Sexual Competitive Ability of Mass-Reared Males and Mate Preference in Wild Females: Their Effects on Eradication of Melon Flies¹

Yoshitaka TSUBAKI² and Suvarin BUNROONGSOOK³

*Laboratory of Applied Entomology and Nematology, Faculty of Agriculture,
Nagoya University, Nagoya 464, Japan*

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A simulation model of sterile insect releases was constructed based on a logistic equation of population growth. Reduction of sexual competitive ability in mass-reared and sterilized males and evolutionary change of mate preference in wild females were incorporated in the model. The results suggested that the effect of the reduction of competitive ability of sterile males on the effectiveness of the sterile insect release method (SIRM) is substantial but that the effect of female mate preference is slight. The number of sterile males released should be increased to overcome the evolution of mate preference in wild females. However, this does not appear to be a serious obstacle for eradication of the melon fly.

INTRODUCTION

One of the many obstacles for the successful application of the sterile insect release method (SIRM) for eradication of insect pests is the reduction of mating competitiveness in mass-reared and sterilized males (hereafter sterilized males). This reduction may be due to reduced viability including longevity and dispersal ability (ECONOMOPOULOS, 1972; NAKAMORI and SOEMORI, 1981), and mating behaviour which changes during long-term mass-rearing programs under laboratory conditions (BOLLER, 1972; SOEMORI et al., 1980; SUZUKI and KOYAMA, 1980, 1981; KUBA et al., 1984).

SOEMORI et al. (1980) showed that mass-reared melon fly *Dacus cucurbitae* males in small cages copulated with females more than wild males did; mass-reared males may be adapted to copulate in a small space rather than in the field. As flight activity was greater in wild males than in mass-reared ones (NAKAMORI and SOEMORI, 1981), the former may encounter females more frequently. Mass-reared males experiencing artificial conditions such as constant temperature and/or artificial diet may lose the physiological and behavioural characteristics needed for normal mating in the field (NAKAMORI, 1988).

In addition to this, IWAHASHI and MAJIMA (1986) observed lek forming behaviour

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² Present address: *Wildlife Conservation Laboratory, National Institute for Environmental Studies, Onogawa, Tsukuba 305, Japan*

³ Present address: *Department of Plant Pest Management Technology, Faculty of Agriculture, King Mongkut's Institute of Technology, Bangkaen, Bangkok, Thailand*

in the field, where visiting females have opportunity to select mates. HIBINO and IWAHASHI (1988, and in preparation) recently obtained evidence which suggests the evolution of female mate preference. Wild females collected in Okinawa, where wild flies have been reduced by SIRM, rejected courtship with mass-reared males. Wild females collected in Ishigaki, where SIRM has not yet been applied, accepted wild and mass-reared males equally. It was hypothesized that wild females have evolved to reject courtship of mass-reared males as the eradication program has progressed.

In this paper, we report the results of analysis of a model which simulates the population dynamics of the melon fly under SIRM. We estimate how many extra sterile males should be released in order to overcome the reduction of mating competitiveness in sterile males and the evolution of mate preference in wild females.

MODEL

Population growth. A modified logistic equation for discrete generations was applied to describe the population process (MORISITA, 1965). The logistic equation is known to fit melon fly population under eradication (ITÔ, 1977; ITÔ and KAWAMOTO, 1979). The seasonal fluctuation of the density of the melon fly population which occurs in nature (IWAHASHI, 1977) was not considered, in order to simplify our arguments.

The population changes in size under the influence of a net reproductive rate, R , can be written as,

$$N_{t+1} = R \cdot N_t \quad (1)$$

where N_t and N_{t+1} indicate population size at generation t and $t+1$, respectively. If we assume that N_t influences the inverse of generation increase ($1/R$) in a linear fashion, we can rewrite equation (1) as,

$$N_{t+1} = \frac{N_t \cdot R}{1 + (R-1)N_t/K} \quad (2)$$

where K is the population size at carrying capacity.

