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SIMPLE MATHEMATICAL MODELS TO DESCRIBE THE RATE OF MATING IN INSECT POPULATIONS[1]

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INTRODUCTION

As a starting point of sexual reproduction, mating constitutes one of the fundamental processes governing the growth and maintenance of insect populations. When or where their densities are extraordinarily low, the process will significantly affect their dynamics in an inversely density-dependent way.

Rather few studies, however, have so far been accumulated on such quantitative aspects of this process in either natural or theoretical populations, and this makes a contrast with the remarkable development recently attained in ethological or physiological studies on the mating systems of insects.

My purpose here is to derive simple mathematical models relating the rate of mating to a few basic parameters for general use in theoretical studies on the mating as a population process. These models will then be used to deduce some principles which seem to underlie the mating process in insect populations.

MODEL CONSTRUCTION

In modelling the process of reproduction in insect populations, FUJITA (1953) formulated the relation of mating rate of females (P) to adult density (N)as an exponential equation, $P=e^{-a/N}$, which shows a rise from the origin towards unity with a gradually decreasing rate. Later NISHIGAKI (1963) used an empirical equation, $P=K(1-e^{-a(N-b)})$, to describe the relation which he observed in an experimental population of been weevils. If $K=1$ and $b=0$ this equation becomes equivalent to the well-known NICHOLSON and BAILEY's (1935) model for insect parasitism, which was applied by PHILIP (1957) and SCOTT (1977) without any modification to the description of mating process. These models so far used are, however, too simple in structure to represent fundamental components of the process, so it will be needed to develop more appropriate models based on biologically valid assumptions.

The models here looked for are such that include parameters to represent basic components of the mating in insect populations, and yet that are mathematically as simple as possible. At first we assume that

(1) The habitat for the population is closed and has a finite size.

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(2) Individuals of either sex are distributed at random within the habitat and their number does not change during the period concerned.

(3) Searching by individual males for their mates (for simplicity we assume here that males search for females and not *vice versa*) is random and independent of each other, and its efficiency in terms of the area searched per unit time is constant for all the individuals.

Then, by assuming further that males can fertilize all the females they found during the period, we have the simplest model called "model 0" here. For the model to be biologically more meaningful, it will be necessary to include a restriction in the male's capacity on mating frequency. This may be done most simply by adding another assumption:

(4) During the period concerned each male makes a certain constant number of searches, in each of which he can mate only once even if more than one females are found.

The models satisfying the above four basic assumptions can further be classified into two types, "model 1" in which the female is assumed to have the ability of mating more than once, and "model 2" in which only the virgin female is subject to attack by the male. To summarize,

$$\begin{array}{l}\text{Male's capacity on}\\ \text{mating freqency}\end{array}\left\{\begin{array}{l}\text{unrestricted}\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\text{ model 0}\\[1em] \text{restricted}\left\{\begin{array}{l}\text{Female's capacity on}\\ \text{mating frequency}\end{array}\right.\left\{\begin{array}{l}\text{unrestricted}\cdots\cdots\text{ model 1}\\ \text{restricted (once)}\cdots\cdots\text{model 2}\end{array}\right.\end{array}\right.$$

These three models are formulated as follows.

Model 0:

Let the area of the habitat be S, the numbers of males and females be M and F respectively, and the area searched by each male during the period concerned be s_T. Then, the mating rate in females or the proportion of females mated at least once till the end of the period is given by

$$P=1-\left(1-\frac{s_T}{S}\right)^M=1-(1-a_T)^M \qquad (1)$$

where a_T is the proportion of area searched by each male and represents the efficiency of mate-searching. This equation is equivalent to STOY's (1932) formula for insect parasitism relating parasitism rate to parasite density. If the area of the habitat, S, and hence both M and F are very large, eq. (1) is approximated to

$$P=1-e^{-s_T m} \qquad (2)$$

where m is the density of males per unit area $(=M/S)$. This limiting form, which is referred to as "model 0′" hereafter, is equivalent to NICHOLSON and BAILEY's (1935) model for insect parasitism, and hence to the model used by PHILIP (1957) and SCOTT (1977).

