Field trials and model simulations for controlling the fall webworm, *Hyphantria cunea* (Drury) with synthetic sex pheromone

合成性フェロモンを用いたアメリカシロヒトリ個体群の制御：
野外試験とシミュレーションモデルによる検討

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GENERAL INTRODUCTION

Sex pheromone in their use for pest management

Sex pheromones consist of chemicals that virtually have no toxicity and act mostly for the target insect with a minute amount. It is said that the pest control programs using sex pheromone bring about little damage to the natural environment and do not have a damaging effect upon the ecological system. Furthermore, since the sex pheromone plays a basic role in sexual communications, it is thought that it should not become ineffective so fast to the target pests as compared to the conventional insecticides (Jones, 1998). Initially, the mass-trapping method using sex pheromone was expected to become the new insect control method. The mass-trapping method, in concept, is rather simple: a high density of traps is placed in a crop field to achieve a measure of protection through the removal of a sufficiently high proportion of individuals from the population by trapping. However, mass-trapping "using sex pheromone" is a little more complicated. Traps cannot remove the larvae that cause damage to agricultural crops, but can remove only the adult male moths. Removal of high proportion of male moths biases the sex ratio, and the bias inhibits many females from being inseminated. A reduction in population size will be seen in the next generation. As the pheromone components of various moths were identified, practical use of this method was started against pest moth species that have been damaging crops and forests since the early 1970's (Beroza and Knipling, 1972; Beroza et al., 1975).

Many mass-trapping attempts have been performed, but only a few of them have proven clearly effective, e.g. in the red banded leafroller (Trammel et al., 1974), the codling moth (MacLelan, 1976) and the cotton leafworm (Sato and Fujiwara, 1978). However, it was noted in the reports that this method is doubtful of the efficacy in some environmental conditions or of its ability to suppress the damages under the tolerable level.

Jones (1998) pointed out some difficulties in achieving the efficacy in mass-trapping using sex pheromone, as follows: (1) Lack of attraction of females by the attractant source used, (2) Lack of highly efficient traps, (3) Problem of high insect populations and trap saturation, (4) Need for a high density of traps per unit of surface area, which in turn renders the technique too costly.

H. cunea in Japan

The fall webworm (*Hyphantria cunea* (Drury)) was accidentally introduced into Tokyo from North America in 1945, and extended its northern and southern distribution to become one of the most serious insect pests of street and garden trees in urban areas of Japan (Ishii, 1966). The larvae voraciously feed on various kinds of deciduous trees and aggregate within nest-webs until the fifth larval instar. After the sixth instar, they abandon the nests and live solitarily. At the seventh

instar, mature larvae creep down to the ground and wander around to find stones or bricks under which they pupate (Umeya and Watanabe, 1973). The adults emerge from pupae in a few hours after sunset, and succeedingly fly away the same day. In the first and second generation, after a few hours they settle on the undersides of leaves of host plants. Female moths are not required to fly in order to mate and lay eggs. In contrast, male moths begin the "random flight" a few hours before dawn to find calling female moths. However, in the third (overwintering) generation the mating behavior is observed in the late evening (Arai and Mabuchi, 1979).

The fall webworm was bivoltine through their distribution in Japan until the early 1970's. In late 1970's, trivoltine populations prevailed gradually in southwestern areas, and the population in Tokyo is trivoltine at present (Arai and Akiyama, 1976). The seasonal trends of the peak occurrence of this moth in Tokyo are three times as follows; in the mid of May, (third = overwintering generation), in late July, (first generation), in early September (second generation) (Gomi, 1997).

Controlling *H. cunea* with synthetic sex pheromone

In the fall webworm, I thought there might be some advantages to apply the mass-trapping method in street trees, as follows: (1) Since female moths lay egg masses after mating without dispersal (Masaki, 1975). We can disregard the baneful danger of fertilized females migrating into the treated areas, (2) Highly effective synthetic sex pheromone is available. (3) The synthetic pheromone, however, costs too much to use a large amount of it such as in the mating disruption method. (4) There are many obstacles such as tall buildings and crowded roads for male moths to disperse, and these conditions may minimize the risk of immigration from non-target areas.

Computer simulation as a powerful tool for making a guideline of pest management

Simulation is a kind of imitation of events that can occur in the real world. We can examine our hypothesis elaborately and can replicate enormous times in the virtual world. Actual experiments are easily disturbed by stochastic factors in the field and it always costs lots of expenses and labor to conduct an extensive experiment in the real world. Instead of actual experiments, model simulations have been used in physics, chemistry, astronomy and engineering practically. These schemes have become more and more popular in ecological sciences since 1970's, especially in ecosystem studies.

Simple mathematical models such as Lotka-Volterra model (Lotka, 1925; Volterra, 1928) and Nicholson-Bailey model (Nicholson and Bailey, 1935) have ruled the thinking device of ecologists for more than a half century. These theoretical models provided them for the first time with the same tools that had proved so effective in analyzing processes in physics. Though these simple mathematical models are still largely valid even now, when we tackle with natural and

complicated ecological systems, they are powerless in predicting these dynamics quantitatively in high reality.

Temporal and spatial structures have been found to be essential for the complicated natural population dynamics. Recent advances allow ecologists to understand population dynamics of animals in time series. Following Takens (1981), Schaffer (1984, 1985) embedded Canadian lynx fur dynamics that had been recorded over 130 yr. into a differential equation with multiple time-lags and depicted Poincaré section in terms of one-dimensional maps. Schaffer concluded that the cycle of Canadian lynx exhibits a low dimensional strange attractor. Turchin and Taylor (1992) developed response-surface methodology, and Ellner et al (1992) did LENNS based on feed-forward neural networks, both of which could extract the endogenous dynamics from noisy ecological time series. Ellner and Turchin (1995) tested 14 insect and 22 vertebrate populations using these methods, and concluded that a wide spectrum of dynamical behaviors, ranging from exponential stability through cycles to chaos, is likely to be found among natural populations.

Studies of dynamics incorporating a spatial structure such as CML (coupled map lattice) or CA (cellular automata) have reported that the spatial structure contributes to generation of self-organized spatial structures from which and global stability results (Hassell et al., 1991; Solé et al., 1992; Solé and Valls, 1992).

Many spatially structured models have been developed for predicting metapopulation dynamics both in basic ecology (Hanski et al., 1995) and in applied ecology, especially conservation biology (McKelvey et al., 1993; Lahye et al., 1994).

However, some difficulties still remain to apply such theoretical approaches to assessment for pest control programs. Time series data with sufficient lengths are hardly available, and we still cannot understand the complicated community structure including the pest population, which lives in spatial heterogeneity.

As opposed to theoretical approaches described above, another approach using computer simulation has been developed: systems analysis (Patten 1971). Odum (1969) proposed that materials cycles and energy flows can be integrated whole complicated system (ecosystem), and could be divided into sub-systems in each trophic level. Odum thought that the whole system could be described as "systems model" if we construct sub-models one by one and synthesize them. So many works has been done with "systems model" in environmental science and ecosystem ecology. Systems model has been one of the most powerful tools for policymaking in the integrated pest management (IPM). It has become popular to use this approach among national research institutes of Japan. For example, Miyashita (1994) constructed a simulation model for forecasting the occurrence and its prevalence of the rice leaf roller, *Cnaphalococis medinalis* (G.). Koizumi (1980) developed a computer simulation for analyzing prevalence of the citrus melanose and its chemical control, and Hashimoto et al. (1986) constructed a simulation model to predict the rice leaf blast

development in relation with propagation by *Nephotettix cincticeps* (U.). Though these systems models can depict the natural system well, the models are likely to be somewhat phenomenological and sometime hard to get general principles and biological implications by these procedures.

In this thesis, I constructed three models, spatially-structured individual-based model (IBM), a lattice model and a temporally-structured population dynamics model. The IBM was constructed to analyze the effect of individual flight patterns on the management program of *H. cunea*. It incorporated complicated behavioral characters of individual males in flight. The lattice model was constructed with simpler assumptions compared to the IBM, but it allowed us to manage larger number of individuals and to execute larger-scale simulations than the IBM. The temporally-structured model had a daily-based age-structure of each cohort and contained detail processes of the insect population, and we could analyze synthetic effects of different pest management methods on the complicated pest population dynamics.

These newly emerged methods to construct our model could be achieved by the admirable progresses in the performance of personal computers. These models were not constructed only for solving problems in applied science like systems models but for aiming rather theoretical goals. I think the models will give us biologically reasonable implications, which are also important for practical *H. cunea* management program.

PART 1: FIELD EXPERIMENTS

CHAPTER 1

Mass-trapping trials in urban street trees

1.1 INTRODUCTION

Though I did not know the exact density of this insect pest in my study field, which may result in the saturation of the traps used and also may be too high to be effective for this method, I conducted my mass-trapping experiments with the maximum density of traps I could use as the first step for the actual application of this method.

In this study, I wanted to know whether the mass-trapping method could reduce the damage to street trees by this insect and, through these trials, the actual occurrence and damage to street trees of this insect in Tokyo at present.

1.2 MATERIALS AND METHODS

Trap

The sex pheromone of the fall webworm is composed of five components (Hill et al., 1982; Tóth et al., 1989). The lure used in my experiments (Nitto-lure; ameshiro®), however, contained three of these components, (3Z,6Z)-3.6-9,10-epoxyheneicosadiene, (9Z,12Z,15Z)-9,12,15-octadecatrienal and (3Z,6Z)-1,3,6-9,10-epoxyeicosatrien. The lure was a sheet of laminated plastic made of polyester and PET. The lure was proven in the field experiments to be as effective as the lure which contained the five components (Zhang and Schlyter, 1996; Zhang et al., 1996). The traps used in my experiments were sticky delta-traps (with a sticky surface of 30.0 × 18.5 cm) . The lure was hung in the middle of the inside of the trap's ceiling. The traps and the lures were provided by Nitto Denko Corp.

Study field

Experiments in 1994 and 1995

The experiments were conducted in about 1.2 km of Harumi Street located in Toyosu, Koto-Ku, Tokyo (Fig. 1-1). I divided this study field into 4 experimental areas, and named as Area-1, Area-2, Area-3 and Area-4 from north to south. There were buffer areas between the neighboring experimental areas. Each area had twenty plane trees (*Platanus acerifolia*) (ten trees in each side) and was about 150 m in length. I placed a pheromone trap on each tree in Area-2 and Area-3 (Treated areas). The average distance between trees was about 6 m (ranging 4 m to 30 m). As the control, I did nothing in Area-1 and Area-4 (Non-treated areas). During the larval period, I counted the number of webs both in the treated areas and in the non-treated areas to estimate the

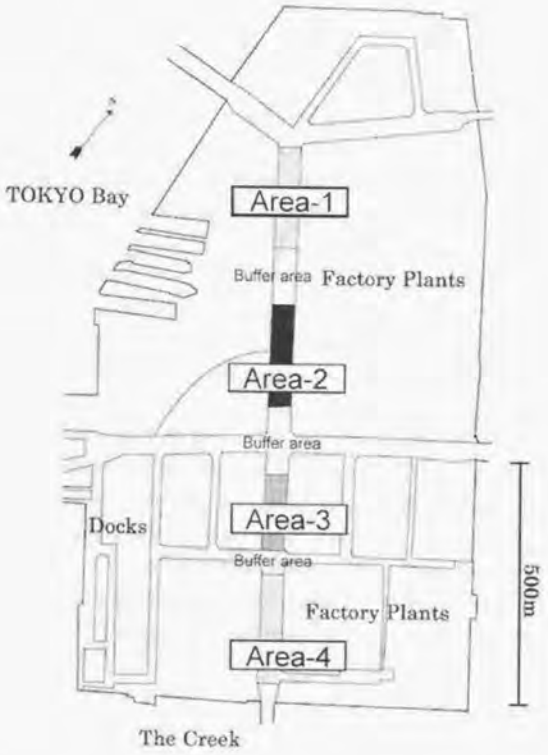


Fig. 1-1. Map of the study field in 1994 and 1995. Area-1 and Area-4 are the non-treated areas. Area-2 and Area-3 are the treated areas.

degree of fall webworm breakout.

Experiments in 1996

I extended the experimental areas to eliminate interference between areas as in 1994 and 1995. Namely, I divided the study field into two experimental areas, one treated area and the other non-treated area. I placed barrier traps to prevent male moths' immigration into treated area (Fig. 1-2). The treated area had 88 plane trees (44 trees in each side) and each tree was treated with a pheromone trap. The non-treated area had 64 plane trees (31 trees in the east side, and 33 trees in the west side). I counted the webs of larvae in the same manner as in 1994 and 1995.

Tethered-female experiment

Tethered-female experiments were conducted around the peak period of male catches. Three-day-old virgin females reared in the laboratory (15L : 9D, 25℃) were used. They were collected as larvae in Ibaraki prefecture, and fed artificial diets (Insecta LF ; Nihon-Nosan Corp.). Females were tethered by fine polyester threads (50 grade, approximately 30 cm long) near the base of a forewing. The other end of the thread was tied to the branch of each plane tree in the experimental areas. The height of the tethered female position was 1.5m to 2.0m. The above procedures allowed the females to move freely on the leaf near the branch and, also, to call and mate. In 1994 and 1995, 20 virgin females were placed in each of Area-1 (non-treated area) and Area-2 (treated area) in each area. One female was put onto each tree. In the 1996, 40 virgin females were placed in each of the treated and the non-treated areas. Females that survived were collected one or two days later and dissected in the laboratory to examine spermatophores in the bursa copulatrix.

1.3 RESULTS

Seasonal prevalence of male catches

Captures of males by the traps are shown in Fig. 1-3. As reported previously (Gomi, 1997), it was confirmed that the fall webworm had three generations a year in Tokyo. In the overwinter generations, not so many males were captured every year and the duration of adult moths' occurrence was longer than in other generations. In 1994 and 1996, the largest numbers of males were captured in the first generations, whereas in 1995 more males were captured in the second generation.

The average number of males captured in 1996 was small in every generation when compared with those in 1994 and 1995. However, I did not take this as a sign of decline in the fall webworm population. Since more than four times larger number of traps were used in one treated area in 1996 than in 1994 or 1995, the traps might scramble more intensively for male moths.

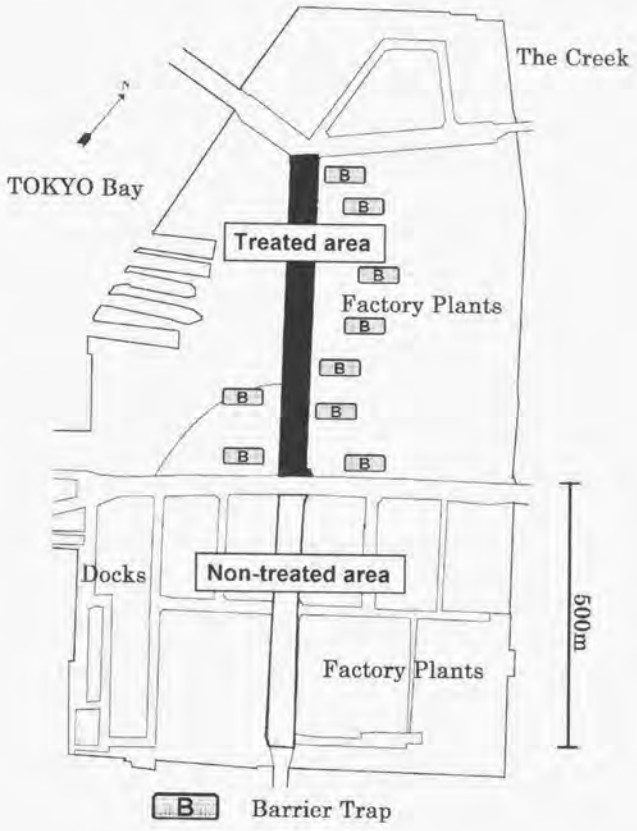


Fig. 1-2. Map of the study field in 1996.

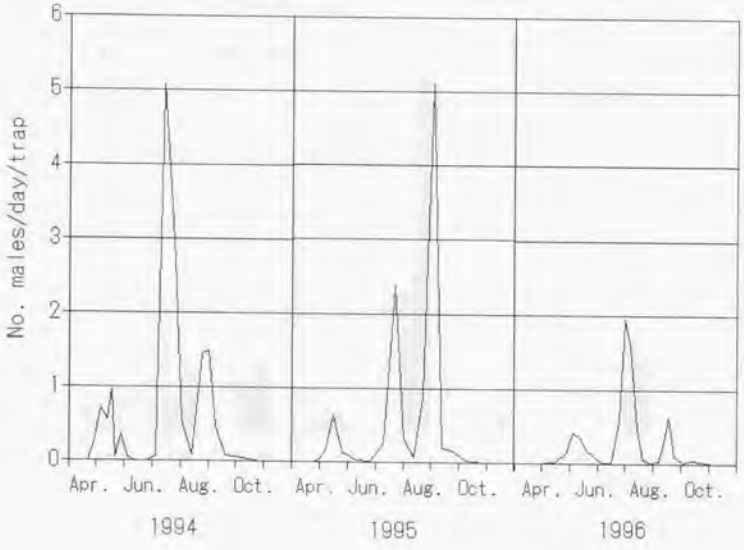


Fig. 1-3. Seasonal prevalence of males captured by pheromone traps in the treated areas from 1994 to 1996.

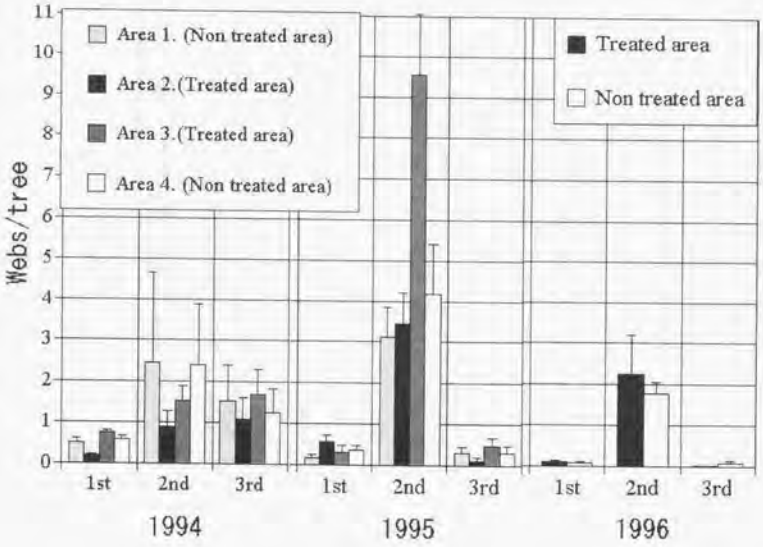


Fig. 1-4. Seasonal occurrence of webs of *H. cunea* larvae in the experimental areas from 1994 to 1996. Error bars indicate S.E.M.

Table 1-1. Effect of mass-trapping on mating success of tethered females of *H. cunea* in 1994 and 1995.

Date (Generation of feral males)		% of females mated (No. recovered females) [a]			
		Treated area		Non-treated area	
1994/9/8	(2nd)	13.3	(15)	26.3	(19)
1994/9/12	(2nd)	14.3	(7)	11.1	(9)
1995/7/19	(1st)	47.4	(19)	69.2	(13)
1995/9/8	(2nd)	46.2	(13)	22.2	(9)

[a] Twenty virgin females were tethered one on every tree in each of the treated and the non-treated areas.

Table 1-2. Effect of mass-trapping on mating success of tethered females in 1996.

Date (Generation of feral males)		% of females mated (No. recovered females)[a]			
		Treated area		Non-treated area	
1996/7/20*	(1st)	35.7	(28)	80.0	(20)
1996/7/25	(1st)	30.0	(30)	46.7	(30)
1996/9/8	(2nd)	32.4	(37)	45.9	(37)

Forty virgin females were tethered one on every tree in each of treated and non-treated areas. * indicates significant difference by Fisher's exact probability test ($p < 0.05$).

Degrees of larval outbreaks

The degrees of larval outbreaks were estimated by counting the number of webs. Heavy damage was observed in the study field through 1994 to 1996. This occurred to the largest extent in the second generations, with many plane trees being defoliated by the fall webworm not only in the non-treated areas but also in the treated areas.

The number of webs per tree is summarized in Fig. 1-4. Only in the second generation of 1994, the number of webs in the treated areas was less than that of the non-treated areas. On the contrary, in the second generation of 1995 and in the second generation of 1996, many more webs were found in the treated areas. However, no significant differences were observed between the treated areas and the non-treated areas in every generation (Kruskal-Wallis test; $p>0.05$).

Mating rate of tethered females

The results of tethered-female experiments are summarized in Table 1-1 and Table 1-2. I could not recover all of the females because some of them slipped out of threads or were eaten by predacious birds. The percentage of mating was calculated based on the females that survived. In the experiments of 1994/9/8 and 1995/7/19, the percentage of mating in the treated area (Area-2) was lower than in the non-treated area (Area-1), but there were no significant differences ($p>0.05$, by Fisher's exact probability test). On the other hand, in the experiments of 1994/9/12 and 1995/9/8, the percentage of mating was higher in the treated area (Area-1).

In the three experiments conducted in 1996, the percentage of mating in the treated area was lower than the non-treated area. Nonetheless, there were no significant differences except in the experiment of 1996/7/20 ($p<0.05$, by Fisher's exact probability test).

1.4 DISCUSSION

I carried out the mass-trapping experiments using synthetic sex pheromone through 1994 to 1996. As a result, I could not significantly reduce the damage to street trees (as reduction of larval webs) in every treated area and generation compared with those in the non-treated areas. In addition, I could not find a sign of decline in the fall webworm population from year to year. From these results, I suggested that it is difficult to control this insect population only by the mass-trapping method.

I conjecture two major reasons leading to the present results. First, I think that the density of the fall webworm population in the study field was too high to control by the mass-trapping method alone. The fall webworm often outbreaks under urban conditions. Adult moths have sharp peaks of occurrence; especially, in the first and the second generations. Furthermore, male moths take their random flight simultaneously in crowed groups to find female moths, within a

short period just before dawn in the first and the second generations. In the mating time during the peak periods, so many male moths might take their mating flight that it was difficult to decrease the mating success by the mass-trapping system. Some model analyses showed that the key to success in the mass-trapping method depends on the density of moths (Knipling and McGuire, 1966; Nakamura and Oyama, 1978; Nakasuji and Fujita, 1980; Barclay and Driesshe, 1983). These models show that the traps cannot catch a sufficient number of males to decrease the matings as the density of moths increase.

On the other hand, I can say from the results of the tethered female experiments that the mass-trapping trials might disturb the matings when the treated area was large enough as in 1996. If we can reduce the population of this insect by other methods like insecticide sprays or prunings (direct removal of webs) as a subsidiary means of control, then the mass-trapping system may be more effective. To construct an integrated control program for *H. cunea*, it may be useful to analyze the temporally structured simulation model that includes the ecological processes and life cycle of this insect. Using such a model, I can evaluate the maximum density at which mass-trapping can exert it's proper efficacy.

Second, I think that male moths might immigrate into the treated areas. Though I assumed that I could minimize the risk of immigration from non-target areas in urban conditions, I did not know the flight ability and preference of this insect. If many more male moths could get into the treated areas than I anticipated, the density of male moths could not be reduced drastically. In such a case, I may be able to overcome this problem by making the treated area larger or by placing more barrier traps. Actually, in the experiments of 1996 that had a treated area four times larger than that of 1994 and 1995, all three experiments resulted in the percentage of mating being lower in the treated area than the non-treated area. If the traps had been arranged more effectively, I think that I could have detected the significant differences between the treated areas and the non-treated areas in all experiments.

I could not reduce the damages of street trees by the mass-trapping method only. On the other hand, conventional control of this insect using pesticide does not seem very effective. Fukuyama (1996) showed that the damages by this insect are increasing as environment conditions become increasing urbanized. He conjectured that the fall webworm could not be kept at a low density by natural enemies in urban areas, because the urban conditions have a relatively poor ecological community system. Moreover, if I could reduce the frequency of insecticide spray by using the mass-trapping method, it still has potential viability in an integrated management program even if it cannot reduce the damages drastically by itself.

CHAPTER 2

Flight Ability and Dispersal Patterns

2.1 INTRODUCTION

It is highly recommended to investigate the flight ability and dispersal patterns of adults, when we design a management program for an insect pest. Especially, pest management for moths using synthetic sex pheromone such as mating disruption or mass-trapping is thought to be very sensitive to the immigration from non-target areas. High immigration of active males and fertile females makes nonsense efficacy of the method (Barclay, 1984). Moreover, it will be further serious in the case that male can mate many females (Jones, 1998: Barclay and Driesshe, 1983).

I conducted mass-trapping trials with synthetic sex pheromone to control *H. cunea* but failed to reduce damages by the larvae (Chapter 1). I thought that one of the reasons of this failure was the immigration of male moths, since *H. cunea* females do not disperse after copulation (Masaki, 1975). To evaluate this possibility, I needed to know the flight ability and dispersal patterns of *H. cunea* males.

Using flight-mill system is convenient to determine the maximum dispersal ability and the velocity of flying insects (Kawamoto et al., 1987). However, flight ability in the flight-mill system can be an overestimation of dispersal in the field, since insects are enforced to fly unnaturally in this system. Dispersal ability should be estimated by coupling field mark-recapture experiments with the flight-mill experiment, then, it can be concluded comprehensively how the insects disperse (Shirai et al., 1998).

In this chapter, I first used the flight-mill system for analyzing the potential flight ability of *H. cunea* males. Secondly, I conducted the wind-tunnel experiment to investigate daily patterns of male flight activities for mating behavior. Finally, field trials of mark-recapture were conducted to determine dispersal patterns of *H. cunea* males in the field.

2.2 MATERIALS AND METHODS

Flight-mill experiment.

Flight ability of virgin male moths was determined using the flight mill system almost the same as that used by Noda and Kamano (1991) for *Spodoptera litura* (F.). The device had a rotor made of balsa wood (5mm in diam. 30cm in length), and a male moth was attached to the end of it at the pronotum with adhesive (Bond G17 *, Konishi K.K.). The number of revolutions was counted by an auto-detect sensor and the data was collected automatically by a personal computer that was

connected to this device. Insects used for this experiment were collected as larvae in Koto-ku, Tokyo in 1997, and were maintained for a few generations in the laboratory condition (15L: 9D, 25°C) with artificial diets (Insecta L. F. ®; Nihon-Nosan Corp.).

