Male Catches of *Spodoptera litura* (F.) in Pheromone Traps under Fluctuating Wind Velocity: Validity of the Active Space Model

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In order to know whether the “active space model” for male orientation to a pheromone source, which was developed by NAKAMURA and KAWASAKI (1977), can be applied to a situation of fluctuating wind conditions during short periods, *Spodoptera litura* male catches in a pheromone trap during 10 min periods were analyzed. Males did not come continuously to the trap but did come intermittently, the longest period when none were attracted being during 5 or 6 min. The wind velocity changed from a high to a low level during these periods.

The active space model was modified to apply to a situation of fluctuating wind velocity, and catches obtained experimentally from different release points from the trap were compared with those obtained from a computer simulation using this model. In more than half the cases experimental results differed significantly from the simulated results. Thus, the active space model, which does not describe instantaneous pheromone behaviour, is not really applicable to fluctuating wind conditions during short periods. However, the distance within which released males were captured in the trap was not greatly different between experimental and simulated results except at the time of weak wind. These facts led to the conclusion that this model is valuable in representing the “time-average” active space (or pheromone plumes) during a certain period.

**INTRODUCTION**

NAKAMURA and KAWASAKI (1977) built a model for the active space of a sex pheromone of *Spodoptera litura* (F.) based on a modified SUTTON’s equation for gas diffusion in which the deposition effect of pheromone was included. Roughly described, this model was applied to the recapture of males in a pheromone trap which were released at several points distant from the trap under various wind conditions. These applications, however, were conducted on data obtained during a half hour at the time of highest male activity by assuming a constant active space with a constant (mean) wind velocity. Thus, this model can be called the “static” active space model.
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Table 1. Outline of experiments and weather conditions on experimental nights

<table>
<thead>
<tr>
<th>Date</th>
<th>No. of females baited to trap</th>
<th>Counting of males taking off</th>
<th>Wind velocity (cm/sec)</th>
<th>Weather</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aug. 3, 1973</td>
<td>5</td>
<td>No</td>
<td>21–145</td>
<td>Cloudy</td>
</tr>
<tr>
<td>Aug. 29</td>
<td>2</td>
<td>Yes</td>
<td>1–96</td>
<td>Cloudy</td>
</tr>
<tr>
<td>Aug. 31</td>
<td>2</td>
<td>Yes</td>
<td>3–52</td>
<td>Cloudy</td>
</tr>
</tbody>
</table>

It has been revealed by many authors that the plume of pheromone fluctuates and meanders dynamically by turbulent dispersion, and the male orientation towards a pheromone source is greatly affected by fluctuations in this pheromone plume (e.g., AYLOR, 1976; AYLOR et al., 1976; CARDE, 1979). Therefore, the number of males caught at each instant in time is expected to differ from those estimated from the "static" active space model.

In this paper, male catches in a pheromone trap during a short time interval, such as 10 min or less, are analysed in relation to wind velocity at that time, using the data obtained on *S. litura* by NAKAMURA and KAWASAKI (1977). These catches are compared with the simulation results using their active space model to know whether or not the model is applicable to these short time intervals. These analyses will throw light upon the validity of this model.

**MATERIALS AND METHODS**

The data used here were obtained from experiments conducted by NAKAMURA and KAWASAKI (1977). In these experiments male adults of *S. litura* were released at several points distant from a pheromone trap baited with virgin females, and recaptured thereafter in the trap each 10 min for 1 or 1.5 hr about one hour after sunset. This period of recapture coincides with the highest time in the male's mating activity (YUSHIMA et al., 1973). The captures were also made by two or three persons who stood around the trap and caught males coming near it (within ca. 1 m) with sweep nets. The mean wind velocity during each 5 or 10 min was measured with a BRAM anemometer placed 2 m from the trap. These experiments were conducted in a meadow of ca. 2.25 ha at Chiba Prefectural Agricultural Experiment Station planted with 50 cm high grasses, in August, 1973.

The weather conditions of the nights when the experiments were conducted are shown in Table 1. In two of the three experiments, the number of males which took off at a release point 60 m downwind from the trap were counted each 10 min.

