An Equation for the Competition between Pheromone Traps and Adult Females for Adult Males

KAZUO NAKAMURA

Division of Entomology, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo 114, Japan

Mitsuo OYAMA

Shikoku Agricultural Experimental Station, Zentsuji, Kagawa 768, Japan

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KNIPLING and McGuire's (1966) equation describing the competition between pheromone traps and adult females for adult males was critically discussed. It was revealed that their equation could not properly deal with such competition because of the unrealistic assumptions they adopted in it. A new equation was developed in this paper, and the relationship between the number of males captured in traps and the number of females mating was derived from it. Data from competition experiments were applied to this new equation and it was shown that it is applicable to a wide variety of trap-female competition situations.

INTRODUCTION

In recent years, traps baited with virgin females or with a sex pheromone have been widely used for monitoring insect populations and for the control of pest insects. The efficiency of attraction of these pheromone traps is largely influenced by such factors as temperature (ÔTAKÉ and OYAMA, 1974), wind velocity (NAKAMURA, 1976) and competition between the trap and native, free-living females. Of these factors, the latter is an essential component when considering pheromone traps. KNIPLING and McGuire (1966) pointed out the importance of this component in the attraction of males to pheromone traps, and they proposed a simple equation describing the competition between pheromone traps and virgin females. Using this equation, they evaluated the effects of pheromone traps on the suppression of insect population. This equation has been widely used, not only in the case of constructing a population model to include the control effect of pheromone traps (ROELLOFS et al., 1970), but also in estimating trap efficiency (HOWELL, 1974).

However, KNIPLING and McGuire's equation is inadequate as a trap-female competition equation (see discussion following). Trap efficiency cannot be estimated correctly using this equation. Therefore, a more practicable equation was developed in this paper. This new equation was applied to experimental results and a practical problem.
EQUATIONS FOR COMPETITION BETWEEN PHEROMONE TRAPS AND ADULT FEMALES FOR ADULT MALES

1. Knipling and McGuire's equation

Knipling and McGuire (1966) estimated the effects of male captures in pheromone traps, on a decrease in an insect pest population. In this estimation they used the following equation for trap efficiency, $E$:

$$ E = \frac{V_0}{F_0 + V_0} \quad (1) $$

when there exists $F_0$ native females capable of mating and $V_0$ pheromone traps in an area. (It is assumed in the following discussions that $F_0$ and the number of males ($M_0$) are enough large to mate each other). In eq. (1) $V_0$ represents the number of virgin females baited in all traps. The attractiveness of a virgin female baited in a trap is assumed to be equal to that of a native female. If all males, $M_0$ individuals, existing in an area, are capable either of mating with native females or of being captured in traps during a certain period, and there are no males escaping either mating or capture during this period, then the number of males captured in traps, $R$, can be written as follows:

$$ R = EM_0 = \frac{V_0}{F_0 + V_0} M_0 = \frac{F_0 V_0}{F_0 + V_0}, \quad (2) $$

if $M_0 = F_0$.

In the more general situation where the sex ratio of adult insects is not 1:1, but $M_0/F_0 = c$ ($c$ is a constant), $R$ is expressed in the following manner:

$$ R = \frac{cF_0 V_0}{F_0 + V_0} \quad (3) $$

On the other hand, the number of females mating with males, $m$, can be expressed as

$$ m = \frac{F_0 M_0}{F_0 + V_0} \quad (4) $$

This equation explicitly shows that the number of females mating increases with an increase in the number of native males, limitlessly. In other words, it is assumed in Knipling-McGuire equation that females are capable of mating repeatedly, without limit. It would seem that this assumption is unrealistic, because females of almost all insect species have a certain period, say one day after their last mating, during which they can not mate.

From eqs. (2) and (4) we obtain an equation describing the relationship between the number of captures, $R$, and the number of females mating, $m$, expressed as follows:

$$ m = \frac{F_0}{V_0} R \quad (5) $$

This equation indicates that, as $R$ increases there is a proportional increase in $m$ (see Fig. 1), but this situation does not represent the true relationship seen in nature. The reason for the difference in nature is that it is impossible for a female to mate repeatedly, without limit.