I used four groups of males in this experiments to investigate flight abilities of males that were applied to the field mark-recapture trials (later): newly emerged males (designated as 'the first day'), males kept in the conditions of 15L : 9D cycles and 25°C for three days (the third day), males kept in a cool condition (15L : 9D cycles, 12°C) after emergence for three days (cooled), males marked with a fluorescent pigment (Keikou-Toryou ®; Kurachi Corp., Osaka) and kept in a cool condition for three days (as cooled & marked). Experiments were started at the 13h in the photophase, continued throughout 9 hours in scotophase, and finished 1h in photophase (12h in total).

The collected data were summarized as flight distances in 12h, flight duration and flight velocities. The flight distance was calculated as a product of number of rotor revolutions and the circumference of the rotor. The flight duration was the summation of 'quarter hour units' (i.e., 15min intervals) in which the numbers of revolutions exceeded a hundred times. Namely, if it took over 9sec. (15min/100) for one revolution on average, I judged this insect had ceased to fly at that 15min unit. The flight velocity was calculated from the data in this flight duration.

Each treatment was replicated 34, 24, 28 and 28 times in the first day, the third day, the cooled and the cooled & marked conditions, respectively. Statistical significance was tested by ANOVA and Turky-Kramer's test for the flight distance, the flight duration and the flight velocity.

Wind-tunnel experiment

An indoor wind tunnel (30 cm in diam. × 2 m in length) was used to investigate daily patterns of male flight activities. Insects used for a this experiment were collected as larvae in Ibaraki prefecture in 1995, and was maintained for few generations in the laboratory condition (15L : 9D, 25 °C) on Insecta LF ®. Adult moths were kept in the same condition as in the larval stage.

The wind tunnel experiment was carried out under conditions of 25°C, >40% r.h., and at a wind speed of 0.30 m/sec. The light condition of the wind tunnel was controlled at 10 lux constantly throughout the experiment. Four male moths within two or three days after emergence were put into the wind tunnel just at the timing of 6 h, 7 h, 8 h in scotophase, light-on, and 1 h, 2 h, 3 h in photophase. I used either four virgin females in a screen cage (9 cm in height: 8 cm in diam.) or synthetic sex pheromone lure (Nitto-Lure; Ameshiro®, Nitto DenkoCorp.) as pheromone sources. The pheromone sources were put into the wind tunnel 1.2 m upwind to the release point of males. Total numbers of pheromone source contacts by four males were counted as male activity.

Each treatment was replicated seven times except for four replicates in the lure at 6 h in scotophase and 3 h in photophase. I tested the statistical differences in time series of the

photoperiod in each treatment by Scheffé's test. In addition, Mann-Whitney's U-test was applied to test a significant difference between the lure and the virgin female conditions in each photoperiod.

Field mark-recapture trials.

Mark-recapture experiments were conducted twice in July (Summer experiment) and September (Autumn experiment), 1998, in Hongo campus of the University of Tokyo, Bunkyo-ku Tokyo (Fig. 2-1). There are a lot of cherry, plane and zolkovas trees, etc., which are favorite hosts of *H. cunea* larvae, and I found webs of the larvae in preliminary observation. The synthetic sex pheromone traps were sticky delta-traps (with a sticky surface of 30.0 × 18.5 cm). The lure was proven to be as effective as virgin females not only by Zhang and Schlyter (1996) but also in my preliminary survey.

I conducted the mark-recapture experiment in a small local area, where the largest distance from the release point was 500 m (Fig. 2-1). Various mark-recapture experiments have been conducted in much larger areas than the present study (Wakamura et al., 1990; King et al., 1990; Shirai and Kawamoto, 1989). However, the aim of the present experiment is to estimate the male dispersal pattern in a few days rather than the maximum dispersal ability.

Males used for the mark-recapture experiment were collected as larvae in Koto-ku, Tokyo, in 1997, and was maintained for a few generations in the laboratory condition (15L: 9D, 25 °C) on Insecta LF ®. Same as the cooled and marked males in the flight-mill experiment, males were marked with Keikou-Toryou ® and kept in the cool condition (15L : 9D cycles, 12°C) for one to three days to prevent exhaustion by flying around in a small cage.

I released 1110 and 996 marked males at 0:00 am in 7 July and 10 September 1998, respectively (see Fig. 2-1 for the release point). Recapture censuses were conducted for all the traps on one, two, four, six, eight and ten days after the release. Sticky sheets were brought back to the laboratory and checked under ultraviolet light to distinguish marked males from wild ones.

I used the meteorological data (temperature, precipitation, wind velocity and the direction of the maximum wind) that was recorded in Tokyo Station of Meteorological Office (Chiyoda-ku, Tokyo).

2.3 RESULTS

Flight-mill experiment.

Though average flight distance of the first day males was the largest, it was almost the same to those of the cooled males and the cooled & marked males (Fig. 2-2(a)). The third day males flew a rather shorter distance on average, though there was no significant difference between this and the others (Turky-Kramer's test; $p>0.05$). One of the first day males flew over 23 km, which was the maximum among all males.

Fig. 2-1. The map of study area for the two marking-recapture experiments in 1998. + : the release point. •: the synthetic sex pheromone traps. SE 1 indicates the trap that caught the largest number of males.

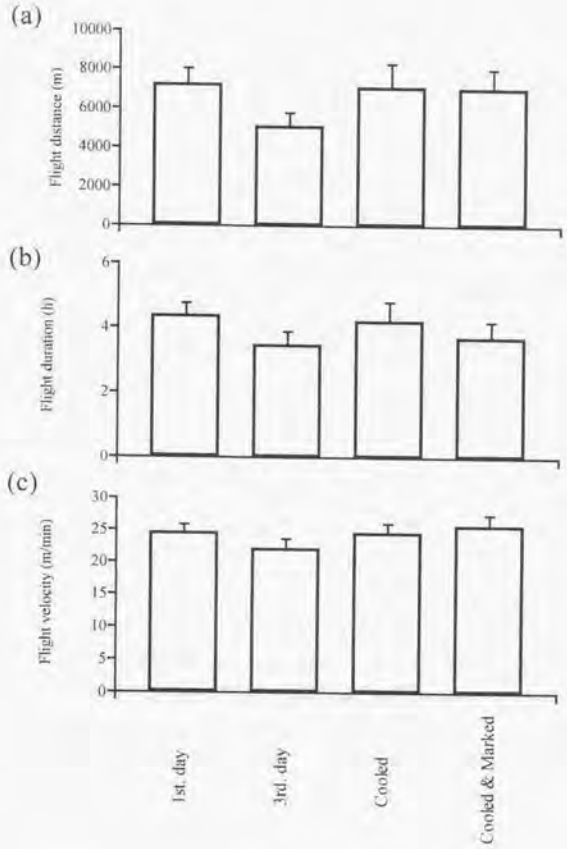


Fig. 2-2. Flight ability of male moths of *H. cunea* in the "first day", in the "third day", in the "cooled" and in the "cooled & marked". (a): the flight distances in 12h. (b): the flight durations (c): the flight velocities in the flying period. Error bar indicates S.E.

Though the average flight duration of the first day and the cooled males had a tendency to be longer than the third day and the cooled & marked, but there were no significant differences among the four treatments (Fig. 2-2(b), Turky-Kramer's test; $p>0.05$). One of the cooled males flew over 11.5 h, which was the longest of all males.

There were no significant differences among treatments in the flight velocity (Fig. 2-2(c), Turky-Kramer's test; $p>0.05$). Though two parameters, the flight distance and the flight duration, had large variations among individuals, the flight velocity was rather invariable around the total mean value, 24.4 m/min. Judging from the result, I thought that the male's activity would not be affected by marking with a fluorescent pigment and keeping in a cool condition for one to three days to use in the mark-recapture experiment.

Examples of the flight patterns observed in the experiment are depicted in Fig. 2-3. Most of the males ceased flying after the first 2h. Some of them continued flying intermittently thoughout the experiment. Some did not fly for a few hours and suddenly restarted during the experiment. The other did not restart flying at all. These patterns seemed to have no relationship with the photoperiod cycle of the rearing condition.

Wind-tunnel experiment.

Responese on the males to the synthetic lure were always significantly higher than those to virgin females (Fig. 2-4, Mann-Whitney's U-test; $p<0.05$). It should be noted that the males rarely responded to the virgin females over 1 h out from the light-on, on the other hand, substantial numbers of males were constantly attracted to the synthetic lure. I concluded from the result that the synthetic lure was sufficiently effective for the use in the later mark-recapture experiment.

There was a clear peak of male activities around the light-on timing (Fig. 2-4) and responses to virgin females and to the synthetic lure at the light-on timing were significantly higher than the other periods (Scheffé's test; $p<0.001$). There were no significant differences between other photoperiods (Scheffé's test; $p>0.05$).

Mark-recapture experiment.

The meteorological data during the experiments are shown in Table 2-1. Fig. 2-5 shows the details of trap catches of marked males in the study area, and Table 2-2 summarizes the daily recaptured numbers. The largest number of males was recaptured on the second day in the two experiments. Mean distance of recaptures from the release point was larger than the distance of eight traps located on the nearest concentric on the first and second day, but shorter than the second-nearest one both in two experiments. The furthest trap capturing male on the first day in the Summer experiment was the most northwest trap (located 502m from release point), and on the first day in the Autumn experiment was the most north trap (located 380m from release point).

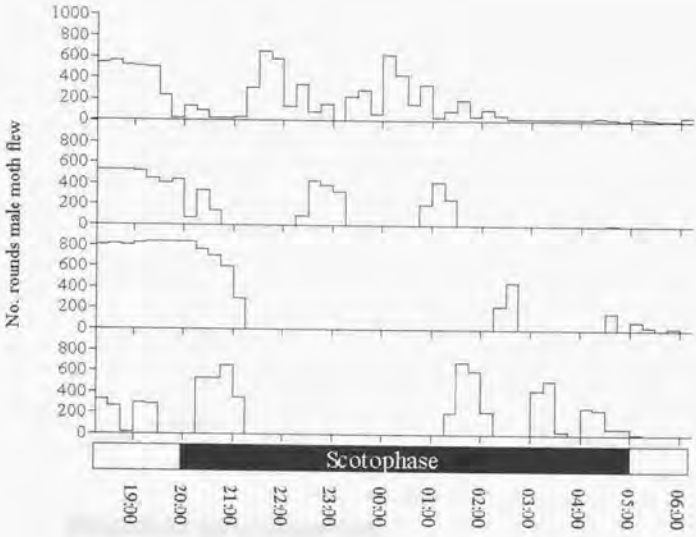


Fig. 2-3. Four examples of males' activities in flight-mill experiment for 12h. The ordinate represents number of rounds made by a male in quarter hour units (i.e. 15 min intervals).

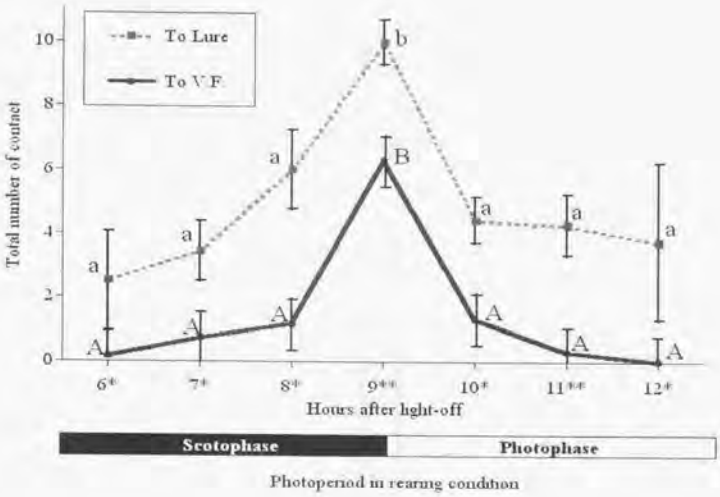


Fig. 2-4. Temporal changes in the male responses to pheromone source. The experiment was carried out under 10 lux lighting regardless of the photoperiodic cycles of rearing. Error bar indicates SE. * and ** in each time point indicates that responses to virgin females and that to the lure are significantly different at 5% and 1 %, respectively, according to Mann-Whitney's U test. Responses at each time point with the same letter are not significantly different by Scheffé's test. The lower bar represents the photoperiod of the rearing condition (D-: scotophase, L-: photophase).

Table 2-1. Meteorological data at Tokyo during the two mark-recapture experiments.

Summer experiment (July 1998)	7 Jul. The day released	Days after release 1	2	3	4	5	6	7	8	9	10
Temperature											
Max	31.6	31.4	35.2	28.9	30.1	24.0	22.1	25.6	23.0	20.5	22.7
Min	26.0	25.6	25.3	22.7	22.4	17.5	17.0	18.1	19.2	18.1	17.8
Mean	28.2	28.1	29.6	26.4	26.6	20.5	19.0	21.3	20.7	19.0	20.4
Rainfall (mm)	0.0	0.0	2.0	30.0	6.0	0.5	0.0	0.0	0.0	6.5	7.5
Mean wind velocity (m/s)	2.2	2.1	2.2	2.1	2.6	4.4	3.3	2.5	2.8	2.8	4.0
The direction of max wind	S	S	NNW	ENE	NE	ENE	ENE	ESE	ENE	NE	NNE

Summer experiment (July 1998)	10 Sept. The day released	Days after release 1	2	3	4	5	6	7	8	9	10
Temperature											
Max	30.8	30.2	28.5	30.7	29.7	27.9	32.8	28.8	24.0	31.0	31.4
Min	22.5	22.1	23.3	22.6	22.7	21.4	22.3	21.8	20.5	22.1	24.4
Mean	26.0	25.1	25.3	25.8	25.4	25.1	27.3	25.5	22.3	26.2	27.2
Rainfall (mm)	0.0	0.0	0.0	0.0	0.0	35.5	94.0	0.0	5.0	0.0	0.0
Mean wind velocity (m/s)	3.0	3.6	2.8	3.2	3.1	2.2	6.7	2.9	2.5	2.9	3.4
The direction of max wind	ENE	ENE	NE	ENE	ESE	E	W	S	NNE	S	S

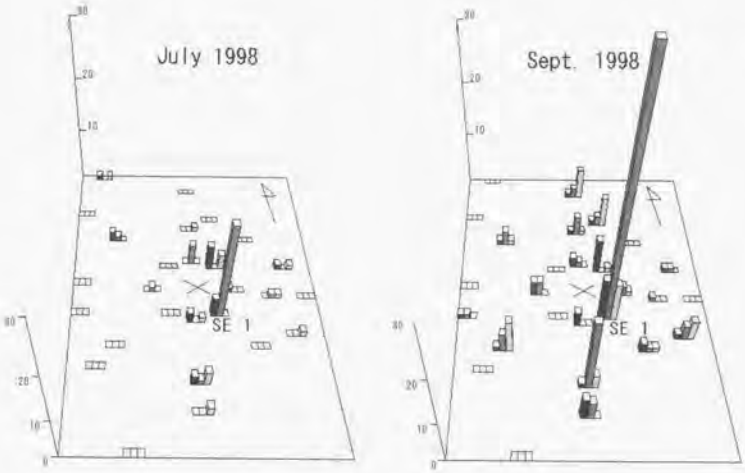


Fig. 2-5. Capture of marked males by pheromone traps in the two experiments. × : release point. Dark gray bar in the left of each point means the number of males captured on the first day of the release. The gray bar in the middle and light gray bar in the right mean on the second day and the summation from the third day to the last day, respectively. SE 1 means the trap that caught extra large number of males.

Table 2-2. Numbers of marked males recaptured and mean distances from the release point in the two experiments.

Summer experiment	Days after release						Total
(release: 7 Jul.)	1	2	4	6	8	10	
No. males recaptured (1110 males released)	18	27	9	5	0	0	59
Mean distance	175.9	123.0	240.7	282.7	-	-	-
(S.D)	(107.5)	(51.9)	(129.2)	(46.4)	-	-	-

Autumn experiment	Days after release						Total
(release: 10 Sept.)	1	2	4	6	8	10	
No. males recaptured (996 males released)	48	96	26	5	2	1	172
Mean distance	190.1	179.6	239.1	244.7	169.1	380.0	-
(S.D)	(93.4)	(89.8)	(101.4)	(87.9)	(66.5)	(0.0)	-

There was significant difference of trap catches between East and North in two-way ANOVA (F=4.423; df=1, 23; p=0.0466), when I divided the trap catches data into four directional categories from the release point. Clear relationship was hardly seen between the trap catches (Table 2-2) and the wind direction or precipitation data (Table 2-1), though, low temperature from the fifth day to the end of the Summer experiment seemed to affect the trap catches, for there was no trap catch in these periods, and there were certain traps, which caught quite large numbers of males. Such traps might affect the difference in direction. Especially, the southeast trap in the nearest concentric (SE 1 in Figs.1 and 5) caught the largest numbers.

2.4 DISCUSSION

Flight ability.

There are some flight-mill experiments on migratory species, cabbage webworm (*Hellula undalis* (F.)) and diamondback moth (*Plutella xylostella* (L.)), but these could not be compared to my flight-mill experiment directly, since there were differences in experimental conditions. However, *H. cunea* males seemed to have the same flight abilities as *H. undalis* (Kawamoto et al., 1987). *H. undalis* flew over 20 km on average for 24 hours in their experiments. *H. cunea* could fly further than *P. xylostella* (Shirai, 1993). *P. xylostella* flew about 10 km on average for 48 hours. Though *H. undalis* and *P. xylostella* have smaller body sizes than *H. cunea*, they are thought to fly long distance into northern part of Japan, where they cannot overwinter. On the other hand, *H. cunea* is regarded as resident species, but potentially can fly long distances comparable to these migratory species.

It has been observed that the *H. cunea* males in summer and autumn generations fly their mating flight in a short period of the dawn (Hidaka, 1972; Zhang and Schlyter, 1996; Chapter 1). The flight-mill experiment showed that temporal activities of individual flight patterns were not limited around the light-on timing, but extensively varied among individuals during the experiment, and they could potentially fly over 7 km throughout the nights.

Temporal flight pattern.

Hidaka (1972) reported that the adult moths began their courtship at dawn (4:00 a.m.) and lasted until about 5:00 in the summer generation. He suggested that the change of luminosity at dawn was the essential factor for eliciting mating behavior. Also in my wind tunnel experiment, a sharp peak of the male response was also observed around the light-on timing both to the synthetic lure and to virgin females. However, my wind-tunnel experiment was conducted constantly under 10 lux lighting, and every male tested at the timing in scotophase experienced the change of light condition. As Arai and Mabuchi (1979) concluded that circadian rhythm was present for *H. cunea* mating behavior, my experiments showed that *H. cunea* males retained circadian rhythm even if they

received a change of light condition (in the case, from complete dark to 10 lux).

Zhang et al. (1998) reported that the synthetic sex pheromone traps caught some males, while the virgin female traps caught no male early in night that had been regarded as the dispersal period after emergence (Arai and Mabuchi, 1979). My experiments also confirmed the possibility that the synthetic sex pheromone traps could catch the males even in the non-mating period. Significant numbers of contacts to the synthetic lure were constantly seen over 1h out from the light-on timing, while they rarely responded to the virgin females in the wind-tunnel experiment. The flight-mill experiment showed that the *H. cunea* males could potentially fly throughout the night.

From these results, I conjectured that the flight duration of males was limited in short period less than one hour or so in the dawn in natural condition, but, there remained some possibilities of male's responding to the synthetic lure even out of such a limited period.

Field dispersal.

There are many mark-recapture experiments to estimate the dispersal patterns in other lepidopteran species. *Spodoptera litura* (F.) was estimated to fly 3.5 km to 5.9 km in one night (Wakamura et al., 1990). *Helicoverpa armigera* (H.) were scarcely recaptured in 1.74 ha field of pigeon pea where insects were marked, but recaptured in surrounding traps. The cabbage webworm *Hellula undalis* (F.) flew 2 km to 3 km and never caught by the traps within 500 m from the release point (Shirai and Kawamoto, 1989). These insects were thought to fly long distance, and these experiments were conducted in rather opened, wide crop fields. *H. cunea* outbreaks in urban conditions, where there are many obstacles such as tall buildings and crowded roads for male moths to disperse and these obstacles are also likely to split *H. cunea* habitats.

In the mark-recapture experiment, the mean distance of trap catches was larger than the distance of eight traps located nearest concentric, but shorter than the second nearest ones (See Fig. 2-1). It could be explained that the traps in the nearest concentric were set more densely than second nearest ones, and more males were captured in eight traps located nearest concentric. However, trap catches in the second day was larger than the first day, and mean distance in the second day was shorter than the first day. From these data, I thought that most of *H. cunea* males did not fly long distances in one day (about several hundred meters), although Hirooka (1987) conjectured that males would fly more than 5 km at mating period in the summer generation.

It should be mentioned that many marked males were eaten by avian predators such as tree sparrows, when I observed on the release day of my mark-recapture experiment. Hasegawa and Itô (1967) reported that adults suffered from heavy predation by birds just after emergence. Adults may be active only short distance dispersal due to heavy pressure of predation by birds.

H. cunea males can fly long distance comparable to the migratory species, but they undergo short distance dispersal due to their circadian rhythm under heavy pressure of predation by

birds. On the other hand, they will be captured by the synthetic sex pheromone trap even out from the mating period. Such properties of this insect may be tractable for pest management with synthetic sex pheromones. However, another experiment should be done for overwinter generation of this insect, which has different mating period (Masaki, 1975; Zhang et al., 1996) and I did not elucidate flight ability and dispersal patterns of them.

CHAPTER 3

Assessment of the synthetic sex pheromone traps

3.1 INTRODUCTION

In this chapter, I attempt to clarify whether synthetic sex pheromone traps could reduce the ratio of mating success in an urban local area. I investigated two aspects of mass-trapping with a synthetic sex pheromone: male-removal effect and "male-attraction effect" described below. I expected that the effect of mass-trapping would be brought about by removing plenty of males, but there seemed alternative explanation for the low mating success in the treated area of my experiment in 1996. Kitamura and Kobayashi (1985) reported in *Spodoptera litura* F. that there was no overall difference in mating percentage between a communication-disruption plot and a mass-trapping plot. They suggested that the mating suppression in the mass-trapping plot came from the communication disruption effect of the synthetic sex pheromone lures in the traps. I thought that such communication disruption effect was caused by "false trail following" by males to the synthetic sex pheromone lures. I named it as "male attraction effect".

I performed an additional field experiment with the synthetic sex pheromone traps and assessed their efficacy, examining the number of males that were captured in virgin-female traps.

3.2 MATERIALS AND METHODS

Study field

I conducted the experiment on Harumi Street in Koto-ku, Tokyo, in 1999. I set up three groups, Treatment I, Treatment II and Control, and each group had two experimental sites (Fig. 3-1). Therefore, this study field was divided into six experimental sites each of which had ten plane trees (*Platanus acerifolia*) on either side of the street (about 150 m length). I placed a buffer area (about 150m) between the two neighboring experimental sites (Fig. 3-1). I employed two replications of each group to avoid initial environmental differences. The arrangement of experimental sites was randomly designed.

Treatments with synthetic sex pheromone traps

The synthetic sex pheromone trap used in the experiment was a sticky delta-trap, NITTO-LURE® (with a sticky sheet of 30.0 × 18.5 cm inside). The synthetic sex pheromone lure contained three components, (3Z,6Z)-3,6-9,10-epoxyheneicosadiene, (9Z,12Z,15Z)-9,12,15-octadecatrienal and (3Z,6Z)-1,3,6-9,10-epoxyeicosatrien, and this lure had been found to be effective in the field

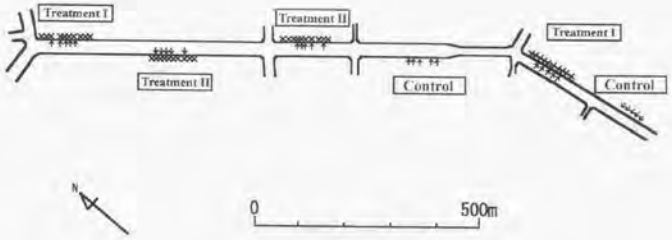


Fig. 3-1. Map of the study field. ✕ and ↗ indicate a synthetic sex pheromone trap (without sticky sheets in Treatment II) and virgin female trap, respectively.

experiments (Zhang and Schlyter, 1996; Zhang et al., 1996). The lure was hung from the trap's ceiling at the center. The traps and the lures were provided by Nitto Denko, Co.

I placed one synthetic sex pheromone trap without an interior sticky sheet on each of ten trees in Treatment I. In Treatment II, I placed one synthetic sex pheromone trap with a sticky sheet in each of the tree. The trees in Control did not receive any traps. Treatment I (without a sticky sheet) was designed to quantify the effect of the synthetic sex pheromone traps only with male attraction, but not with trap catches. It also corresponds to the case where the traps caught so many male moths that the sticky sheets were covered with scales and captured males, and no more male moths could be captured. In Treatment II, to avoid trap saturation, I replaced each sticky sheet whenever more than 30 males were captured. Each treatment was started 29 June and continued until 21 July 1999.

Assessment using virgin-female traps

Two virgin *H. cunea* females were put into a screen cage (5.0 × 5.0 × 8.0 cm) and the screen cage was placed on the center of the aforementioned sticky sheet. The virgin females were collected as larvae in Koto-Ku, Tokyo. The larvae were reared on an artificial diet (Insecta LF; Nihon-Nosan Co.)in the laboratory (15L : 9D cycles, 25 °C), and the emerged female moths were kept in a cool condition (15L : 9D cycles, 15 °C) for one to three days in order to keep them from exhausting themselves by flying around inside a small cage.

In order to quantify male-removal effect and male-attraction effect, five traps with two virgin females in each were placed in five trees so that each tree had one trap in each experimental site (see Fig. 3-1). This procedure was carried out twice: between 14 and 17, and between 17 and 21, July 1999. I determined the start of the first trial according to the field observations of pupal development and *H. cunea* males captured by sticky sheets in Treatment II. In the experimental sites of Treatment I and Treatment II, the virgin-female traps were placed so that they were not at the end of the each site and placed on a branch apart from the previously set synthetic sex pheromone trap. The virgin-female traps were first placed on 14 July and were maintained for three days in each experimental site. Then, after counting the number of males captured in the virgin-female traps, I replaced the sticky sheets and virgin females with new ones on 17 July as the second trial. The final counting of the number of males captured in the second trial virgin-female traps was performed on 21 July.

3.3 RESULTS

The numbers of males captured in the virgin-female traps are shown in Table 3-1 (a). The total number of males (pooling two replicate sites) for each trial are presented in the left-side column and the capture numbers in each trap are presented on its right. Both the first and second

Table 3-1.

(a) The number of males captured in virgin-female traps in Treatment I, Treatment II and Control (no synthetic pheromone trap).

