A Population Model to Assess the Effect of Sex Pheromones on Population Suppression

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A population model to assess the effect of sex pheromones on the suppression of insect pest population was presented and simulation tests were conducted with the model. The effect of population size on the degree of suppression was stronger in the mass trapping method than in the disruption method. The trap efficiency in capturing males and relative attractiveness of the trap to the wild females within an area permeated with both pheromones had less effect on suppression rate. The ratio of males captured by the traps to the total number of males emerged, or the rate of females mated per day is not a good measure of the degree of population suppression in the next generation.

INTRODUCTION

KNIPLING and McGUIRE (1966) presented a simple population model which can be applied to assess the effectiveness of mass trapping as a method of controlling insect pests. ROELOFS et al. (1970) and MERTINS et al. (1975) used this model to demonstrate the effect of removing males with sex pheromone-baited traps on populations of the redbanded leaf-roller moth *Argyrotaenia velutinana* and the pine sawfly *Diprion similis*, respectively. However, the KNIPLING and McGUIRE model had an important limitation, namely the number of females mated was determined only by multiplying the probability of a male being attracted to a virgin female by the number of males. Under this assumption, the number of females mated increases unlimitedly with an increase in the number of males. NAKAMURA and OYAMA (1978) presented an improved model of mating in which its efficiency decreased with an increase in the number of males. However, this model is still unrealistic because the mating capacity of males is assumed to be unrestricted.

KUNO (1978) recently proposed a set of models to analyze the mating process of animals. In the present paper, we use one of this equation for mating and develop a population model which can be used to assess the effects of both mass trapping and disruption methods by means of sex pheromones. Simulation tests were conducted to assess the scope and limitations of mass trapping and disruption methods.

POPULATION MODEL

The emergence curve of adults was taken to be a Gaussian distribution with a

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total number of adults N and standard deviation of the time of emergence SD days. The sex ratio of adults emerging was assumed to be 1:1 and the daily survival rate of adults was tentatively taken as 0.9. The number of eggs laid per day per female was determined in an age-dependent manner by the following equation:

$$N_E = 533 - 44.4t, \quad (t \geq 3) \quad (1)$$

where N_E is the number of eggs laid on the t th day from emergence. This equation is based on the actual data for the tobacco cutworm, *Spodoptera litura* (NAKASUJI, 1975), though the curve of oviposition rate is somewhat simplified. Females which mate on the t th day immediately lay eggs at the rate of oviposition for the t th day.

KUNO (1978) proposed a model for the mating rate (P) of females under the assumption that the female, once mated, disappears immediately from the sight of searching males, as follows:

$$P = \frac{F_m}{F} = \frac{1}{F \ln(1-a)} \ln [(1-a)^{kM} \{1 - (1-a)^F\} + (1-a)^F] \quad (2)$$

where F , M and F_m are the number of females, males and mated females, respectively, and k is the number of searches made by each male during a period. The parameter a is the relative area covered by each successive searches of a male. In equation (2), the upper limits of mating frequencies for males and females are assumed to be k and 1, respectively. We assumed the parameter k was also 1 per day in the present model. The parameter a relates to the area permeated with the sex pheromone of a female

Fig. 1. The numbers of males and females emerging daily, of females mating and of eggs laid per day. The emergence curve of adults was generated using random numbers from a Gaussian distribution. The total number of adults emerging (N) and sex ratio of adults were 1,000 and 1:1, respectively and the mean and standard deviation of emergence time were 50 and 10 days, respectively.

in the present case, because males are assumed to find females only by means of the sex pheromone of virgin females. A standard value of a was taken to be 0.033, at which all females can mate during the preovipositional period in the largest population size ($N=1,000$) used in the present model.

The numbers of males and females emerging, of females mated, and of eggs laid by females are shown in Fig. 1 when N and SD are 1,000 and 10, respectively.