Model 1:

In models 1 and 2, two parameters must be defined to describe mate-searching activity, i. e. the number of searches made by each male during the period, k, and the area covered by each of these successive searches, s, or its relative expression, $a=s/S$. Then, the probability for a male to catch a female at each search is $1-(1-a)^F$, and hence the probability for a female to mate at that search is $\{1-(1-a)^F\}/F$. Thus, the overall mating rate in females for model 1 is given by

$$P=1-[1-\frac{1}{F}\{1-(1-a)^F\}]^{kM} \tag{3}$$

The limiting form of (3) for $S\rightarrow\infty$ (model 1′) is

$$P=1-e^{-km(1-e^{-fs})/f} \tag{4}$$

where m and f are the densities of males and females per unit area respectively. Equation (4) is formally equivalent to ROYAMA's (1971) model for parasitism derived by the generalization of IVLEV's (1955) empirical formula.

Model 2:

It is assumed here that the females once mated disppear immediately from the sight of searching males. Then, the strict expression of the mating rate in females in this case will be

$$P=\frac{1}{F}\sum_{F_m=0}^{F}F_m p(F_m|kM) \tag{5}$$

where $p(F_m|kM)$ is the probability that exactly F_m females are mated till the end of the period, i. e., after kM searches were made by the males in total, which can be written as

$$p(F_m|kM)=p(F_m-1|kM-1)\{1-(1-a)^{F-F_m+1}\}+p(F_m|kM-1)(1-a)^{F-F_m}$$

Starting from calculation of $p(0|1)$ and $p(1|1)$, it is possible to calculate $p(F_m|kM)$ for any value of F_m and then P from eq. (5), but the calculation is very laborious unless both F and M are small. A much simpler alternative of eq. (5) can be obtained as follows. Let the number of virgin females at time t be F_t. Then, the expectation of the change of F_t (either 0 or -1) after the next search by a male is

$$\Delta F_t=-\{1-(1-a)^{F_t}\}\Delta t$$

where Δt is the interval between t and the time at the next search. As an approximation this may be replaced by a differential equation

$$dF_t=-\{1-(1-a)^{F_t}\}dt$$

which gives

$$kM=-\int_{F}^{F-F_m}\frac{dF_t}{1-(1-a)^{F_t}}$$

Solving this, we have

$$(1-a)^{kM}=\frac{(1-a)^{F_m}-(1-a)^F}{1-(1-a)^F}$$

Thus, the mating rate in females in question is

$$P=\frac{F_m}{F}=\frac{1}{F\ln(1-a)}\ln[(1-a)^{kM}\{1-(1-a)^F\}+(1-a)^F] \tag{6}$$

The goodness of approximation of eq. (6) to eq. (5) is generally satisfactory. For example, if $a=0.1$, $k=1$ and $F=M=2$, P from (5) is $(1\times 0.3249+2\times 0.0190)/2=0.1815$, while P from (6) is 0.1745, the difference being only 0.0130.

Since the discrepancy becomes much smaller for larger values of k, M and F, the alternative use of eq. (6) for eq. (5) will be justified, at least in most cases. The limiting form of eq. (6) for $S\rightarrow\infty$ (model 2′) is

$$P=-\frac{1}{fs}\ln\{e^{-ksm}(1-e^{-sf})+e^{-sf}\} \tag{7}$$

Since m and f are continuous variables here, this is no longer an approximate, but an exact relation. This limiting form is again equivalent to ROYAMA's (1971) model based on IVLEV's formula, but here to the model for predation.

