Population Dynamics of Adult Spodoptera litura (Fabricius) (Lepidoptera: Noctuidae): Estimation of Male Density by Using Release-Recapture Data

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Applying Hartstack's method to release-recapture data of male Spodoptera litura, male density was estimated for revealing the relationship between trap catch with synthetic sex pheromone and wild male density. The release-recapture experiments were conducted once a month from May through September, 1985. Estimated densities were 0.013, 0.009, 0.031, 0.60, and 2.0 males/ha for May, June, July, August and September, respectively, and were thought to be generally overestimated. These estimates showed generally similar, but smaller, fluctuation to the considerably overestimated projections obtained by Petersen's method. Ratios of trap catch (N_d) to the estimated density (D_H) by Hartstack's method fluctuated: N_d/D_H values were 108, 232, 225, 94 and 86 in May, June, July, August and September, respectively. These values would be useful for the tentative estimation of male density based on catch with the synthetic sex pheromone trap.

Key words: Spodoptera litura, male density, release-recapture

INTRODUCTION

Spodoptera litura is one of the most serious pests of soybean, taro, vegetables and forage crops. The density of this insect gradually increases from spring to early summer and rapidly from mid-summer to autumn in the southwestern districts of Japan, and often causes damage. Forecasting the outbreaks of this pest is necessary for improving the pest management system.

The sex pheromone of S. litura was identified by Tamaki et al. (1973), and established as an effective lure by Yushima et al. (1974). Thereafter, the sex pheromone trap has been extensively used for monitoring the population density. Various environmental factors such as temperature (Oyama and Wakamura, 1976), wind (Nakamura, 1976), and vegetation (HiRano, 1976) have been revealed to affect the male catches of this trap. Nakasugi and Kirifani (1978) proposed a forecasting model to predict the population level of S. litura larvae, in which the egg mass density was predicted based on a linear regression of egg mass densities on male catches. However, few researchers have succeeded in revealing a relationship between trap catch and wild

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male density. We considered that an estimation of male density was necessary for revealing the feasibility of the sex pheromone trap for forecasting.

We have reported release-recapture experiments of male *S. litura* to reveal their dispersal distance (WAKAMURA et al., 1990). HARTSTACK and WITZ (1981) estimated male *Heliothis virescens* density using the "area-ratio model" (HARTSTACK et al., 1971). In this paper, we describe an attempt to estimate the absolute density of male *S. litura*, applying HARTSTACK’s method to the release-recapture data, and evaluate its validity. PETERSEN’s method (PETERSEN, 1896; LINCOLN, 1930) is also applied.

**MATERIALS AND METHODS**

*Experiment area.* All the experiments were conducted in Kagawa Prefecture in 1985 (Fig. 1). *Spodoptera litura* larvae feed mainly on soybean which was cultivated in 534 ha: ca. 4% of the farming area and ca. 1% of the total land area indicated in Fig. 1.

*Release and recapture of males.* Detailed description of the release-recapture experiments has been given in our previous paper (WAKAMURA et al., 1990).

Insects were reared according to the method described by OYAMA and KAMANO (1976) and KOZAI and WAKAMURA (1989). Males were marked on the forewing(s) with oily dye using a felt-tip pen within 24 h after emergence. Different marks were made on different release dates and sites. The mark was not removed even after the insects were caught with traps. Males were released on the next evening when they were 2 days old.

![Fig. 1. Release-recapture experiment showing trap and release sites (1985, Kagawa, Japan). The target area for density estimation is indicated with broken lines (ca. 100 km²). Inset is a magnification of the area near the release point A. △: release point, ●: trap site, dotted area: forest, hatched area: urban and industrial area.](image-url)
Estimation of Male S. litura Density

Water-pan traps were set about 1 m above the ground at 24 sites in the experiment area (Fig. 1). A rubber septum impregnated with 5 mg of "liture", a 10:1 mixture of (Z,E)-9,11- and (Z,E)-9,12-tetradeциdenyl acetates (YUSHIMA et al., 1974), was baited in each trap.