Non-random mating. We assumed that a female copulates once in her life. Released sterile males mix rapidly with wild males in the field. The proportion of wild males to sterile males in the field (x) can be written as,

$$x = W/S \quad (3)$$

where W and S represent the number of wild and sterile males, respectively. Females will copulate with wild males with a probability P_w . If there is no difference in competitive ability between wild and sterile males, and there is no female mate choice (random mating), P_w can be written as,

$$P_w = \frac{x}{x+1}$$

If sterile melon fly males have less mating competitiveness under natural conditions (IWAHASHI et al., 1983) than wild males, or if females prefer wild males to sterile males (HIBINO and IWAHASHI, 1988), random mating cannot be assumed. Assuming that females are likely to copulate with wild males A times more than with sterile males, the factors leading to non-random mating can be simply represented by a single parameter, A , in the following equation,

Fig. 1. The relation of the probability of females to mate with wild males, Pw , to the proportion of wild males to total males in the field, x , with a varying parameter of non-random mating, A .

$$Pw = \frac{A \cdot x}{A \cdot x + 1} \quad (A \geq 1) \quad (4)$$

With this equation, we assumed that the probability of females copulating with wild males is influenced both by the proportion of wild males to total males and the degree of non-random mating.

Figure 1 shows the relationship between x and Pw for different A values. If $A > 1$, females tend to mate with wild males at a higher probability than with sterile males. If $A = 1$, females mate with wild and sterile males indiscriminately.

Male-male competition and female choice. We assumed that A can be separated into two factors: the difference in competitive ability between wild and sterile males, a , and the degree of mate preference in females, b , as,

$$A = a \cdot b.$$

We also assumed that there are two classes of females in the field; indiscriminate and selective. Indiscriminate females do not show any preference for wild males, but may still tend to copulate with wild males because of their high competitive ability, a ($A = a$). In contrast, selective females tend to copulate with wild males more than indiscriminate females ($A = a \cdot b$). Therefore, the probability of mating with wild males for selective females can be represented as

$$Pw = \frac{(a \cdot b)x}{(a \cdot b)x + 1} \quad (a \geq 1, b \geq 1) \quad (5)$$

For indiscriminate females we can use this equation after establishing b as 1.

Reproductive success of indiscriminate and selective females. Only females which copulated with wild males leave progeny. Therefore, N_{t+1} can be written by multiplying (2) and (5) as,

$$N_{t+1} = Pw N_t R / (1 + (R-1)N_t/K) \quad (6)$$

If we denote the number of indiscriminate and selective females as Fn_t and Fc_t , respec-

tively, we can express the number of these females as

$$F_t = Fn_t + Fc_t,$$

where F_t indicates the number of total females at the t -th generation.

Assuming a 1:1 sex ratio, the number of wild males, W_t , and population size of wild flies, N_t , are calculated as

$$W_t = F_t$$

and

$$N_t = W_t + F_t.$$

From (3),

$$x_t = W_t/S \quad (7)$$

where S is assumed to be constant throughout the eradication program.

If we represent the probability of mating with wild males for indiscriminate and selective females as Pwn_t and Pwc_t , respectively, then

$$Pwn_t = \frac{ax}{ax+1} \quad (8a)$$

and

$$Pwc_t = \frac{(ab)x}{(ab)x+1} \quad (8b)$$

Finally, from (6) and (8a, b), we can calculate the change in number of indiscriminate and selective females separately as,

$$Fn_{t+1} = Fn_t Pwn_t R / (1 + (R-1)N_t/K) \quad (9a)$$

$$Fc_{t+1} = Fc_t Pwc_t R / (1 + (R-1)N_t/K) \quad (9b)$$

By this equation, we assumed that mate preference is heritable only through females and is not genetically influenced by males. If this is not the case, we may have overestimated (approximately by a factor of two) the rate of evolution in female mate preference. However, this does not influence the major conclusions of our analysis.

Population dynamics. Based on the above assumptions, simulations were carried out to examine the effects of the number of sterile males released (S), on the population dynamics of the melon fly in relation to the relative competitive ability of sterile males (a), and the degree of female mate preference (b). We assumed that the population size is at carrying capacity, K , and selective females are rare at the initial period of the eradication program. The following values were used as an initial condition of the eradication program.

$$Fn_0 = 9,995$$

$$Fc_0 = 5$$

$$W_0 = 10,000$$

$$N_0 = 20,000$$

For the constant values,

$$R = 4 \text{ (estimated from IWAHASHI, 1977)}$$

$$K = 20,000$$

S = from 1,000 to 30,000 with increments of 1,000

a = from 1 to 10 with increments of 1

b = from 1 to 10 with increments of 1.