SIMULATION METHODS

Mass trapping method

The number of traps (X) is given in terms of the number of virgin females equivalent to the amount of synthetic sex pheromone used as bait in the traps. When the areas permeated with pheromone from trap and from a wild female overlap, the probability of a male being caught by the trap (P_T) is given thus:

$$P_T = cP_X \left(1 - \frac{FP_X P_F}{FP_X + bXP_F} \right) \quad (3)^1$$

where P_X and P_F are the probabilities of a male being attracted to traps and to wild females when traps and wild females distribute randomly and independently of each other and these are as follows: $P_X = 1 - (1-a)^X$ and $P_F = 1 - (1-a)^F$. The parameter b is the relative attractiveness of the trap to the wild female within the area permeated with pheromones from both and c is the efficiency of the trap in capturing males. The coefficient of relative attractiveness (b) is 0.5 when competitiveness of the trap is equal to the wild female within an overlapping area and it becomes lower than 0.5 when the trap baited with the synthetic pheromone is less attractive than the natural pheromone from wild females. The value c will increase when the structure of the trap is improved. In the present calculation, males which are not caught are assumed to stay in the neighbourhood of the trap during one day.

Disruption method

In this method the pre-mating communication between the sexes is disrupted by permeating the atmosphere with natural sex pheromone (GASTON et al., 1967), which prevents males from orienting to females. Sometimes, the use of one of pheromone components (YUSHIMA et al., 1975) or of different isomers of the these components (MINKS et al., 1976) can play a similar role. In all cases, the effect of disruption is considered to be attained by a reduction in the effective area permeated by pheromone from wild females. Thus, in the present simulation we supposed that the parameter a in the equation (2), i.e. the area permeated with pheromone of a wild

¹ We assumed that the number of males being attracted to the traps within overlapping areas of the traps and wild females depends both on the relative density and on the relative attractiveness of traps to wild females. Because the relative densities of wild females and traps are $F/P_F S (=f)$ and $X/P_X S (=x)$ where S is the area of habitat, and relative attractiveness of trap to the wild female is b , the probability of a male being caught by the trap (P_T) is

$$P_T = c \left\{ P_X (1 - P_F) + \frac{bx}{f + bx} P_X P_F \right\}$$

where c is the efficiency of the trap in capturing males ($0 \leq c \leq 1$). The equation (3) is given by the relationship mentioned above.

female, was reduced when the disruption method was applied.

RESULTS OF THE SIMULATIONS

Mass trapping

Suppression of the population was expressed by the proportional decrease in the number of eggs laid per female when a certain control method was applied.

The relationship between suppression of the population and the number of traps, in terms of virgin females equivalent, is shown in Fig. 2. The computation was carried out for three population sizes of adults, i.e. $N=1,000$, 200 and 100 with a standard deviation (SD) of emergence time of 10 days. For the values of other parameters see the legend of Fig. 2.

The suppression increased with an increase in the number of traps, but that for the largest population, i.e. 1,000 individuals, is considerably lower than for the smaller populations, i.e. 200 and 100 individuals. For example, 80 percent suppression can be attained by 27 and 50 traps for the population sizes of 100 and 200 individuals, but it cannot be obtained even by 500 traps for the population size of 1,000 individuals.

Next, the effect of varying the trap efficiency (c) on population suppression was tested (Fig. 3). Although the suppression rate increased gradually with an increase in trap efficiency, the effect is small, an increase in efficiency from 0.5 to 1.0 giving only 20 percent greater suppression for a population of 1,000 individuals.

The effect of relative attractiveness of the trap baited with synthetic pheromone to that of wild females (b) was assessed for three population sizes (Fig. 4). A value of b , for example of 0.33 means that the attractiveness of the trap is one half that of wild females within areas permeated with both pheromones. Generally, attractiveness of the trap baited with synthetic pheromone will be less than that of wild females which excrete the natural pheromone. Fig. 4, however, shows that lower competitiveness

Fig. 2. The relationship between population suppression expressed as the proportional reduction in mean fecundity of females, and the number of traps where b and c in the equation (3) (see text) are 0.5 and 0.8, respectively.

