tin boxes with moist plaster of paris. The origin of the mites and their relation, if any, to the eggs was not determined.

Domestic chickens were observed eating adult
billbugs in the field on several occasions, but were probably of little importance in control.

Several species of Carabid beetles and at least one species of Dermaptera were taken from burrows in corn roots where dead billbug larvae or pupae were found. Although they were never actually observed preying on the pest, it seemed likely that this sometimes occurred.
SUMMARY

The corn billbug occurs in most of the counties in the eastern part of South Carolina, where it often causes serious injury to corn.

Only one generation was observed under field conditions, however a second generation occurred in the insectary when succulent food was provided throughout the season.

The adults emerged from hibernation during April and May, and oviposited in the corn plants all during spring and summer.

Each individual completed its entire development in the root of a single corn plant. The total developmental period for the first generation in the insectary averaged about 53 days during the three years. There were 3 to 6 larval instars. The number of instars influenced the total larval growth and also the growth of each instar for any individual.

In the field, adults which transformed from the pupal stage usually remained in the soil to pass the winter.

In the insectary, larvae which were fed only on the root of the corn plant required several days longer to complete their development than larvae fed on the above ground parts of the plant.

Life history activities in the field were usually somewhat behind those in the insectary.
Of 343 individuals reared to maturity in the insectary, 53 percent were males and 47 percent females.

The maximum number of eggs laid by one female was 370. The average for spring emerged females was about 135.

Although oviposition occurred from April to October, most eggs were laid in May, June and July.

Many females survived the second winter of hibernation and laid eggs the following spring, but these individuals usually died within a few weeks after emerging. A large percent of them died without ovipositing.

The period of greatest daily activity of the adults was from 9 to 11 A.M. However, some individuals were found active at nearly every hour during the day and night. Oviposition took place about equally during the day and night.

The adult was not observed to fly under field conditions. Caged individuals were observed to fly a few inches.

The longevity of beetles, collected from the field in early spring, without food averaged 52 days as compared with more than 81 days with food.

The longevity of beetles, emerged (in outdoor cage) from their second winter of hibernation, without food averaged 15.6 days as compared with 29.8 days with food.

Adults survived 7 days of total submergence in
water and began ovipositing 24 hours afterward. They survived somewhat longer in soil which was covered with water, than in plain water.

Corn was injured by the adult in feeding and ovipositing when the plants were small. The females were more injurious than the males.

Injury by the larvae, which fed in the roots, continued throughout the season.

Corn planted as late as July was seriously injured.

Effective control was obtained by a combination of cultural practices, the most important of which were crop rotation, early planting and trap-rows planted between infested and non-infested fields.
ACKNOWLEDGMENTS

The writer wishes to acknowledge his sincere appreciation to the South Carolina Experiment Station for permission to use the data herein presented for a thesis. I am particularly grateful to Mr. O. L. Cartwright, under whose supervision the studies were conducted, for his cooperation and valuable suggestions throughout the time the work was in progress. Also does the writer wish to acknowledge the criticisms and advice sought of Mr. F. B. Whittington and Mr. G. W. Haug of the Ohio State University Graduate School, the suggestions sought of Mr. C. F. Rainwater of the Bureau of Entomology and Mr. J. G. Watts of the South Carolina Experiment Station, and the valuable advice and criticisms sought of my advisor, Dr. D. M. DeLong of the Ohio State University, Department of Entomology.

To Mr. W. E. Hall, Superintendent of the Pee Dee Branch of the South Carolina Experiment Station, where the studies were conducted, is due much credit for his cooperation and assistance in carrying on the research.