SOME ANALYSES ON THE MODELS

Comparison of the Three Models

At first we make clear the relations of models 1 and 2 to model 0. Formally, model 0 is included in either of the other two models as its special case in which parameter k is increased to infinity under the condition that the total area searched by each male during the period (i. e. the area covered by k independent searches) is finite. This is proved as follows. If k is increased under the above condition, then $(1-a)^F\approx 1-aF$ because a becomes small here, so that eq. (3) for model 1 reduces to

$$P\approx 1-[1-\frac{1}{F}\{1-(1-aF)\}]^{kM}=1-(1-a)^{kM}$$

Thus, since the total area searched by each male, a_{T}, is equal to $1-(1-a)^k$, we have

$$P=1-(1-a_{\mathrm{T}})^M$$

which is equivalent to eq. (1) for model 0. Similarly, under the same condition, $\ln(1-a)\approx -a$ in eq. (6) for model 2, so that we have

$$\begin{aligned}P&\approx-\frac{1}{aF}\ln[(1-a)^{kM}\{1-(1-aF)\}+1-aF]\\&=\ln[1-aF\{1-(1-a)^{kM}\}]^{-1/aF}\\&\approx\ln\{e^{1-(1-a)^{kM}}\}=1-(1-a)^{kM}=1-(1-a_{\mathrm{T}})^M\end{aligned}$$

Although these models have apparently similar patterns in the mating rate (P)-to-population size (N) relation (Fig. 1), there are distinct differences in the properties between model 0 and models 1 and 2. Firstly, while the P-values in models 1 and 2 are affected by both male (M) and female (F) population sizes, the value in model 0 is determined only by the male population size (compare eq. (1) with eq. (3) or (6)). Thus, while in model 0 the number of females mated (FP) increases linearly if F is increased for fixed M, in model 1 or 2 there is an upper limit ($=kM$) for FP to which it approaches gradually—the relation comparable to "functional response curve" in the case of predation (Fig. 2). Secondly, P in model 0 invariably approaches 1 with increasing N, regardless of the sex ratio, but in model 1 or 2 this is not necessarily true, i. e., a certain proportion of females may remain unmated however

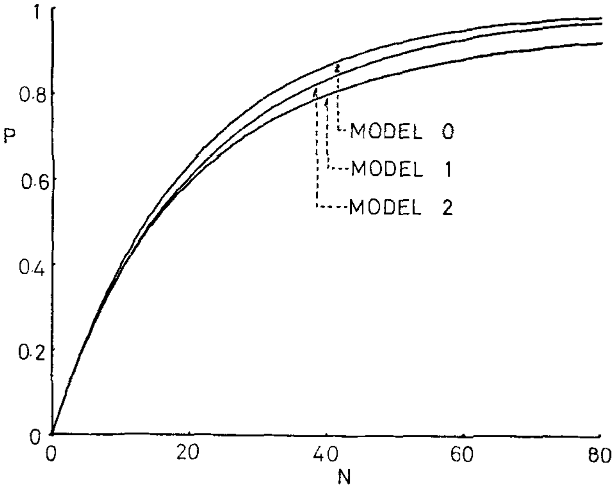

Fig. 1. Relation of mating rate of females (P) to population size ($N=F+M$). $F:M=1:1$, $a=0.025$, $k=4$ ($a_T=0.0963$).

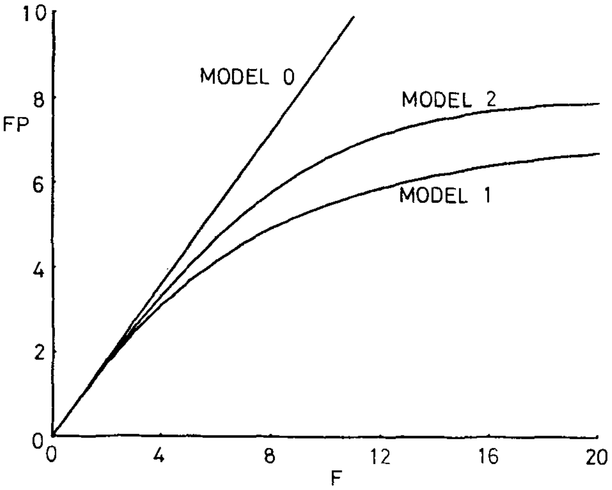

Fig. 2. Relation of number of mated females (FP) to number of females (F) when varying number of females are exposed to a single male. $a=0.25$, $k=8$ ($a_T=0.900$).

