Survival Rate and Reproductivity of the Adult Southern Green Stink Bug, *Nezara viridula*, in the Field Cage

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INTRODUCTION

The duration of developmental period of the southern green stink bug from egg to adult emergence requires between five and six weeks in mid-summer (KIRITANI & HOKYO, 1962). An adult bug, on the other hand, lives relatively long in comparison with its duration of immature stage. KIRITANI (in press, a) studied oviposition habit of the bug relative to its generation, and has shown that the duration of preoviposition period for the first generation is about three weeks which are relatively short in comparison with four weeks for the second generation. Therefore, assessment of the age-specific fecundity and survival rate of adults in addition to the proportion of fertile females under natural conditions is a matter of the most importance to understand the population dynamics of the southern green stink bug. The third generation bugs pass the winter as adults with sexual immaturity and they resume their reproductive activity in the following spring. They suffer considerable loss during their hibernating period (KIRITANI *et al.*, 1962). An estimate of the fecundity of the hibernated adults under natural conditions will be published elsewhere (KIRITANI, in press, b). Accordingly, our present work is limited to the adults of non-hibernating generations which are the first and the second generation in a year.

MATERIAL AND METHOD

Experimentation in field cages

Larvae of the fifth instar were collected in the paddy fields of early planting rice of several varieties differing in the dates of ear formation and transplantation. Field cages which were used for the breeding of insects were covered with the net of vinyl chloride of 16 meshes, and the size of each cage was 4 m² in area and 2 m high. Each field cage covered 36 stubbles of rice plant with young ears that were served to adult bugs as food. The number of larvae kept in a cage was limited in order to avoid a deleterious effect of crowding.

Every newly emerged adult was marked with dyes diluted with aceton solution which are found in common market under various names, such as “marking ink”. Every field cage was examined every three days, and survival and mating of each bug were recorded. At the same time, the numbers of eggs and egg masses that were laid during the successive examinations were recorded through careful searching. Details of the experimental design of the field cage were shown in Table 1. All of the eggs were eradicated from the field cages with the exception of the No. 1 cage in which some of the eggs were left. Also, in this cage the adults that emerged from these eggs were kept under observation with their parents.

Experiment in laboratory

Experiments were conducted on the first generation bugs at 25°C and the second ones under the room temperature both on pods of the common haricot beans. The number of pairs observed was 15 for the first and 27 for the second generation. The results which were based upon
Table 1. Design of experiment in the field cages.

<table>
<thead>
<tr>
<th>Cage no.</th>
<th>Variety of rice plant in the cage</th>
<th>Date of ear</th>
<th>Initial no. of insects kept in the field cage (mass)</th>
<th>Egg 5th instar larva</th>
<th>Generation of adult</th>
<th>Initial date of adult emergence</th>
<th>No. of adults produced</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sinei &amp; Toyosato*</td>
<td>July 1</td>
<td>—</td>
<td>36**</td>
<td>1st</td>
<td>July 26</td>
<td>16 : 15</td>
</tr>
<tr>
<td>2</td>
<td>Honen</td>
<td>Sept. 1</td>
<td>433 (5)</td>
<td>—</td>
<td>2nd</td>
<td>Aug. 17</td>
<td>15 : 10</td>
</tr>
<tr>
<td>3</td>
<td>Homarenisiki</td>
<td>Aug. 6</td>
<td>—</td>
<td>63</td>
<td>2nd</td>
<td>Aug. 14</td>
<td>28 : 29***</td>
</tr>
</tbody>
</table>

* Transferred on Sept. 5 from Sinei to Toyosato.
** Larvae produced under natural conditions from 714 eggs (9 egg masses) that were laid for the period June 18 to June 27 in the paddy field of var. Sinei.
*** One female and two males died accidentally after emergence.

the daily examination of each pair with regard to its frequency of mating and number of eggs deposited were used for the interpretation of data obtained in the field cages. The other details of the experiment were published in a previously announced paper.

RESULT

Survival and death rate

As it is the case with the natural populations, the life span of the adults in the field cages is much shorter than that of the laboratory populations. The duration of adult life span in the field cages was almost one half of the life span of the laboratory populations irrespective of sex.

On the other hand, the coefficient of variation in the longevity of laboratory populations was less than one-half that of the field populations (Table 2). The reason of this difference can be well represented by the survivorship curves for the both populations (Fig. 1).