Fig. 3. The relationship between population suppression and the efficiency of the trap in capturing males (c) when X and b (see text) are 80 and 0.5, respectively.

Fig. 4. The relationship between population suppression and the relative attractiveness (b) of the trap to the wild female within an area permeated with pheromones from both sources. X and c (see text) are 80 and 0.8, respectively.

of the trap may not be critical in the mass trapping method.

Disruption method

In order to assess the effect of population suppression by means of the disruption method, the parameter a in the equation (2) was varied. Starting with the value

Fig. 5. The relationship between population suppression and the relative value of the parameter a which is the area permeated with the pheromone of a wild female. The actual (maximum) value of a is 0.033 (see text).

of 0.033, the parameter was decreased gradually to one-thousandth of this standard value. The calculation was performed for three population sizes and changes in the rate of population suppression in relation to the changes in a are shown in Fig. 5.

The change in suppression rate was again influenced by the population size in this case, but the effect was smaller than that of the mass trapping method (Fig. 2). The suppression rate increased above 80 percent when the parameter a decreased to 1/110, 1/40 and 1/30 of the standard value for the population sizes of 1,000, 200 and 100 individuals, respectively. The suppression rate for any initial population size approached a high value when the value of a was decreased further.

Fig. 6. The relationship between the rate of population suppression and the ratio of males captured by the traps to the total number of males emerging. The data were obtained from the simulation test shown in Fig. 2.

Some problems in the evaluation of the population suppression experiment in fields

The effect of the mass trapping and disruption methods is usually assessed by the rate of capturing males by traps relative to a known male population (PROVERBS et al., 1975; MADSEN et al., 1976), and the mating rate of the tethered or wild females during a certain period, e.g. one night (BEROZA et al., 1974; CAMERON and SCHWALBE, 1974; OYAMA and WAKAMURA, 1977). Whether these rates correspond precisely to the rate of population suppression of the ensuing

progeny was tested in the present section.

The relationship between the rate of population suppression and the ratio of males caught to the total number of males emerging was obtained from the results of the simulation tests shown in Fig. 2 and was presented in Fig. 6. The suppression rate increased with increase in the capturing rate, but the relationship between two items was non-linear and differed considerably with population size.

Next, the relationship between the population suppression rate and the mating rate of females was examined. The data were obtained from the result of the simulation test shown in Fig. 5. The relationship between the suppression rate and the mean mating rate of females per night for 10 days at the peak of emergence was shown in Fig. 7.

The relationship between the two is concave and this suggests that the decrease in the mating rate does not bring about a proportional decrease in the population density in the ensuing generation. For example, 90 percent inhibition of mating per night corresponds to only 60 percent decrease in the number of eggs laid per female.

Fig. 7. The relationship between the rate of population suppression and the mating rate of females per day. The data were obtained from the simulation test shown in Fig. 5 and the mating rates were averaged for 10 days at the peak of the emergence.

DISCUSSION

So far, over 40 trials of insect pest control with synthetic pheromones have been carried out in upland fields, orchards and forests throughout the world (NAKASUJI, 1979). The first experiment with the mating disruption was conducted as early as 1967 in California for the cabbage looper, *Trichoplusia ni* (GASTON et al., 1967). Their experiment showed that disruption of mating using the synthetic sex pheromone was a promising method for suppressing the population. On the other hand, GRASS et al. (1970) tried to control an insect pest of apple, the red-banded leafroller moth *A. velutinana*, by means of mass trapping in 1968 in New York State. Though the result of the experiment in 1968 was not satisfactory, successful control was attained in 1969 when the moth density was lower than in 1968 (ROELOFS et al., 1970). After that, many trials using both mating disruption and mass trapping were carried out for about 25 species of insect pests (NAKASUJI, 1979). These experiments, however, have been conducted in a trial and error manner without an assessment of the likely applicability and limitation of the method.