large N becomes. Namely, the P-values for infinite N for the three models are

Model 0 : $\lim_{N\to\infty} P=1$

Model 1 : $\lim_{N\to\infty} P=1-e^{-k(1-w)/w}$

Model 2 : $\lim_{N\to\infty} P=1 \qquad \text{for } k\geq w/(1-w)$

$= k(1-w)/w \qquad \text{for } k<w/(1-w)$

where w is the sex ratio ($=F/(F+M)$).

Thus the asymptote for P is always smaller than 1 in model 1, and is either equal to or smaller than 1 in model 2, the difference from 1 depending on the values of both w and k.

The above comparison shows that in contrast with model 1 or 2, model 0 has properties that are biologically inadequate. This, however, may not always negate its use, but there still seem to be a number of aspects in theoretical studies to which this symplest model can be usefully applied.

If model 1 and model 2 are compared with each other, the P-value for the same values of the parameters is always higher in the latter (see Fig. 1). This of course results from the increase in mate-searching efficiency in model 2 by concentrating the male's attack to virgin females. The difference, however, becomes slight as k, the male's capacity on mating frequency, becomes large, in which case both of the models converge to model 0 as proved earlier.

Effect of Population Size

The next problem is to examine how the fundamental factors in the mating process, which are represented by the parameters in these models, affect the overall mating rate in the population. Both model 1 and model 2 derived here have four parameters, M, F, a and k, but it is more convenient for the discussion that follows to replace the first two by N, total population size, and w, sex ratio. Then, eq. (3) and eq. (6) for model 1 and model 2 become respectively

$$P=1-[1-\frac{1}{wN}\{1-(1-a)^{wN}\}]^{k(1-w)N} \tag{3'}$$

and

$$P=\frac{1}{wN\ln(1-a)}\ln[(1-a)^{k(1-w)N}\{1-(1-a)^{wN}\}+(1-a)^{wN}] \tag{6'}$$

The effect of population size N on the mating rate P has already been shown in Fig. 1 for both of the models. Its notable characteristic is that at low levels of N where P is also low, N governs P nearly linearly or proportionally, but as N increases and P approaches to the respective asymptote ($1-e^{-k(1-w)/w}$ in model 1, or 1 or $k(1-w)/w$ in model 2), its action upon P becomes more and more ineffective.

Effect of Searching Efficiency

In the present models the efficiency of mate-searching is represented by parameter a, the relative area which a male can cover in a single search. The P—a relation (Fig. 3) is very similar in its form to the P—N relation discussed above. P rises from the origin with a gradually decreasing rate, the maximum (the value when $a=1$) being $1-\{1-1/(wN)\}^{k(1-w)N}$ in model 1 and either 1 or $k(1-w)/w$ in model 2. These maximum values also are nearly (model 1) or exactly (model 2) equal to the asymptotes for the P—N relation.

Effect of Male's Capacity on Mating Frequency

The relation of P to k, the number of searches a male can make during the period, is shown in Fig. 4. It is again similar to the P—N relation, and hence to the

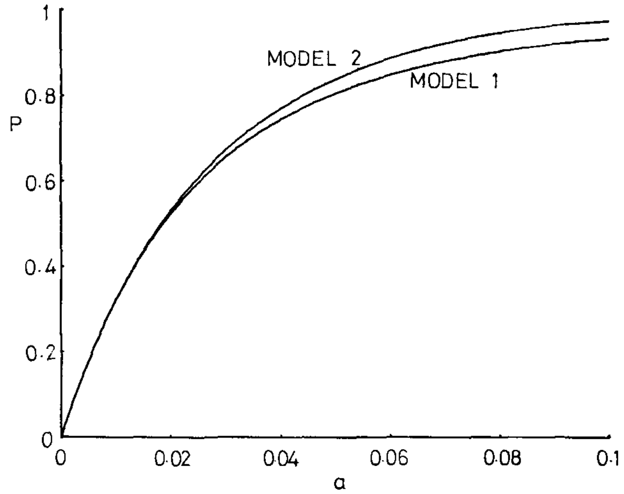

Fig. 3. Relation of mating rate of females (P) to male's searching efficiency (a). $F = M = 10$, $k = 4$.