Treatment	First trial (14th to 17th July)						Second trial (17th to 20th July)					
	Total	No. moths in each trap *)					Total	No. moths in each trap				
Treatment I	1	(0	1	0	0	0)	43	(36	1	3	0	0)
(traps without sticky sheets)		(0	0	0	0	0)		(0	0	1	2	0)
Treatment II	4	(2	1	0	0	0)	43	(1	6	15	11	8)
(normal traps)		(0	0	1	0	0)		(1	1	0	0	0)
Control	15	(5	1	7	0	0)	62	(28	2	3	0	13)
(no pheromone trap)		(0	0	2	0	0)		(5	0	9	1	1)

*)Upper and lower five numbers, respectively, show the number of males captured in each trap in either of two experimental sites.

trial, the number of males captured in Control tended to be larger than in Treatment I and Treatment II. A randomized t-test, however, showed that there was not significant differences either between Treatment I and Control (p=0.140 and p=0.312, respectively) nor between Treatment II and Control (p=0.635 and p=0.613, respectively) in both the first and the second trials (Manly, 1997). There was no differences between Treatment I and Treatment II in both the first and the second trials (p=0.458 and p=1, respectively). I, therefore, pooled the data of Treatment I and Treatment II as a new category, Treatment, then tested between Treatment and Control (Table 3-1 (b)). In the first trial, I found a significant difference between Treatment and Control (p=0.040), though no significant difference was detected in the second trial (p=0.610).

3.4 DISCUSSION

The number of males captured by the traps showed large variation (Table 3-1 (a)). The efficacy of the pheromone traps depends on various factors such as temperature, light intensity, humidity, direction and strength of wind, and their placement (McNeil, 1991). I could not determine the main factors that created the large variation among traps. However, the virgin-female traps located at the end of experimental sites sometimes caught extraordinarily large numbers of males (Table 3-1(a)). Wall and Perry (1980) reported that the trap at the most upwind site often caught the largest number of males. Considering such spatial heterogeneity, I performed the randomization test instead of a usual non-parametric test. Because the randomization test repeats random shuffling of actual data, this method can detect a significant difference, if any, even under conditions with such spatial heterogeneity (Manly, 1997).

Randomization test showed no significant difference between Treatment I and Treatment II in both two trials, although the synthetic sex pheromone traps without sticky sheets never caught any males in Treatment I. This result suggests that the male-removal effect had no significant effects on reducing mating success in Treatment II.

On the other hand, pooling the data of Treatments I and II as Treatments, I found a significant difference between Treatments and Control in the first trial. This part of the experiment was performed at the beginning of the first-generation moth emergence, judging from field observations, and the adult density was still low. I considered that the traps of Treatments could effectively inhibit males to approach virgin females. Many male moths might be attracted to the synthetic sex pheromone, expending most of their energy and time around the trap, rather than searching for virgin females.

However, I could not find a significant difference in the second trial. It was conducted in the midst of adult emergence, judging from the sharp outbreak that follows within several days the increase of emergence in the yearly average pattern. Unfortunately, I accidentally abandoned the sticky sheets of the synthetic sex pheromone traps in Treatment II. However, the quick increase of

Table 3-1.(Continued)

(b) Randomization test using t-score

Randomization test	First trial (14th to 17th July)		Second trial (17th to 20th July)	
	Mean probability[1)]	Range[2)]	Mean probability	Range
Treatment I vs. Treatment II	0.458	(4491-4639)	1	-
(Treatment I +Treatment II) vs. Control	0.040	(385-430)	0.610	(6015-6166)

1) Original data were randomized 9999 times and the procedures were replicated ten times.

2) Numbers in parentheses show the range of orders of actual t-score among 10,000 t-scores in ten-time repeats.

adult density was also evident according to the score of captured males in Control (Table 3-1 (a)), and my previous mass-trapping experiments (Chapter 1). There might be such a preponderance of males that many other males might not be attracted to the synthetic sex pheromone, and thus male-attraction effect might disappear.

It has been claimed that a large-scale program should be conducted to achieve the mass-trapping success (Jones, 1998). In this study, I treated the synthetic sex pheromone traps in a locally limited area. The synthetic sex pheromone traps, however, reduced the mating success by male-attraction effect during the low adult density period. Considering that the male-attraction effect has a possibility to be more effective than the effect of male-removal effect on reducing the mating success of *H. cunea* in local area, it is important for the optimal design of synthetic sex pheromone treatment to elucidate how large a treatment area should be and how I should place synthetic sex pheromone lures, depending on moth density.

These considerations do not deny the possibility of also using the male-removal effect, if much more traps were to be treated. However, when we account for *H. cunea*, it is less efficient to treat more traps in one tree than my experiments, counting the cost-performance of the traps. Spatially structured simulation model will be useful for assessing manners of locations and abundance of pheromone traps.

PART 2: MODEL ANALYSIS

CHAPTER 4

An individual-based model for pheromone-mediated flight patterns of male moths in a local area

4.1 INTRODUCTION

Jones (1998) pointed out some difficulties in achieving the efficacy in mass-trapping using sex pheromones, as mentioned in General Introduction: (1) Lack of attraction of females by the attractant source used, (2) Lack of highly efficient traps, (3) Problem of high density of insect populations and trap saturation, and (4) Need for a high density of traps per unit area, which in turn renders the technique too costly.

I thought of another reason of the failure in the previous mass-trapping experiments (Chapter 1) in addition to those of Jones (1998). Pheromone traps can actually remove many males from the target area. However, if we could not neglect immigration from the surrounding areas, the attraction effect of the pheromone trap might cause a surplus increase of males. Namely, the mating success will not decrease even though a large number of males are captured, because pheromone traps may constantly amass males in the target area. Since the males' activities were largely affected by environmental conditions, it is difficult to detect such an effect in the field. This is why I constructed a model here to elucidate the effect of male attraction.

There are some models for pheromone-mediated flight patterns of male moths. Nakamura and Kawasaki (1977) constructed an individual-based model to determine the virtual active space of pheromone traps in *Spodoptera litura* (F.). Perry and Wall (1984) constructed a mathematical model for the pea moth, *Cydia nigricana* (F.) with respect to the interaction between traps and the effect of crops. Byers (1993) constructed an individual-based model to estimate the capturing efficiency of pheromone traps for the bark beetles, *Ips typographus* L. These models, however, assumed the pheromone diffusion pattern as "effective attraction radius", or the average boundary of threshold in constant wind direction. They also disregarded detailed flight processes of the males. Hirooka (1987) constructed an individual-based model for *H. cunea*, which included some realism: turnings of male moths in their pheromone-mediated flight after encountering "pheromone puffs", though he assumed constant wind direction. I thought that the "male attraction effect" should be strongly affected by the pheromone diffusion pattern in changing wind direction and the detailed male flight patterns.

In this chapter, I constructed an individual-based model describing pheromone plume

movements and detailed mechanisms of pheromone-mediated flight patterns of male moths, and analyzed how such process affects the spatial distribution of males and pheromone trap catches.

4.2 MODEL FORMULATION

I constructed a simulation model in which individual male moths moved in a two-dimensional virtual experimental area. My program was developed with Visual C++ (version 4.0, Microsoft). I put one synthetic sex pheromone trap at the center of the virtual experimental area and assumed that one time step as 1 sec. and the boundary condition of the area as torus. The schematic flow chart of the simulation processes is shown in Fig. 4-1.

Movement of pheromone plumes

The pheromone diffusion pattern and pheromone-mediated flight patterns of male moths have been gradually revealed. At the beginning of insect pheromone studies, insect pheromones were thought to produce an active space in which the concentration was above threshold for the male's responsiveness, and the boundaries of which could be described approximately (Bossert and Wilson, 1963). This postulation has been found inadequate, because it describes the concentration of odor molecules averaged over time periods. Insects respond instantaneously, when they get a sensory input by encountering intermittent or turbulent pheromone molecules (Wyatt 1994). In fact, the pheromone flows like smoke, and this structure was called as "pheromone plume" (Murlis et al., 1992). Moreover, the wind direction is not constant but "swings", causing a plume to meander and snake in the field (David et al., 1982).

Elkinton et al. (1987) suggested that few males came up to the trap from any distance, when the wind direction deviated widely. I also regarded the change of wind direction as one of the important factors for males' pheromone-mediated flight patterns. In the simulation, I assumed that the wind flows at a constant speed (W_{speed}), but changed its direction (Fig. 4-2). I set up the mean wind direction W_{direct}, and changed the direction every certain period (W_{freq}) according to the Gaussian distribution (SD: W_{sd}).

Pheromone plumes flow intermittently or turbulently like a cigarette smoke. They are regarded, however, to flow away somewhat keeping its concentration to far downwind (about several dozen meters) compared to merely normal diffusion (Howse, 1998). I could not quantify how far or how long the plume kept its structure, because such characters of the plume would change depending on the situation and the meteorological conditions (Uchijima, 1993). In the simulations, I assumed that the pheromone plume consisted of circular pheromone puffs. Fig. 4-2 shows the idealized representation of the trajectories of pheromone puffs used in the simulations, which follows the idea of David et al. (1982). The radius of each pheromone puff grew proportional to the elapsed times, and the concentration of each pheromone puff was diluted in inverse proportion to

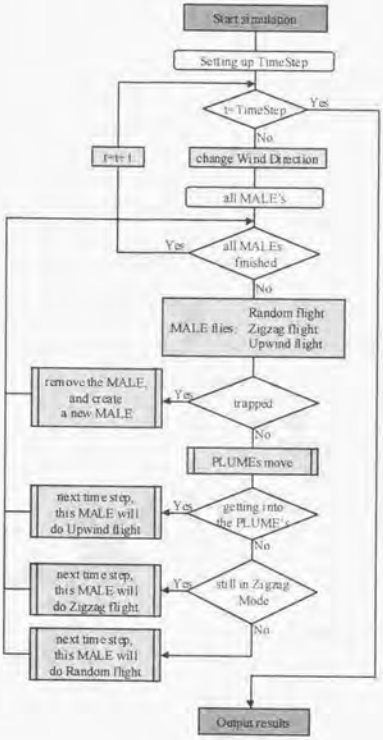


Fig. 4-1. The flowchart of our simulation model.

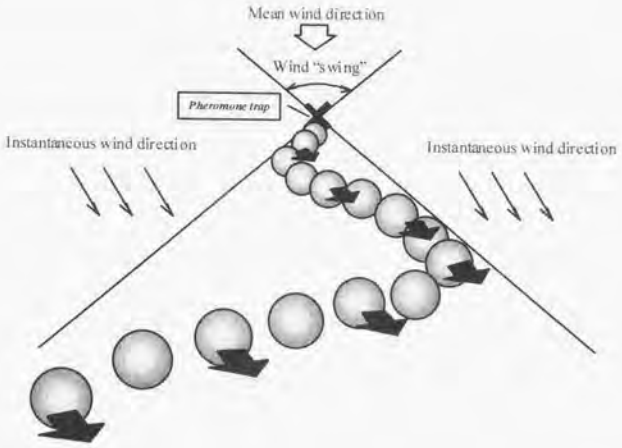


Fig. 4-2. Idealized representation of the trajectories of pheromone puffs used in our simulations. Each puff changes its direction according to the instantaneous wind direction.

its area. These relationships are given in the following equation (Fig .4-3).

$$R=at+R_0 \tag{1}$$

The wind sweep down the puff but never changes its amount of molecules, then

$$\pi R^2 D=\pi {R_0}^2 D_0$$

$$D=\frac{\pi {R_0}^2 D_0}{\pi R^2} \tag{2}$$

where R is the pheromone puff radius, a is diffusion constant, t is time steps, R_0 is the initial radius of pheromone puff, D is the density of the pheromone puff, D_0 is the initial density of the pheromone puff (see Table 1). Pheromone puffs were generated one per one time step (1 sec.), and were effective on male attraction until its density became lower than a certain threshold (D_{thres}). For example, if a=0.03, R_0=2 cm, D_0=10000 ng, D_{thres} =7ng, a puff can exists 25 sec. It was calculated in the following by equation (1) and (2):

$$t=\frac{\sqrt{\frac{\pi {R_0}^2 D_0}{\pi D_{thres}}}-R_0}{a}=\frac{\sqrt{\frac{\pi 0.02^2\times 10000}{\pi 7}}-0.02}{0.03}=24.531 \tag{3}$$

Then, there exist 25 puffs simultaneously in the virtual area. These procedures are depicted in Fig. 4-3.

Movement of males

When the males detect the pheromone plume, they start the upwind flight guided by anemotaxis. Loss of contact with the pheromone results in the cross-wind turning known as casting movements or the zigzag flight (Kennedy, 1977). This maneuver increases a probability to encounter the pheromone plume again. The upwind flight and casting movements, which derived from the internal couterturning program, were mediated by two aspects of chemical signals: the odor concentration within the plume and the odor "pulse" frequency (Vickers and Baker, 1992; Mafra-Neto and Cardé, 1994). They proposed that the males' straight upwind flight would occur when they were encountering sufficient concentration of pheromone pulses at intervals in turbulent plumes and the casting movements would take place, when they are flying along small continuous plumes or low-frequency pulsed plumes.

I categorized the male flight patterns in three types, random flight, zigzag flight and upwind flight. In the mating period, males flew the random flight until they encounter a pheromone puff. The length of the random flight in one time step ($Random_{Speed}$) was generated

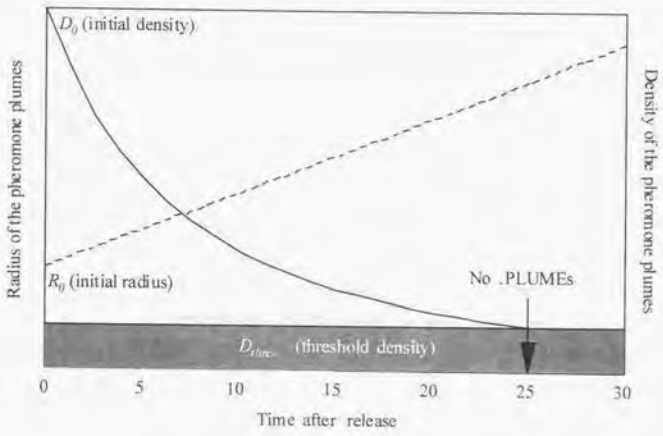


Fig. 4-3. The procedure generating pheromone puffs and calculating the number of plumes existed in a certain time step. R_0: initial radius of pheromone plume, D_0: initial density of pheromone plume, D_{thres}: a threshold density, for males' detection.

according to Gaussian distribution (mean: $Random_{Mean}$, S.D.: $Random_{SD}$). Males changed its direction by θ according to Gaussian distribution (mean: 0°, S.D.: $Random_{Angle}$) between the steps (Fig. 4-4(a)).

When they encountered the pheromone puff, they instantly stopped their random flight and started the upwind flight (Fig. 4-4(b)). Net length of the upwind flight in one time step was constant (*Upwind*), and males flew against the instantaneous wind direction. A male's encountering with a pheromone puff was judged not only when they were in a pheromone puff at a certain time step (t) but also when they passed through the trajectory of the pheromone puff (between t-1 and t). If they also encountered a pheromone puff at the next time step (t+1), they kept on the upwind flight.

Whereas, if they could not encounter a pheromone puff at next time step, they started the zigzag flight (Fig. 4-4(c)). Net length of the zigzag flight in one time step ($Zigzag_{Speed}$) was generated according to Gaussian distribution (mean: $Zigzag_{Mean}$, S.D.: $Zigzag_{SD}$) and males flew across the instantaneous wind direction one side to the other (Fig. 4-4(c)). Males flew the zigzag flight until they encountered a pheromone puff, but they returned to the random flight after zigzagging several times ($Zigzag_{Number}$).

If the males, in the upwind or the zigzag flight, got in or passed through the sticky area of the pheromone trap (*TrapArea*) placed at the center of the virtual area, they were regarded to be captured by the traps and removed from the area. When one male was removed from the virtual area, I placed a new male at a randomly chosen point inside the area. This replacement procedure corresponds to the immigrations from outside to the target area constantly, and the density of males is kept at the same level.

4.3 PARAMETER ESTIMATIONS

I focused my simulations on the situation where the traps capture the summer generation of *H. cunea* in a local area, and estimated the parameters according to the preceding studies by other researchers and our experiments. For the first step, I set default values, which could be regarded as biologically reasonable. Then, I changed some parameters, which was thought to be important for the outputs. The list of the model parameters and the default values are shown in Table 4-1.

Setting-up the simulation

Male moths begin the random flight just before dawn to find calling females in the summer generation (Arai and Mabuchi, 1979). I set the duration of our simulation time as 30 minutes (*TimeStep*=1800), during which time the mating activity of males was high. In the previous field experiment (Chapter 1), I observed that 10 to 20 males were simultaneously flying around a synthetic sex pheromone trap in the peak occurrence, and the pheromone-mediated flight

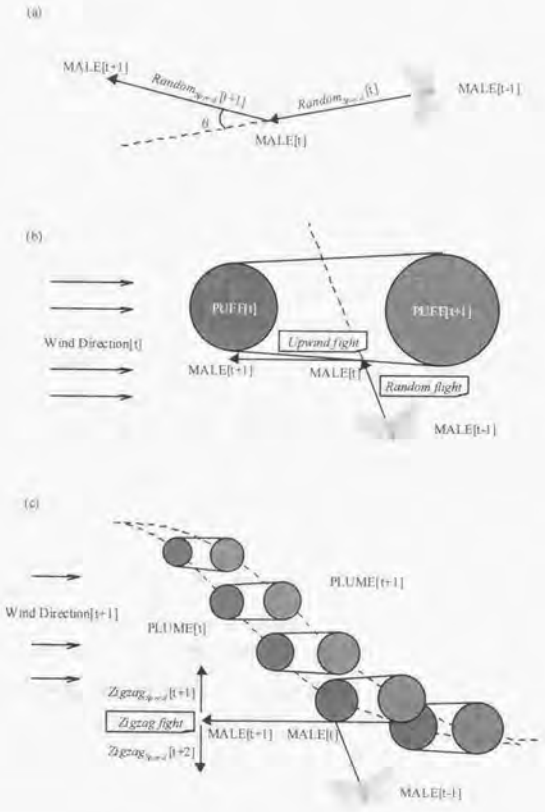


Fig. 4-4. Movement of males in our simulation. (a). a male flies the random flight with $Random_{Speed}$, and changes its direction by θ. (b). a male encounters a pheromone puff and flies the upwind flight in next step. (c). a male losses a pheromone puff and starts the zigzag flight with $Zigzag_{Speed}$ across the wind.

Table 4-1. Descriptions of model parameters and the default values used in our simulation model.

Parameter	Descriptions	Default Value	Units
	Simulation Settings		
$TimeStep$	Simulation duration	1800	sec.
$Males$	No. males constantly exists in simulation	10	-
$Area$	Simulation area	40.0 × 40.0	m
W_{Speed}	Wind speed	1.0	m/sec
W_{Direc}	Mean wind direction	0.0 (East)	degree
W_{Freq}	Frequency of wind direction changing	3	sec
W_{SD}	Wind "swing", standard deviation	45.0	degree
	Characteristics of H. cunea *male*		
$Random_{Mean}$	Mean speed of males in the random flight	1.38	m/sec
$Random_{SD}$	Standard deviation in the random flight	0.36	m/sec
$Random_{Angle}$	Standard deviation of the direction changing in the random flight	30.0	degree
$Upwind$	Constant speed of males in upwind flight		
$Zigzag_{Mean}$	Mean speed of males in the zigzag flight	0.47	m/sec
$Zigzag_{SD}$	Standard deviation in the zigzag flight	0.98	m/sec
$Zigzag_{number}$	No. turnings before giving up the zigzag flight	25	-
	Characteristics of pheromone trap		
$TrapArea$	Area of sticky sheet in the pheromone trap	0.3 × 0.18	m
D_0	Initial density of the pheromone plume	10000.0	ng/sec
R_0	Initial radius of the pheromone plume	0.02	m
D_{thres}	Threshold density detected by males	10.0	ng/sec
α	Diffusion constant	0.03	m/sec

was observed in 7-12 m apart from the trap (data not shown; 25 to 30 July, 1996). I set the number of males (*Males*) as 10 for the default value (Table 4-1), which constantly existed in the virtual area (*Area*: 40.0 m × 40.0 m).

Because I supposed that the average wind direction was somewhat fixed but frequently changing slightly. Thus I set W_{Speed}=1.0 m, W_{Direc}=East, W_{Freq}=3 sec, W_{SD}=45° as the default values and changed W_{SD} to analyze the effect of the wind swinging.

Characteristics of *H. cunea* male

Hirooka (1981) reported intensive observations of mating behavior of *H. cunea* males. Male moths fly the random flight like gaseous molecules moving along host trees outside the range of virgin females. When they get into the close range of virgin females, they suddenly changed their flight way and mode, and approached the virgin females with the zigzag flights (Hidaka, 1972). According to the Hirooka's results, I set $Random_{Mean}$=1.38, $Random_{SD}$=0.36, $Zigzag_{Mean}$=0.47, $Zigzag_{SD}$=0.98 (Table 4-1). I set $Random_{Angle}$=30° by executing the simulations and comparing simulated flight pattern with the flight trails of the males depicted by Hidaka (1972). Hirooka (1987) reported that the males of *H. cunea* zigzagged 25 times before starting the upwind flight beyond 2m down the wind from the pheromone source. I set $Zigzag_{Number}$=25 as default value (Table 4-1) and changed it step by step to analyze its effect.

Pheromone trap and release of the pheromone plume

The traps used in the field experiments from 1994 to 1996 (Chapter 1) were delta-traps with a sticky sheet of 30.0 × 18.5 cm. I set *TrapArea*: 0.3 × 0.185. The lure (Nitto-lure; ameshiro®; Nitto-Denko Corp., Osaka) contained 6mg of components, (9*Z*,12*Z*,15*Z*)-9,12,15-octadecatrienal, (3*Z*,6*Z*)-3,6-9,10-epoxyheneicosadiene and (3*Z*,6*Z*)-1,3,6-9,10-epoxyeicosatrien in the ratio of 10:1:1.

I did not know the actual release rate of pheromones into the air, and the threshold concentration at which males could detect (see Fig. 4-3). Thus, I conducted a dose-response experiment.

Experiment

An indoor wind tunnel (0.30 m in daim. × 2.00 m in length) was used to investigate the daily pattern of male activities for mating. The wind tunnel experiment was carried out under conditions of 25 °C, 40% r.h. minimum, and at a wind speed of 0.30m/sec. Insects used in this experiment were collected as larvae in Ibaraki prefecture in 1995 and reared on artificial diets (Insecta LF ®; Nihon-Nosan Corp.) in the laboratory (15L : 9D, 25 °C). After the adult moth emergence, a laboratory population was maintained under the same conditions.

Four male moths that emerged in two or three days were put into the wind tunnel at the mating period. Total numbers of contacts by four males to the pheromone source were counted as a male's activity for mating. Either various doses of three synthetic components, four virgin females in a screen cage (9 cm in height: 8 cm in diam.), or commercially available pheromone lures (Nitto-lure: ameshiro® ,Nitto-Denko Corp., Osaka), which were the same as those used in the field experiments (Chapter 1), were used as pheromone sources. Three components of *H. cunea* synthetic sex pheromone were mixed according to the ratio as of Nitto-lure: ameshiro®, diluted with hexane and loaded onto filter paper strips. Dose of the mixture was represented by that of the major component, (9*Z*,12*Z*,15*Z*)-9,12,15-octadecatrienal (TAL).

Each treatment was replicated eight times. Mann-Whitney's U-test was applied to detect a significant difference between treatments.

Results

The male activity to 10000 ng lure was as high as that to four virgin females, but significantly lower than that to Nitto-lure (Fig. 4-5). Only small numbers of males responded to 0.1 to 100 ng, and these were not significantly different from the control.

I set D_0=10000ng, D_{time}=10ng based of this result. And I set a=0.03 and R_0=0.02, because I assumed that the puffs kept its structure and shape far down from the source. Number of puffs existed in a moment were 20 and the radius of the plume at the down wind end was 62.0 cm in this parameter set.

4.4 STATISTICAL ANALYSIS

My aim in this chapter was to analyze spatial distribution of males and the efficacy of pheromone trap catches, with the key parameters for the pheromone- mediated flight pattern being changed. Replicating the simulation for ten times, significant differences in pheromone trap catches among parameter changes were tested by Tukey's test. Randomized nearest-neighbor test is one of the most powerful method to detect the clustering pattern of individuals in coordination-mapped data (Manly, 1997). In the present case, I applied the nearest-neighbor test to the trap position instead of clustering of individuals.

I replicated the simulation for ten times and calculated distances between each male and the pheromone trap at the center of the virtual area. Then, I sorted the distances in the increasing order, and calculated the q statistic(q_i), the average distance of ten replicates in the i-th nearest order. On the other hand, random distributions were generated 1000 times, and distribution of q statistics was approximated. I detected the significant difference of the male distribution pattern, comparing q_i calculated by our simulations with those of random distributions.

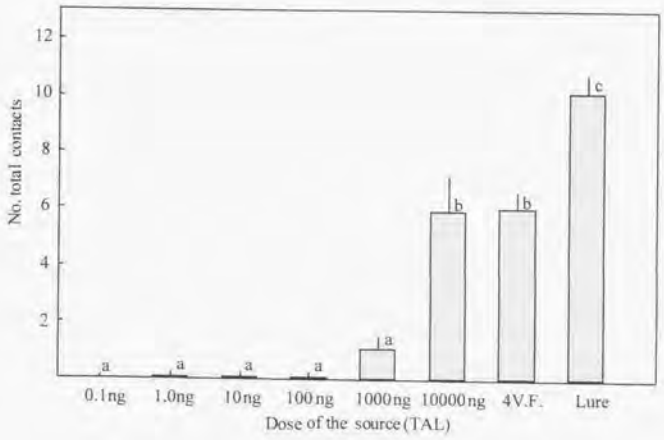


Fig. 4-5. Dose-response relationships in an indoor wind-tunnel. Three synthetic components of the sex pheromone were used. Error bars indicate S.E. Dose of the mixture was represented by that of the major component, (9*Z*,12*Z*,15*Z*)-9,12,15-octadecatrienal (TAL).

4.5 RESULTS

Fig. 4-6 depicted a temporal change of males' distribution with default parameters (Table 4-1). The movements of males and the pheromone plume on the computer display were quite satisfactory. I could mimic well the pheromone-mediated flight pattern of males and movement of the pheromone plume, though I myself have never observed the actual flowing pattern of a pheromone plume directly. Nevertheless, it meandered and was similar to the smoke plume from a factory chimney.