We used a combination of values of S , a and b in each simulation. For the biological meanings of a and b , see Fig. 1 by substituting $A=a$, or $A=ab$.

RESULTS

Population dynamics

In each simulation, population changes were monitored until the entire population went extinct ($N_t < 1$) or population size became stable ($|N_{t+1} - N_t| < 0.1$), and the number of generations necessary to attain eradication was obtained. In addition, changes in numbers of indiscriminate and selective females were calculated.

Without female choice. In Fig. 2, we show examples of calculations using several combinations of parameters a and S . The results indicate that both the number of males released and degree of mate preference had effects on the population change. When S was small, the population (number of females) became stable. The stable population size was always smaller than carrying capacity, K , depending on a and S . When S was large, the population went extinct. The number of sterile males necessary to attain eradication was largely influenced by a (Table 1). For example, when $a=1$ (random mating), we needed only 4,000 sterile males to make the population of initial size 20,000 go extinct. However, when $a=6$, 21,000 sterile males were necessary to attain eradication.

Effect of female choice. Here, we assumed $a=3$. This is roughly equivalent to the actual situation when the melon fly eradication was conducted (IWAHASHI et al., 1983). In other words, sterile males released in the eradication program were about three times less competitive than wild males. In addition, we assumed that the selective females are more likely to copulate with wild males than are indiscriminate females.

Fig. 2. Examples of simulated population changes under the eradication program with combinations of parameters a and S . Females are assumed to show no mate preference, but sterile males are assumed to be less competitive against wild males.

Table 1. Number of generations necessary to attain eradication in relation to the difference in competitive ability of wild and sterile males, a

No. sterile males released	a									
	1	2	3	4	5	6	7	8	9	10
1,000	—	—	—	—	—	—	—	—	—	—
2,000	—	—	—	—	—	—	—	—	—	—
3,000	—	—	—	—	—	—	—	—	—	—
4,000	19	—	—	—	—	—	—	—	—	—
5,000	12	—	—	—	—	—	—	—	—	—
6,000	10	—	—	—	—	—	—	—	—	—
7,000	9	39	—	—	—	—	—	—	—	—
8,000	8	19	—	—	—	—	—	—	—	—
9,000	7	15	—	—	—	—	—	—	—	—
10,000	7	12	—	—	—	—	—	—	—	—
11,000	6	11	27	—	—	—	—	—	—	—
12,000	6	10	19	—	—	—	—	—	—	—
13,000	6	9	16	—	—	—	—	—	—	—
14,000	6	9	14	39	—	—	—	—	—	—
15,000	5	8	12	24	—	—	—	—	—	—
16,000	5	8	11	19	—	—	—	—	—	—
17,000	5	7	10	16	62	—	—	—	—	—
18,000	5	7	10	15	31	—	—	—	—	—
19,000	5	7	9	13	23	—	—	—	—	—
20,000	5	7	9	12	19	—	—	—	—	—
21,000	5	7	9	11	17	39	—	—	—	—
22,000	5	6	8	11	15	27	—	—	—	—
23,000	5	6	8	10	14	22	—	—	—	—
24,000	4	6	8	10	13	19	52	—	—	—
25,000	4	6	7	9	12	17	32	—	—	—
26,000	4	6	7	9	12	16	26	—	—	—
27,000	4	6	7	9	11	15	22	78	—	—
28,000	4	6	7	9	11	14	19	39	—	—
29,000	4	6	7	8	10	13	17	29	—	—
30,000	4	5	7	8	10	12	16	24	—	—
31,000	4	5	7	8	10	12	15	21	48	—
32,000	4	5	6	8	9	11	14	19	34	—
33,000	4	5	6	8	9	11	13	18	27	—
34,000	4	5	6	7	9	10	13	16	24	62
35,000	4	5	6	7	9	10	12	15	21	39
36,000	4	5	6	7	8	10	12	15	19	31
37,000	4	5	6	7	8	10	11	14	18	26
38,000	4	5	6	7	8	9	11	13	17	23

The number of generations was calculated as a function of the number of sterile males released in each generation. Net reproductive rate, $R=4$. Initial population size, $N_1=20,000$. Bars indicate failure to achieve eradication.

Fig. 3. Examples of simulated population changes under the eradication program with combinations of parameters b and S . Selective females are assumed to show mate preference, but indiscriminate females show no mate preference. Sterile males are assumed to be less competitive against wild males ($a=3$).