The number of catches, *C*, were corrected to a value, *y*, by regarding that a total of 100 males were released. Thus, the *y*-value at the *i*-th time unit, *y*<sub>i</sub>, was calculated using the following equation:

\[ y_i = \frac{100}{R_{00}} \cdot C_i \]

where *R*<sub>00</sub> is the number of males available to be caught at the beginning of *i*-th time unit. *R*<sub>00</sub> is given by the following:

\[ R_{00} = R_0 - \sum_{j=1}^{i-1} C_j \]
Table 2. An example of males released at one release point in the simulation of the Aug. 29, 1973 experiment.

<table>
<thead>
<tr>
<th>Time unit</th>
<th>Time</th>
<th>Wind velocity, $u$ (cm/sec)</th>
<th>Males released</th>
<th>Flying time $b$ (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1820–1830</td>
<td>0</td>
<td>1</td>
<td>70</td>
</tr>
<tr>
<td>2</td>
<td>30–40</td>
<td>0</td>
<td>3</td>
<td>60</td>
</tr>
<tr>
<td>3</td>
<td>40–50</td>
<td>3</td>
<td>9</td>
<td>50</td>
</tr>
<tr>
<td>4</td>
<td>50–1900</td>
<td>5</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>5</td>
<td>1900–10</td>
<td>96</td>
<td>12</td>
<td>30</td>
</tr>
<tr>
<td>6</td>
<td>10–20</td>
<td>94</td>
<td>9</td>
<td>20</td>
</tr>
<tr>
<td>7</td>
<td>20–30</td>
<td>1</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>49</td>
<td></td>
</tr>
</tbody>
</table>

* Different numbers of males were released at the beginning of each time unit.
*b The time period during which males released at each time unit are moved in the simulation.
*c Virgin females in the trap were assumed to release no pheromones during these periods.

Fig. 1. The number of males caught every minute and wind velocity (cm/sec) every 5 min on Aug. 3, 1973.

where $R_0$ is the total number of males released. All analyses on the catches in this paper were done using the values of $y$.

Simulation model. NAKAMURA and KAWASAKI's model was modified to apply in a situation of fluctuating wind velocity. Thus, the active space was changed each 10 min according to the mean wind velocity during the period, but the fluctuation of wind direction was neglected. Fifty males were released at each release point during the experimental period. The number released at each unit of time (10 min) was, however, changed from time to time (Table 2). These values were determined on the basis of the actual number of males taking off at a corresponding time, assuming that this number follows the normal distribution (NAKAMURA and KAWASAKI, 1984). Males were released at the beginning of each unit of time and moved in a random direction outside the active space until they entered that space or the experimental time limit had expired. The time in which males moved within this limit of time was to change
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![Graph](image_url)

Fig. 2. The relationship between the mean wind velocities and the number of males caught during 5 min on Aug. 3, 1973. The dotted line was drawn freehand.

According to the release time, as seen in "flying time" in Table 2. When a male entered the active space, he was regarded as having been caught in the trap. Other framework details of the model and simulation procedures were the same as the original.

RESULTS

**Relationship between male catches and wind velocity**

The number of males coming near the pheromone trap (within ca. 1 m) caught by persons with sweep nets and the time each male was caught was recorded from 1900 to 2100 on Aug. 3, 1973. Mean wind velocity during each 5 min was also recorded during the period. Figure 1 shows the number of males caught each minute and the mean wind velocity during 5 min. It is apparent from this figure that the males did not come continuously to the trap, but did intermittently, so that the longest period in which none were attracted was 5 or 6 min. It seems that in a period during which no males came the wind velocity had decreased from the immediately previous higher level. This is seen, for example, in the periods from 1941 to 1945, 1951 to 1954 and 2020 to 2025. Thus, catches at each instant were greatly affected by the wind velocity at that time.