Next, let us examine the relationship between the number of native females, $F_0$, and the number of captured males, $R$. Eq. (3) can be rewritten as
K. Nakamura and M. Oyama

\[ F_0 = \frac{RV_0}{c V_0 - R} \]  

(6)

Plotting \( F_0 \) (on a logarithmic scale) against \( R \), we obtain the curve of \( F_0 \) approaching a certain value of \( R \), as shown in Fig. 2. The trend of the \( F_0 \) curve is explicitly shown by eq. (3), since \( R \) approaches \( c V_0 \) as \( F_0 \) increases infinitely. In other words, the number of captures never exceeds a certain value which is determined by the number of traps and the sex ratio of adults. This unrealistic trend of the \( F_0 \) curve was first noted by Howell (1974) and led him to conclude that the pheromone trap could not be used as a monitoring tool in insect populations. However, this trend is not due to a characteristic of pheromone traps, but rather to an unrealistic assumption adopted in Knipling-McGuire equation. In their equation (i.e., eq. (1)), it is assumed that native females for mating are equivalent to pheromone traps: that is, both females and traps can “mate” repeatedly without limit. In the preceding discussion it was pointed out that this is true for pheromone traps, but not for females.

Therefore, more realistic equations based on reasonable assumptions need to be developed.

2. A new equation

Consider a closed area having a size of \( S \) m\(^2\), that \( F_0 \) females and \( M_0 \) males, capable of mating, are randomly distributed within it and that pheromone traps are laid in it. (Again, both \( F_0 \) and \( M_0 \) are assumed to be enough large to mate each other.) Assume that neither immigration nor emigration of either males or females occurs into or from this area during a certain period of \( P \), say one night. Also assume that no deaths, except captures in traps, occur during this period. Thus, \( F_0 \) holds constant and \( M_0 \) decreases only by captures during a period of \( P \). Furthermore, assume that both females and males are incapable of mating more than once during this period. Then, each female has a pheromone active space, \( a \) m\(^2\), and if a male enter it, he will be attracted to the female and will mate with her. Similarly, the sum of all pheromone trap active spaces is \( b \) m\(^2\). The area of active space overlap, between females, between
traps and between females and traps, is assumed to be small enough to be ignored. Let \( m_t \) be the number of females mating until time \( t \) and \( R_t \), the number of males captured in traps until time \( t \) (\( t \leq P \)). Then, the rate of females mating during the small time interval from \( t \) to \( t + \Delta t \) will equal the number of males in the pheromone active space of the females at time \( t \): that is,

\[
\frac{m_{t+\Delta t} - m_t}{\Delta t} = \frac{a}{S} F_t M_t = \alpha F_t M_t \tag{7a}
\]

where \( F_t \) and \( M_t \) are the numbers of females and males at time \( t \), respectively, and \( \alpha = \frac{a}{S} \).

Similarly, the rate of males captured in the trap during a time interval from \( t \) to \( t + \Delta t \) will equal the number of males entering the active space of the traps: that is,

\[
\frac{R_{t+\Delta t} - R_t}{\Delta t} = \frac{b}{S} M_t = \beta M_t \tag{7b}
\]

where \( \beta = \frac{b}{S} \).

If \( \Delta t \) approaches 0, we get the following equations from eqs. (7a) and (7b):

\[
\frac{dm_t}{dt} = \alpha F_t M_t \tag{8a}
\]

\[
\frac{dR_t}{dt} = \beta M_t \tag{8b}
\]

Since both female and male are assumed to be incapable of mating for a certain period after their last mating, \( F_t \) equals \( F_0 - m_t \) during this period. On the other hand, the remaining males capable of mating at time \( t \) are those which escaped both mating and capture in the trap until time \( t \): i.e., \( M_0 - m_t - R_t \). Therefore, eqs. (8a) and (8b) can be rewritten as follows:

\[
\frac{dm_t}{dt} = \alpha (F_0 - m_t)(M_0 - m_t - R_t) \tag{9a}
\]

\[
\frac{dR_t}{dt} = \beta (M_0 - m_t - R_t). \tag{9b}
\]

From eqs. (9a) and (9b), we get an equation for the relationship between \( R_t \) and \( m_t \) as

\[
m_t = F_0(1 - e^{-\frac{\alpha}{\beta} R_t}). \tag{10}
\]

In this equation \( m \) approaches \( F_0 \) as \( R_t \) increases infinitely (Fig. 1). This result is reasonable because females are assumed to mate only once during a certain period and because the number of females having mated never exceeds the initial number of females, \( F_0 \).