![Survivorship curves (left) and mortality curves (right) drawn by the running average of three points of the populations in laboratory and field cage. Ordinate: per cent, Abscissa: day.](image-url)
Table 2. Comparison of adult longevity between laboratory and field cage. Part of the data for the laboratory populations recited from Kiritani (in press, a).

<table>
<thead>
<tr>
<th>Rearing condition</th>
<th>No. of adults</th>
<th>Generation</th>
<th>Longevity (M±s.d.)</th>
<th>Mean fecundity/female</th>
</tr>
</thead>
<tbody>
<tr>
<td>At 25°C, with common haricot bean pods</td>
<td>15 pairs</td>
<td>1st</td>
<td>33.7±8.5</td>
<td>41.1±7.3</td>
</tr>
<tr>
<td>At room temperature with common haricot bean pods</td>
<td>27 pairs</td>
<td>2nd</td>
<td>38.6±10.9</td>
<td>47.8±13.6</td>
</tr>
<tr>
<td>Mean</td>
<td>42 pairs</td>
<td></td>
<td>36.6±10.9</td>
<td>45.4±12.2</td>
</tr>
</tbody>
</table>

Field cage No. 1-1                     | F : 16        | 1st        | 19.32              | 21.75                | 59.0                  |
| Field cage No. 1-2                     | M : 15        | 2nd        | 14.40              | 29.28                | 81.4                  |
| Field cage No. 2                       | F : 15        |            |                    |                      |                      |
| Field cage No. 3                       | M : 10        |            |                    |                      |                      |
| Field cage No. 2                       | F : 27        | 2nd        | 21.91              | 31.83                | 124.3                 |
| Field cage No. 3                       | M : 27        |            |                    |                      |                      |
| Field cage No. 3                       | F : 12        |            |                    |                      |                      |
| Field cage No. 3                       | M : 11        |            |                    |                      |                      |
| Field cage No. 3                       | F : 70        | 2nd        | 13.77              | 23.25                | 20.0                  |
| Field cage No. 3                       | M : 63        |            |                    |                      |                      |

To make ease the comparison of survivorship curves between the populations of both laboratory and field cage, calculation was made including both populations of the first and the second generations for each sex. It can be seen that the longest duration of adult longevity in the field cage is almost the same as that of laboratory, but the shape of survivorship curves in the field cage is characterized by their rather concaved type or steep fall at the early period of adult life. The death rate curves of the both laboratory and field cage populations are expressed by a running average of three points (Fig. 1). Although there can be seen an early loss at the start for the females of field population, the death rate remains almost constant with respect to age until about 30th day for females and 25th day for males, and then rises steeply with increasing age. A similar trend can be seen also for the laboratory populations. It is noteworthy, however, that the death rate curves of the male of the both populations have the peak mortality or rather steep falls in the late period of life. There is no relevant explanation as to whether this is a mere chance or an underlying physiological process in itself.

Estimate of the fraction of a reproductive population

It can be said that there are adult individuals which die without participating in reproduction, and the amount of fraction of those adults, especially the females, plays an important role in determining the number of individuals in the next generation.

A rough estimate of this fraction can be made. First, from the fraction of those died before the beginning of oviposition in each field cage—Method 1. Secondly, from those died within two weeks, which are the shortest duration of preoviposition period observed in the laboratory populations—Method 2 (Table 4). The first method gives a value of 25.7% when considered altogether, and the second one gives 32.9% females as sterile or died without egg laying.

Kiritani (in press, a) reported that mating frequency becomes high about one week before the first egg laying and becomes the lowest the day before oviposition and again reaches to the highest as soon as eggs are deposited. Changes in the number of oviposited eggs and that of mating individuals as percentage of the total population are represented in Fig. 2.
It can be seen that the oviposition curve has a similar trend to the curve of mating frequency. As the relation between mating and oviposition is so close that we can use mating frequency observed for each individual as an index of its reproductive activity. It was observed that there is a great variation in the sexual activity among individuals of both sexes. About half or more adults of both sexes could not be observed their mating during the course of successive surveys, including a male and a female that were found separately 17 times and 21 times, respectively (Table 3). On the other hand, the most active male mated 7 times out of 10, and the female 4 times out of 11 consecutive surveys. As the intervals of successive surveys in the field cages were three days, those females which were not observed mating can not necessarily be regarded as sterile. In fact, a female that was found 17 times without mating was laying eggs on 15th discovery. Therefore, in order to obtain more accurate estimate of the proportion of reproductive females, it becomes necessary to know the fraction of reproductive females among the non-mating females. The following procedure should be employed in order to obtain the estimate mentioned above.