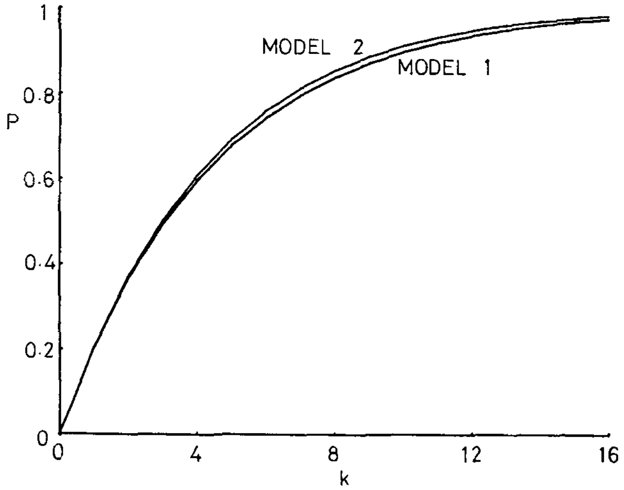

Fig. 4. Relation of mating rate of femeles (P) to male's capacity on mating frequency (k). $F = M = 10$, $a = 0.025$.

P—a relation, showing a curve rising towards the asymptote with a gradually decreasing rate. The only difference is found in the asymptote value which is always 1 here in both models.

Effect of Sex Ratio

The relation of P to sex ratio, w, shows a monotonously decreasing curve in either model (Fig. 5). Here, however, it is more significant ecologically to consider the proportion of mated females to the whole population, wP, rather than P, because it represents the population's reproductivity more directly. Unlike the P—w relation,

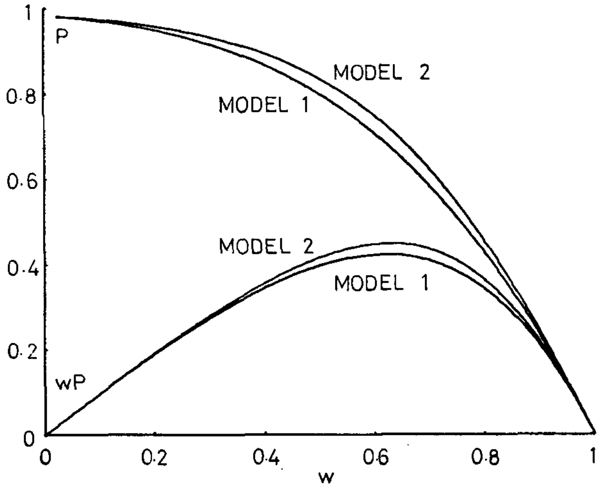

Fig. 5. Relations of mating rate of females (P) and proportion of mated females in the total population (wP) to sex ratio ($w=F/(F+M)$). $N=F+M=40$, $a=0.025$, $k=4$.

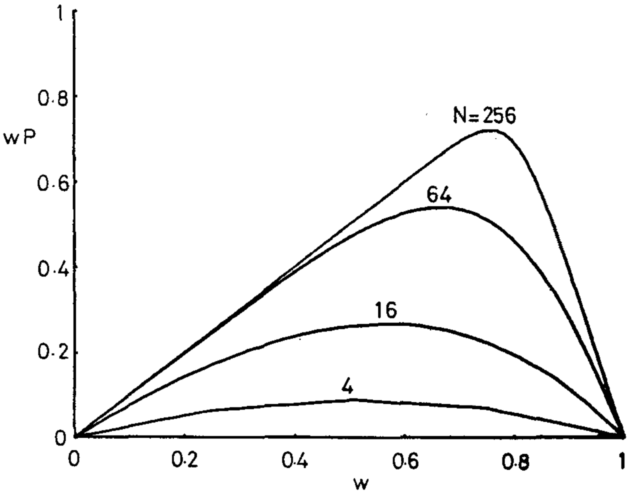

Fig. 6. Relations of proportion of mated females in the total population (wP) to sex ratio (w) for different population sizes (N) (model 2). $a=0.025$, $k=4$.