The first mathematical model to assess the effect of mass trapping was developed by KNIPLING and McGUIRE (1966). ROELOFS et al. (1970) used this model to predict the effect of mass trapping on the population of *A. velutinana* in apple orchards and they suggested that over 50 traps should be placed on each tree to attain 95 percent

control in severely infested orchards which have 32 percent damage of apples. MERTINS et al. (1975) modified the KNIPLING and McGUIRE model slightly and used it to design a mass trapping method for control of the pine sawfly, *D. similis*. They assumed that male sawfly does not mate or attempt to copulate more than once in 24 hours and mated females loss their attractiveness to a male. This assumption is the same in the present study. *D. similis* is an arrhenotokous insect and unfertilized females produce male progeny. Under the assumptions mentioned above, they calculated the generation by generation trend in the sawfly population using the KNIPLING and McGUIRE model and predicted that four generations of intensive trapping would be sufficient to eliminate the sawfly from an isolated area.

In the present study, a new population model was built and some simulation tests were conducted to assess the effect of mass trapping and disruption methods.

The simulation tests suggested that mass trapping method would be more strongly influenced by the size of target population than the disruption method. Actually, the number of traps placed in fields will be restricted by economic limitations and, generally, it will be considerably less than the number of wild females. Under such conditions and especially when population densities are high, the mass trapping method is likely to be ineffective.

The disruption method will be applicable to both large and small population sizes. The number of progeny can be greatly reduced using large amount synthetic pheromone even when population densities are high and the technical and economic problems of an extensive treatment of synthetic pheromone are being solved for some insect pests (BEROZA, 1976). Theoretically, complete suppression would be expected when parameter a is infinitely decreased. This situation, however, will not be attained in practice, because males can find and copulate with females at a short distance by other means than sex pheromones, e.g. visual (HIDAKA, 1972) or contact stimuli (ONO, 1977).

The effect of mass trapping on population suppression is usually measured by the number of males captured by the traps (TASCHENBERG et al., 1974) or the rate of males captured by traps to a known male population, e.g. by using mark-recapture technique (PROVERBS et al., 1975). On the other hand, the effects of the disruption method have been evaluated by the decreasing number of males captured by the traps baited with the synthetic pheromone in the treated area (CARDÉ et al., 1977) or by the mating rate of the tethered females (OYAMA and WAKAMURA, 1977) and of the wild females (BEROZA et al., 1974). The simulation tests in the present study suggest that the capturing rate of males or mating rate of females during a short period, e.g. one night, cannot be a good measure of the degree of population suppression in the ensuing generation. Some censuses for the density in the next generation, e.g. egg or larval density, should be added to these measure to evaluate precisely the effect or population suppression by means of sex pheromones. Examples of such precise evaluations have been reported by some authors (BEROZA et al., 1974; ROTHSCHILD, 1975; MINKS et al., 1976 and MACLELLAN, 1976).