In order to adjust the daily record of mating of each pair of the laboratory populations to the mating frequency of the field cages, each total number of mating was grouped together as 0-2, 3-5, 6-8 and 9-11 so as to be able to compare each other in the frequency of mating (Table 3). As it is the case with male sex, the males died earlier than the females. In the laboratory, the period of co-existence of both sexes was used instead of the net life span of the both sexes, because mating behaviour can only be expected to occur in this period. Similarly, the duration from emergence to the time when all the males died out in each field cage was adopted as the maximum duration of the surviving females.

The fraction of egg laying females in relation to the specified frequency-group of mating during the period of co-existence can be obtained from the laboratory observation. All the females that were observed to mate more than 3 times by daily examination and that lived not less than 17 days oviposited fertile eggs. Among the females that mated less than 2 times,
Table 3. Mating frequency in relation to the duration of co-existence of both sexes and the percentage of sterile females. Intervals of successive examinations are three days in the field and daily in the laboratory.

<table>
<thead>
<tr>
<th>Code no. of cage</th>
<th>Duration of co-existence</th>
<th>No. of adults</th>
<th>0</th>
<th>1</th>
<th>Mating frequency</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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<td>7</td>
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<td>1-2</td>
<td>1-5</td>
<td>15</td>
<td>4</td>
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<td>Total of females</td>
<td>1-5</td>
<td>70</td>
<td>21</td>
<td>3</td>
<td>3</td>
<td>7</td>
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<tr>
<td>Mean mating freq. = 0.986</td>
<td></td>
<td>35</td>
<td>19</td>
<td>5</td>
<td>6</td>
<td>3</td>
<td>2</td>
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<tr>
<td>Total of males</td>
<td>1-5</td>
<td>63</td>
<td>28</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>7</td>
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<tr>
<td>Mean mating freq. = 1.095</td>
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<td>35</td>
<td>13</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td></td>
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<tr>
<td>Laboratory population (1st + 2nd generation)</td>
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<tr>
<td>Duration of co-existence</td>
<td>No. of adults</td>
<td>Mating frequency</td>
<td>% of sterile females in 0-2 group</td>
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<tr>
<td>1-16</td>
<td>42</td>
<td>1 (1)*</td>
<td>100.0</td>
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</tr>
<tr>
<td>17-31</td>
<td>8 (4)*</td>
<td>4 (1-0.50)</td>
<td>50.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>32-46</td>
<td>8 (3)*</td>
<td>8 (1-0.375)</td>
<td>37.5</td>
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</tr>
<tr>
<td>47-</td>
<td>3 (1)*</td>
<td>1 (1-0.333)</td>
<td>33.3</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>20</td>
<td>13</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean net mat. freq. = 3.24</td>
<td>mean adjusted mat. freq. = 0.76</td>
<td>8</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

* Figures in parentheses denote the number of sterile females.

there exist some sterile females and the percentage of these females decreases with the prolongation of co-existing period which approximates to the longevity (Table 3). Using these estimates of percentage of sterile females, the number of ovipositing females in each field cage was calculated. For example, the number of ovipositing females in the cage No. 2 can be estimated from Table 3 as follows:

\[
\{6 \times (1-1.00)\} + \{4 \times (1-0.50)\} + \{1 \times (1-0.375)\} + \{1 \times (1-0.333)\} + 15 = 18.292 \text{ or } 18.292/27 = 67.8\% \text{(method 3)}.
\]

The estimate by the method 3, as a matter of fact, was considered to give an overestimated value, because of the possible sterility among those females that mated only once and was found alive less
Table 4. Estimation of the percentage of reproductive females and their fecundity.