From May through September, between 650 and 2259 males were released from 4 points (Fig. 1) for 3 or 4 successive days once a month. The recapture rate \( P \) was calculated using the following equation:

\[
P = \frac{m}{M}
\]

where \( M \) is the total number of marked males released for 3 or 4 successive evenings from a releasing point, and \( m \) is the total number of marked males recaptured with a trap by the next morning.

Estimation of male density. Male density was estimated by applying the "area-ratio model" proposed by HARTSTACK et al. (1971) (see the footnote of Table 1) to the release-recapture data. In this study, Tone's (1981) microcomputer program of non-linear least squares method was used for the estimation of both the "capture efficiency of pheromone trap", \( E \), and the "effective radius of pheromone plume", \( R \). Although all the release-recapture data were used for the estimations of \( E \) and \( R \), mean numbers of wild males caught with 17 traps in the target area (ca. 100 km\(^2\); Fig. 1) were used for the calculation of male density.

The PETERSEN method (LINCOLN index) (PETERSSEN, 1896; LINCOLN, 1930) was also used for the estimation of male density.

![Graph](image_url)

Fig. 2. An example of fitting HARTSTACK's "area-ratio model", \( P = \frac{ER^2}{(X+R)^2} \), to the release-recapture data, where \( P \) = recapture rate of marked males, \( X \) = distance from release point (km), \( E \) = "capture efficiency of pheromone trap", and \( R \) = "effective radius of pheromone plume" (km) (June, 1985).
RESULTS

Estimation by HARTSTACK's method

An example of fitting the HARTSTACK's method is shown in Fig. 2, and the estimates for “capture efficiency” (\( \bar{E} \)) and “effective radius” (\( \bar{R} \)) in HARTSTACK’s method are shown in Table 1. The estimated density (\( \bar{d}_h \)) was ca. 0.01 males/ha in May and June, and increased gradually to 2.0 males/ha in September (Table 1).

Estimation by Petersen’s method

The estimated densities (\( \bar{d}_p \)) are shown in Table 2: ca. 0.02 males/ha in May and June, followed by an increase to ca. 1.9 males/ha in September. They were generally larger than those from HARTSTACK’s method except for September.

Rate of trap catches to the estimated densities

The rates of the mean trap catches to the estimated densities by HARTSTACK’s and

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Table 1. Summary of recovery and estimation of male density of Spodoptera litura
by HARTSTACK's method* (1985, Kagawa)

<table>
<thead>
<tr>
<th>Month</th>
<th>Released no.</th>
<th>Recovered no.</th>
<th>Maximum flight distanceb: ( X_{\text{max}} ) (km)</th>
<th>No./trap nightc: ( N_e )</th>
<th>“Capture efficiency”: ( \bar{E} )</th>
<th>“Effective radius”: ( \bar{R} ) (m)</th>
<th>Male density: ( \bar{d}_h ) (males/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>5621</td>
<td>640</td>
<td>16.0</td>
<td>1.41 (1.90)</td>
<td>0.217</td>
<td>569</td>
<td>0.013</td>
</tr>
<tr>
<td>June</td>
<td>7259</td>
<td>1788</td>
<td>18.5</td>
<td>2.09 (2.09)</td>
<td>0.311</td>
<td>713</td>
<td>0.009</td>
</tr>
<tr>
<td>July</td>
<td>4760</td>
<td>1179</td>
<td>13.9</td>
<td>6.98 (4.52)</td>
<td>0.291</td>
<td>792</td>
<td>0.031</td>
</tr>
<tr>
<td>August</td>
<td>5878</td>
<td>603</td>
<td>10.1</td>
<td>56.4 (43.8)</td>
<td>0.105</td>
<td>971</td>
<td>0.60</td>
</tr>
<tr>
<td>September</td>
<td>5263</td>
<td>857</td>
<td>13.4</td>
<td>171.3 (88.0)</td>
<td>0.427</td>
<td>343</td>
<td>2.00</td>
</tr>
</tbody>
</table>