The pheromone plume does not develop enough in the down-wind for the first 20 sec. as a transient phase, and there were small numbers of males in the upwind or zigzag flight (Fig. 4-5(a), (b)). The distributions of males within 20 sec. were not significantly different from random distribution. A few males began the zigzag or the upwind flights and trapped after 50 sec. (Fig. 4-5(c)). Several males somewhat gathered nearby and down-wind of the pheromone trap. The distribution of males after 50 sec. appeared not to change drastically (Fig. 4-5(d), (e) and (f)), possibly because I placed a new male randomly in the virtual area when a male was removed by the trap.

Male density-dependent distribution patterns

Clustering patterns of males with different numbers of males (changing *Males*) are shown in Fig. 4-7. When *Males* = 5, there were no significant differences at any of nearest orders to the trap (Fig. 4-7(a)). However, significant differences were detected from the fourth to the ninth-nearest orders when *Males* = 10 (default) (Fig. 4-7(b)), and the clustering tendency became more eminent as *Males* became larger (20 in Fig. 4-7(c) and 40 in (d)). Significant differences were mainly detected among middle orders, and could not be detected in the nearest and farthest, which was a similar pattern to Manly's (1997) clustering example.

Effect of wind swing (changing W_{SD})

Effect of the wind swinging on males' distribution and trap catches was analyzed by changing W_{SD}, and results are summarized in Table 4-2. If the wind direction did not change (W_{SD} = 0°), the largest number of males was captured, and the clustering around the trap was less conspicuous than other cases. Because there are wind swingings more or less in the natural environment, males are likely to cluster around the trap the field. A clustering tendency seemed to be weakened, as W_{SD} became >90°, and the numbers of males captured by the trap gradually decreased, although not significantly.

Effect of the number of turnings (changing $Zigzag_{Number}$)

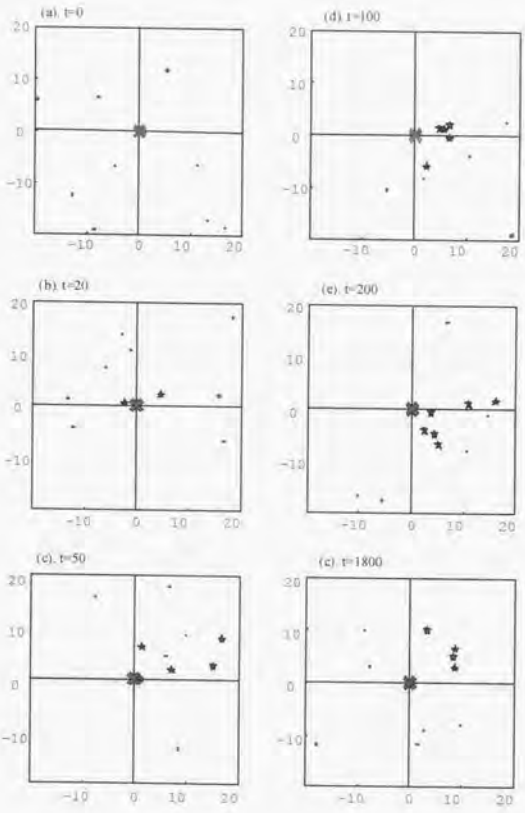


Fig. 4-6. The snap shot of males' distribution with default parameters in each time step (See Table 1 for default values). ×: Pheromone trap. : Male in the Random. ☆: Male in the Zigzag or the Upwind.

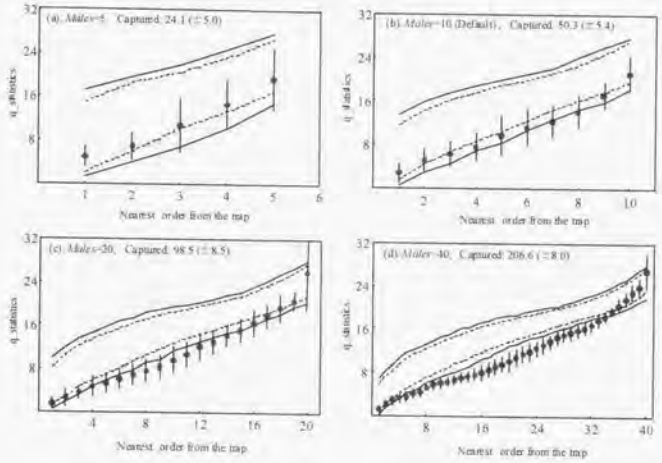


Fig. 4-7. Clustering patterns of males in different numbers of males (*Males*). Black dots and error bars indicate the q statistics (q_i), *i*-th nearest distance order, and its S.D. calculated for 10 times simulations. Solid and dashed lines show 99 % and 95 % confidence limits, respectively, calculated by 1000 times replicated random allocations.

Table 4-2. Effect of wind "swing" on males' distribution and trap catches in our simulations.

Wind "swing"	Nearest order from the trap										Mean no.males captured
S.D. (W_{SD})	q1	q2	q3	q4	q5	q6	q7	q8	q9	q10	(± S.D) [1]
0°	2.52	3.58*	7.01	9.48	11.15	12.49	14.10*	15.83*	17.58*	20.09	146.6 (±14.4)[a]
22.5°	2.63	5.16	6.00*	7.01*	8.87*	10.37**	12.05**	14.05**	16.00**	22.57	64.4 (±5.7)[b]
45° (Default)	*2.75*	*5.09*	*6.31*	*7.53**	*9.68**	*11.15**	*12.40***	*14.13***	*17.16**	*21.13*	*50.3 (±5.4)*[c]
67.5°	3.03	4.60	5.94*	7.04*	8.83*	9.74*	11.60**	14.41**	16.60*	20.30	47.3 (±6.4)[c]
90°	2.03	3.50	5.45	8.08*	10.37*	12.02*	14.45	17.24	19.46	21.66	40.4 (±7.5)[c]
180°	2.38	5.51	7.24	9.21	11.47	13.18	14.56	16.44	18.63	25.38	41.1 (±4.7)[c]

See text and Fig. 7 for the procedures to detect significant differences.

[1] Different letters indicate significantly different according to Tukey's test at 5 %.

* and ** indicate significantly different at 95 % and 99 %, respectively, from random distribution.

I summarized the effect of the number of turnings in the zigzag flight ($Zigzag_{Number}$) on males' distribution and trap catches in Table 4-3. The clustering tendency was not observed so far as the males did not take the zigzag flight ($Zigzag_{Number} = 0$), and the number of males captured by the trap was the smallest. A clustering tendency seemed to be increased, as $Zigzag_{Number}$ became larger, while the number of males captured did not increase monotonous.

Effect of initial lure concentration (changing D_0)

Table 4-4 shows the effect of intial lure concentration (D_0) on males' distribution and trap catches. Changing D_0 affected the number of puffs that existed simultaneously. No puff existed at $D_0 = 0$, one effective puff at $D_0 = 1000$, 20 at $D_0 = 10000$ (default), 29 at $D_0 = 20000$. In the case of $D_0 = 20000$, a few puffs went away from the virtual area and reappeared from the opposite side because the boundary condition was torus. I did not execute the simulation with further higher concentration, considering the artifact effects of reappearance of puffs.

When no puff was produced ($D_0 = 0$), no male was captured by the trap and the clustering tendency was not observed at all (almost similar q_i values were almost similar to the mean q_i values of random distributions). It was surprising that the trap could catch as many males as in the case $D_0 = 10000$ (default) when only one puff was produced ($D_0 = 1000$), while no clustering tendency was observed (Table 4-4). In contrast, when 29 effective puffs existed in the virtual area ($D_0 = 20000$), the trap caught not so many males as in the case $D_0 = 10000$ (default), while the clustering tendency was most conspicuous among the four cases.

4.6 DISCUSSION

Importance of the males zigzag flight in the male clustering

It has been argued which is important for male moths to find the way to the pheromone at a distant point; chemotactic plume-following or anemotaxis mechanism (Shorey, 1973; Kennedy, 1977; Jones, 1998). Lately, it is regarded that the both may be used in harmony by male moths. Recent studies have revealed that odor concentration within the plume and odor "pulse" frequency were essential factors for the upwind flight and casting movements (Vickers and Baker, 1992; Mafra-Neto and Cardé, 1994). I did not incorporate any chemotaxsis caused by the concentration gradient within the plume into the simulation model, but incorporated the processes of the upwind and casting movement that are evoked encountering and loosing the puffs.

Males in the virtual area could find the pinpoint source in the simulations. For example, a trap with the *TrapArea*=1.0 × 1.0cm caught 49.8 males on average, which was not significantly different to the case of 30.0 × 18.5cm (default) according to Student's t-test (the former 49.8 vs. the latter 50.3, t=0.099, p>0.924).

It also should be noted that I did not incorporate the effect of males' "sensory fatigues" in

Table 4-3. Effect of No. turnings in the zigzag flight on males' distribution and trap catches in our simulations.

No. turnings	Nearest order from the trap										Mean no.males captured
($Zigzag_{Number}$)	q1	q2	q3	q4	q5	q6	q7	q8	q9	q10	(± S.D) [1]
0	2.99	5.86	8.66	10.60	12.02	13.86	15.48	17.34	19.76	21.87	38.6 (±6.7) [a]
5	2.28	4.76	6.11*	7.93	11.03	12.97	14.82	17.69	18.62	21.01	47.1 (±5.8) [b]
10	4.18	6.40	7.99	8.88	11.68	14.90	16.63	17.98	19.10	20.71	46.8 (±6.5) [ab]
25 (Default)	*2.75*	*5.09*	*6.31*	*7.53**	*9.68**	*11.15**	*12.40***	*14.13***	*17.16**	*21.13*	*50.3 (±5.4)* [b]
50	2.97	4.82	5.96*	7.67*	9.09*	10.69*	11.77**	13.64**	16.11*	19.16*	43.4 (±6.7) [ab]

See text and Fig. 7 for the procedures to detect significant differences.

[1] Different letters indicate significantly different according to Tukey's test at 5 %.

* and ** indicate significantly different at 95 % and 99 %, respectively, from random distribution.

Table 4-4. Effect of initial lure concentration on males' distribution and trap catches in our simulations.

Initial concentration of the pheromone plumes(D_0)	Nearest order from the trap										Mean no.males captured (± S.D) [1]
	q1	q2	q3	q4	q5	q6	q7	q8	q9	q10	
0	6.05	9.72	12.71	14.02	15.34	17.03	18.71	19.92	21.18	22.95	0.0 (±0.0) [a]
1000	2.25	6.26	7.87	12.07	14.07	15.19	17.42	18.50	21.21	23.44	51.3 (±5.1) [b]
10000 (Default)	*2.75*	*5.09*	*6.31*	*7.53**	*9.68**	*11.15**	*12.40***	*14.13***	*17.16**	*21.13*	*50.3 (±5.4)* [b]
20000	2.59	3.66*	5.56*	6.60**	8.44*	10.06**	12.16**	14.03**	15.88*	21.76	44.2 (±5.5) [c]

See text and Fig. 7 for the procedures to detect significant differences.

[1] Different letters indicate significantly different according to Tukey's test at 5 %.

* and ** indicate significantly different at 95 % and 99 %, respectively, from random distribution.

the model. The sensory fatigue caused by exposure to high concentration pheromone for a long time may decrease the number of turning (Sanders, 1997). However, I did not have enough data in available about that effect and the model would be too complicated to show the simple tendency of males' clustering. In spite of above deficiencies, I thought the upwind and the zigzag flight processes incorporated in this model were enough to describe the pheromone -mediated flight of males phenomenologically.

The number of turnings ($Zigzag_{Number}$) affected the number of males captured by the trap (Table 4-3). This effect was more distinct when the wind direction changed in a wide range; only 22.1 males were captured on average ($Zigzag_{Number}$=0; W_{SD} =360°). This result can be interpreted that the males with no zigzag flight could scarcely approach the source when the wind was swinging largely. Thus, I conclude that the zigzag flight played an important role in the approach to the source.

The zigzag flight also affected the clustering of males around the trap. The clustering tendency became more distinct as the number of turnings increased, while trap catches did not change largely when the number of turning was between 5 to 50 (Table 4-3). Then a question arose from the result of the clustering in the simulations: Can the sex pheromone trap reduce the mating success by removing males, or enhance it by amassing males from the outside of the area?

Two aspects of the mass-trapping: male removal and attraction

I evaluated two aspects of the pheromone trap in mass-trapping: male-removal effect and male-attraction effects that was revealed in Chapter 3. The male-attraction effect is thought to be one of the mechanisms of communication-disruption theresults from male's expending most energy and time around the trap rather than searching for virgin females. From the experiment, I concluded that the synthetic sex pheromone traps could reduce the mating success through male-attraction effect rather than male-removal effect, when the adult moth density was low. The male-attraction effect was also evidenced in *Spodoptera litura* by Kitamura and Kobayashi (1985). They suggested that the mating suppression in the mass-trapping plot came from the communication-disruption effect of the synthetic sex pheromone lures in the traps. On the other hand, the field experiment suggested that male-attraction effect might disappear when the density of adult moths was high. It might be the case where the mating success will not be reduced albeit a large number of males are captured, because pheromone traps may constantly amass males around the traps. The male-attraction effect may be amplified by the process of the zigzag flight.

In the simulations, I have shown that the zigzag flight made the clustering of males around the trap. The males swarming around the trap were thought to be arrested to the "remnant" of the pheromone plume by their internal counterturning program, and they could not fly away to find virgin females. There was no significant difference in the first nearest order throughout the simulations,

and there seemed some tendency that males were swarming around the trap among the middle range of q, from the trap (See Fig. 4-7(b), for example). If a large number of males immigrate into the target area, and if the zigzag flight makes a stock of males around the trap but most of them are not removed by the trap, some of the males may cease their zigzagging and start to search virgin females near the trap.

I need to consider the ratios of immigration, trapping and zigzagging in males to elucidate whether the clustering of males have positive effects or negative ones on pest control success. Though my model was not constructed to analyze such problem, male density-dependent distribution patterns in Fig. 4-7 show that the more males were put into the virtual area, the larger the clustering tendency became. This phenomenon may explain ineffectiveness of male-attraction effect at a high male density (Chapter 3). I must construct another model for larger spatial structure which contains multiple traps and virgin females to analyze how the clustering pattern affects the control program of lepidopterous pests.

Higher density pheromone lure may not capture more males

The simulations also suggested that the high density pheromone sources could not catch more males, but made the clustering distribution more conspicuous (Table 4-4). This result was consistent with the suggestion by Elkinton et al. (1987). They conjectured higher release rates of pheromone might elicit response at greater distances in down-wind but might not result in increased trap catch when the plume of pheromone meandered violently in the forest. Judging from this result, I did not expect that I get higher effectiveness by using higher density release pheromone source.

These results may be important suggestion in the practical pest control using sex pheromone traps.

CHAPTER 5

A spatially structured model for controlling a pest with synthetic sex pheromones

5.1 INTRODUCTION

In Chapter 4, I constructed an individual-based model (IBM) for describing pheromone plume movements and detailed processes of pheromone-mediated flight patterns of male moths. The spatial distribution of males and pheromone trap catches were analyzed therein. Simulations with the IBM showed a possibility of male clustering around the trap, which was caused by the males' zigzag flight for finding a pheromone plume. Then, a question arose from the IBM simulations: can the sex pheromone trap reduce the mating success by removing males, or enhance it by amassing males from the outside of the area?

It is a problem about the ratios of immigration, trapping and zigzagging in males, when I elucidate whether the clustering of males has positive or negative effects on pest control success. Therefore, I constructed a lattice model in a larger spatial and temporal scale that contained multiple traps and virgin females to analyze how the clustering pattern affects the control program of lepidopterous pests in this chapter.

5.2 MODEL FORMULATION

A schematic flow chart of the simulation processes is shown in Fig. 5-1, and all the parameters in the simulations are listed in Table 5-1. I assumed a two-dimensional cellular experimental area. Simulations were continued for adult emergence period (*Days*), and each day (*d*) consisted of the *TimeSteps* number of time steps (One time step is 15 sec). Individual male moths are allowed to move within the cell and can emigrate to eight neighbor cells at every time step (*t*). I placed one synthetic sex pheromone trap in each cell. The cells with a trap were distributed in various formations (described later). The boundary condition of total area (*Area*) was reflective. The program was developed with Visual C++ (version 4.0, Microsoft).

5.2.1 Moths emergence and death

Male (newmale[*d*]) and female (newfemale[*d*]) moths emerge on day *d* according to the Gaussian distribution (normal[*x*] on the day *x*, mean: *Peak*, S.D.: *PeakSD*) and are placed within cells randomly.

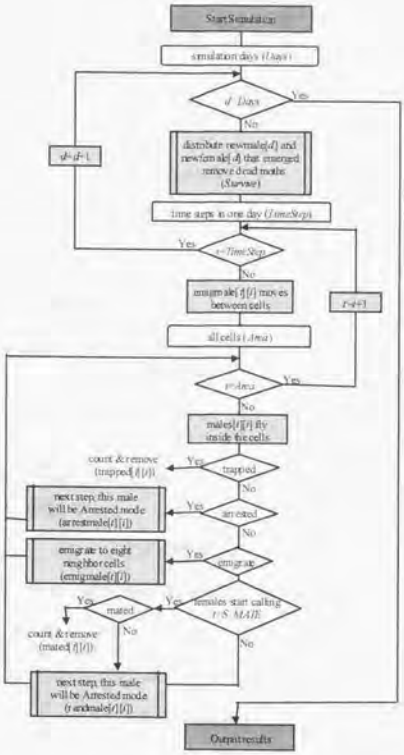


Fig. 5-1. The flowchart of the simulation model.

Table 5-1. Descriptions of model parameters and the default values used in our simulation model

Parameter	Description	Default Value	Unit
	Simulation Settings		
Days	Simulation period	30	day
TimeSteps	Time steps in one day	120	*Time*
Area	No. cells used in our simulation	41 ×41	cells
CellArea	Area of the cell	40×40	m
Traps	No. traps distributed in the simulation area	25	-
Emergence	No. moths (males and females according to the ratio 1:1) emerged in one day	10000	-
	Characteristics of H. cunea		
S_MATE	Time lag to start calling behavior by female	40	time step
Survive	Survival rate in one day	0.694	-
Peak	Peak day of moths' emergence	15	days
PeakSD	Standard deviation of moths' emergence	6.1	days
a	Relative permeating area of pheromone	0.0024	m^2/Area

Table 5-1. (Continued)

Parameter	Description	Default Value	Unit
	Parameters in a cell without trap		
Emigrate	Emigration ratio in one step at a cell without trap	0.630	-
	Parameters of males in Random mode in a cell with trap		
R_Emigrate	Ratio of males in Random mode to emigrate to eight neighbor cells in next time step	0.280	-
R_Random	Ratio of males in Random mode to keep on Random mode in next time step	0.407	-
R_Arrested	Ratio of males in Random mode to be in Arrested mode in next time step	0.308	-
R_Trapped	Ratio of males in Random mode to be trapped	0.005	-
	Parameters of males in Arrested mode in a cell with trap		
A_Emigrate	Ratio of males in Random mode to emigrate to eight neighbor cells in next time step	0.004	-
A_Random	Ratio of males in Random mode to keep on Random mode in next time step	0.076	-
A_Arrested	Ratio of males in Random mode to be in Arrested mode in next time step	0.893	-
A_Trapped	Ratio of males in Random mode to be trapped	0.027	-

$$\text{normal}[x] = \frac{1}{\sqrt{2\pi} \cdot PeakSD} \exp\left[-\frac{(x - Peak)^2}{2\,PeakSD^2}\right] \tag{5-1}$$

$$\text{newmale}[d] = \text{newfemale}[d] = Moth \times \int_{d-1}^{d} \text{normal}[x]\,dx \tag{5-2}$$

Moths suffer from natural mortality by a factor (1-*Survive*) every day. Then the numbers of males and females on day *d* are

$$\text{male}[d] = Survive \cdot (\text{male}[d\text{-}1] + \text{mated}[d\text{-}1]) + \text{newmale}[d] \tag{5-3}$$

$$\text{female}[d] = Survive \cdot \text{female}[d\text{-}1] + \text{newfemale}[d] \tag{5-4}$$

Since mated males (mated[*d*-1]) could still mate again on the next day (*d*) while mated females no longer mate with males (Masaki, 1975), I added mated[*d*-1] to the males on the pervious day (male[*d*-1]).

5.2.2 Male moths behavior in a cell

Fig. 5-2 shows projection procedures for male moths' behavioral categories in a cell with a trap. Behavior of males in a cell with a trap is categorized into Emigrate, Random, Arrested or Trapped according to stochastic ratios, *R_Emigrate*, *R_Random*, *R_Arrested* and *R_Trapped*, respectively, at time-step *t*. All males start their mating behavior in the Random at *t*=0. Males categorized in the Random still fly the random flight in the cell until the next time step and will be categorized into either Emigrate, Random, Arrested or Trapped at time-step *t*+1. Only the male in the Random can mate with a virgin female in the same cell after the virgin females start their calling behavior (*S_MATE*). Males in the Emigrate fly away to the 8 neighbor cells with a uniform probability. Males in the Arrested were assumed to fly the upwind or the zigzag flight to the synthetic sex pheromone trap. They must still be in the same cell, but cannot mate with females. Males in the Trapped are regarded as captured by the trap and are removed from the simulation area after counting. Males in the Arrested are likely to be also in the Arrested at the next time step, and then to be at a higher probability in the Trapped than in the Random. Therefore, I defined another probability set, *A_Emigrate*, *A_Random*, *A_Arrested* and *A_Trapped*, to categorize the males at *t*+1 time-step that was in the Arrested at *t*.

Behavior of males in a cell without a trap is only categorized into either the Emigrate or the Random, and the probabilities are *Emigrate* and (1-*Emigrate*), respectively. The males in the Emigrate or the Random behave in the same way as the males in a cell with a trap.

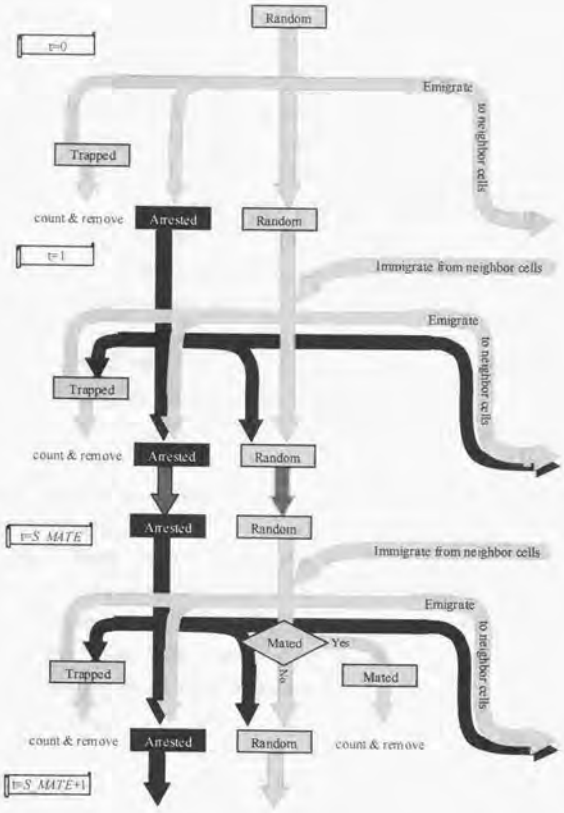


Fig. 5-2. The schematic flow chart of categorizing males' behavior in the cells with a trap.

5.2.3 Mating behavior

Males start their mating behavior prior to females' calling behavior on each day in the simulations. It is common for male insects to start their mating behavior a little before the females' calling (Chapman, 1969), and Hidaka (1972) reported that *H. cunea* males set to fly a little earlier than the onset of the females courting. The results in the wind tunnel experiments in Chapter 2 showed that the males responded to the synthetic sex pheromone source one hour earlier than the light-on timing. From these considerations, I set the period (*S_MATE*) in which the males respond only to the synthetic sex pheromone because females have not started their calling behavior yet.

I applied Kuno's random mating model (1978) to the mating efficiency in the case which males and females mate one time in one night.

$$P = \frac{F_m}{F} = \frac{1}{F \ln(1-a)} \ln[(1-a)^M \{1-(1-a)^F\} + (1-a)^F] \tag{5-5}$$

where *Fm*: number of mating, *M*: number of males and *F*: number of females in the cell i at t. The parameter a is a kind of searching efficacy, but it relates not only a relative searching area of males to the whole area, but also the area that is permeated with the sex pheromone of a female. My model assumed that each individual acted as one object that was expressed by an integer number. Mating did not take place frequently when I used the original Kuno's equation, because small number of males or females produces the number of matings smaller than 0.5. From this consideration, I introduced a stochastic process for calculating the number of matings.

Number of matings in cell i at time-step t was calculated by the following procedures. Males in the Random (randmale[t][i]) start their mating behavior one by one in turn. (1) a probability (p) of a male that can mate was calculated by,

$$p = 1 - (1 - a)^{\text{female}[t][i]} \tag{5-6}$$

(2) The decision whether the male mated or not was determined in probabilities. (3) If the male mated with a virgin female, it was removed from the simulation area until next day (d+1). The females were counted as the mated females and were removed from the simulation area thereafter. Next male starts the mating behavior according to Eq. (5-6) with the actual number of females. After all males in the Random at time-step t finish their mating behavior, the number of males in the Random (randmale[t+1][i]) and the virgin females (female[t+1][i]) at t+1 can be calculated by,

$$\text{randmale}[t+1][i] = \text{randmale}[t][i] - \text{mated}[t][i] \tag{5-7}$$

$$\text{female}[t+1][i] = \text{female}[t][i] - \text{mated}[t][i] \tag{5-8}$$

Then the total number of matings on day d is

$$\text{mated}[d] = \sum_{t=0}^{TimeStep} \sum_{i=0}^{Area} \text{mated}[t][i] \qquad (5\text{-}9)$$

5.3 PARAMETERS ESTIMATION AND DEFINITION

The list of the model parameters and the default values are shown in Table 5-1. This chapter specifically focused on the situation where the traps capture the summer generation of *H.cunea*, so I estimated the parameters according to the precedent studies on the IBM in Chapter 4. A whole area was assumed as 1640m × 1640m, and divided into 41 × 41 cells (=*Area*). One time step (*t*) was regarded as 15sec. Their setting corresponds to the IBM (Chapter 4) in which the simulation area was 40m and it took 14.49sec to fly away from the cell for males in the center of the cell. The total time steps (*TimeSteps*) was 120 *Time* (30min) in one day, because *H. cunea* males will fly their mating flight within a short period just before the dawn in the summer generation. The period (*S_MATE*) proceeding to the females calling was set as 40 time-steps (10min).