<table>
<thead>
<tr>
<th>Code no. of cage</th>
<th>No. of females</th>
<th>No. of eggs (egg masses) deposited</th>
<th>Mean size of egg mass</th>
<th>Estimated % of reproductive females</th>
<th>No. of eggs (egg masses) per reproductive female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>M. 1</td>
<td>M. 2</td>
</tr>
<tr>
<td>1-1</td>
<td>16</td>
<td>944(11)</td>
<td>85.8</td>
<td>56.3</td>
<td>56.3</td>
</tr>
<tr>
<td>1-2</td>
<td>15</td>
<td>1,221(22)</td>
<td>55.5</td>
<td>60.0</td>
<td>66.7</td>
</tr>
<tr>
<td>2</td>
<td>27</td>
<td>3,356(48)</td>
<td>69.9</td>
<td>88.9</td>
<td>74.1</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>240(4)</td>
<td>60.0</td>
<td>83.3</td>
<td>66.7</td>
</tr>
<tr>
<td>Total &amp; Mean</td>
<td>70</td>
<td>5,823(85)</td>
<td>67.8</td>
<td>74.3</td>
<td>67.1</td>
</tr>
</tbody>
</table>

Method 1: Percentage of the females that died before the beginning of the first egg laying.
Method 2: Percentage of the females that died within two weeks.
Method 3: Using lower estimate of the sterile females.
Method 4: Using upper estimate of the sterile females.

than 5 times or 15 days, which are the shortest duration of preoviposition period observed in the laboratory populations. If we allow a discount of this fraction off the number of ovipositing females estimated by the method 3, we can obtain the fourth estimate, viz. in the example mentioned above 18.292−1=17.292 or 17.292/27=64.0% (method 4). These estimates as well as the number of eggs per reproducing female obtained by different methods are shown in Table 4.

The percentage of sterile females in the laboratory was only 21.4%, being the figure much smaller than those observed in the field cages. The severe mortality in the early period of adult life in the field cages accounts for this fact largely. The difference of over 10% between the figures based on the method 2 and those on the method 4, however, is important because it suggests that there are sterile females in such a high proportion in the natural populations, notwithstanding no difference can be seen in their external appearance. Furthermore, the figures in Table 3 for the male sex also show the existence of those individuals that are sexually inactive in much the same proportion besides the short-lived ones.

Variation in the mean fecundity which was observed among the caged populations was so great as 20 eggs per female in cage No. 3 to 124 in cage No. 2. It can be seen that the mean fecundity as well as the length of life span for the second generation decreases as the date of adult emergence retarded (Tables 1 and 2). KIRITANI (in press, a) reported that parental age of a bug has a great influence upon the viability of eggs, duration of incubation period and larval stage. And he further reports, the old females lay eggs with a high fraction of viability as well as short incubation period, and the larvae produced from these eggs develop faster than those from the eggs laid early. But it is unknown as to whether or not the variation of fecundity observed in the present study can be explained relevantly by such a sort of phenomenon.

In the cages Nos. 1-2 and 2, the estimated number of egg masses deposited by the reproductive females was approximately three. The validity of this estimate can be supported by the fact that the egg laying curve in Fig. 2 shows that there were three peaks in egg laying activities among field cage populations. In this connection, it must be noted that the estimate of the mean number of egg masses per reproductive female in the cage No. 3 was less than a unity, and the actual number of egg masses deposited in this cage was
only four. And this should be considered as the maximum number of reproductive females. Thus, yet the value of 43.8% obtained by the method 4 is higher than the actual value, 33.3% or 4/12 at most would be more valid estimate of the fraction of reproductive females.

As stated above, there was a parallel relation between the mean longevity of females and their mean fecundity. Kiritani (in press, a), however, could not find any relationship between the length of longevity and fecundity among the laboratory populations of the first and the second generations. But among the hibernated adults there was a close relation between the two items. Incidently, it is interesting to know whether such a relationship can be hold among the field cage populations. As a nature of this sort of experiment, only the mean value for each population is available. Equation of a regression line using the figures in Table 2 was calculated as follows:

\[ Y = 71.2 + 7.5103(X - 26.5) \]

or \[ Y = 7.51X - 127.82 \]

where Y is the mean fecundity per female and X is the mean length of female longevity. When Y = 0, X = 17.0 which denotes the mean preoviposition period.