* HARTSTACK's method (HARTSTACK et al., 1971): According to their “area-ratio model”, the basic assumption is

\[
P = \frac{ER^2}{(X+R)^2}
\]

where \( P \) is the probability for a male to be caught with a certain trap at distance \( X \) from the original location of the male, \( E \) is the “capture efficiency of pheromone trap”, and \( R \) is the “effective radius of pheromone plume”. \( P \) is determined as the recapture rate in a release-recapture experiment. Trap catch of wild males with a certain trap (\( N_\text{e} \)) should be given by the integration of the product of the number of males at distance \( X \) from the trap \((2\pi Xd)\) and the probability of capture \( (P) \) from distance zero to the maximum flight distance \( X_{\text{max}} \):

\[
N_\text{e} = \int_0^{X_{\text{max}}} 2\pi X \cdot d \cdot P \cdot dX = 2\pi \cdot d \cdot E \cdot R^2 \int_0^{X_{\text{max}}} X \cdot (X+R)^2 dX
\]

where \( d \) is the population density. Solving equation (2), \( d \) is given:

\[
d = N_\text{e} [2\pi ER^2 \left( \ln((X_{\text{max}}+R)/R) - X_{\text{max}}/(X_{\text{max}}+R) \right)]
\]

In the table, \( \bar{E}, \bar{R} \) and \( \bar{d}_h \) are the estimated values for \( E, R \) and \( d \), respectively.

b Distance from the release point to the farthest trap with which one or more marked male(s) was caught.

c Means and standard deviations in parentheses with 17 traps in the target area (Fig. 1.).
Estimation of Male *S. litura* Density

Table 2. Estimated density ($\hat{d}_p$, males/ha) of male *Spodoptera litura* by Petersen's method (LINCOLN index) (1985, Kagawa)

<table>
<thead>
<tr>
<th>Date</th>
<th>$M_0^a$</th>
<th>$m^a$</th>
<th>$u^a$</th>
<th>$\hat{U}^a$</th>
<th>$\hat{d}_p^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5/13</td>
<td>650</td>
<td>108</td>
<td>18</td>
<td>108</td>
<td>0.011</td>
</tr>
<tr>
<td>5/14</td>
<td>1483</td>
<td>195</td>
<td>15</td>
<td>114</td>
<td>0.011</td>
</tr>
<tr>
<td>5/16</td>
<td>1836</td>
<td>101</td>
<td>26</td>
<td>473</td>
<td>0.047</td>
</tr>
<tr>
<td>mean±S.D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.015±0.020</td>
</tr>
<tr>
<td>6/16</td>
<td>1934</td>
<td>426</td>
<td>41</td>
<td>186</td>
<td>0.019</td>
</tr>
<tr>
<td>6/17</td>
<td>1968</td>
<td>518</td>
<td>41</td>
<td>156</td>
<td>0.016</td>
</tr>
<tr>
<td>6/18</td>
<td>2259</td>
<td>584</td>
<td>34</td>
<td>132</td>
<td>0.013</td>
</tr>
<tr>
<td>6/19</td>
<td>1098</td>
<td>248</td>
<td>26</td>
<td>115</td>
<td>0.012</td>
</tr>
<tr>
<td>mean±S.D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.015±0.003</td>
</tr>
<tr>
<td>7/15</td>
<td>764</td>
<td>204</td>
<td>144</td>
<td>539</td>
<td>0.054</td>
</tr>
<tr>
<td>7/16</td>
<td>2226</td>
<td>501</td>
<td>107</td>
<td>475</td>
<td>0.048</td>
</tr>
<tr>
<td>7/17</td>
<td>1770</td>
<td>466</td>
<td>105</td>
<td>399</td>
<td>0.040</td>
</tr>
<tr>
<td>mean±S.D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.047±0.007</td>
</tr>
<tr>
<td>8/21</td>
<td>1185</td>
<td>104</td>
<td>748</td>
<td>8523</td>
<td>0.852</td>
</tr>
<tr>
<td>8/22</td>
<td>1905</td>
<td>207</td>
<td>966</td>
<td>8890</td>
<td>0.889</td>
</tr>
<tr>
<td>8/23</td>
<td>1772</td>
<td>199</td>
<td>1008</td>
<td>8976</td>
<td>0.898</td>
</tr>
<tr>
<td>8/24</td>
<td>1016</td>
<td>89</td>
<td>1114</td>
<td>12717</td>
<td>1.272</td>
</tr>
<tr>
<td>mean±S.D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.978±0.197</td>
</tr>
<tr>
<td>9/11</td>
<td>2145</td>
<td>464</td>
<td>2727</td>
<td>12606</td>
<td>1.261</td>
</tr>
<tr>
<td>9/12</td>
<td>1861</td>
<td>236</td>
<td>2428</td>
<td>19993</td>
<td>1.999</td>
</tr>
<tr>
<td>9/13</td>
<td>1257</td>
<td>165</td>
<td>3582</td>
<td>22947</td>
<td>2.295</td>
</tr>
<tr>
<td>mean±S.D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.852±0.533</td>
</tr>
</tbody>
</table>