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REFERENCES

- BEROZA, M., C. S. HOOD, D. TREFREY, D. E. LEONARD, E. F. KNIPLING, W. KLASSES and L. J. STEVENS (1974) Large field trial with microencapsulated sex pheromone to prevent mating of the gypsy moth. *J. econ. Entomol.* **67** : 659-664.
- BEROZA, M. (ed.) (1976) Pest management with insect sex attractants. *ACS Symp. Ser.* **23**, Am. Chem Soc., 192 p.
- CAMERON, E. A. and C. P. SCHWALBE (1974) Disruption of gypsy moth mating with microencapsulated disparlure. *Science* **183** : 972-973.
- CARDÉ, R. T., T. C. BAKER and P. J. CASTROVILLO (1977) Disruption of sexual communication in *Laspeyresia pomonella* (Codling moth), *Grapholitha molesta* (Oriental fruit moth) and *G. prunivola* (Lesser appleworm) with hollow fiber attractant sources. *Ent. exp. & appl.* **22** : 280-288.
- GASTON, L. K., H. H. SHOREY and C. A. SAARIO (1967) Insect population control by the use of sex pheromones to inhibit orientation between the sexes. *Nature* **213** : 1155.
- GLASS, E. H., W. L. ROELOFS, H. ARN and A. COMEAU (1970) Sex pheromone trapping red-banded leaf roller moths and development of a long-lasting polyethylene wick. *J. econ. Entomol.* **63** : 370-373.
- HIDAKA, T. (1972) Biology of *Hyphantria cunea* Drury (Lepidoptera : Archiidae) in Japan. XIV. Mating behavior. *Appl. Ent. Zool.* **7** : 116-132.
- KNIPLING, E. F. and MCGUIRE, Jr. (1966) Population models to test theoretical effects of sex attractants used for insect control. *USDA Agr. Inf. Bull.* No. **308**, 20 p.
- KUNO, E. (1978) Simple mathematical models to describe the rate of mating in insect populations. *Res. Popul. Ecol.* **20** : 50-60.
- MACLELLAN, C. R. (1976) Suppression of codling moth (Lepidoptera : Olethreutidae) by sex pheromone trapping of males. *Can. Ent.* **108** : 1037-1040.
- MADSEN, H. F., J. M. VAKENTI and F. E. PETERS (1976) Codling moth : Suppression by male removal with sex pheromone traps in an isolated apple orchard. *J. econ. Entomol.* **69** : 597-599.
- MERTINS, J. W., H. C. COPPEL and M. G. KARANDINOS (1975) Potential for suppression *Diprion similis* (Hymenoptera : Diprionidae) with pheromone trapping : A population model. *Res. Popul. Ecol.* **17** : 77-84.
- MINKS, A. K., S. VOERMAN and J. A. KLUM (1976) Disruption of pheromone communication with micro-encapsulated antipheromone against *Adoxophyes orana*. *Ent. exp. & appl.* **20** : 163-169.
- NAKAMURA, K. and M. OYAMA (1978) An equation for the competition between pheromone traps and adult females for adult mates. *Appl. Ent. Zool.* **13** : 176-184.
- NAKASUJI, F. (1975) Life history and ecology of the tobacco cutworm *Spodoptera litura*. In : *Ecology and Control of the Tobacco Cutworm, Turnip Moth and Greasy Cutworm*. (ed. OZAKI, K.) Special Rep. Ministry Agr. and Forestry. pp. 7-51 (in Japanese).
- NAKASUJI, F. (1979) Control of insect pest by means of sex pheromone. *Farming Japan* **13**(4) : 26-40 (in Japanese).
- ONO, T. (1977) The scales as a releaser of the copulation attempt in Lepidoptera. *Naturwissenschaften* **64** : 386.
- OYAMA, M. and S. WAKAMURA (1977) Effective range for mating suppression of *Spodoptera litura* by evaporating (Z,E)-9,12-Tetradecadienyl Acetate. *Appl. Ent. Zool.* **12** : 372-374.
- PROVERBS, M. D., D. M. LOGAN and J. R. NEWTON (1975) A study to suppress codling moth (Lepidoptera : Olethreutidae) with sex pheromone traps. *Can. Ent.* **107** : 1265-1269.
- ROELOFS, W. L., E. H. GRASS, J. TETTE and A. COMEAU (1970) Sex pheromone trapping for red-banded leaf roller control : Theoretical and actual. *J. econ. Entomol.* **63** : 1162-1167.
- ROTHSCHILD, G. H. L. (1975) Control of oriental fruit moth (*Cydia molesta* (Busck) (Lepidoptera, Tortricidae)) with synthetic female pheromone. *Bull. ent. Res.* **65** : 473-490.
- TASCHENBERG, E. F., R. T. CARDÉ and W. L. ROELOFS (1974) Sex pheromone mass trapping and mating disruption for control of the redbanded leafroller and grape berry moth in vineyards. *Environ. Entomol.* **3** : 239-242.
- YUSHIMA, T., Y. TAMAKI, S. KAMANO and M. OYAMA (1975) Suppression of mating of the armyworm moth, *Spodoptera litura* (F.), by a component of its sex pheromone. *Appl. Ent. Zool.* **10** : 237-239.