**Net reproduction rate (Ro) and intrinsic rate of natural increase (r)**

Kiritani and Hokyo (1962) estimated the mortality (M) from egg to adult emergence over 99%, 91% and 94% among the first, the second and the third generations, respectively. Preliminary calculations of the M made for the first and the second generations in 1962 suggest 98% and 94% for the respective generation (Kiritani et al., unpublished). Some of the examples which are ready to hand in demonstrating these orders of mortality can be seen in Table 1, viz. in cage No. 1, 31 adults were produced from 714 eggs with 96.4% mortality for the latest broods of the first generation under natural conditions, and 25 adults from 433 eggs with 94.2% mortality for the second generation in the field cage. Accordingly, we can calculate the net reproduction rate or multiplication per generation (Ro) and the intrinsic rate of natural increase (r) for the first and the second generations using these estimates in addition to the age-specific fecundity and survival rate of adults obtained from the present study.

The female life table and the age-specific fecundity table give a probability of a female at birth \((l_x)\) being alive at any stated age \(x\). The age-specific fecundity table gives the mean number of female offspring \((m_x)\) produced per unit time by a female of age \(x\). Figures of \(l_x\) are adjusted to pre-adult mortality and the sex ratio unity (Table 5). Ro is the ratio of the total female births in two successive generations. It is the multiplication per generation or net reproduction rate. It can be described as follows:

\[ \frac{N_t}{N_0} = e^{rT} \]

\(T\) is the mean length of a generation which

<table>
<thead>
<tr>
<th>Pivotal age in 6 days</th>
<th>(l_x)</th>
<th>(m_x)</th>
<th>(l_x \cdot m_x)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>0.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 stages</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>0.0154*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>39</td>
<td>0.0142</td>
<td>14.497</td>
<td>0.2050</td>
</tr>
<tr>
<td>45</td>
<td>0.0129</td>
<td>27.967</td>
<td>0.3643</td>
</tr>
<tr>
<td>51</td>
<td>0.0113</td>
<td>9.628</td>
<td>0.1079</td>
</tr>
<tr>
<td>57</td>
<td>0.0103</td>
<td>34.324</td>
<td>0.3328</td>
</tr>
<tr>
<td>63</td>
<td>0.0087</td>
<td>29.655</td>
<td>0.2581</td>
</tr>
<tr>
<td>69</td>
<td>0.0063</td>
<td>19.150</td>
<td>0.1161</td>
</tr>
<tr>
<td>75</td>
<td>0.0042</td>
<td>38.471</td>
<td>0.1582</td>
</tr>
<tr>
<td>81</td>
<td>0.0019</td>
<td>25.075</td>
<td>0.0449</td>
</tr>
<tr>
<td>87</td>
<td>0.0008</td>
<td>17.000</td>
<td>0.0102</td>
</tr>
<tr>
<td>93</td>
<td>0.0002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ Ro = \sum l_x \cdot m_x = 1.6175 \]

* Sex ratio = 0.5, death in prereproductive period = 0.271
Table 6. Values of Ro, r and $\lambda$ with varying durations of immature stages and rates of mortality. Unit time of both r and $\lambda$ is 6 days.

<table>
<thead>
<tr>
<th>Mortality</th>
<th>Ro</th>
<th>r</th>
<th>$\lambda$</th>
<th>Duration of immature stages (day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>30</td>
<td>36</td>
<td>42</td>
</tr>
<tr>
<td>99%</td>
<td>0.404</td>
<td>-0.170</td>
<td>-0.147</td>
<td>-0.130</td>
</tr>
<tr>
<td></td>
<td>0.844</td>
<td>0.863</td>
<td>0.878</td>
<td>0.895</td>
</tr>
<tr>
<td>98%</td>
<td>0.809</td>
<td>-0.064</td>
<td>-0.059</td>
<td>-0.052</td>
</tr>
<tr>
<td></td>
<td>0.938</td>
<td>0.943</td>
<td>0.949</td>
<td>0.957</td>
</tr>
<tr>
<td>96%</td>
<td>1.617</td>
<td>0.045</td>
<td>0.039</td>
<td>0.035</td>
</tr>
<tr>
<td></td>
<td>1.046</td>
<td>1.040</td>
<td>1.036</td>
<td>1.032</td>
</tr>
<tr>
<td>94%</td>
<td>2.426</td>
<td>0.106</td>
<td>0.092</td>
<td>0.081</td>
</tr>
<tr>
<td></td>
<td>1.111</td>
<td>1.096</td>
<td>1.084</td>
<td>1.075</td>
</tr>
<tr>
<td>92%</td>
<td>3.234</td>
<td>0.152</td>
<td>0.132</td>
<td>0.117</td>
</tr>
<tr>
<td></td>
<td>1.163</td>
<td>1.140</td>
<td>1.123</td>
<td>1.110</td>
</tr>
</tbody>
</table>