$^a$ $M_0$: no. of marked males released, $m$: no. of marked males recaptured, $u$: no. of unmarked (wild) males captured, $U$: estimated no. of males ($U=M_0/u$), and $\hat{d}_p$: estimated male density ($\hat{d}_p=U/10^4$ males/ha).

Table 3. Ratios of trap catches ($N_e$) to estimated densities of male *Spodoptera litura* by Hartstack's ($\hat{d}_H$) and Petersen's ($\hat{d}_p$) methods (1985, Kagawa)

<table>
<thead>
<tr>
<th>Date</th>
<th>$N_e$</th>
<th>$\hat{d}_H$</th>
<th>$k_H^a$</th>
<th>$\hat{d}_p$</th>
<th>$k_P^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>1.41</td>
<td>0.013</td>
<td>106</td>
<td>0.023</td>
<td>61</td>
</tr>
<tr>
<td>June</td>
<td>2.09</td>
<td>0.009</td>
<td>232</td>
<td>0.015</td>
<td>139</td>
</tr>
<tr>
<td>July</td>
<td>6.98</td>
<td>0.031</td>
<td>225</td>
<td>0.047</td>
<td>149</td>
</tr>
<tr>
<td>August</td>
<td>56.4</td>
<td>0.60</td>
<td>94</td>
<td>0.98</td>
<td>58</td>
</tr>
<tr>
<td>September</td>
<td>171.3</td>
<td>2.00</td>
<td>86</td>
<td>1.85</td>
<td>93</td>
</tr>
</tbody>
</table>

$^a$ $k_H=N_e/\hat{d}_H$, $k_P=N_e/\hat{d}_p$
Petersen's methods fluctuated as shown in Table 3. The rates in June and July were about double those of May, August and September.

DISCUSSION

Validity of the estimates by Hartstack's method

"Capture efficiency" (E) is the expected recapture rate when males were released from the immediate vicinity of a trap, according to the definition by Hartstack et al. (1971). This parameter E should be dependent on various factors, such as evaporation rate of sex pheromone, type of trap, activity of male moths to sex pheromone, and environmental factors such as temperature, wind, vegetation, etc.

Hidaka (1976) observed that male moths started orientation flight toward sex pheromone sources at about 10 m leeward, while Nakamura and Kawasaki (1977), using a computer simulation model, estimated that the maximum attractive area was about 80 m leeward of a female moth. Therefore, the values for the "effective radius of pheromone plume" (R) estimated in this study (Table 1) were much larger than those assumed by behavioral observation or computer simulation.

Interferences among sex pheromone traps are neglected in Hartstack's method. If the interferences were not negligible, estimated density would include bias. A trap between a release point and a distant trap might reduce the recovery rate with the latter trap. Therefore, the "effective radius" (R) should be underestimated, which would result in an overestimation for population density.