the wP—w relation gives a mountain-shaped curve, indicating the existence of an optimum sex ratio for population reproduction (Figs. 5 and 6). In Fig. 6 it is also important to note that this optimum ratio changes with a change in population size, N, from near $1/(k+1)$ for very large N (in model 2) to about 0.5 for very small N. This means that in very sparse populations their reproduction will become most efficient when both sexes exist in even proportions, regardless of the values of other parameters.

DISCUSSION

The above examination seems to have shown us two basic principles concerning the mating process in insect populations. One is that the relations of the female's mating rate, P, to the three parameters, N, a and k are essentially similar in their patterns, or in other words, population size N governs P as critically as do the parameters a and k representing the mate-searching activity for each individual. Thus, the necessary value of either a or k to attain a given, fixed level of P changes nearly in an inverse ratio to the change of N, meaning, for example, that a or k must be increased twice in order to compensate the reduction of P due to population decrease to half the original size (Fig. 7). The other principle is that the efficiency of increasing N on the increase of P, as well as the efficiency of increasing a or k, falls acceleratively as P rises to high levels. Thus, while the two-fold increase of either N, a or k results in nearly the same-fold rise of P when P is at a low level (say, less than 0.1), it gives rise to only a slight increase in P, by several percent at best, if P has already attained a high level of 0.9 or so (see Fig. 1).

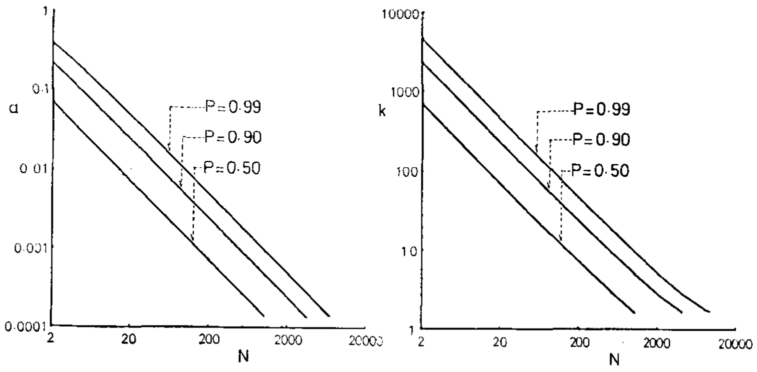

Fig. 7. Necessary value of a(left; $k=10$) or k (right; $a=0.001$) to attain a fixed level of P, in relation to population size (N) (model 2).

It is a well-known fact that populations of many insects are subjected to severe density fluctuations from generation to generation (e.g. VARLEY *et al.*, 1973). In connection with the above principles, this suggests how serious and severe a problem it may actually be for many insect populations to secure consistently high levels of mating rate and avoid extinction over a vast number of generations. Owing to the inversely density-dependent nature of the process, an extreme reduction of P, even for a short period, might lead the population to crash and so cannot be allowed for its persistence.