Next, let us consider the relationship between \( R_t \) and \( F_0 \). Assuming that all males are capable either of mating with females or of being captured in traps, we can write the following expressions:

\[
F_0 = R_t e^{\frac{\alpha}{\beta} R_t} \quad \text{(when} \ F_0 \leq M_0) \tag{11a}
\]

\[
F_0 = (R_t + C) e^{\frac{\alpha}{\beta} R_t} \quad \text{(when} \ F_0 > M_0), \tag{11b}
\]

where \( C \) is the difference between \( F_0 \) and \( M_0 \) (i.e., \( C = F_0 - M_0 \)). The curve of \( F_0 \) is shown in Fig. 2. In this figure, the \( F_0 \) curve increases with an increase in \( R_t \) without limit. This result is realistic and expected in nature.
APPLICATION OF THESE NEW EQUATIONS TO EXPERIMENTAL DATA AND
A PRACTICAL PROBLEM

A. Experimental data

1. Competition for adult male Spodoptera litura

A pheromone baited with 20 virgin female S. litura was placed near the pe-
riphery of a closed 330-m² greenhouse in which taro, Colocasia antiquorum Schott, was
planted. 20 virgin females of S. litura, each of which was tethered to a pole, were
systematically distributed throughout the greenhouse. Two hundred males were released
in the evening. The number of males captured in the trap and the number of females
mating during the night were counted the next morning. Three similar experi-
ments were conducted using 50, 100 and 200 females respectively. In each case, the
number of males was held constant at 200. These experiments were repeated four
times for each number of females.

Table 1. Experimental Data from Spodoptera litura Trap-Female Competition
AND THE ESTIMATE OF $\beta^*/\alpha^*$

<table>
<thead>
<tr>
<th>No. of tethered females</th>
<th>No. of females baited in</th>
<th>Rate of mating</th>
<th>No. of captures</th>
<th>$\beta^<em>/\alpha^</em>$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_0$</td>
<td>$V_0$</td>
<td>$m/F_0$</td>
<td>$R$</td>
<td>New eq.</td>
</tr>
<tr>
<td>20</td>
<td>20</td>
<td>0.88</td>
<td>34</td>
<td>0.802</td>
</tr>
<tr>
<td>50</td>
<td>20</td>
<td>0.78</td>
<td>28</td>
<td>0.925</td>
</tr>
<tr>
<td>100</td>
<td>20</td>
<td>0.66</td>
<td>12</td>
<td>0.556</td>
</tr>
<tr>
<td>200</td>
<td>20</td>
<td>0.52</td>
<td>10</td>
<td>0.681</td>
</tr>
</tbody>
</table>

$^a$ 200 males were released in each experiment.

$^b$ $\beta^*/\alpha$ (the ratio of the attractiveness of one virgin female as bait in a trap to that of one
tethered female) was estimated using a new equation and using the KNIPLING-McGUIRE equation
(K-MG eq.).

Table 1 shows the mean ratio of females mating, $m/F_0$, and the mean number
of males captured in the trap, $R$. Substituting these values in eq. (10), we obtained
the attractiveness ratio of the trap to a tethered female, $\beta/\alpha$. The corresponding value
to $\beta/\alpha$ in KNIPLING-McGUIRE equation is, by definition, $V_0$. Then, the expected
value of $V_0$ was obtained by substituting the value of $m$ and that of $R$ in eq. (5). The
values obtained ($\beta/\alpha$ or $V_0$) were divided by the number of females baited in the trap
so as to produce the attractiveness ratio of a virgin female, baited in the trap, to that
of a tethered female. (Let us denote this by $\beta^*/\alpha$.) The values of $\beta^*/\alpha$ are presented
in Table 1. If the attractiveness of a female does not differ between the trap and
one tethered, then $\beta^*/\alpha$ is expected to take a value around unity. As seen in Table 1,
the values of $\beta^*/\alpha$ obtained using the new equation were less than 1. In contrast,
the values obtained using the KNIPLING-McGUIRE equation were greater than 1,
where there were a significantly larger number of males than tethered females. These
unexpected results were apparently caused by the unrealistic assumption adopted
in KNIPLING-McGUIRE equation; that is, that both native females and females
baited in traps are capable of mating without limit. These results clearly show that
the equation developed in this paper is more applicable to experimental data than
is the KNIPLING-McGUIRE equation.