is defined as the mean period elapsing from birth of parent to birth of offspring. N is the mean number of reproducing females, and r is the intrinsic rate of increase which is a natural logarithm of the self-multiplicative rate of increase $\lambda$. The estimate of Ro can be given by summing up the $lx \cdot mx$ products for each age-group (Table 5). Value of r is calculated by the methods given in detail by Birch (1948) and by Howe (1953 b).

The value of Ro can be calculated straightforwardly as (survival rate of immature stages) $\times$ (sex ratio) $\times$ (mean fecundity per female), thus for the first generation $0.01 \times 0.5 \times 82.3 = 0.4115$ is comparable with 0.4043 from $lx \cdot mx$ in Table 5. Similary, Ro for the second generation, when the survival rate of immature stages is 6%, is $0.06 \times 0.5 \times 82.3 = 2.469$, or $0.4043 \times 6 = 2.4258$. The net reproduction rates calculated by the former method with varying values of M were represented in Table 6. The value of M which makes the value of Ro unity is 97.57%.

By definition, the intrinsic rate of increase (r) is the actual rate of increase of a population with a stable age distribution, since the age distribution in the population of the southern green stink bug changes with time and never attains to the stable age distribution. In spite of this situation, the statistic r serves to compare the effect of duration of immature stages upon the r value among the populations having the same schedule of lx and mx.

The range of variation in the duration of immature stages observed under natural conditions is very great. The latest broods of the third generation take as much as 80 days in their development because of the low temperature in that period. Except the third generation, the longest duration of developmental stages of 56 days for the first generation and the shortest, 26.5 days for the second generation were actually observed. The mean duration of the first generation in 1962 was about 42 days and that of the second in 1961 was 36.5 days. In Table 6, values of Ro, and those of r and $\lambda$ per 6 days were given with varying duration of immature stage and mortality. The value of r becomes negative when the mortality of immature stages exceeds 97.57%.

DISCUSSION

It can be assumed that the population density of an insect is determined by fecundity on one hand and mortality on the other. Utida (1957) postulated that importance of the changes in physiological conditions, in particular that of fecundity play in initiation and termination of the gradation of insects referring to many evidences cited from Eidmann (1937), Voelkel (1930), Nechleba (1927), Shelford and Flint (1943) and Wellenstein (1942). Recently, Utida (1959) elucidated that in the rice stem borer, Chilo suppressalis, the
percentage reduction from the potential fecundity can be estimated over 99% in a normal year and in the pre- and post-gradation year, whereas during the gradation year it is barely 90% or less. This surprising level of reduction before the egg stage seems to be the point that has been overlooked in the study of population dynamics of the rice stem borer. The other point which is relevant to the present study was elucidated by Zimmerman (1932, cited from Kendiegh, 1961). He stated that although the breeding population of a species concerned with its reproductivity, often there was a substantial, though inconspicuous, non-breeding population that ought to be taken into consideration in any understanding of community dynamics. Studies of animals, especially of birds, have shown that the non-breeding population consists principally of young animals that have been slow in reaching sexual maturity, of surplus individuals of either sex in monogamous species, and of adults which have been lacking in reproductive vigor or have been unsuccessful in establishing proper breeding relation (Kendiegh, 1961). It is worthy to mention that these observations were mainly made for the higher animals having territorial behaviour or a complex social relation in their breeding season.

As it is often the case with an oviposition experiment of an insect species in the laboratory, it can be found that some of the individuals die without egg laying. In the present study of laboratory populations, 21% of the females were sterile. This 21% sterility can not be attributed to the physiological deterioration by crowding or malnutrition in the larval stage, because the larvae of the second generation were collected from the paddy field under the natural conditions, and those of the first generation reared at such density as has no measurable crowding effect and produces normal adults, and further an oviposition experiment was conducted with each pair of adults supplied with surplus food. Adults in the field cages are protected in some respects from the natural environmental resistance, such as birds. About 43% of the females that emerged in the field cages estimated to have died without participating in reproduction, and the death during the period of preoviposition accounted for about 33% of them. The remainder of 10% was considered to be sterile females showing no apparent difference from normal fertile ones. In addition to this, as mentioned in the earlier part, evidence obtained from the observation in regard to mating frequency of male suggests the existence of individuals that are sexually weak or impotent in much the same proportion as females.