5.3.1 Field experiment for adult survivorship and density estimations

Experiment

I conducted another field experiment to estimate adult survivorship and density at Toyosu, Koto-Ku in 1996. Male moths used for this experiment were collected as larvae in Ibaraki prefecture in 1995, reared on artificial diet (Insecta LF ®; Nihon-Nosan Corp.) under the laboratory conditions (15L:9D, 25°C), and were maintained for a few generations. Males were kept under a cool condition for one to three days after their emergence, so that they were not exhausted by flying around in small cages. Males were marked at the tip of a forewing with a felt pen (Magic INK®, UCHIDA YOKO Corp. Tokyo). Marked males (197 on 22nd July and 203 on 26th July) were divided into ten groups, and were released from the 10 release points in the mass-trapping treated area of Chapter 1 (88 traps were treated on each of all the 88 trees in the treated area, Fig. 5-3). Recapture censuses were conducted for all the traps every other day after the release.

Results

Table 5-2 summarizes the daily recaptures. Two release days, 22nd and 26th July, were just at the peak of feral males, judging from the pheromone trap catches in 1996 (see Fig 1-3 in Chapter 1). I estimated the males' survivorship and density according to Yamamura (1992). It was estimated that 912.4 and 1008.7 feral males existed on 22nd and 26th July, respectively. The survivorship was 0.747 and 0.694 per day, respectively.

5.3.2 Moths emergence and death

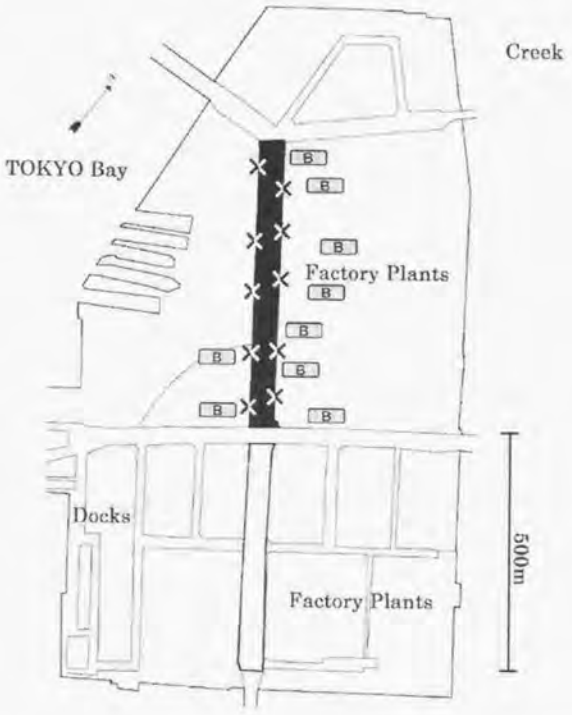


Fig. 5-3. The map in the marking-recapture experiments in 1996. × : the release point. [B]; barrier traps.

Table 5-2. Number of marked and non-marked males captured by the pheromone traps in the mass-trapping area in 1996.

Date	Non-marked	Black marked	Non-marked	Red marked
July 22	-	*197**	-	
July 24	340	41		
July 26	355	15		*203**
July 28	383	0	383	36
July 30			245	7
Aug. 1			291	1

**Italic* figure means the number of released males.

I set the daily survivorship of moths at 0.694, the lower value of two estimates in the experiment mentioned above and the total number of males and females that emerged were 10000, respectively, as default. It was because the number of males estimated was around 1000 on a day during the peak period in Toyosu area (about 1.2ha), then the simulation area (2.7ha) should have 10000 males as the total emergence at least. Male and female moths emerge on day d according to the Gaussian distribution Eq. (5-1). The standard deviation of the emergence was estimated as 6.1 days (*PeakSD*) from the field catches by synthetic sex pheromone traps on Toyosu, Koto-Ku, Tokyo, in 1996 (Chapter 1). I set the simulation period (*Days*) at 30 days, and the peak day (*Peak*) at day 15 to cover the almost all of the moths' entire emergence.

5.3.3 Parameters for males' behavior

It is difficult to determine the parameters of males' behaviors in nature. These must be changeable, depending on variable environmental conditions. I estimated them from the IBM simulations in Chapter 4.

I executed the IBM simulations with D_0=20000, $Zigzag_{number}$ =50 with the absorptive boundary condition. The other parameters followed default values. This parameter set was selected so that it could result in the most conspicuous clustering patterns (see Chapter 4), because the main aim of the present chapter is to know how the eminent clustering pattern would affect on the control with synthetic sex pheromone traps. The simulation was run for 50sec precedently to develop the pheromone plume enough the down-wind. Then, I checked the number of males in the random flight and traced them in successive 15sec. After that, I checked the number of males in the zigzag flight or the up-wind flight, which were assumed to be arrested to the pheromone trap, and trace them in another 15sec. I observed 1000 males in the random fight and the results are summarized in Table 5-3. According to these results, I set *Emigrate* = 0.630, *R_Emigrate* = 0.280, *R_Random* = 0.407, *R_Arrested* = 0.308, *R_Trapped* = 0.005, *A_Emigrate* = 0.004, *A_Random* = 0.076, *A_Arrested* = 0.893 and *A_Trapped* = 0.027.

5.3.4 Parameter for mating behavior

Parameter a was estimated by executing the lattice model simulation constructed above. I set up the same-scale area for a lattice model simulation Toyosu area (Chapter 1). Then, 1000 males and 1000 females, which were agreeable numbers to those estimated in the previous section (*5.3.1*), were distributed randomly in the cellular area. I ran this simulations for 30 min for one day simulation, and estimated the mating ratio changing a step by step. Mating ratios in the treated area and non-treated area were estimated as 30.0% and 46.7%, respectively, on 25th July in the tethered female experiments in Chapter 1 (see Table 1-2 in Chapter 1). Therefore, I set at a=0.0024, which produced 40.3% matings on average in the lattice model simulations.

Table 5-3. The mode of males' behavior at time-step t in the IBM (Chapter 4)

Mode of males at previous time step (t-1)	Mode of males at t				
	No. males examined	Emigrate	Random	Arrested	Trapped
Random (in the cell without trap)	1000	628	234	-	-
Random (in the cell with trap)	1000	290	407	308	5
Arrested (in the cell with trap)	308	12	23	275	8

5.4 MODEL ANALYSIS

The target area (11 × 11 cells) to be controlled by the pheromone traps was assumed inside the total virtual area (41 × 41 cells) (Fig. 5-4). Traps were distributed to control the target area. Then, simulations were executed with *Emergence* = 5000 (as low density), *Emergence* = 10000 (as the default) and *Emergence* = 20000 (as high density) in each simulation.

5.4.1 Effects of distribution and number of traps

First, I examined the control effects with synthetic sex pheromone traps on the reduction of mating success. The main aim of the simulation in this section is to determine the most desirable trap disposition that can maximally reduce the mating success with a smaller number of traps (i.e., with a lower cost). I tested five types of the trap formation (Fig. 5-4). (a) nine traps were distributed in a grid formation, (b) eight traps were distributed just outside the margin and one trap was placed at the center of the target area, (c) 25 traps were distributed in a grid formation, (d) 24 traps were distributed just outside the peripheral margin and one trap was put at the center of the target area, (e) 121 traps were placed at every cell of the target area. Simulations were replicated 20 times in each formation and significant differences were detected by Student's t-test or Tukey's test for multiple comparisons.

The number of mated females in each of the five treatments, including no-trap simulation, was summarized in Table 5-4. Treatment of the traps in every formation reduced the number of mated females within the target area. The number of mated females should be directly related to the damages in the target area in the next generation, because *H. cunea* mated females lay one egg mass each without dispersal (Masaki, 1975). The treatment that achieved the maximum reduction in mating success was (d) (see Fig. 5-4(d)). It was surprising that the formation (d) could reduce the mating success at a higher rate than the treatment (e), which had about 5 times larger number of traps. Table 5-5 compares total number of males captured by the traps between the two formations. The surrounding formation, (b) and (d), caught larger number of males than the grid formations, (a) and (c), with the equal total number of traps. It is also interesting that the treatment (d) could catch significantly more males than the treatment (e) (Table 5-5).

5.4.2 Distributions of males and mated females

The spatial distributions of males and mated females were examined. Fig. 5-5 shows a snap shot of distribution of the mated females in each all on day 30 (*Emergence*=10000). Every treatment of traps seemed to make low-density area of mated females around the target area (NOTICE: the darker, the smaller the number) compared to the no-trap simulation (Fig. 5-5(f)). However, in the cells with a trap occasionally occurred a large number of matings in the grid

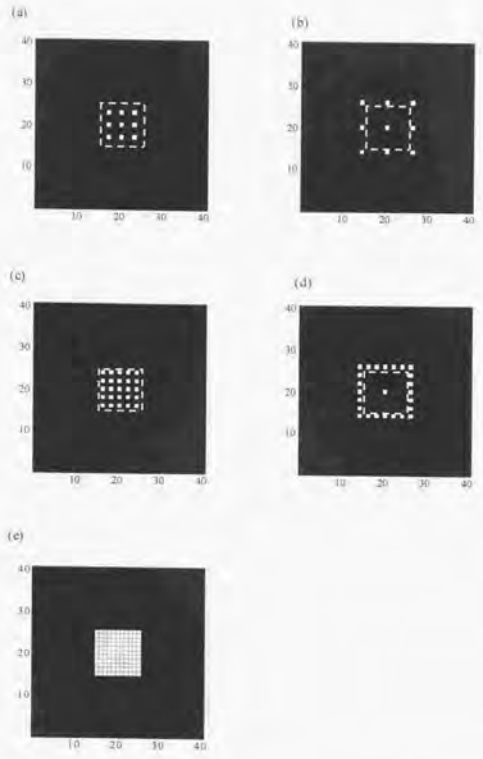


Fig. 5-4. Various strategies of trap formations in the simulations. (a): 9 traps in grid, (b): 9 traps in surrounding, (c): default, (d); 25 traps in surrounding and (e); 121 traps in all cells. The area compartmented by dashed line is the target area to control with sex pheromone traps.

Table 5-4 Total number of mated females in each treatment.

Formations of the traps	Total moths that emerged (*Emergence*)		
	5000	10000	20000
No-trap	24.2 (± 5.4)[a]	88.5 (± 10.4)[a]	315.6 (± 20.3)[a]
(a) 9 traps in the grid	16.9 (± 3.7)[b]	57.8 (± 8.2)[b]	211.3 (± 9.6)[b]
(b) 9 traps in the surrounding	15.9 (± 4.1)[b]	55.1 (± 8.4)[b]	202.9 (± 16.4)[b]
(c) 25 traps in the grid	11.2 (± 3.3)[c]	44.8 (± 7.2)[c]	159.5 (± 16.0)[c]
(d) 25 traps in the surrounding	5.1 (± 2.8)[d]	22.4 (± 3.3)[d]	87.6 (± 8.5)[d]
(e) 121 traps in all cells	8.5 (± 2.6)[d]	36.1 (± 5.2)[c]	129.6 (± 14.1)[e]

Mean ± SD is shown.

Different letters on the right side of the data mean significant difference by Tukey's test at $P<0.05$.

Table 5-5 Comparison of total number of males captured between formations.

Formations of the traps	Total moths that emerged (*Emergence*)		
	5000	10000	20000
(a) 9 traps in the grid	797.8 (± 36.1)	1597.9 (± 61.2)	3158.1 (± 104.2)
(b) 9 traps in the surrounding	998.5 (± 39.8)*	1975.8 (± 69.8)*	3910.3 (± 95.2)*
(c) 25 traps in the grid	1289.5 (± 32.5)	2546.6 (± 50.3)	5079.9 (± 97.4)
(d) 25 traps in the surrounding	2067.9 (± 32.9)*	4100.8 (± 58.9)*	8175.2 (± 109.9)*
(e) 121 traps in all cells	1851.1 (± 31.8)	3695.6 (± 44.6)	7295.0 (± 67.6)

Mean ± SD is shown.

* A significantly larger value between the grid and the surrounding formation by Student's t-test at $P<0.001$.

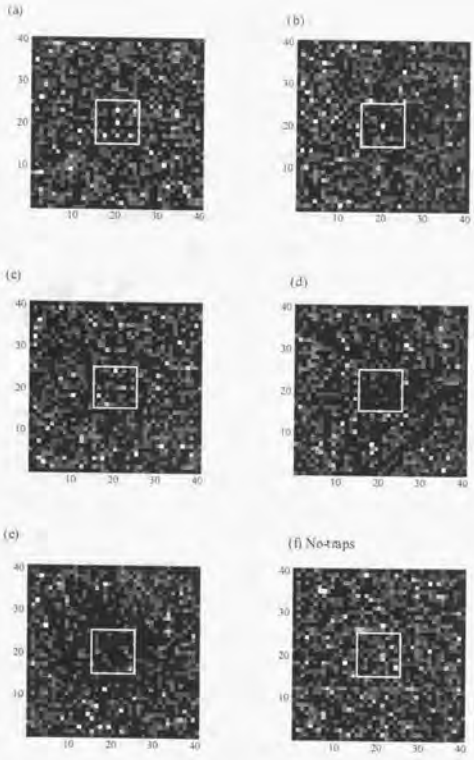


Fig. 5-5. Spatial distribution of mated females in the simulations. Complete black and white grids indicates 0 and more than 3 females, respectively. The whiteness of the gray grid shows abundance of the mated females. (a): 9 traps in grid, (b): 9 traps in surrounding, (c): default, (d); 25 traps in surrounding, (e); 121 traps in all cells and (f); No-traps were distributed.

formations (Figs. 5-5 (a) and (c)). These grid formations could reduce the mating success around the target area, but male attraction effect amassed males in that trap-treated cell itself and could not reduce it within the cell. A kind of "doughnut" structure also took place about 10 cell-distant around the target area. On the contrary, 24 traps in the surrounding formation (d) could effectively reduce the mating success, and no cell with a large number of matings was observed inside the target area. The treatment (b) allowed a few matings inside the target area and the number of mating in the center cell was the largest (5). The eight traps surrounding the target area seem to be insufficient to protect from immigrating males.

Changes in distributions of the males in (c) and (d) with time lapse are shown in Fig. 5-6. The figures suggested that the traps in the surrounding formation (d) could arrest the males that were attracted from inside the target area and also could protect from immigrating males, while traps in the grid formation (c) allowed males to stock inside the target area. Such phenomena were remarkable at the peak of moth emergence, d=15 (Figs 5-6 (c.2) and (d.2)).

5.4.3 Simulations for traps without sticky sheet

I executed another parameter setting (arrest setting) for assuming a case that the trap without sticky sheet never catch any male but arrest them around the trap. The rate of males in the Arrested in this simulation was *R_Arrested* + *R_Trapped* in the place of *R_Arrested*, and for the males already arrested in the previous time step *A_Arrested* + *A_Trapped*. Namely, I set that there are no males in the Trapped (*R_Trapped*=0 and *A_Trapped*=0). The simulations were conducted under the 25 traps in the grid formation (c-n) and in the surrounding formation (d-n).

The results are summarized in Table 5-6. The treatment of traps without sticky sheets in the grid formations (c-n) allowed the largest number of matings, i.e., larger than the no-trap simulation. On the other hand, those in the surrounding formation (d-n) could reduce the matings compared to the no-trap simulation, although the numbers were significantly larger than those of the treatments with normal traps that could catch males. Fig. 5-7 shows the changes in males distribution in the (c-n) and (d-n) treatments with day passing. The cells with a trap apparently gathered a large number of males from the neighboring cells. The grid formation of traps (Fig. 5-7(c-n. 2)) seemed to allow the males to stay inside the target area.

5.5 DISCUSSION

5.5.1 Male-attraction effect on mass-trapping success

The IBM of Chapter 4 revealed the possibility that the clustering pattern was caused by the males' zigzag flight behavior. The lattice model in this chapter also suggested the male-attraction effect in the cell with a trap. Though the result of the lattice model is natural because I constructed the model based on the IBM that incorporates the parameters of the Arrested behavior, the lattice

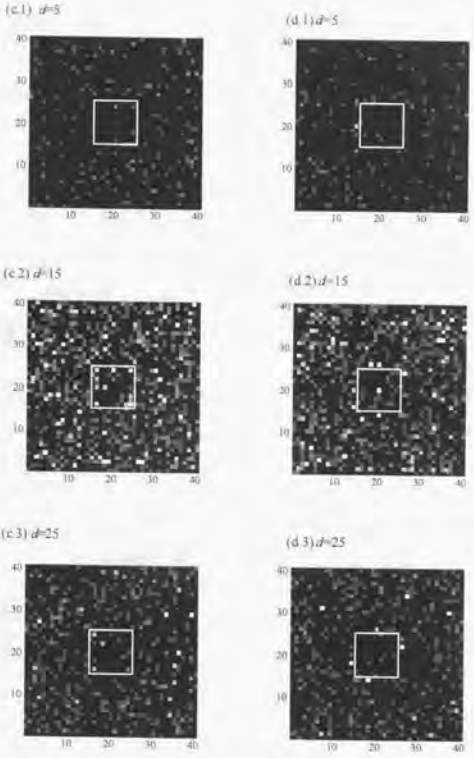


Fig. 5-6. Spatial distribution of males in the simulations (*Emergence*=10000). Complete black and white grids indicates 0 and more than 3 males, respectively. The whiteness of the gray grid shows abundance of the males. (c.1), (c.2) and (c.3) show snapshots of the male distribution along the d=5, d=15 and d=25 in the simulation of the 25 trap grid formation. (d.1), (d.2) and (d.3) shows those in the simulation of the 25 trap surrounding formation.

Table 5-6 Total number of mated females in the treatment of normal traps and of traps without sticky sheet.

Formations of the traps	Total moths that emerged (*Emergence*)		
	5000	10000	20000
No-trap	24.2 (± 5.4)[a]	88.5 (± 10.4)[a]	315.6 (± 20.3)[a]
(c) 25 traps in the grid	11.2 (± 3.3)[b]	44.8 (± 7.2)[b]	159.5 (± 16.0)[b]
(d) 25 traps in the surrounding	5.1 (± 2.8)[c]	22.4 (± 3.3)[c]	87.6 (± 8.5)[c]
(c-n) 25 traps without capturing in the grid	31.9 (± 6.1)[d]	109.9 (± 8.9)[d]	353.8 (± 19.4)[d]
(d-n) 25 traps without capturing in the surrounding	19.3 (± 3.8)[e]	68.5 (± 8.7)[e]	243.7 (± 19.6)[e]

Mean ± SD is shown.

Different letters on the right side of the data mean significant difference by Tukey's test at $P<0.05$.

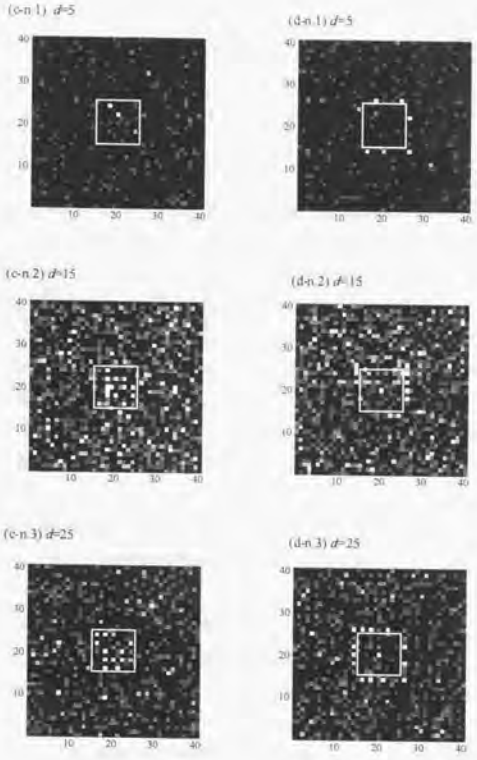


Fig. 5-7. Spatial distribution of males in the simulations for traps without sticky sheet (*Emergence*=10000). Complete black and white grids indicates that it has 0 and more than 3 males, respectively. The whiteness of the gray grid shows abundance of the males. (c-n.1), (c-n.2) and (c-n.3) show snapshots of the males distribution along the d=5, d=15 and d=25 in the simulation of the 25 trap grid formation. (d-n.1), (d-n.2) and (d-n.3) shows those in the simulation of the 25 trap surrounding formation.

model simulation that assumed a whole generation period might accelerate the male attraction. Since a male was assumed to mate several times during his life span and the pheromone traps had an attractive period preceding to the females' calling, the male attraction in the cell with a trap became more distinct with day passing in the simulations (Figs 5-6 and 5-7). The male attractions observed in this lattice model simulation might have a more important meaning to the pest control than those observed by the IBM in the short period.

The male-attraction effect on the mating success in the target area is now evident. The cells with a trap amass the males from surrounding areas, and the male densities in the adjacent cells became lower. Consequently, the mating success in the local area will be reduced (Fig. 5-8(a)). However, when the target area was located within a large area where *H. cunea* infested and emerged randomly, the mating success will be more complicatedly affected. Males emerged from outside constantly immigrate into the target area, then the cells with a trap keep a large number of males that escaped from removal by the traps, and allow the males to mate (Fig. 5-8(b)). Reduction of mating success stands on the balance between the removal rate of males by the trap and the immigration rate of the males. I conjectured that removal rate by the traps exceeded the immigrating rate of the males with the parameter set used in my simulations, since all the five treatments ((a), (b), (c), (d) and (e)) achieved significantly reduced number of matings, compared to the no-trap simulation (Table 5-4). However, further field experiments should be done to analyze how the male-attraction effect act in the practical controls with synthetic sex pheromone traps.

5.5.2 Model implications for practical control with synthetic sex pheromone traps

Can the sex pheromone trap reduce the mating success by removing males, or enhance it by amassing males from the surrounding areas? The suggestion from the lattice model simulations was that it depended on the trap disposition. The 25 traps in the surrounding formation (d) achieved the lowest matings among the five treatments in Table 5-4. I conjectured two reasons for this success in (d). One was the absorbing effect. The surrounding formation of the traps attracted the males from *inside* the target area to them, while the grid formation of the traps seemed to produce the "doughnut" structure *outside* the target area, but they amassed the males inside the target area. The other was the barrier effect. Males immigrating from the outside stopped and remained for a long time at the cell with a trap that was located at the surrounding cells of the target area. The target area was protected consequently. However, traps must be located densely. The eight traps in the surrounding allowed as high mating success as the eight traps in the grid (Table 5-4).

It was surprising that the treatment (d) reduced the mating success better than the treatment (e), which suggested that intensive treatment of pheromone traps dose not always reduce the mating success compared to the less intensive but surrounding formation. One of the reasons of

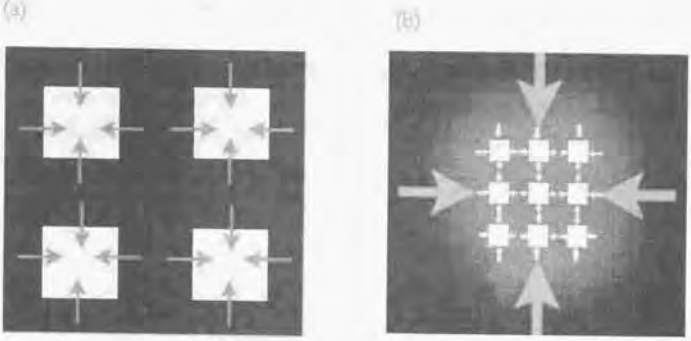


Fig. 5-8. Conceptual explanations of the male-attraction effect on the mating success. (a) shows the positive effect in a local area. (b) shows the negative effect in a wider area.

this phenomenon may be competition among traps. Some previous studies showed that multiple treatment of traps reduced the per-capita catches of males because of competition among them (Wall and Perry, 1980; Elkinton and Cardé 1988; McNeil, 1991). The grid formations, (a) and (c), caught smaller numbers of males than the surrounding formations did (Table 5-5). The cells with a trap may keep the males in them stickily and did not release to the outside in the intensive treatment (e), then sufficient number of males was not removed, compared to the treatment (d). The importance of the barrier traps and the surrounding formation have already been suggested in the field studies from the beginning of the pheromone use in pest controls (Trammel, 1974; Nemoto, et al., 1980; Negishi et al., 1980). The lattice model simulations was able to explain the importance mechanistically.

From these considerations, I concluded that pheromone traps in the *H. cunea* control in a local area like the field experiments from 1994 to 1996 (Chapter 1) should be arranged in the surrounding formation, though further experiments are necessary to estimate the removal rate of males by the trap and immigration rate of the males.

CHAPTER 6

A temporally structured model for predicting outbreaks

6.1 INTRODUCTION

The fall webworm, *Hyphantria cunea* (Drury), was accidentally introduced into Tokyo from North America in 1945, and has extended its distribution rapidly toward north and south and has become one of the most serious insect pests of street and garden trees in urban areas of Japan (Ishii, 1966). *H. cunea* was regarded as bivoltine throughout its distribution in Japan until early 1970s. In late 1970s, trivoltine populations prevailed gradually in southwestern Japan, and the population currently is trivoltine in Tokyo (Arai and Akiyama, 1976). Seasonal the adult abundance of *H. cunea* populations in Tokyo has cleary three times a year: in mid May, (the overwintering generation), mid to late July, (the first generation), and early September (the second generation) (Gomi, 1997).

The change of insect voltinism is closely related to evolutionary changes in developmental characters such as the larval growth rate, the lower thermal threshold for larval development, the critical day-length for diapause, and so on. Age-structured model analysis is one of the powerful tools for understanding the effects of such life history changes on population dynamic patterns (Gurney et al., 1983; Godfray and Hassell, 1987; Constantino et al., 1997). It is very interesting to apply a temporally structured model as a felicitous example to the *H. cunea* populations in Japan, because this insect quickly changed generation cycles within only 20 years (Masaki, 1975; Uezumi, 1976; Arai, 1981; Gomi and Takeda, 1991; Gomi and Takeda, 1996; Gomi, 1997).

It is also useful to apply such a temporally structured model to the analysis of a pest insect control. The temporally structured model allows us to predict the timing and population abundance of insect outbreaks (Yano, 1989(a), 1989(b); Trichilo and Wilson, 1993; Söndgerath and Müller-Pietralla, 1996).

In this chapter, I constructed a temporally structured model for *H. cunea* incorporating its daily age-structure, life histories, larval development, the meteorological data and the seasonal phenology of host trees. I analyzed effects of changing parameters such as the growth rate, critical day-length and the development of host tree foliage on the population dynamics of *H. cunea*.

6.2 MODEL FORMULATIONS

The model has 275 time steps for one-year season (*SEASON*), and each time step (t) corresponds to each day from 1st March, to 31st November. I assumed a local urban area in Tokyo.

Daily temperature (temp[t]) and day-length (daylength[t]) data at a day (t) used in the simulations were the mean from 1993 to 1996, which were recorded in Tokyo Station of Meteorological Office, Chiyoda-ku, Tokyo.