Howell (1974) placed 14 traps, each baited with 10 virgin codling moth females, Laspeyresia pononella (L.), in an orchard where codling moths were absent. A certain number of females and males were released in the orchard and the number of males captured in traps was recorded. On another occasion males alone were released and the number captured in traps was recorded. Howell calculated the percent capture of males, using Knipling-McGuire equation, when both females and males were released. In this calculation he used the estimated number of males remaining in the orchard, rather than the actual number of males released. This estimate was obtained by multiplying the number of males released by their rate of capture in traps when males alone were released. His experimental data and calculations are presented in Table 2. This table shows that the expected (calculated) percents captured were much smaller than the actual percent captured.

<table>
<thead>
<tr>
<th>Date</th>
<th>No. of females</th>
<th>Expected females remaining</th>
<th>No. of males</th>
<th>Expected males remaining</th>
<th>% of captures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P₀</td>
<td></td>
<td>M₀</td>
<td></td>
<td>Actual</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>New eq.</td>
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<td></td>
<td></td>
<td></td>
<td>K-MG eq.</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Howell's calculation</td>
</tr>
<tr>
<td>July</td>
<td>1000</td>
<td>305</td>
<td>200</td>
<td>61</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>10.1</td>
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<td></td>
<td>9.5</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.7</td>
</tr>
<tr>
<td>Aug.</td>
<td>1000</td>
<td>505</td>
<td>200</td>
<td>101</td>
<td>16.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.2</td>
</tr>
<tr>
<td>Aug.</td>
<td>500</td>
<td>35</td>
<td>100</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.7</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>4.7</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9</td>
</tr>
</tbody>
</table>

a McPherson's orchard.
b Weeks' orchard.
c Estimated using the new equation and using Knipling-McGuire equation (K-MG eq.).

However, his calculation is not correct, since a certain number of females released would also leave the orchard. Therefore, we need to estimate the number of females remaining in the orchard and to use this estimate in the calculation. Hence, the rate of capture of males in traps was used in this paper in estimating the number of females remaining. The percent captured was recalculated applying the estimated numbers of females and males remaining in the orchard to Knipling-McGuire equation. Similarly, the percent captured was obtained using eqs. (11) (the new equation developed here). The results of these calculations are presented in Table 2. The values obtained did not differ greatly between Knipling-McGuire equation and the new equation. Also, the actual values for percent captured did not differ greatly. In these experiments the number of males released was far smaller than the number of females. Thus, in this situation, we expect no large difference, between the equations, in the number captured, R. From the preceding we can see that the calculations obtained in this paper are expected and to be reasonable.

B. Problem: The effect of time lag, in the start of female mating activities, on the rate of capture

In almost all insects the start of the mating activity in adult males will synchronize with that of adult females. However, it has been reported that males of Holomeina aurantiaca begin their search for females earlier than the females begin their calling (Cardé, 1974). Similar phenomena are also known in Synantheson hector (Yaginuma et al., 1977) and Plutella xylostella (Yamada, personal communication). In these
cases it is expected that the male adult, initiating his mating activity before that of the female, is attracted only to the trap baited with synthetic sex pheromones. Therefore, the capture of males in traps will highly suppress mating with native females in these species (Tamaki and Nakamura, 1976).