It is almost an established fact that the fecundity of an insect species is affected by the density during the developmental stages as well as the adult stage. We have the other unpublished evidence, that larvae developed in crowding condition in a large field cage produced by the preceding generation's surplus egg laying would give adults which are light in weight and their fecundity would be considerably lowered. So far, the low fecundity attended by high density is liable to be considered simply as a shift of mean fecundity, but the present study implies that such a shift of mean is not only responsible for the change (decrease) in mean fecundity per reproducing female, but also for the change (increase) in the proportion of sterile females in the pertinent population.

The biotic potential of the southern green stink bug can be assumed tentatively as 550 which is a value approximate to the highest fecundity realized for the second generation in the laboratory, except the hibernated adults which often lay eggs more than 800 (Kiritani, in press, a). Now, the percentage reduction from the potential in the present case is calculated as \((550 - 82)/550 \times 100 = 85\%\) (cf. Table 2). This figure, though fairly low as compared with an estimate in Chilo suppressalis, represents...
the severity of the environmental resistance during the adult stage.

The mortality curve shows an increase in death rate during the early period of adult life. The critical period of adult life is at emergence. As the larvae before moulting to adult become sluggish as newly emerged adults, they are susceptible to the environmental factors such as flooding, heavy precipitation, predators etc. Therefore, the 10% loss in the number of emerged adults from that of the fifth instar larvae and 13.4% of the adults can be directly attributed to the death caused in this susceptible period by drowning in water, failure in transformation and predation by frogs. After passing this period, adults die almost at a constant rate until the time when the death rate suddenly increases as the aging of adults. Mortality rate of adult bugs is relatively constant until the time about 60% reduction of the adults of both sexes and eventually the rate increases afterward. It is interesting that this type of mortality is rather similar to those observed among adults of wild birds (Lack, 1954).

The first generation of the southern green stink bug suffers heavy mortality as compared with consecutive generations. This high mortality is largely attributed to the activity of egg parasites (Kiritani & Hokyo, 1962). Consequently, the net reproduction rate (Ro) for the first generation produces only 0.4 eggs in the second generation. But this does not mean that one female of the first generation produces 0.4 females in the next generation, because the hibernated adults seem to be more fertile than the adults of successive generations (Kiritani, in press, b). It must not be overlooked, however, that the hibernated females are the survivors that suffered already from more than 50% mortality during their hibernating (Kiritani et al., 1962). Mortality of developmental stages in the second generation is estimated as 91% in 1961 (Kiritani & Hokyo, 1962). But this level of mortality can be considered a value which was underestimated, because of the difficulty in estimating the number of adults produced in the census field. We have obtained a more accurate approximate value in 1962 by improving the census method and a makeshift calculation gives about 94% mortality for the second generation. Using this value, the net reproduction rate is expected to be 2.4 fold per second generation. The product of both values of Ro, 0.4 x 2.4 = 0.96, approaches unity. Therefore, the decrease in the population of the first generation is compensated by the increasing trend in the population of the second generation. This surprising high value of Ro in the second generation explains the increase of population density and damage by this insect in the southern parts of Japan where the cultivation of early planting rice is prevailing in recent years.

The effect of the duration of immature stages on the value of r of the bug assuming the same level of mortality of immature stages is not so great as postulated by Birch (1948) in Sitophilus sasakii (small strain of S. oryzae), because the egg laying occurs relatively in long terms as compared with the rice weevil. The possibility of survival, however, may be expected to depend more or less on the duration of immature stages. Consequently, the actual influence of the prolongation of developmental stages upon the value of r can be expected to be far greater than the calculation suggests. Usefulness of r in the analysis of the population dynamics of the southern green stink bug, however, is considerably limited on account of the unstable age distribution of this insect. The values of r so far obtained from insects almost confined to the species of stored product pests, such as Tribolium castaneum, Sitophilus spp., Rhizopertha dominica and nine ptinid species (Birch, 1948, '53, '54; Howe, 1953a; Leslie & Park, 1949). It is noteworthy that values of r obtained by these authors are invariably large as
compared with the value obtained from the southern green stink bug, even adjusted to the value of r per week. The reason for this difference is the high mortality of immature stages in the natural populations of the latter.