The model consists of the *H. cunea* sub-model and the host tree sub-model. The *H. cunea* sub-model further consists of four parts: Egg, Larva, Pupa and Adult-processes. Population dynamics of *H. cunea* in the next year takes over the abundance of hibernating pupae in the previous-year process. No individuals in other stages can survive over the winter season (from 1st December to 28th February). These procedures are shown in Fig. 6-1 as a flow chart, and all the parameters used in the simulations are listed in Table 6-1.

6.2.1 Host tree phenology

There have been many models for describing annual phenology of plants (Ross, 1967; Van Dyne, 1969; Lüdeke et al., 1994). However, these models need many parameters for characterizing the target plant or plant community, and contain some uncertainty to express biologically reasonable processes. My aim is neither to make a model representing the whole system of a specific plant population, nor to describe seasonal dynamics of plant biomass in nature with high accuracy, but to construct a simple and easy model to alter its developmental characteristics with changing a few parameters. Thus, I constructed an original, simple model with difference equations.

H. cunea larvae infest deciduous trees, which are regarded as storing a stock that is transformed from the photosynthetic part (leaves) into the trunk and the root after summer. They start the foliation using the stock next spring. The phenology of foliage development of the host tree is shown in Fig. 6-2 and formulated as follows:

The host tree started their photosynthesis in 1st March, using the *STOCK*. The amount of host-biomass (foliage[t]) in t-th time step changes according to a logistic-difference equation.

$$\text{foliage}[t+1] = \frac{R \times \text{foliage}[t]}{1 + (R-1) \times \frac{\text{foliage}[t]}{K\_F}} \qquad (1)$$

where R is the growth rate of host tree and K_F is the carring capacity of host-biomass. The host tree stops photosynthesis and starts transformation of the products in autumn.

$$\text{foliage}[t+1] = \text{foliage}[t] - TRANS \qquad (2)$$

where *TRANS* is the transformation rate of products per day. I prevented the foliage[t] from becoming less than *STOCK*.

6.2.2 Egg laying and larval development

A *H. cunea* female lays one egg-mass (*EGG_LAY*) once in her lifetime. The larvae

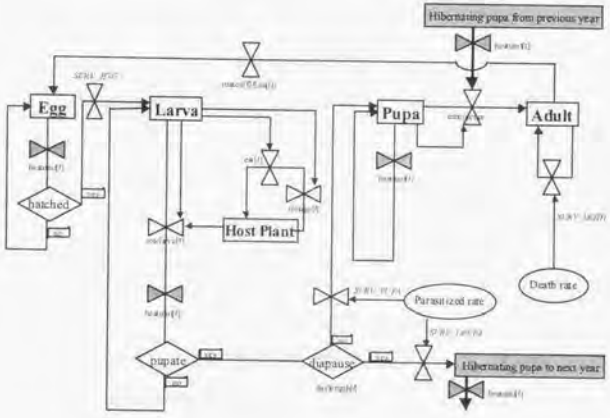


Fig. 6-1. Schematic flow chart of the model in one year. Each arrow steps forward in one time step (1 day).

Table 6-1. A list of the model parameters and the default values used in simulations

Parameter	Description	Default Value	Unit
	Simulation Settings		
SEASON	Simulation period in one year	275	day
PUPAINI	Initial input number of pupae in diapause	1000	-
LONGDAY	The longest day-length in Tokyo (on the 22nd, June)	15.85	h.
	Parameters for host tree		
STOCK	Fundamental biomass of host-biomass stock	1000.0	leaves
K_F	Carrying capacity of host-biomass	10000.0	leaves
R	Growth rate of host-biomass	1.04	-
TRANS	The rate of transformation of products per day (started in 23. Sept. (200 time step))	*K_F* / *SEASON*-200	time step
	Characteristics for Adults		
EGG_LAY	Number of eggs laid by an female	700	-
a	Relative permeating area of pheromone	0.005	-
	Parameters for interactions between larvae and host-biomass		
K_L	Maximum number of larvae that can exist in the most suitable condition	5000.0	-
S0	Survival rate in the larval stage at one time step in a density-independent situation	0.99	-
SC	Survival rate in the larval stage at one time step in the host biomass weighted by *b*	0.83	-
b	Intensity of density-dependence among larvae	1.8	-
EAT_MAX	Amount of food required for the 7th instar larvae in one time step	0.5	g
EAT_MIN	Amount of food required for the first instar larvae in one time step	0.000001	g

Table 6-1. (Continued)

Parameter	Description	Default Value	Unit
	Heat units required for each stage of H.cunea *and thermal constant*		
TH_ZERO	Lower thermal threshold of development	10.0	°C
TH_CONS	Thermal constant of *H.cunea* to complete the whole stages	690.0	day-degree
HEAT_EGG	Cumulative heat unit required to complete the egg stage	150.0	day-degree
HEAT_LARVA_S	Cumulative heat unit required to complete the younger instars	175.0	day-degree
HEAT_LARVA	Cumulative heat unit required to complete the older larval instars	165.0	day-degree
HEAT_PUPA	Cumulative heat unit required to complete the pupal stage	210.0	day-degree
HEAT_PUPA_DEV	S.D of the *HEAT_PUPA*	60.0	day-degree
DIAPAUSE	Ciritical day length for diapause in Tokyo	14.30	h.
	Density-independent survival rate in each stage		
SURV_EGG	Survival rate in the egg stage	0.7	/stage
SURV_PUPA	Survival rate of non-diapause pupa	0.8	/stage
SURV_DPUPA	Survival rate of diapause pupa	0.7	/stage
SURV_MOTH	Survival rate of adults per time unit	0.7	/time step

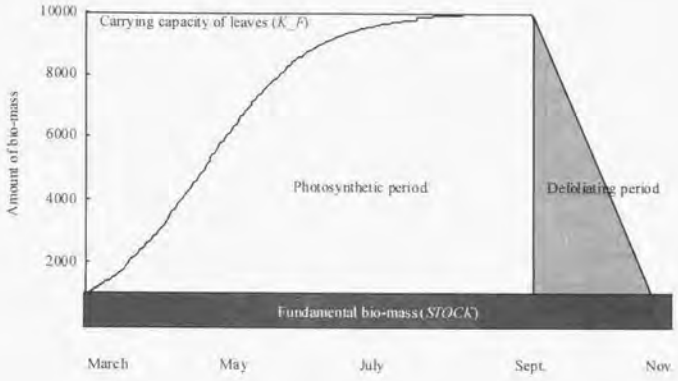


Fig. 6-2. Phenology of the host tree in the model. It starts photosynthesis using the reserves (*STOCK*) on 1st March and stops photosynthesis and starts transformation of products on 23th October.

voraciously feed on various kinds of deciduous trees and aggregate within nest-webs until the fifth instar. They disperse from the nests thereafter and live solitarily. At the seventh instar, mature larvae creep down on the ground and wander around to find stones or bricks under which they pupate (Umeya and Watanabe, 1973).

A group of individuals that were laid as eggs by parents at the same time step (i) is called a "cohort" (larva[t][i]), and grow up simultaneously according to the temperature of the day in the egg and pupal stages. It is well known that the growth rate of insects is proportional to the temperature and can be expressed by a liner regression.

$$D = \frac{TH\_CONS}{T - TH\_ZERO} \tag{3}$$

where D is the duration of development in days, T is the constant rearing temperature in the laboratory conditions, and *TH_CONS* is called as cumulative thermal constant for the completion of development, and *TH_ZERO* as the lower thermal threshold for larval development. *TH_CONS* and *TH_ZERO* can be estimated by the linear regression of D against T.

I divided *TH_CONS* into *HEAT_EGG*, *HEAT_LARVA_S*, *HEAT_LARVA* and *HEAT_PUPA* as for the cumulative heat unit required for completing the egg, the younger larval, the older larval and the pupal stages, respectively. I determined the stage of i-th cohort judging from the cumulative heat unit (heatunit[t][i]) cumulated until the t-th time step, but since the temperature (temp[t]) in the field condition changes day by day, heatunit[$t+1$][i] is calculated by

$$\text{heatunit}[t+1][i] = \text{heatunit}[t][i] + \max\{0, \text{temp}[t] - TH\_ZERO\} \tag{4}$$

Except for the larval stage, *H. cunea* individuals suffer from density-independent mortality factors by multiplying survival rates, *SURV_D*, *SURV_PUPA*, and *SURV_DPUPA* in the egg, pupal, and diapausing pupal stages, respectively. The larvae suffer a density-dependent mortality in relation to host-biomass, and this will be described in section *6.2.5*.

6.2.3 Pupal development

Each pupa in the same i-th cohort (pupa[t][i]) grew up simultaneously just the same as in the egg and larval stages. However, they never emerge simultaneously but they do with variations as reported by several authors (Itô et al., 1969; Itô and Endo, 1970). In the model (Fig. 6-3), I assumed that the emergence (emergence[t]) at the t-th time step take place according to the Gaussian distribution (normal[x] on heat-unit, x) that depends on the cumulative heat unit of individuals in the same cohort (mean: *HEAT_PUPA*, S.D.: *HEAT_PUPA_DEV*).

$$\text{normal}[x] = \frac{1}{\sqrt{2\pi} \cdot HEAT\_PUPA\_DEV} \exp\left[-\frac{(x - HEAT\_PUPA)^2}{2\,HEAT\_PUPA\_DEV^2}\right] \tag{5}$$

The number of pupae pupated on the i-th day is pupa[i][i], which represents the total number of

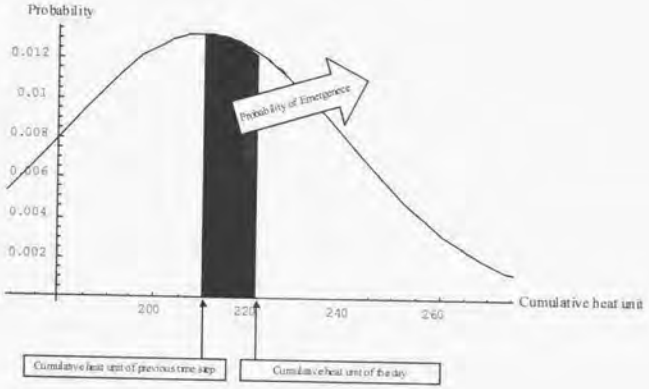


Fig. 6-3. The procedure to generate the emergence of adults. Probability of emergence was determined by the heat-unit (degree-day) which was acquired the cohort in a day. Gaussian distribution was assumed as the emergence pattern.

pupae to emerge. There are t cohorts at the pupal stage (including empty cohorts) until day t. Then,

$$\text{emergnece}[t] = \sum_{i=0}^{t} \left(\text{pupa}[i][t] \times \int_{\text{heatunit}[t][i]}^{\text{heatunit}[t+1][i]} \text{normal}[x]\, dx \right) \quad (6)$$

The number of pupae in the t-th day is obtained by subtracting the number of adults emerged, as the following equation,

$$\text{pupa}[t+1][i] = \text{pupa}[t][i] - \text{pupa}[i][i] \times \int_{\text{heatunit}[t][i]}^{\text{heatunit}[t+1][i]} \text{normal}[x]\, dx \quad (7)$$

H. cunea overwinters at the pupal stage in diapause, and entering diapause is determined by the photoperiod during the early larval stages (Masaki, 1975). In the model, individuals in a cohort are destined to be either diapause pupae or non-diapause pupae when heatunit[t][i] exceeded *HEAT_LARVA_S*, the cumulative heat unit required for completing the young larval stage (from the first to 5th instar) from hatching. If the day-length at the t-th time step (daylength[t]) was shorter than the critical day-length for diapause (*DIAPAUSE*), the individuals in the cohort are destined to diapause, and vice versa.

6.2.4 Mating behaviour of adults

Males and females of *H. cunea* mate only once a day. I used the random mating model, which was proposed by Kuno (1978), as follows:

$$\text{mated}[f[t],\ m[t]] = \frac{1}{\ln(1-a)} \ln\left[(1-a)^{m[t]}\left\{1-(1-a)^{m[t]}\right\} + (1-a)^{f[t]}\right] \quad (8)$$

where, f[t], m[t], and mated[t] are the number of females, males and mated females in the day t, respectively. The parameter a is a kind of searching efficacy, but it relates not only to a searching area of males relative to the whole area but also to the area that is permeated with the sex pheromone of a female.

Since mated females do not mate with males any more (Masaki, 1975), I removed the mated females from the simulation after oviposition, while mated males could still mate again thereafter. Adults suffered from density-independent mortality by a factor *SURV_MOTH* every day.

6.2.5 Interaction between larvae and host-biomass

Intensive surveys on factors that influence the population dynamics of *H. cunea* have reported that the mortality rate was remarkably low in the early larval period, and the population process from the egg to the young larvae seemed to be density-independent (Itô and Miyashita, 1968; Itô et al., 1969; Arai and Akiyama, 1976; Ouchi, et al., 1978; Suzuki and Uematsu, 1981).

My pervious field experiments also suggested that the larvae voraciously feed on the leaves in the webs and seemed not to be controlled by density effects of the larvae themselves or by natural enemies (observations in the experiments of Chapter 1). However, I observed that the older instar larvae wonder around the street after they ate up almost all of the foliage in the street trees. I supposed that a *H. cunea* population shows "scramble-type competition" (Nicholson, 1954) in the older larval stages. Namely, *H. cunea* might eat the leaves without intraspecific competition so long as the resources last, but almost all of them die from hunger in case of the abrupt shortage. Shimada (1989) proposed a generalized competition equation that was modified from a logistic-difference equation. First, I set the total number of larvae (totallarvae[t]) in all cohorts at the t-th time step. Since there are t cohorts in larval stage (including empty cohorts) until t-th day, then,

$$\text{totallarvae}[t] = \sum_{i=0}^{t} \text{larva}[t][i] \tag{9}$$

According to Shimada's equation, I calculated totallarvae[t], as shown in Fig. 6-4

$$\text{totallarvae}[t+1] = \frac{S0 \times \text{totallarvae}[t]}{\left[1+\left(\frac{S0}{SC}-1\right)\frac{\text{totallarvae}[t]}{\frac{K\_L}{K\_F}\text{foliage}[t]}\right]^b} \tag{10}$$

where b is the intensity of density-dependence among larvae (b>1 for scramble competition). $S0$ is the survival rate at the larval stage in one time step in a density-independent situation. SC is the density-dependent survival rate at one time step at the host biomass weighted by b. K_L is a maximum number of larvae that can exist in the most suitable condition, and K_F is a carring capacity of host-biomass. Then, $\frac{K\_L}{K\_F}\text{foliage}[t]$ in the Eq. (10) means the maximum number of larvae that can be achieved at the amount of host-biomass of foliage[t]. Individuals of each cohort are assumed to die at the same ratio totallarvae[t+1] / totallarvae[t].

$$\text{larva}[t+1][i] = \frac{\text{totallarvae}[t+1]}{\text{totallarvae}[t]} \times \text{larva}[t][i] \tag{11}$$

The amount of host-biomass consumed by a larva was assumed to increase exponentially according to its development and was calculated by

$$\text{eat}[t][i] = EAT\_B \cdot \exp\{EAT\_A \cdot \text{heatunit}[t][i]\} \tag{12}$$

where EAT_A and EAT_B are the constants estimated from the data, that is the amount of host-biomass consumed per day by the first instar larva (EAT_MIN) and by the final instar (EAT_MAX) according to the algebraic solution. The amount of host-biomass was obtained subtracting the amount consumed by larvae.

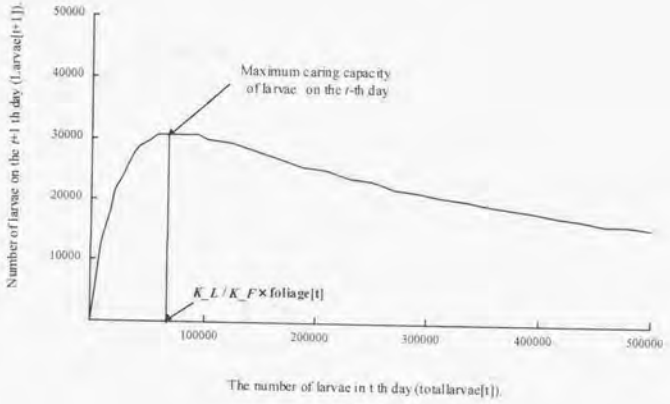


Fig. 6-4. "Scramble" type competition curve used in the model. Maximum carring capacity of larvae on the *t*-th day was determined by the amount of host tree biomass.

$$\text{foliage}[t+1] = \text{foliage}[t] - \sum_{i=0}^{t} \text{eat}[t][i] \qquad (13)$$

6.3 PARAMETER ESTIMATIONS

The list of default values of the parameters is shown in Table 6-1. The initial diapause pupae (*PUPAINI*) put into the simulations were constantly 1000.

6.3.1 Default values for host tree

I focused on the biomass development of a plane tree (*Platanus orientalis* L.). The simulation had 10000 units of foliage biomass (*K_F*) at maximum in the area. Haddad et al. (1995) reported that the plane tree started the transformation after summer far preceding to the defoliation. I assumed that the date for starting the transformation was 23rd September in the simulations. It is considered that the transformation also corresponds to the deterioration of leaves. I set the default values of *STOCK*=1000.0, *TRANS* = 133.3 and *R* = 1.04 (Table 6-1), so that they match the phenology of the plane tree (Haddad, et al., 1995) and other deciduous trees, *Cornus controversa* (Kotani and Togashi, 1995), *Acer mono* (Seiwa, 1998) and *Prosopis glandulosa* (Nilsen et al., 1987).

6.3.2 Default values for Adults

The number of eggs in one egg-mass was reported to range from 300 to 1300, and the mean number was around 700 (Itô et al., 1969; Arai, 1981; Ishii, 1966). So I set *LAY*=700. It was quite difficult for us to estimate the actual value of searching efficacy for males (a) in Eq. (8), and there were no useful reference. I thus conducted the tethered-female experiments in the field (Chapter 1). The mating rate per day was from 0.111 to 0.800, and the mode was around 0.4. For example, substituting 150 males, 150 females and 65 matings (43.3%) into Eq. (8), then I get a=0.005. I set this value as the default.

6.3.3 Parameters for interaction between larvae and host plant

Parameters in Eq. (10) were also difficult to estimate, since I did not have any data about it. Though Shimada (1989) showed how to estimate the parameters in laboratory experiments using azuki bean weevil, *Callosobruchus chinensis*, it is difficult to conduct such experiments in the field. So I changed the parameters of Eq. (10) step by step in the simulations and determined the biologically reasonable defaults so that the output population dynamics became stationary after a transient phase.

6.3.4 Heat units required for each stage of H. cunea *and thermal constant*

Gomi and Takeda (1990) reported that the first generation of the Kobe population required

a thermal quantity of 686 degree-days. I set *TH_CONS* = 690, *TH_ZERO* = 10.0°C, and then divided *TH_CONS* into four stages, (*HEAT_EGG* = 150.0, *HEAT_LARVA_S* = 175.0, *HEAT_LARVA* = 165.0 and *HEAT_PUPA* = 210.0), referring to the detailed data of Itô et al. (1968) who used the bivoltine population of Tokyo in the past as well as my rearing data (data not shown).

I set *DIAPAUSE* = 14.3h according to Gomi and Takeda (1991). They reported that the critical day-length for diapause was 14h 23min and 14h 24min in Kobe and Wakayama, respectively, where populations were trivoltine. Though these data were not for the Tokyo populations, I thought that the Tokyo population had similar characteristics to them.

6.3.5 Density-dependent survival rate in each stage

Itô and Miyashita (1968) and Itô et al. (1969) made life tables of *H. cunea* in the field. Mortality at each stage in the simulation, however, could not be estimated directly from these life tables, because the field population might suffered from both density-dependent and -independent factors, and there were no detailed data related to the abundance of host-biomass. I set arbitrarily *SURV_EGG* = 0.7, *SURV_PUPA* = 0.8, *SURV_DPUPA* = 0.7 as the default values while consulting for their life tables.

I conducted two mark-recapture experiments for population estimation in 1996, and the survivorship of males in one day was estimated to be 0.747 and 0.694 (Chapter 5). Then I set *SURV_MOTH* = 0.7 per day.

6.4 MODEL ANALYSIS

6.4.1 Results with default values

Simulation results with default parameters are shown in Fig. 6-5 together with the actual phenology of males in 1994. Concordance of the simulation result with the field phenology of *H. cunea* was satisfactory. I recorded the number of males captured by pheromone traps from 1994 to 1996 at Koto-ku, Tokyo (Chapter 1). Overwintering generation adults emerged without forming a sharp peak in May, and the number of adults was smaller compared with the other two generations in the three-year observation. The first-generation adults had a sharp peak of prevalence in July, and the number was always larger than that of the overwintering generation. The emergence of the second-generation adults varied year to year from August to September. The largest peak was observed in 1995, while peaks in 1994 and 1996 were smaller. The simulation well represented the timing and the dynamical characteristics of seasonal prevalence in the Tokyo population.

Interactions between the larvae and host-biomass are shown in Fig. 6-6. I observed in the field that the second-generation larvae (the offspring of the first-generation adults) intensively comsumed a plenty of leaves in the study area. In that year, the subsequent third-generation larvae could not increase largely in number. The simulation described the process well (Fig. 6-6). The second-generation larvae ate up the host foliage, and only a small amount of the foliage was

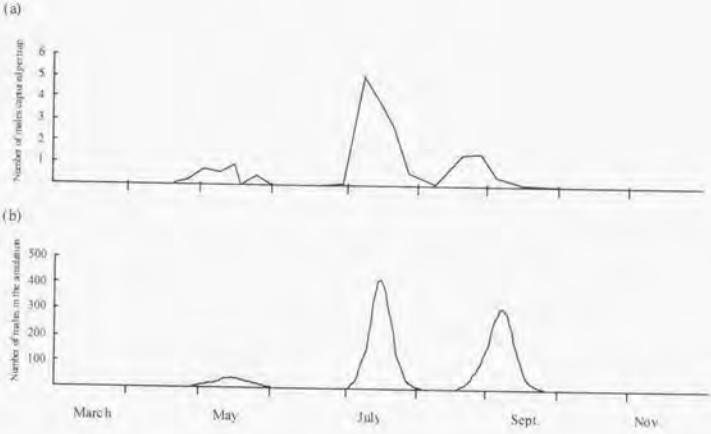


Fig. 6-5. Comparison between the field data and the simulation result. The field data was collected in Toyosu, Koto-ku, Tokyo in 1994 as the number of males captured by the pheromone trap. The simulation result was represented by the number of males. All parameters were default values.

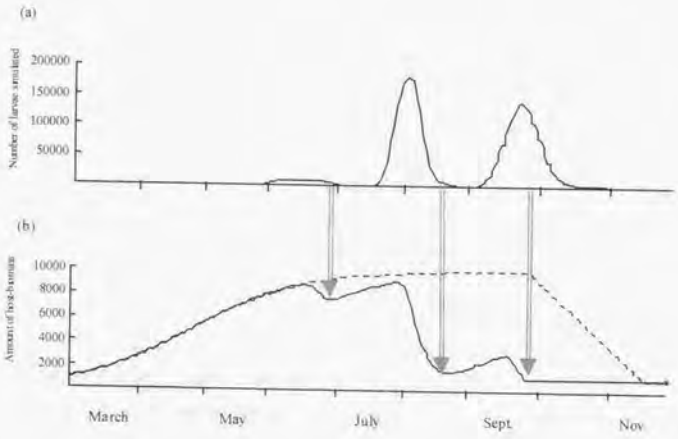


Fig. 6-6. Interaction between the larvae and the host tree in the simulation. The arrows indicate the intensive period of larval feedings. All parameters were default.

produced until the third-generation larval period. Therefore, a lot of the third-generation larvae starved to death.

Decrease in the host-biomass occurred behind to the larval peaks in the simulation. I considered that it was due to two reasons. One was that the amount of host-biomass consumed by larvae increased exponentially with their development. Since older larvae consumed a larger amount of host-biomass, the tree might be damaged severely in the later half of the larval period. The other was that the amount of host strictly regulated the larval density according to Eq. (10). The severe infestation of larvae accelerated intraspecific competition through the host depletion.

6.4.2 Effects of host-biomass dynamics (STOCK)

I examined various patterns of host-biomass dynamics. These affected the population abundance in three generations of *H. cunea*, but if some amount of host remained after final consumption by larvae, *H. cunea* population could be sustained. In the host-biomass equations (Eq. (1), (2) and (13)), *STOCK* was the key for maintaining the population. Fig. 6-7 shows the effect of *STOCK* on population dynamics of *H. cunea* in the simulations. If *STOCK* is smaller than about 650, the population goes to extinction in a few years (Fig. 6-7(a)). When the *STOCK* is larger than this threshold, *H. cunea* population could persist over 100 years, while the heights of the three peaks varied (Fig 6-7(b), (c) and (d)).

6.4.3 Effects of the thermal constant (TH_CONS) *and critical day-length* (DIAPAUSE)

When I shortened the critical day-length (*DIAPAUSE*) or when I decreased the thermal constants (*TH_ZERO*), population dynamics of *H. cunea* changed from two generations to three generations a year. Fig. 6-8(a) shows the typical case of trivoltinism (default) and Fig. 6-8(b) shows the typical case of bivoltinism. A dynamical pattern that might correspond to a transient phase from bivoltine to trivoltine was generated during the course of changing from trivoltine to bivoltine dynamics (Fig. 6-8(c)). Though I could see three peaks of adult emergence in the partially trivoltine dynamics (Fig. 6-8(c) left), the dynamics of pupae showed that the adult in the third peak never produced any diapause pupae (Fig. 6-8(c) right). Some of the second-generation pupae that pupated earlier could emerge, and might produce eggs. The eggs could not develop into the diapause pupae.

In the simulation, I examined the population dynamics every 0.25h in *DIAPAUSE* and every 12.5 degree-day in *TH_CONS* (Fig. 6-9). I have shown that both the thermal constant (*TH_CONS*) and the critical day-length (*DIAPAUSE*) affect the voltinism of *H. cunea*, and a transient dynamical zone is present between bivoltine and trivoltine.