We have ample evidence to recognize how complicated and elaborate devices insects have evolved to raise the efficiency of mating (e.g. ENGELMAN, 1970). Many insect species have developed surprisingly sensitive means of between-sexes communication using sight, sound, pheromones *etc.*, which may assure a high efficiency for mate-searching corresponding to the parameter a (or more exactly s in $a=s/S$) in the present models. Spatial convergence in the distributions of both sexes in the period for mating may also be interpreted as an effective device to improve the searching efficiency a, here by decreasing S, the whole area for searching. Efficient behavioural processes for copulation, in which only a little time and energy are consumed, may be significant for raising the overall mating rate by increasing the male's capacity on mating frequency or k in these models. Also, the habits such as concentration of adult emergence to a short period of a season or restriction of mating activity to a narrow time range of a day, which are common in insects, may be regarded as those to raise the mating efficiency by increasing the effective value of population size N. In view of Fig. 6, it seems possible to explain, at least partly, the fact that populations of most insects have sex ratio near 1:1, too, in connection with the optimization of reproductive efficiency, since the optimum ratio will practically be 1 : 1 when N is so small that the population is exposed to the danger of extinction. It is, however, likely that there are some specific modes of life which are often accompanied with the population instability so severe that any such devices might be still insufficient to secure consistently high mating rates. In species with such modes of life the only possible way to avoid extinction will be to acquire the habit of asexual reproduction in some part, at least, of their life cycles, though it necessarily sacrifices the genetical merit of sexual reproduction to a lesser or greater extent. Various types of parthenogenesis observed among insects, particularly among aphids and parasitic wasps, may be interpreted as such degeneration to secure population persistence.

All these facts indicate that for populations of many insects consistent attainment of high mating rates has actually been a serious difficulty which could have been overcome only with great efforts in various aspects of their behaviour, supporting the predictions deduced from the simple models here presented. This may confirm the significance of making further theoretical studies in various quantitative aspects of the mating process, including the effects of population distribution, migration, survival, intra- and interspecies interaction, *etc.*, based on these models. Such studies will help understanding of the mating strategies in insects in relation to their population dynamics.

SUMMARY

Simple models are constructed to describe the rate of mating in insect populations. The models are based on the assumption of random mate-searching in a closed habitat, including four parameters, i.e., population size, sex ratio, searching efficiency and male's capacity on mating frequency. The modes of effects of these parameters on the rate of mating are analyzed and some principles deduced are discussed in relation

to the mating process in natural populations.

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REFERENCES

ENGELMAN, F. (1970) *The physiology of insect reproduction.* Pergamon Press.

FUJITA, H. (1953) Factors affecting the type of population density effect upon average rate of oviposition. *Res. Popul. Ecol.* 2: 1-7. (In Japanese with English summary.)

IVLEV, V. S. (1955) *Experimental ecology of the feeding of fishes.* (English translation by D. SCOTT, 1961) Yale Univ. Press, New York.

NICHOLSON, A. J. and V. A. BAILEY (1935) The balance of animal populations. Part 1. *Proc. Zool. Soc. London,* 1935: 551-598.

NISHIGAKI, J. (1963) The effect of low population density on the mating chance and the fecundity of the azuki been weevil, *Callosobruchus chinensis* L. *Jap. J. Ecol.* 13: 178-184. (In Japanese with English summary.)

PHILIP, J. R. (1957) Sociality and sparse populations. *Ecology* 38: 107-111.

ROYAMA, T. (1971) A comparative study of models for predation and parasitism. *Res. Popul. Ecol.* Suppl. 1: 1-91.

SCOTT, J. A. (1977) Competitive exclusion due to mate searching behaviour, male-female emergence lags and fluctuation in number of progeny in model invertebrate populations. *J. Anim. Ecol.* 46: 909-924.

STOY, R. H. (1932) Appendix to G. SALT's paper (Superparasitism by *Collyria calcitrator* GRAV.). *Bull. Ent. Res.* 23: 215-216.

VARLEY, G. C., G. R. GRADWELL and M. P. HASSEL (1973) *Insect population ecology: an analytical approach.* Blackwell Scientific Publications.

昆虫個体群における交尾率を記述するための単純な数理モデル

久野英二

均質な閉鎖空間における昆虫個体群の交尾率を記述する数理モデルを作製した。モデルはランダムな異性探索行動の仮定に立脚しており，個体群サイズ，性比，異性発見効率，交尾頻度に関する雄の能力，という4つのパラメータを含む。これらの各パラメータの交尾率に対する影響のしかたを解析し，そこで導いたいくつかの原則を自然個体群における交尾過程との関連において論じた。