In order to establish what effect could be expected, we calculated the number of females mating, \( m \), and the number of males captured, \( R \), when the mating activity of the male begins earlier than that of the female. For these calculations, eqs. (9a) and (9b) were modified somewhat. Thus, if the time interval from the start of the male mating activity to that of the female is represented by \( T \), \( \alpha \) in eq. (9a) is replaced with 0, when \( t < T \). When \( t \geq T \), \( \alpha \) takes a certain constant value. Then, eqs. (9a) and (9b) can be solved simultaneously using a hybrid computer, HIDAS 2000X. Some examples of such calculations are shown in Fig. 3. In this figure, it was assumed that the female continues to release pheromone for a period of four hours and that the male can search for a female during this period. The value of \( \alpha \) was calculated from Kawasaki and Miyashita’s (1976) Spodoptera litura field data and the value obtained (i.e., \( \alpha = 0.01275/\text{hr} \)) was used in the calculations here. The attractiveness of the trap, \( \beta \), was taken to equal \( \alpha \) in Fig. 3. As seen in this figure, the ratio of capture increased with an increase in \( T \) (i.e., the time interval from the start of male mating activity to that of the female). However, the ratio of females mating decreased with an increase in \( T \).

Fig. 4 shows the ratio of female mating when both \( T \) and \( \beta \) were changed. When \( \beta \) is smaller than \( \alpha \), the decrease in the ratio of mating is not large, even if \( T \) is taken to be 4 hrs. However, the suppression of mating increases with an increase in \( \beta \). As a result, when \( \beta \geq 10 \alpha \), no female is expected to mate with a male at \( T > 20 \) min. Apparently, this calculation shows that the more the number of traps placed, the higher the suppression of female mating. This increase in suppression is due to the time lag effect in the start of female mating activity.

![Figure 3](image-url)  
**Fig. 3.** The ratio of capture, \( R/M_0 \), and the ratio of female mating, \( m/F_0 \), at time \( t \) when the male begins mating behaviour earlier than the female. \( T \) represents the time lag until female mating behaviour commences. The attractiveness of a trap is assumed to be equal to that of a native female (i.e., \( \alpha = \beta \)).

![Figure 4](image-url)  
**Fig. 4.** The relationship between the time lag in female mating behaviour commencing, \( T \), and the ratio of female mating, \( m/F_0 \), when the attractiveness of a trap, \( \beta \), was changed from \( 1/50 \alpha \) to \( 20 \alpha \) (\( \alpha \) is the attractiveness of a native female).
DISCUSSION

The new equation developed in this paper, for competition between pheromone traps and adult females for adult males, compensates sufficiently for the unrealistic assumptions included in the Knipping-McGuire equation. However, this new equation is based on two important assumptions. First, it was assumed that both females and males neither emigrate from nor immigrate into the area concerned during the experimental period. This assumption will not hold for many insect species. However, since $M_t$ is not included in eqs. (10), (11a) and (11b), these equations hold independently of the number of males. In other words, it is necessary to examine only the number of females emigrating and immigrating in order to obtain more exact relationships between $m$ and $R$ and between $F_0$ and $R$. This is an important problem which should be investigated in the future.

The second assumption upon which the new equation is based is that the overlap between the pheromone active space of a trap and that of a female is small enough to be neglected. This assumption also does not hold in many cases. For example, the maximum distance from source of the pheromone active space of a Spodoptera litura female is estimated to be ca. 60 m (Nakamura and Kawasaki, 1977). Therefore, it must be expected in species with large active spaces that trap-female active space overlap will be significant. Similarly, trap-female overlap will be significant in species where the population density is high.

However, if a male entering a region of trap-female overlap is randomly attracted to either of the pheromone sources then, eqs. (9a) and (9b) (and also their derivative equations) are still valid. Therefore, what we must reveal here is the way in which a male orients himself when he enters a region of trap-female pheromone overlap. Oyama’s (1974) experimental results on S. littoralis suggest that a male orients towards the source of pheromone emitting the higher concentration (i.e., a pheromone trap), and is attracted to it. In these cases, $\beta^*$ (the attractiveness of one female baited in the trap) is not taken to equal $\alpha$ (the attractiveness of one active female). Therefore, it is necessary to examine the behaviour of males entering the region of active space overlap in order to obtain the exact value of $\beta^*/\alpha$. Of course, $\beta^*/\alpha$ will not be constant, but rather expressed as a function of female density. The estimation of $\beta^*/\alpha$ is an important problem in obtaining exact relationship between $R$ and $m$, and between $R$ and $F_0$.

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