6.5 DISCUSSION

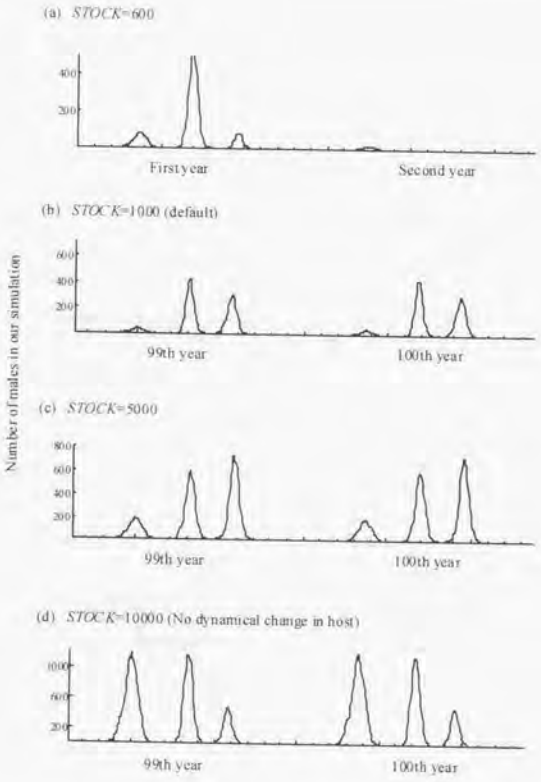


Fig. 6-7. Effect of amount of the resource (*STOCK*). Other parameters were default. Populations could not sustain unless there existed a certain amount of *STOCK*.

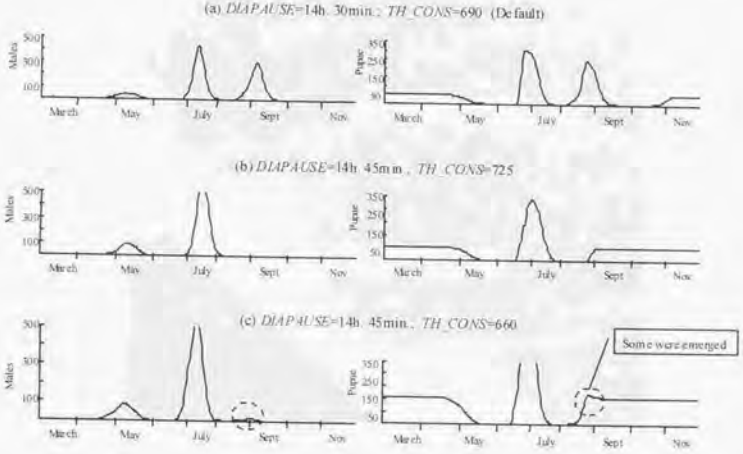


Fig. 6-8. Examples of dynamics observed by changing the critical day length (*DIAPAUSE*) and the thermal constant (*THE_CONS*). Dynamics of the males are shown in the left, and those of pupae in the right. (a): typical trivoltine with default values, (b): typical bivoltin, (c): a transient phase from bivoltine to trivoltine. Dashed circle indicates the evidence of 2nd generation adult emergence in the same year.

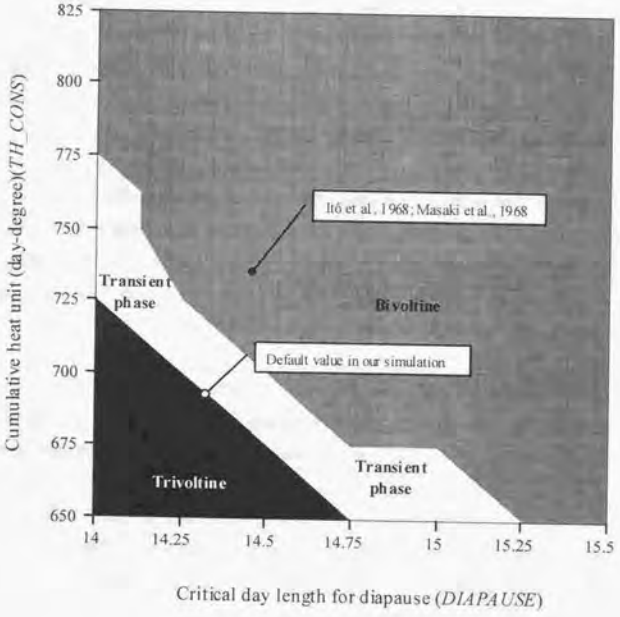


Fig. 6-9. Effects of the critical day length (*DIAPAUSE*) and the thermal constant (*THE_CONS*) on the population dynamics in the simulation presented in a kind of phase-plot. Other parameters were default.

6.5.1 Implication of STOCK *for persistence of* H. cunea *population*

I found that *STOCK* strongly affected the persistence of *H. cunea* population, while it was defined as merely an amount of reserves in the root and trunk. Although this result could be regarded as some artifact of my model formulation, I thought *STOCK* played an essential role for preventing larvae from extinction. When I changed the assumption of *STOCK* to be inedible for larvae, the population became unstable and was hard to persist longer than five years. These results suggested that the population was unstable in the model because of "scramble-type competition" in Eq. (10), and they required some food "refuge" when they ate up all biomass of the host tree. Intensive studies in the field populations (Itô, Y. and K. Miyashita, 1969; Itô et al., 1969; Itô et al., 1970) suggested that the field population was not regulated by density-dependent factors (inverse density dependence) but behaved a graduation-like pattern. I thought that spatial heterogeneity was one of the factors that regulate the potentially unstable population. When they eat up all of the host leaves, they can avoid extinction by migrating to the neighboring areas and can survive by feeding on a wide variety of plants in nature. *H. cunea* larvae were reported to eat even herbal plants such as artemisia, sweet corn, egg plant, watermelon and cucurbits (Kitao et al., 1962). I conjectured that *STOCK* in the model could be equivalent to those extra biomass that existed around the host tree.

From these considerations, I plan to construct a temporally and spatially structured model that incorporates the more realistic assumptions about host trees, in which larvae cannot feed on *STOCK* but migrate to the neighbor areas when they starve.

6.5.2 Transition from bivoltinism to trivoltinism

Itô et al. (1968) reported that the lower thermal threshold for larval development equals to 10°C, and a thermal quantity of 800 degree-days was required for one generation of *H.cunea* in Tokyo. Masaki et al. (1968) reported that the critical day length was between 14hr 30 min and 14 hr 45 min in Yokohama, when the population was bivoltine. I plotted these values into the simulation results in Fig. 6-9. The value in 1960s was in the region of bivoltine. On the other hand, when I set the default values according to the population of Kobe or Wakayama (Gomi and Takeda, 1990, 1991) in the simulation, the result lied just on the margin of the trivoltine region. I supposed from the simulations that the Tokyo population of *H. cunea* changed from the typical bivoltine to the trivoltine, and it was caused by shortening of the critical day length and decease in the thermal constant.

A possibility of the presence of transient phase had been already reported on the Tokyo population in 1967 (Itô et al, 1968). Arai and Akiyama (1971) reported that some pupae in the third generation entered diapause in a mulberry field of Kumagaya, Saitama-prefecture. In addition, the current population in the Tokyo exhibits the steady trivoltine dynamics (Chapter 1). Tokyo

population seemed to have changed their voltinims from the transient phase between biovoltine and trivioltine to the steady trivoltine, while the model population with 1960s parameter set behaved typical biivoltine and the the model population with 1990s parameter set was on the margin of trivoltinism (Fig. 6-9). I conjectured that this inconsistency was caused by the fact that thermal constant and the critical day length used in the simulation were all estimated by the laboratory experiments. Masaki et al. (1968) suggested that the critical day length in the field should be estimated by taking into account of the duration of twilight in the evening and at dawn. I could make simulation results agreeable with the field data, when I added 30 min to the longest day-length in Tokyo (i.e., *LONGDAY* was altered to 16.05) in the simulations considering the effect of such crepuscule.

An alternative explanation of this inconsistency may be temperature dependency of diapause induction. It has been said that high temperature shortened the critical photoperiod for diapause of *H. cunea* (Morris, 1967). In addition, recent studies have revealed that temperature dependence for diapause induction was greater in a trivoltine population than in a bivoltine population (Gomi, 1997; Gomi and Takeda, 1996). Though I did not incorporate the temperature-dependency in the present model, the result of the simulations would be expected to shift in the direction to the trivolitinism if I did.

6.5.3 Temporally structured model approach to H. cunea populations

There have been some model approaches to dynamical properties of insect populations (Shimada and Fujii, 1985; Shimada, 1989; Yano, 1989 a, b; Tsuda and Shimada, 1995; Shimada and Tsuda, 1996). These models helped us to understand the characteristics of the insects' growth, the density-dependent processes and interactions with their natural enemies. They, however, were constructed for rather simple systems: laboratory or greenhouse populations.

Itô et al. (1969) constructed a dynamical model based on the regression equations that were derived from the relationship among generations of *H. cunea* natural populations in Tokyo. While this model succeed to predict the dynamics of *H. cunea* population fairly well in 9 out of 13 cases, it could not be applied to the practical control program of *H. cunea*, because it did not have sufficient resolution to describe detailed dynamical processes. Furthermore, I could not use it for analyzing changes of population dynamic patterns in the insect life history, because it did not incorporate meteorological factors and the detailed developmental processes of *H. cunea*.

In this chapter, I constructed a daily-based and age-structured model for describing *H. cunea* natural populations. Populations in the simulations live under the changing day-length and the temperature day by day. They suffer from density-dependent processes that is related to the interaction with the host-biomass. I used biologically reasonable assumptions in each process and integrated them into a whole system, and the output of the simulation was satisfactory. Some

problems still remains to apply this model to the practical pest management; for example, I did not take it into consideration in this chapter how the pest management method affect the model population (see General Discussion) and I should consider about the spatial structure. However, the novel model simulation developed in this chapter will be a useful tool to understand the whole and detailed dynamical properties of insects, and can be applied to the integrated pest management programs.

GENERAL DISCUSSION

-Model implications for the pest control program-

In the latter half of this thesis, I constructed three models, i.e., the IBM in Chapter 4, the lattice model in Chapter 5 and the temporally structured model in Chapter 6. Though these models could describe well the actual behavioral and population patterns of *H. cunea*, they still have some problems when we apply them to a practical control program. For example, the IBM was constructed with some simplified assumptions such as a linear pheromone-puff growth, a constant number of turnings and so on. In addition, the model did not incorporate the effect of males' "sensory fatigues" in the model. The lattice model used parameter values that were not from field experiments but from the simulations of the IBM. The parameters related to the immigration or arresting in the lattice model must be analyzed further in more complicated and changeable environments in nature. The temporally structured model incorporated biologically reasonable assumptions in each process and integrated them into a whole system. However, some unknown parameters and some real biological factors and processes were omitted in the modeling. For example, it should incorporate the spatial structures. In addition, outputs of these models are still opened for empirical evaluations in the field. Practical models used for the actual pest controls require empirical supports by the field experiments.

Notwithstanding such problems that should be solved in future, I propose some implications for *H. cunea* control from the lattice model and the temporally structured model. These models will give some useful suggestions and guidance for the control strategies for *H. cunea* population management, although those ideas are opened for future field-experimental examinations.

G.1 Implications from the spatially structured, lattice model

The lattice model suggested that the disposition of traps was an essential factor to reduce the mating success in a target area (Chapter 5). Major conclusions from the lattice model simulations were (1) traps should not be placed *inside* the target area but just *outside* of the area, and (2) the surrounding formation of traps with well-chosen spacing is the most desirable. From these predictions, I constructed a new lattice model simulation (*TOYOSU_sim*) based on the previous lattice model, to analyze how to arrangement of traps for the best control of *H. cunea* in Toyosu area.

Within the whole virtual *TOYOSU* area (35 × 21 cells), I set a target area (17 cells; linearly set along a street, in the upper-half) to be controlled by the pheromone traps and a non-target area (17 cells in the line; in the bottom-half) for comparison (Fig. G-1(0)). Two streets, one runs across north to south and the other runs from east to west, cross at the center of the virtual *TOYOSU* area. Male and female moths (*Emergence* = 5000) emerge only from trees along the two streets. After

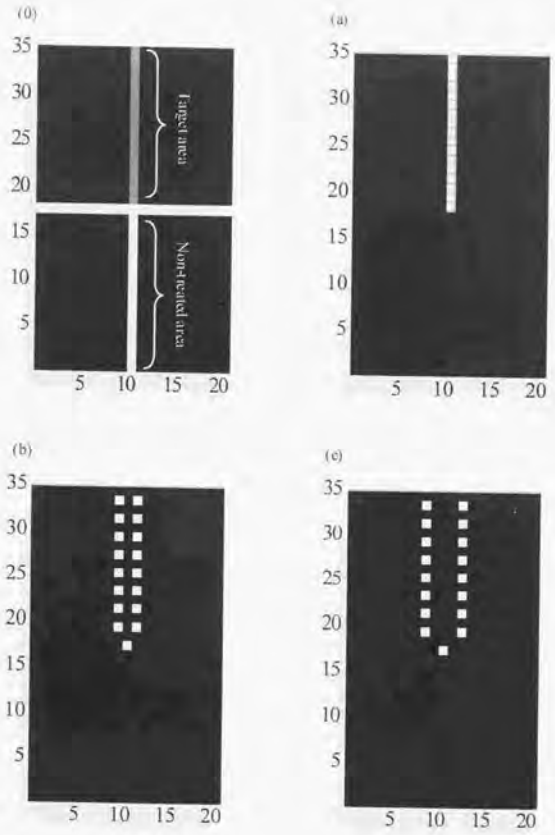


Fig. G-1. Three trap formations examined in the *TOYOSU.sim*. (0): map of the virtual *TOYOSU* area. (a): 17 traps were put on every cell of the target area (default). (b): 16 traps were put on every other cell that located either side of the target area, with one trap placed at the bottom of the target area (surrounding1). (c): 16 traps were put on every other cell that located either side of the target area with one line spacing, with one trap placed at the bottom of the target area (surrounding2). Each white cell in (a), (b), (c) has one pheromone trap in each.

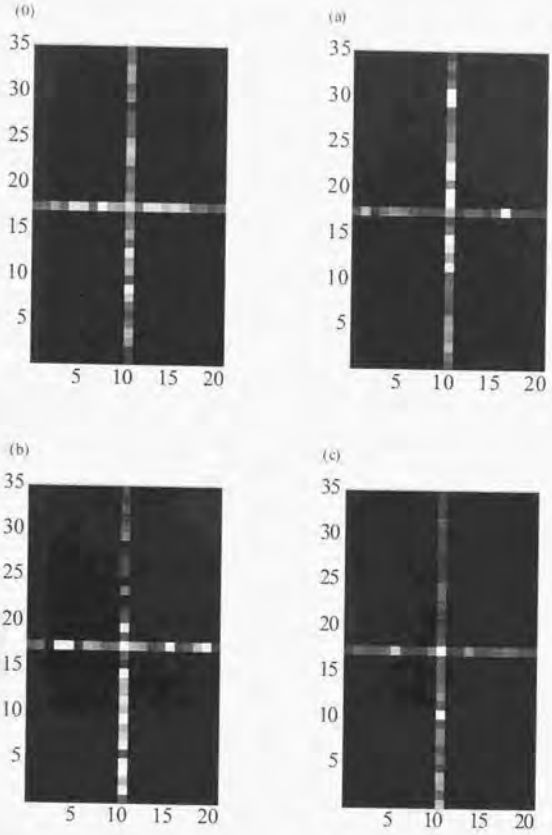


Fig. G-2. Spatial distribution of mated females in the *TOYOSU* sim. Complete black and white grids indicates that it has 0 and more than 19 females, respectively. The whiteness of the gray grid shows abundance of the mated females. (0): no traps, (a): default, (b): surrounding1, (c); surrounding2.

Table G-1 Total number of mated females and trap catches in each treatment of *TOYOSU sim.*

Formations of the traps	No. matings in target area	No. matings in non-target area	Total males captured
No-trap	191.1 (± 12.2)[a]	187.7 (± 20.1)	-
(a) Default	204.8 (± 19.8)[b]	155.9 (± 20.9)*	2257.1 (± 44.1)[a]
(b) Surrounding1	42.1 (± 9.8)[c]	136.8 (± 11.8)*	2163.3 (± 54.8)[b]
(c) Surrounding2	52.9 (± 8.9)[c]	136.3 (± 13.9)*	2191.0 (± 48.8)[b]

Mean ± SD is shown.

Different letters on the right side of the data in target area and total males captured mean significant difference among formations by Tukey's test at $P<0.05$.

* on the right side of data in non-target area means significant difference between the target area and the non-traget area by Student's t-test at $P<0.05$.

emergence, females remain in the street trees but males fly around the whole area. The other parameters and procedures are the same as defaults in the lattice model in Chapter 5.

G.1.1 Simulations of TOYOSU.sim

I examined three types of trap formation here (Fig. G-1). (a) 17 traps were placed on every cell along the target area ('default'), (b) 16 were put on every other cell that located either side of the target area, with one trap placed at the bottom of the target area (surrounding1), (c): 16 traps were put on every other cell that located either side of the target area with one line spacing, with one trap placed at the bottom of the target area (surrounding2). The number of mated females was calculated in each formation, and compared with those in the non-target area and those in no-trap simulation.

The results are summarized in Table G-1. As expected, the surrounding formations, (a) and (b) achieved significant reductions of matings, compared with the non-target area. In contrast, the default setting, which was the same formation as the field experiments in Chapter 1, allowed the highest number of matings among all the formations. Fig. G-2 shows the spatial distribution of mated females. Larger numbers of matings were observed in the central part of the virtual *TOYOSU* area in the default formation ([18, 10]: 21, [19,10]: 25 matings, respectively) (Fig. G-2 (a)). This result indicated that there was intensive immigration of males from non-target area, which was caused by the male-attraction effect of the traps. Fig G-2(b) and (c) suggested that the two surrounding formations of the traps prevented males from stocking up inside the target area. There was no significant difference in the number of mated females between (b) (surrounding1) and (c) (surrounding2) (Table G-1), which suggested surrounding might be better strategy for the pest control.

G.1.2 Can we reduce the mating success of H. cunea *by the synthetic sex pheromone?*

I have always wondered why the synthetic sex pheromone traps could not reduce the damages at the next generation in the field experiment of Chapter 1, notwithstanding that the traps sometimes caught a large number of males (4098 in the 1st. gen., 1994 and 2957 in the 2nd gen., 1995 by 40 traps; see Fig. 1-1 in Chapter 1). In *TOYOSU.sim*, pheromone traps in the default formation allowed higher mating success than those in the non-target area and also in the no-trap simulation, while they caught the largest number of males (Table G-1), which corresponded to removal of 45.2% males from the total emerged males.

The linear formation of traps along the street trees with high density (such as one trap on each tree in the field experiment in Chapter 1) is an example of misapplication. Because the line formation does not produce any structure that was surrounded by the traps, the cell with a trap receives the male-attraction effect more directly, and it becomes far worse than the grid formation of

Chapter 5. In addition, the high-density treatment enhances the competition among traps and reduces the male removal efficiency. The solution from these considerations is simple; "Distribute traps in a surrounding formation".

Notice that *TOYOSU.sim* did not incorporate any factor of males' preference for host plants. Though such preferences are common in barkbeetles or female moths (Shorey, 1973; Farkas and Shorey, 1974), behaviors of male moths may also be affected by the host plant odor (Farkas et al., 1974). Hirooka (1981) observed flights of *H. cunea* males in the field, and found that males have a tendency to fly near the host plants. If *H. cunea* males have some preference to fly around the host tree, the traps that are hung on objects other than the host trees may catch a smaller number of males. A field examination is needed for elucidating the trap formation and the host-tree effects.

G.2 Implications from the temporally structured model

In Tokyo, *H. cunea* is controlled by insecticides and direct removal with infested leaves (pruning) (Edogawa-Ku and Koto-Ku, personal communications). Intensive surveys on factors that influence the population dynamics of *H. cunea* have shown that the mortality was remarkably low in the early larval periods and seemed not to be suffered from natural enemies (Itô and Miyashita, 1968; Itô et al., 1969; Arai and Akiyama, 1976; Ouchi, et al., 1978; Suzuki and Uematsu, 1981). Local governments usually spray insecticides and prune the infested trees in July or August. They do not have any strategy for the timing of the *H. cunea* control but decide it after and increase of complaints from the residents nearby, because they hesitate to use insecticides in residential areas without any consensus of the residents. Control of *H. cunea* in Toyosu was conducted by Koto-Ku government on the 9th August in 1994 and the 24th August in 1996. Whenever I checked *H. cunea* controls in Toyosu, it was conducted around the period of old larval instars in the 2nd-generation or sometimes in the 3rd generation; after they had already infested street trees voraciously.

G.2.1 Simulations for the integrated pest management (IPM)

From the viewpoint of integrated pest management (IPM), I have consider pest control programs with the synthetic sex pheromone trap as well as other pest control methods, such as spraying insecticides and prunings, by expanding the temporary structured model in Chapter 5. I tried to show that the timing control is the key for the success of control, and explored a possibility of *H. cunea* control program with mainly pruning and synthetic sex pheromone traps. A schematic flow chart of the simulation was shown in Fig. G-3. Simulations in Chapter 6 were executed with default values for the first 6 years until the population got through the initial transient phase, and then the control factors were introduced into the simulation after year 7.

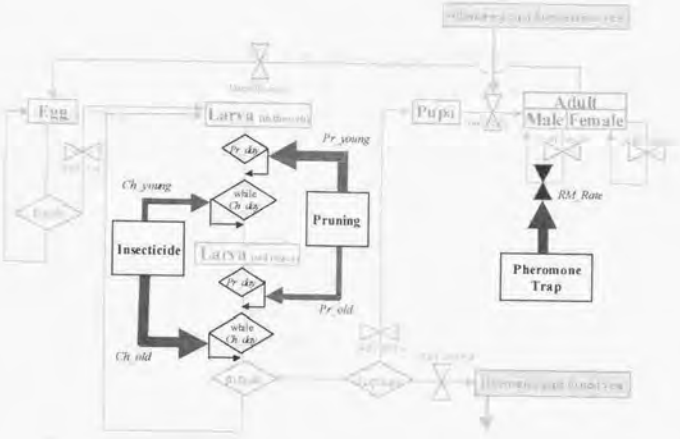


Fig. G-3. Schematic flow chart of pest control simulations in one year.

G.2.2 Pest control with synthetic sex pheromone

From the results of Chapter 4 and Chapter 5, effects of the synthetic sex pheromone were shown to be complex. The disposition of traps has a greater impact on the control success, as shown in Chapter 5 and the preceding part in this Chapter (G.1), whereas placing of a large number of traps dose not always reduce the mating success effectively. However, the present expanded temporally structured model does not incorporate such spatial configurations. I examined the male-removal effect of pheromone traps on population dynamics when we assume removal of males a constant rate (*RM_Rate* = 40%, 60% or 80%), which was achieved in the most desirable formation (Fig. G-1(b)) of the traps.

Though 40% removal of males could reduce the damages caused by the 1st-generation larvae, intensive damages were still observed in the 2nd and the 3rd generations (Fig. G-4(a)). Reduction of the 2nd-generation larvae was improved by removal of the 60% males, but the 3rd generation caused severe damages (Fig. G-4(b)). When the removal rate was increased up to 80%, complete eradication of the population was achieved after 4 years (Fig. G-4(c)). From these results, it was shown that the treatment of sex pheromone alone could exterminate the *H. cunea* population, if it can exhibit such a high removal ability. However, it is actually very hard to remove 80% of males by pheromone traps only, and the IBM (Chapter 4) and the lattice model (Chapter 5) suggested that a high rate of male removal would not always reduce the mating success. From these considerations, I conclude that it is difficult to control *H. cunea* population only by pheromone trap.

G.2.3 Pest control with insecticides

I conducted simulations for treatments with insecticides. Fenitrothion (dimethyl 4-nitro-*m*-tolyl phosphorothioate), DEP (dimethyl 2,2,2-trichloro-1-hydroxyethylphosphonate), DDVP (2, 2-dichlorovinyl dimethyl phosphate) etc., have been used for controlling *H. cunea* larvae (NOUYAKU HANDBOOK, 1994). Ishii (1966) reported that the older instar larvae apparently become more resistant to insecticide, because it was hard to apply insecticide effectively to the larvae within the developed webs. Konno (1998) reported that *H. cunea* Ibaraki population larvae had acquired the resistance for insecticides, especially against fenitrothion and DEP.

In the present simulations, I assumed an insecticide with high efficacy and its aftereffect continued for 6 days. The effect of the insecticide was incorporated as extra-mortality per day for young instar larvae (the survival rate is *Ch_young*) and old instar larvae (the survival rate is *Ch_old*) for 6 days. The insecticide was applied twice (*Ch_day*) during the larval period in the second generation.

The examples of the population dynamics with varied *Ch_young* and *Ch_old* are shown in

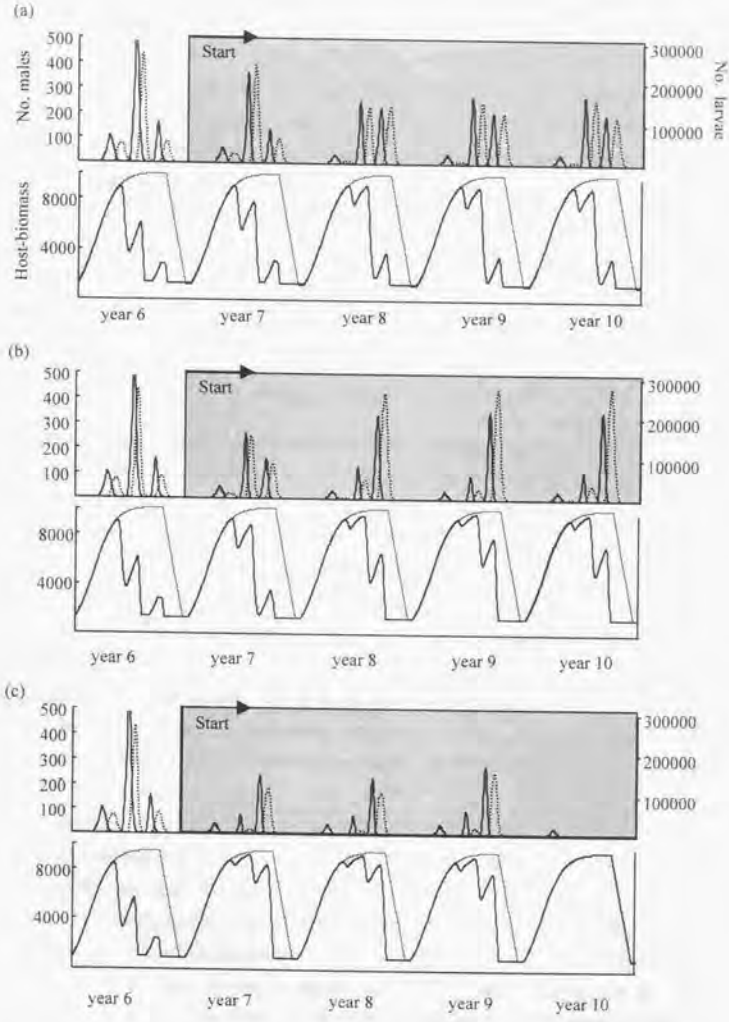


Fig. G-4. Population dynamics under the pest control with the sex pheromone. (a): removal rate was 0.4, (b): 0.6, (c): 0.8. Solid and dashed lines in the upper figure in each treatment indicate dynamics of male moths and those of larvae, respectively. Thick and thin lines in the lower figure in each treatment indicate dynamics of host-biomass with *H. cunea* population and without it, respectively.