The quality of the released males was possibly different from that of wild ones. Oyama (1976) reported that wild S. littura males would be more likely to be caught with sex pheromone traps than the males reared in the laboratory. If S. littura males released were inferior in their response to the sex pheromone, "capture efficiency" (E) would be underestimated and then the density would be overestimated. On the other hand, if released males were inferior in flying long distance, the "effective radius" (R) would be underestimated, which would also result in an overestimation of male density. Then, the density estimated by Hartstack's method (\( \hat{d}_H \)) should be generally overestimated.

Hartstack's method requests an assumption of uniform distribution in the wild population. Apparently, S. littura larvae distributed mainly in the soybean fields scattered in patches over the experiment area. Male moths, however, seem to fly around independently of vegetation since a considerable number of males was caught in the fields of non-host plants (Hirano, 1976; Oyama and Wakamura, 1976). They also showed much flight activity as reported in the previous paper (Wakamura et al., 1990). We therefore thought it necessary to assume an uniform distribution soon after sunset when active flight begins.

Validity of the estimates by Petersen's method

Petersen's method was also applied for the evaluation of the validity of the estimated density obtained by Hartstack's method. When applying the Petersen method to release-recapture data, several strict assumptions should be satisfied. Otherwise, the estimates would involve biases. Nevertheless, they would be valuable, if we can determine whether the values are overestimated or underestimated by judging the assumptions:
Estimation of Male *S. litura* Density

1. *Population is closed i.e. there is neither recruitment nor disappearance.* *S. litura* males were attracted to the sex pheromone traps throughout the night (OYAMA, 1985). Recapture is thought to have started immediately after the male release in the evening. Therefore, the mortality and recruitment would be negligible from release to recovery. Some of the released males were caught with the traps out of the target area of density estimation. The emigration of the released males would have resulted in overestimation of the density. The effect of recruitment is discussed later.

2. *Marked individuals are distributed evenly and the probability of their sampling is equal to that of unmarked ones.* Distribution of marked males was apparently uneven since more marked males were caught with proximate traps and less marked males were caught with distant traps than expected if moths were evenly distributed. This would have resulted in underestimation at places nearby and overestimation at places distant from the release point. In this study, males were released from 4 points and captured with 17 traps located at various distances (Fig. 1). Therefore, overestimation and underestimation seem to cancel out the bias. However, it is difficult to determine the direction toward which the estimated values are biased since it depends on the relative size of target area to male dispersal distance.

3. *Marked males are not different in their behavioral activity from the wild ones and never lose their marks.* If marked males were less active in response to sex pheromone than wild ones, the density would be overestimated as discussed in the case of HARTSTACK’s method. The rate of disappearance of mark was regarded as almost zero, since it was persistent even after the males were caught in the traps.

*Bias in the estimated density caused by the age composition*

Released males were 2 d old, but a wild population must consist of a variety of ages. This difference in age-composition would also cause a bias (ITÔ, 1973). Adults emerge at night. The males, just after emergence (0 day old), show no response to sex pheromone (YUSHIMA et al., 1973). The recovery rate of 1-day-old males was 40% less than those of 2-day-old or older males (OYAMA, 1985). Therefore, the estimated density should have included the bias toward underestimation, the degree of which should be the same in HARTSTACK’s and PETERSEN’s methods.

*Evaluation of Hartstack’s method*

The estimates by PETERSEN’s method are, therefore, thought to include biases that generally lean toward overestimation. This seems reasonable, since the estimates were generally greater than those from HARTSTACK’s method which were also considered to be overestimated (Table 3). The estimated density ($\hat{d}$) and the ratio of trap catches to estimated density ($k_H$) from HARTSTACK’s method seem to be more likely to be related to the wild densities.

The validity of the estimates should be evaluated by any other different sampling method, but it seems impossible to do so at present since we have no other convenient sampling method of male *S. litura* than the sex pheromone trap. Although the catch density ratios ($k_H$ and $k_p$, Table 3) are considered to fluctuate with the seasonal changes in flight distance of males, trap efficiency and other environmental factors, it is difficult to discuss the differences between $k_H$ and $k_p$ since they include biases. Nevertheless, they would be valuable as coefficients for tentative estimation of absolute density of male *S. litura* population.
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