As a result, selective females increased in number because they have higher reproductive success than indiscriminate females, on average.

Figure 3 shows examples of calculations with several combinations of parameters of b and S . When both b and S were small, the number of indiscriminate females decreased slowly, whereas the selective females increased gradually (Fig. 3a). If S was large, both indiscriminate and selective females went extinct (Fig. 3c).

When b was large and S was small, the results were similar to the cases when b was small, however, the indiscriminate females were replaced by selective females more rapidly (cf. Figs. 3a and b). This is because the female mate choice was more intense in this case. When S is large, the number of indiscriminate females decreased quickly, but selective females also increased quickly (cf. Figs. 3b and d), because the intensity of selection for sterile male resistance was higher. When S was large, the population went extinct in all cases (Table 2). In every case of population extinction, selective females increased in number and had a small peak immediately prior to the total extinction of the population (see Fig. 3c, around 10th generation).

Table 2. Number of generations necessary to attain eradication in relation to the degree of mate preference in selective females, b

No. sterile males released	b									
	1	2	3	4	5	6	7	8	9	10
10,000	—	—	—	—	—	—	—	—	—	—
11,000	27	—	—	—	—	—	—	—	—	—
12,000	19	20	—	—	—	—	—	—	—	—
13,000	16	16	17	—	—	—	—	—	—	—
14,000	14	14	14	16	—	—	—	—	—	—
15,000	12	12	13	13	15	20	—	—	—	—
16,000	11	11	12	12	13	14	16	—	—	—
17,000	10	10	11	11	11	12	13	14	—	—
18,000	10	10	10	10	10	11	11	12	14	16
19,000	9	9	9	10	10	10	11	11	12	12
20,000	9	9	9	9	9	10	10	10	11	11
21,000	9	9	9	9	9	9	9	10	10	10
22,000	8	8	8	8	8	9	9	9	9	10
23,000	8	8	8	8	8	8	8	9	9	9
24,000	8	8	8	8	8	8	8	8	9	9
25,000	7	7	8	8	8	8	8	8	8	8
26,000	7	7	7	7	7	8	8	8	8	8

The number of generations was calculated as a function of the number of sterile males released in each generation. Net reproductive rate, $R=4$. Initial population size, $N_1=20,000$. Difference in competitive ability of wild and sterile males, $a=3$. Bars indicate failure to achieve eradication.

Minimum number of released sterile males

Table 2 summarizes the results of simulations with all combinations of b and S values. When the number of sterile males released is less than 11,000 (1.1 times larger than wild males at carrying capacity), the population does not become extinct. The number of sterile males necessary to attain eradication increased with b . In cases where eradication was not successful, selective females increased in number and replaced indiscriminate females. However, even if b is large, however, we can eradicate target insects by releasing larger numbers of sterile males. For example, when $b=5$, which means that selective females copulate with wild males with about 15 times ($=3 \times 5$) higher probability than with sterile males (probably an unrealistically strong female mate preference), we need to increase the number of sterile males 36% above that for the case of $b=1$.

Number of generations necessary to attain eradication

Both the number of sterile males released and the degree of sterile male resistance had an influence on the number of generations necessary to attain eradication. The larger the number of sterile males released, the more quickly eradication was attained. With larger a and b values, the number of generations until extinction was greater. But it is noteworthy that the effect of a was much larger than that of b (Tables 1 and 2).

DISCUSSION

Our model shows that SIRM can be used successfully for melon fly eradication, even though there is suggestive evidence for evolutionary change in mate preference in wild females. However, there are several cases of SIRM in which eradication was not attained despite the release of a very large number of sterile insects (e.g., RHODE et al., 1971; CIRIO and DE MURTAS, 1974). Our analysis of the model indicates that a is much more influential for SIRM than b . This conclusion suggests that failure in SIRM is mainly due to the reduction of competitive ability in sterile males rather than the evolution of mate preference in wild females.

The model also suggests that we should release as large a number of sterile males as possible from the start of an eradication program, in order to prevent the increase of selective females. Probably, the worst option is to start eradication program by releasing a small number of sterile males with a subsequent increase. The melon fly population may decrease from this treatment for the first few generations, but will soon recover as the proportion of selective females increases in the population. We need much larger releases of sterile males in order to eradicate populations in which indiscriminate females have been replaced by selective females.

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