Using the data of Fig. 1, the number of catches during 5 min was plotted against the mean wind velocity during the same period (Fig. 2). As seen in Fig. 2, a small number of males (less than 4) was caught during 5 min when the wind velocity was low. As the wind velocity increased, catches also increased and attained a peak at a velocity of about 95 cm/sec and then decreased thereafter. This relationship is very similar to that between the maximum distance of active space of the *S. litura* sex pheromone and the wind velocity, which was one of the basic assumptions in NAKAMURA and KAWASAKI's model. Therefore, these results may suggest that their model can also be applied to catches in pheromone traps during a short period, if the active space at each period is given.
Fig. 3. A comparison of the number of catches in experiments (solid circles) and in simulation (open circles) during each 10 min from 1840 to 1930, on Aug. 29, 1973. $u$ is the mean wind velocity (cm/sec). The trap was placed at 0 m and the wind blew from the left side (the negative ranges) to the right (the positive ones).
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Fig. 4. Maps of catch rates shown by contours at distances from the pheromone trap as obtained from the simulation model. Open circles represent release points and dark ones the number of males actually caught which were released at the center of these circles. The horizontal line is parallel to the wind direction and the trap is placed at the left most edge of the active space of the pheromone (A.S.). Two different cases of wind velocity on Aug. 29, 1973 are shown here (see also Fig. 3).

Validity of the active space model on male catches during a short time period

Figure 3 shows the catches each 10 min which were released at each release point and caught in the pheromone trap both in the actual experiment on Aug. 29, 1973 and in its computer simulation. In the simulation the active space was changed each 10 min according to the mean wind velocity during the period. When the wind velocity was low such as at 1850, 1900, and 1930, the range of catches in the simulation was restricted to 10 or 20 m distant from the trap. In actuality, however, males from farther release points were caught. When the wind was strong such as at 1910 and 1920, the range within which males were caught is similar in the actual experiment and in the simulation. These trends are shown more clearly in Fig. 4 in which catches in the simulation are represented by contour lines, together with actual catches.

The comparison of distance-catches in experiments with those in simulation for all three experiment nights shows that in 10 of 16 cases observed results differ sig-
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Fig. 5. The relationship between the attraction rate of males entering the active space and the wind velocity. Each point is the rate obtained from the catches during 10 min on the three different nights. In the dark circles the range in which males were caught was not greatly different between experiment and simulation, but in the open circles this range differed considerably.

Figure 5 shows the attraction rate of males plotted against the wind velocity during the same period. Attraction rate represents the rate at which males entering the active space once could reach the trap, and this was calculated by dividing the total

significantly from those expected as a result of \( \chi^2 \)-test. A part of this difference seems to have been caused by small sample sizes (catches) in experiments because of the short 10 min sampling period. However, male catch ranges obtained in the simulation were similar to those actually obtained in 12 of 16 cases. In three of the four cases where the catch range differed greatly, the wind was very weak (Fig. 5).
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Catches from all release points in actual experiments by those in simulations. Although all males entering the active space once were assumed to be caught in the trap in this model, in practice males are thought to often leave this space (Nakamura, 1981). The attraction rates must therefore take smaller values than unity; however, in many cases of weak wind times these values exceeded unity (Fig. 5). This means that the active spaces estimated in these cases were underestimated, as already shown in Fig. 3. Except in this range of wind velocity (less than 20 cm/sec), an increasing tendency of the rate is recognized against the increasing wind velocity (with \( r = 0.6724 \); significant at 5\% error level). Therefore, it can be said that of males entering the active space more are attracted and caught in the trap as the wind velocity increases, when the wind is not as weak.

DISCUSSION

In Nakamura and Kawasaki's model, the active space of the *S. litura* sex pheromone was assumed as a function of wind velocity: that is, the maximum distance downwind of it increases from 0 m until it reaches the maximum at ca. 80 cm/sec and decreases thereafter. This assumption was deduced from field experiments in which male response behaviour in *S. litura* to its sex pheromone were observed at varying distances from the pheromone source under various wind conditions (Nakamura, 1976). The curve of catches during each 5 min against the wind velocity (Fig. 2) is similar to the curve of the maximum distance downwind of the active space mentioned above. This fact suggests that the active space model still holds in a situation where the wind velocity fluctuates considerably in short periods, if the active space size in the model is changed depending on the fluctuating velocity.