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We wish to thank Prof. S. UTIDA, Laboratory of Entomology, College of Agriculture, Kyoto University for his encouragement and valuable criticism in preparation of this paper.

SUMMARY

Age-specific fecundity, survival rate and proportion of the sterile females in the population of Nezara viridula that belongs to the first and the second generations were studied in field cages. Larvae of the fifth instar were kept in each cage and examined at 3 day intervals. Every newly emerged adult was marked to obtain an individual record of life span and mating behaviour. Eggs deposited in the cage were thoroughly examined at each survey and eradicated after taking count. Relation between mating frequency and egg laying obtained from the daily examination of 15 pairs of the first and 27 pairs of the second generation in the laboratory was used for the estimate of the fraction of sterile females in the field cages. Longevity of adults in the field cages was 18.7±14.2 days among males and 27.5±19.2 among females, on the other hand 36.6±10.9 and 45.4±12.2, respectively in the laboratory. The survivorship curves of the cage populations are characterized by rather a concave type or a steep fall at the early period of adult life. After passing this period, adults die almost at a constant rate until about 60% death of the total population results and the rate suddenly increases along with the aging of adults.

There is a great variation in sexual activity among individuals of both sexes. And about half or more adults of both sexes could not be observed during mating. As mating behaviour of females is closely related to egg laying, the fraction of sterile females among those non-mating individuals was estimated from the percentage sterility obtained in the laboratory populations in regard to the mating frequency. It was calculated that a total of 43% of the females had died without reproduction, 33% of which was ascribed to the death in the preoviposition period and 10% was considered to be sterile showing no apparent difference from normal ones. In addition to this, it is suggested that there are males that are sexually weak or impotent in much the same proportion as females.

It is postulated that the low fecundity accompanied by high density should not be interpreted simply as a shift of mean fecundity per female, but such a shift of mean is attributable to a decrease in mean fecundity per reproducing female on one hand, and to an increase in proportion of sterile females in the pertinent population on the other. Using the values of mortality obtained from life tables, net reproduction rate (Ro) was calculated and gave the values of 0.4 and 2.4 for the first and the second generations, respectively. Therefore, the decrease in the population of the first generation is compensated by the increasing trend in the second generation which develops principally in the paddy fields of early planting rice. When the mortality of immature stages is 97.57%, the value of Ro becomes unity. Values of intrinsic rate of natural increase (r) of the southern green stink bug were shown in Table 6 with varying degree of mortality and duration of immature stages.

REFERENCES

133.
Kiritani, K. (in press b) Application of the changes in reproductive systems of the adult to the forecasting of the seasonal history of the southern green stink bug, Nezara viridula.

(* Reference to the original paper was not made.)

摘 要

野外網室におけるミナミアオカメムシ成虫の生存率と生殖能力

桐谷　圭治・法橋　信彦・木村勝平代
和歌山県農業試験場朝来試験地

2m³の網室4個を水稲圃場内に設け、5令幼虫を収容して、羽化成虫雌71、雄65について日令別産卵数、生存率、不妊率をしらべた。調査は3日間隔でおこなった。卵は調査ごとに計数して取り除き、個体ごとの生死、交尾行動を記録した。産卵と交尾の関係を網室内と同じ世代の成虫、すなわち15対（第1世代）、27対（第2世代）を使用して毎日しらべた。

網室内の成虫寿命は雌18.7±14.2日、雄27.5±19.2日、実験室内では雌36.6±10.9、雄45.4±12.2で前者は後者の約半分であるが、変異係数は逆に約2倍に達する。網室内での生存曲線は初期に高い死亡がみられるが、それ以後は約60%が死亡する時期をとらえておより成虫羽化までの死亡率と、ことでえられた日令別産卵数、生存率を使用して世代当たり増加率（R₀）を計算すると第1世代では0.4、第2世代では2.4となり第1世代の減少が、おもに早期水稲で成育する第2世代の高い増殖率によって補償されている。発育前の産卵数が79.57%のとき個体群密度は世代間で平衡を保つことになる発育期間および死亡率を仮定したときの自然増殖率（λ）の値を他の昆虫のそれと比較するため示した。