Fig. G-5. There were some threshold parameter sets to eradicate the population. Population persisted and heavy infestation occurred every year when the set of *Ch_old* and *Ch_young* was above the threshold (Figs G-5(a) and (b)). Fig. G-5(c) shows the case *Ch_old* = 0.0 and *Ch_young* = 0.4, which were below the threshold. I conjectured that the former two cases were closer to the actual dynamical patterns in Toyosu. Koto-Ku and Edogawa-Ku local governments have conducted insecticide application every year at a large expense. For example, it cost over ¥2,500,000 for only *one* park (Komatshu-sakaigawa park in Edogawa-Ku, 1993, personal communication). However, heavy infestations still continues in these areas. I conclude that intensive treatments with insecticides in the period of the 2nd-generation are not effective when we considered a total management efficacy.

G.2.4 Pest control with pruning

Pruning has been regarded as the most powerful method to protect the street trees. Itô (1972) proposed that removal of webs during young larval instars would be the most desirable to reduce insecticide. This method has been frequently described as the control measure for *H. cunea* found in local governments' publications (Yamanashi-prefecture, Kanagawa-prefecture, personal communication). Thus, I conducted simulations for examining the effect of prunings.

Pruning activities were incorporated as the extra-mortality per day for the young larval instars (the survival rate is *Pr_young* = 0.2 per day) and the old larval instars (*Pr_old* = 0.5 per day). *Pr_young* and *Pr_old* were determined from the assumption that the young larvae were likely to stay in the webs and more easily to be removed, but the older larvae might have already dispersed and thus only a small portion of them were removed by pruning. Pruning was applied three times during the peak occurrence of webs in every generation (*Pr_day* = 13th June, 30th July and 25th September).

The damages by the 2nd generation larvae were slightly reduced, but so far no overall improvement was achieved (Fig. G-6(a)). Then, I added one more pruning on 25th July to reduce the damages by the 2nd generation larvae (Fig. G-6(b)). However, the result was no more improved than with 2 time prunings (Fig. G-6(a)). Therefore, I executed pruning on 8th and 13th June, 25th and 30th July to intensively control the populations of the 1st and the 2nd generations. Though the population sustained for longer than 30 years, the damages by the 1st and the 2nd-generation larvae were relieved (Fig. G-6(c)). However, the damage by the 3rd-generation larvae remained. I did not add pruning anymore, since it costs much more for pruning than insecticides or pheromone traps. Pruning requires a lot of labor and practice, and it is difficult to find out webs in the foliage when the larvae are young. I conclude that pruning would not control *H. cunea* populations effectively because some webs inebitably remain unremoved.

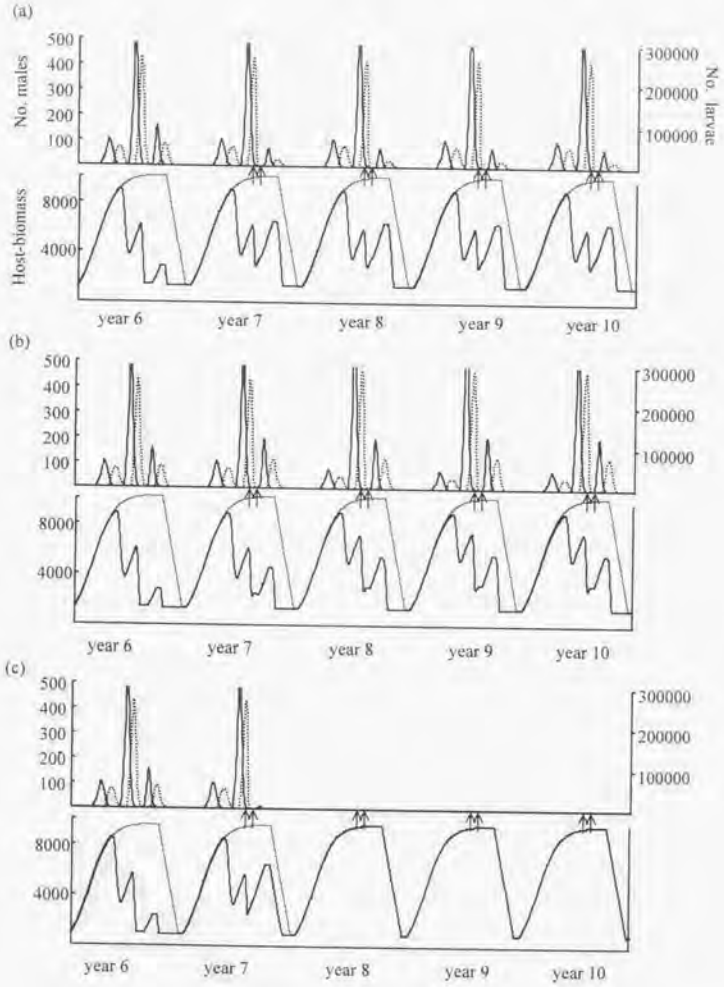


Fig. G-5. Population dynamics under insecticide sprays. (a): *Ch_old* = 0.7 and *Ch_young* = 0.5, (b): *Ch_old* = 0.5 and *Ch_young* = 0.7 (c): *Ch_old* = 0.0 and *Ch_young* = 0.4. *Ch_day* was 5th and 15 th August. Solid and dashed lines in upper figure in each treatment indicate dynamics of male moths and those of larvae, respectively. Thick and thin lines in the lower figure in each treatment indicate dynamics of host-biomass with *H. cunea* population and without it, respectively. Each arrow in the upper figure indicates the timing for spraying the insecticide.

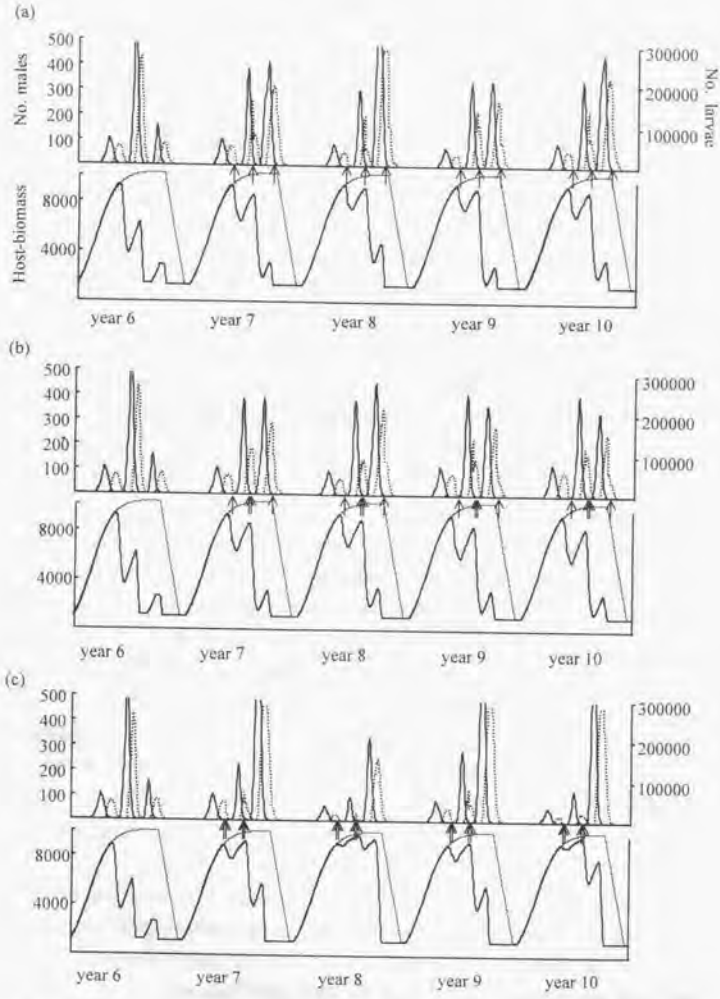


Fig. G-6. Population dynamics under prunings. *Pr_day* was (a): 13th June, 30th July and 25th September, (b): 13th June, 25th and 30th July and 25th September, (c): 8th and 13th June, 25th and 30th July. Solid and dashed lines in the upper figure in each simulation indicate dynamics of male moths and those of larvae, respectively. Thick and thin lines in the lower figure in each simulation indicate dynamics of host-biomass with *H. cunea* population and without it, respectively. Each arrow in the upper figure indicates the timing for pruning.

G.2.5 Integrating the different methods

I have executed heretofore three pest control simulations. These results suggested that if a certain number of individuals are left, the next generation can propagate. In addition, reduction of the host-biomass damage by these control measures would enhance damage in the next-generation because more host-biomass is available for the larvae in the next generation. This result results from the density-dependant process in Eq. 6-10 (Chapter 6), because the larval population was strictly regulated by the host-biomass according to this equation. This phenomenon may correspond to outbreak patterns of *H. cunea* in nature. *H. cunea* larvae have a low mortality in the young instars and infest trees until whole leaves are eaten up. If we remove a large number of them, the remaining larvae can grow up without starvation and will not experience high mortality factors. From these considerations, I propose that the strategy for *H. cunea* control should be eradication instead of leaving them in low densities. The best way to achieve total destruction of *H. cunea* population is to beat them during the low-density period. Therefore, I executed pruning during the 1st generation and treatment with sex pheromone traps.

Fig. G-7 shows results of the simulation. Although one pruning on 13th June plus 40%-removal by sex pheromone traps failed to exterminate the population (Fig. G-7(a)), extinction of *H. cunea* population was achieved when an additional pruning on 8th June was added (Fig. G-7(b)).

I conclude here that intensive pruning in the 1st generation together with treatments of pheromone traps can control the *H. cunea* population. The pheromone trap can also be used as a monitor trap to determine the timing of pruning as well as to confirm the extinction.

G.3 Conclusions

In this thesis, I conducted field experiments and model simulations to examine the feasibility of *H. cunea* control with synthetic sex pheromone traps. I summarize the results and implications derived from the whole of my studies below.

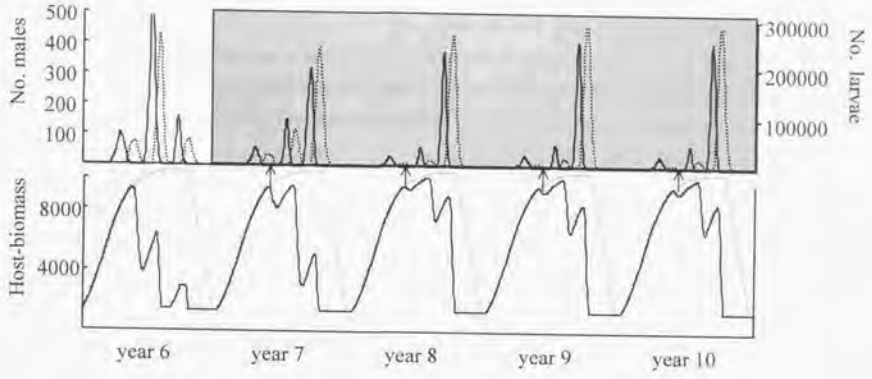
(1) I found some properties of *H. cunea* that should be advantageous for the control by sex pheromone trapping. *H. cunea* males flew for mating just around light-on timing in the 1st and 2nd generations, while they had a potential to fly for 12 h and 7.2km on average (Chapter 2).

(2) It was suggested that the pheromone traps could not always reduce mating success, while traps caught plenty of males (Chapters 1, 5 and G.1).

(3) The possibility of male clustering around the trap was suggested. This phenomenon is likely to be caused by the processes of male moths' pheromone-mediated flight, and would produce male attration effect (Chapter 3, 4 and 5).

(4) Disposition of traps was an essential factor affecting the mating success. The surrounding formation of traps with well-chosen spacing is the most effective. (Chapter 5 and G.1)

(a)



(b)

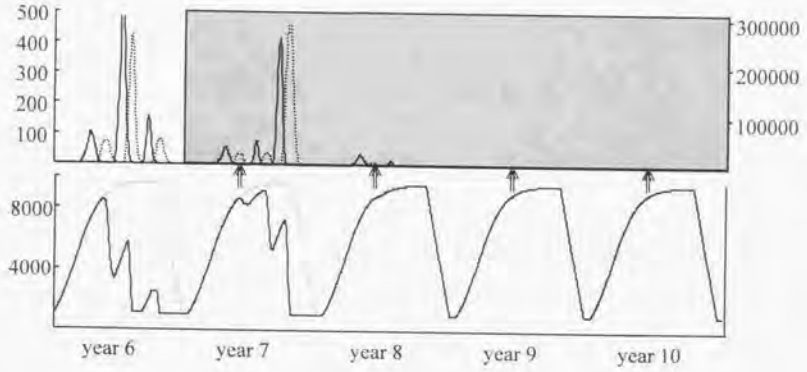


Fig. G-7. Population dynamics under control with prunings and pheromone traps. (a): pruning conducted on 13th June and 40% of males was removed by pheromone traps. (b): additional pruning conducted on 8th June. Solid and dashed lines in the upper figure mean dynamics of male moths and those of larvae, respectively. Thick and thin lines in the lower figure in each simulation indicates dynamics of host-biomass with *H. cunea* population and without it, respectively. Each arrow in the upper figure indicates the timing for pruning.

(5) A daily-based and age-structured model well described the timing and the dynamical characteristics of seasonal prevalence in the Tokyo population. (Chapter 6) The best strategy for controlling *H. cunea* was examined using this model, and intensive pruning in the 1st generation together with treatments of pheromone traps was shown to have an potential to eradicate the *H. cunea* population. (G.2)

Though many of the conclusions obtained here should be evaluated by tests in the field in future, the IBM and the lattice model are very useful for elucidating the negative aspect of the pheromone traps, "male attraction effect", systematically. The effects of pest controls on population dynamics were also exhibited by using the detailed age-structured model. I believe these approaches are novel and powerful for practical pest controls.

ACKNOWLEDGMENTS

I express my sincere thanks to Prof. Sadahiro Tatsuki. He not only led me the way of Applied Entomology, but also supported me mentally. I deeply thank Prof. Masakazu Shimada. He always re-inspired my curiosities to the Insect Ecology, every time I came near to give up my study in half the way of it. I thank all of the members of Laboratory of Applied Entomology, The University of Tokyo. Dr. Y. Ishikawa and Mr. S. Hoshizaki always attended to my study conditions, aided me in my experiments, and gave me their suggestions. Messrs Takanashi, Nomura and Kageyama helped me a lot to prepare this thesis. I thank all of the members of System Science (Biology), The University of Tokyo. Dr. Daniel Borash gave me comments and improved my poor English manuscripts phraseologically. I thank Drs. O. Saito and Y. Shirai of the National Institute of Agro-Environmental Sciences, who kindly gave me their suggestions. I thank Nitto-Denko, Co. for providing me assistance and commodities.

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論文の内容の要旨

生産・環境生物学専攻

平成７年度博士課程　進学

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Field trials and model simulations for controlling the fall webworm,

Hyphantria cunea (Drury) with synthetic sex pheromone

邦題「合成性フェロモンを用いたアメリカシロヒトリ個体群の制御：

野外試験とシミュレーションモデルによる検討」

性フェロモンは環境への毒性が低く、極低濃度で種特異的に働くため、1960 年代以降様々な鱗翅目害虫の性フェロモンが同定されるにつれ、これを害虫防除に利用する動きが高まってきた。学位申請者は、アメリカシロヒトリ(*Hyphantria cunea* (Drury))に対する合成性フェロモン製剤を用いたフェロモン防除法の有効性を確かめるために、野外実験及びモデルのシミュレーション解析を併用した研究を行ってきた。本学位論文は、本種の配偶飛翔の行動特性と個体群動態の理解を通じて、性フェロモンを用いた害虫防除がどのような効果を発揮するかを分析したものである。

アメリカシロヒトリは戦後北米から侵入し、日本各地に分布を広げて、主に市街地において、広範囲の落葉広葉樹を食害する大害虫となった。都市緑地という人間の生活空間で発生する本種の防除にはとくに、環境への影響が少ない性フェロモンを利用した防除の可能性を検討する意義は大きい。さらに、本種は、多くの人工物に囲まれ生息地が分断されている都市環境で発生するため、防除対象外の地域からの移入による被害の発生は少ないと考えられること、高濃度・長期間使用可能な誘引力の高い合成性フェロモン製剤が開発されたこと、雌成虫は交尾後その場に定着して産卵するため、既交尾雌の移動による被害の拡大の恐れがないことなど、性フェロモン利用による防除を行う上で有利な点が多いと思われる。

第１章では、1994 年から 1996 年にかけて東京都江東区豊洲の街路樹を用いて実用面を考慮した野外実験を行った。約 500m に渡って 88 本の街路樹に各 1 個のフェロモントラップを設置し（1996 年の試験）、同じ規模の無処理区と比較した。防除効果を確かめるため、つなぎ雌の交尾率を調査したところ、条件によってはトラップ設置区で交尾抑制効果が示された。しかし、幼虫による街路樹の食害度（木当たり巣網数）を比較すると、一部のケースを除いて、試験区を無処理区よりも有意に低く抑えることは出来なかった（図１）。その原因として、試験区の規模が小さ過ぎたため周囲からの雄成虫の移入による交尾があったこと／雄成虫密度が高い発生の最盛期にはトラップが飽和してしまったこと／トラップ設置区の個体群密度が大量誘殺法の効果を発揮できる範囲を超えた高いレベルにあったこと、の３点が考えられた。

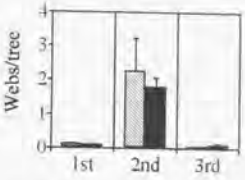


図１　□ 処理区 ■ 無処理における巣網の発生状況（1996）

そこで第２章では、雄成虫の飛翔能力と飛翔による分散様式を調べるため、フライト・ミルを用いた潜在的飛翔力の測定／フェロモン源を置いた室内風洞による交尾飛翔時間帯の把握／野外での標識再捕獲による分散様式の観測、という一連の実験を行った。フライト・ミル実験では、本種雄成虫は 12 時間で平均 7220m 飛び、飛翔性の強い鱗翅目移住種に匹敵する飛翔能力を潜在的に有することが示された。しかし、フェロモン源を置いた風洞実験において、雄成虫の交尾のための飛翔活動は明け方に相当する短い時間帯（約１時間）にのみ集中した。また野外における標識再捕獲でも、フェロモントラップで再捕獲された位置は放逐した場所からあまり大きく離れていなかった。本種雄の交尾のための実際の飛翔距離が潜在飛翔能力に比べるとずっと短いことは、性フェロモンを利用した防除法にとって有利な条件となるはずである。

第３章では、局所的にフェロモントラップを設置した場合の防除メカニズムを調べた。通常の粘着板を付けたフェロモントラップ／粘着板なしのフェロモントラップ／無処理の３条件の試験区を設け（１区あたり１０本の樹にトラップを設置）、同時に、各試験区に処女雌トラップ（処女雌をフェロモン源にしたトラップ）を１区あたり５本の樹に設置して、処女雌トラップに捕獲された雄成虫数を比較した（少ないほど交尾成功率が低いと想定）。本実験は 1999 年７月に第１世代成虫の発生進行に応じて２回試験を行った。その結果、まず、通常のフェロモントラップと粘着板なしのフェロモントラップの試験区間には有意差がなかった。そこで、

これら２つのフェロモントラップ処理区における処女雌トラップの雄成虫捕獲数をプールし、それを無処理区と比較したところ、成虫発生初期の低密度期では処理区の方で処女雌トラップに捕まった雄が有意に少なかった。この結果は、局所的に設置したフェロモントラップは、雄を捕獲するよりもむしろ誘引し惑わすことで、成虫低密度の条件下では雌の交尾成功率が下がって、防除効果が期待できることを示唆している。しかし、羽化発生が進んで高密度期になると有意な抑制効果は得られなくなってしまった。

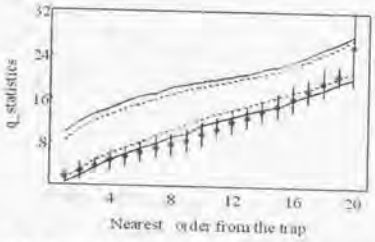


図２　Nearest-neighbor法による雄成虫（20匹を設置）のトラップに対する集中度の解析
トラップからの近接順位 2～17までで顕著なトラップへの集中が見られる
―― 実線は99%信頼限界を
…… 破線は95%信頼限界を示す

第４章では以上の野外実験の結果をうけて、空間的に構造化されたモデルを構築し、侵入・誘引・捕獲がフェロモン防除法に与える影響を考察した。第一のモデルとして、個体ごとの交尾行動の詳細を個別に記述した個体ベースモデルを構築した。このモデルでは、トラップから環境中にフェロモンが風に乗って流れ出ている。雄成虫は、ランダム飛翔／フェロモン物質に接触してあらわれる風上飛翔／フェロモンから外れたときのジグザグ飛翔、という一連の行動を行う。シミュレーションの結果、風がある程度揺らぐ条件下で、雄成虫はトラップの周りに有意に集中分布すること（図２）、高濃度でフェロモンが放出されても雄の捕獲数は上がらないが、トラップ周辺への雄の集中はより顕著になることが示された。また、雄によるジグザグ飛翔の回数を増やすと、トラップ周辺への集中分布はより顕著になった。これらの結果により、これまでフェロモンによる防除のなかであまり考えられてこなかった雄によるジグザグ飛翔が、雄成虫のトラップへの集中分布に強く関与していると示唆された。また、製剤の担持量をある程度以上に増加しても雄の捕獲効率を上げる効果はないこと、トラップの周りに雄成虫を引きつけることで他所にいる処女雌の交尾成功率を下げる可能性のあることが示された。

ところが、「トラップ周辺に多くの雄を引き寄せるけれど、捕獲数は増えない」という状況が、トラップの近くに雌成虫がいた場合の交尾成功率を高めてしまう危険性はないのだろうか？　そこで第５章では、第二のモデルとして、複数のトラップと雌成虫を組み込んだ格子モデルを新たに構築した。このモデルはセル（局所生息場所）状環境を考え、セル間の個体

の移動を考慮しながら、各セル毎に個体数を計算するものである。ここではランダム飛翔／ジグザグ飛翔／交尾／捕獲の４つにカテゴリーを分け、シミュレーション解析を行った。その結果、トラップの配置の仕方によっては防除効果を下げてしまう可能性が示唆された。

第６章では、第三のモデルとして、本種の日齢構成／有効積算温量に基づく成長／寄主植物の季節的消長、を盛り込んだ時間構造化モデルを構築した。これにより予測された本種の個体数の発生消長は現実の年３化の個体群動態と非常に近い挙動をし（図３）、このモデルの記述力の高さが示された。さらに、このモデルにフェロモントラップなどの防除手段の効果を総合的に組み込むことで、本種の個体群動態に与える影響を考察した。その結果、薬剤防除や剪定防除では一時的効果を発揮しても有効性が続かないこと、大量誘殺法単独では十分な防除効果が得られないことが示された。しかし、個々の防除法単独では本種を効果的に抑制することはできなくても、それぞれを補完的に組み合わせることで、本種を低い密度に抑えることが可能であると思われる。

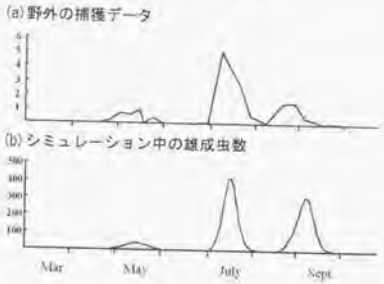
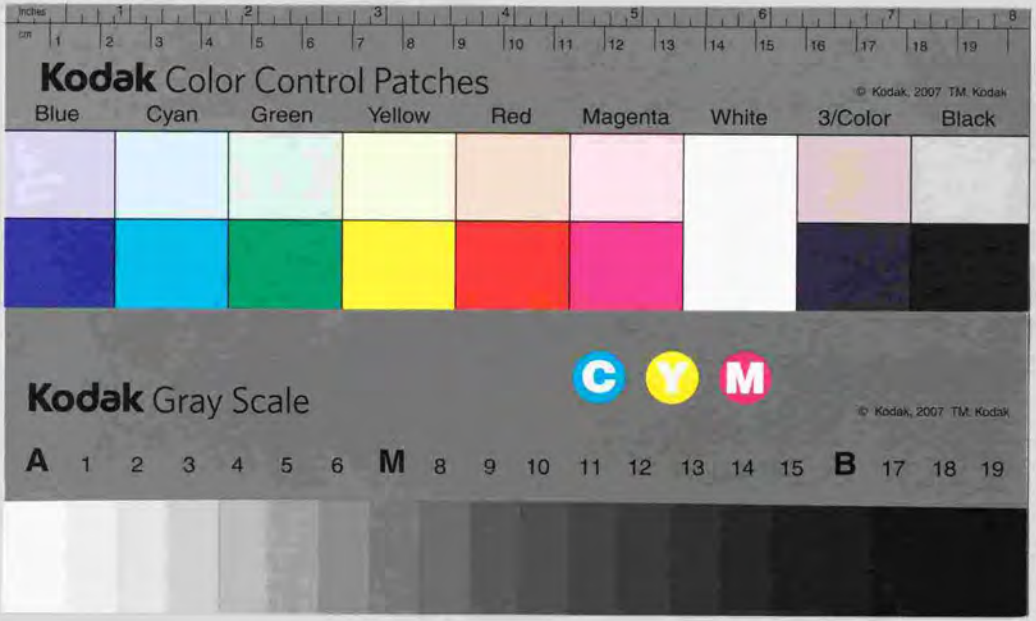


図３　時間構造化モデルによるシミュレーションと現実の雄成虫捕獲消長（1996）
(a) はトラップあたり１日にちあたり捕獲数を
(b) は仮想領域中の総雄成虫数をそれぞれ示す

以上のように本学位論文では、性フェロモンによるアメリカシロヒトリの防除を実際に試み、その結果をもとに防除効果ならびに個体群動態を予測するための３つのモデルを構築した。これらのモデルは生物学的意味を持ちながら、現実の防除プログラムにも応用可能な新しいアプローチである。今後、さらに生物学的な詳細の組み入れ・防除試験の結果のフィードバックを重ねることで、アメリカシロヒトリ防除プログラムを構築する際の中核となりうると考える。


Kodak Color Control Patches
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Yellow
Red
Magenta
White
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