However, the number of males caught in the trap is not determined only by the active space size. Figure 5 shows that the attraction rate of males entering the active space increases with an increase in wind velocity. This phenomenon has also been shown in the diamondback moth, *Plutella xylostella* by Ishii et al. (1981). As Lewis and Macaulay (1976) have revealed, the distinct plume of pheromone is constructed from the pheromone source and a large proportion of males entering it can reach the source when the wind is strong. Contrary to this, under weak wind conditions the pheromone diffuses vaguely around the source and the trap catches few males. The increasing trend of attraction rate with increasing wind velocity obtained in Fig. 5 was probably caused by an increase in the distinctness of the pheromone plume. Thus, the number of males caught in the trap depends not only on the size of active space, but on the distinctness of that space. The number of males caught will therefore reduce under weak wind conditions as a result of the decrease both in size and distinctness of active space. This is shown in Fig. 1 where catches did not occur when the wind velocity decreased.

Since male catch ranges obtained by experiments and by simulations were similar at a wind velocity larger than 20 cm/sec (Fig. 5), we can conclude that the size of active space estimated by Nakamura and Kawasaki's model was not inconsistent with actual space at strong wind times. However, under weak wind conditions of less than 20 cm/sec the estimated active spaces are thought to be smaller than the actual size (Figs. 3–5). This difference seems to be produced by several causations.

First of all, the equation used for estimating the active space in the model may not
be correct under the condition of small wind velocity. The diffusion of the pheromone was expressed there by a modified equation of SUTTON’s by including the deposition effect of the pheromone; this acts stronger and reduces the active space size with a decrease in the wind velocity. However, these approximations may not apply to weak wind conditions of less than 20 cm/sec.

Secondly, the wind velocities used in the simulation are the mean values of 10 min. Therefore, it would occasionally blow stronger than the mean for an instant and the active space would extend farther at that time. This effect of the velocity fluctuation on the catch ranges would be stronger in a weak wind time than in a strong one. This is because the increasing or decreasing rate of active space with increasing wind velocity is greater in a low wind velocity than in a high one (NAKAMURA and KAWASAKI, 1977).

Although the active space estimated by the model was roughly consistent with actual ranges at large wind velocities, this does not directly mean that the behaviour of the pheromone plume can be accurately expressed by this model. The model assumes the wind direction to be constant throughout experimental periods, so that only the size of active space was changed here. Actual wind direction, however, fluctuates significantly and then the pheromone plume does not extend in a straight line, but meanders (AYLOR et al., 1976). The results of catches obtained at 1920 on Aug. 29, 1973 (Fig. 3) may have been caused by this meandering, where the maximum number of catches occurred not at a place nearest to the trap, but at some distance from it. These facts show that the active space model cannot be accurately applied to the instantaneous behaviour of the pheromone plume.

However, the concept of the “active space” of a pheromone is useful when we want to estimate the number of males inhabiting that area from the number of male catches in the pheromone trap, or to obtain an optimum number of traps in applying the mass-trapping method to control an insect pest. The “active space” of the pheromone we need for these aims is a time-average space in which almost all plumes (or their active spaces) at each instant fall during a certain period, such as one night. NAKAMURA and KAWASAKI (1977) conducted simulations of catches of male S. litura in a pheromone trap during 30 min using mean wind velocities and compared those results with actual experimental results. The simulation results did not differ significantly from the observed ones in more than half the cases. This fact shows that the active space obtained from NAKAMURA and KAWASAKI’s model by using the mean wind velocity coincides, roughly speaking, with the “average” active space. This description is only true when the wind is not weak during experimental periods. A model expressing the pheromone diffusions under a weak wind condition should be developed in the near future.

In this work, virgin females were used for the pheromone source. The release rate of pheromone in females is probably affected by certain meteorological factors such as wind conditions and atmospheric temperature. The rate of male takeoff may be affected by the amount of pheromone there which is dispersed from pheromone traps and virgin females inhabiting that area, in addition to the effect of the meteorological factors (NAKAMURA, 1981). Fluctuations in pheromone emission rate and the rate of male takeoff due to these factors might have some effect on male catches. These matters should also be clarified in the future.
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REFERENCES


