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A MARKOV CHAIN MODEL FOR THE MATING BEHAVIOR IN FLIES

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Shiojenn Tseng and Jyh-Ping Hsu (1989) A Markov chain model for the Mating behavior in flies. *Bull. Inst. Zool., Academia Sinica* **28**(3): 183-189. The mating behavior in flies for a closed as well as an open environment are modeled stochastically through a Markov chain representation. The stochastic approach provides not only the mean or macroscopic information about the phenomenon under consideration but also an estimation of its fluctuating characteristic. The applicability of the present stochastic model is justified by analyzing the available experimental data.

Key words: Flies, Markov chain, Mating behavior.

Recently, and increasing interest in modeling the mating behavior in flies has been observed (Eckstrand and Seiger, 1975; Taylor, 1975; Kence and Bryant, 1978; Dowse *et al.*, 1984; Dowse *et al.*, 1986; Hsu and Tseng, 1988). Most of the mating behaviors, however, are described in a deterministic manner (see, Taylor, 1975; Dowse *et al.*, 1986; Hsu and Tseng, 1988). That is, the behavior of a dynamic system is represented by its mean or macroscopic characteristic. Thus, given the initial condition of the system, its status at an arbitrary point on the time scale is uniquely determined. In contrast to a deterministic model, a dynamic system is portrayed through probabilistic statements in a stochastic model. The solution to such a model yields probability distributions describing the variations of the random variables representing the system. In general, the mean or the first moment of the probability distribution of the random variable of a stochastic model reduces to the result predicted by the corresponding deterministic model. Therefore the former is capable of providing more detailed informations about a dynamic system than the latter. In other words, a stochastic model is a generalization of the corresponding deterministic model.

Unlike a lifeless entity, each individual

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fly possesses its characteristic. A deterministic representation is unable to reflect this fact since flies are viewed as identical entities having the mean characteristic of the population of the system. On the other hand, the probabilistic approach in a stochastic representation provides a possibility of portraying the random nature inherent in the phenomenon. Furthermore, it is well known that the mean and the variance of a random variable is on the same order of magnitude. Therefore if the number of flies in a dynamic system is not large enough, the mean of the random variable representing the number of flies is not sufficient in describing its behavior. The random nature of the phenomenon is especially significant in this case. In the present study, we extend our previous deterministic analysis (Hsu and Tseng, 1988) to the corresponding stochastic counterpart, in the form of a Markov chain (Bharucha-Reid, 1960). An attempt is made such that the degree of the fluctuation in the number of mated fly pairs can be estimated.

MARKOV CHAIN REPRESENTATION

The transition stage mating mechanism proposed by Hsu and Tseng (1988) is adopted to describe the mating behavior in flies. According to this mechanism, a male fly and a female fly, when encountered, need to pass through a transition stage before they become a mated pair. Symbolically, we have

$$M+F \longrightarrow MF^* \longrightarrow MF \qquad (1)$$

where M, F, MF^*, and MF denote, respectively, male flies, female flies, fly pairs in the transition stage, and mated fly pairs. It is defined that flies in states 1, 2, and 3, represent male flies, fly pairs in the transition stage, and mated fly pairs respectively. The number of males, pairs in the transition stage, and mated pairs, are denoted by n_1, n_2, and n_3, respectively. The number of females, n_F, can be evaluated by the following expression:

$$\begin{aligned} n_F &= F_0-(M_0-n_1) \\ &= F_0-M_0+n_1 \end{aligned} \qquad (2)$$

where M_0 and F_0 are the males and females initially present in the system. respectively. Define $p_{ij}(m, m+1)$ as the probability that a fly in state i at time $m\Delta t$ will be in state j at time $(m+1)\Delta t$ where Δt is a unit time interval. The evolution of the mating phenomenon is thus described by the following transition probability matrix $P(m, m+1)$:

$$P(m, m+1) = \begin{matrix} & 1 & 2 & 3 \\ 1 & p_{11}(m, m+1) & p_{12}(m, m+1) & p_{13}(m, m+1) \\ 2 & p_{21}(m, m+1) & p_{22}(m, m+1) & p_{23}(m, m+1) \\ 3 & p_{31}(m, m+1) & p_{32}(m, m+1) & p_{33}(m, m+1) \end{matrix} \qquad (3)$$

The rate of formation of the fly pairs in the transition stage is assumed to be proportional to the product of the number of males and the number of females; and the rate of formation of the number of mated pairs is proportional to the number of fly pairs in the transition stage (Hsu and Tseng, 1988). These assumptions lead to the following transition probability matrix:

$$P(m, m+1) = \begin{matrix} & 1 & 2 & 3 \\ 1 & 1-k_1 n_F(m)\Delta t & k_1 n_F(m)\Delta t & 0 \\ 2 & 0 & 1-k_2\Delta t & k_2\Delta t \\ 3 & 0 & 0 & 1 \end{matrix} \qquad (4)$$

where k_1 and k_2 are constant. Clearly, if there are $n_i(m)$ flies in state i at time $m\Delta t$, these flies will be in one of the states j at time $(m+1)\Delta t$ with probability $p_{ij}(m, m+1)$, $i, j=1, 2, 3$. That is, $n_i(m+1)$ is multinomially distributed among the states 1, 2, and 3. Consequently, the conditional mean and the variance of n_j at $(m+1)\Delta t$, given the value of n_i at time $m\Delta t$, $i, j=1, 2, 3$, are respectively (Rohatgi, 1976),

$$E[n_j(m+1)\,|\,n_i(m),\ i=1, 2, 3] = \sum_{i=1}^{3} n_i(m)\, p_{ij}(m, m+1), \quad j=1, 2, 3. \tag{5}$$

and

$$\mathrm{Var}[n_j(m+1)\,|\,n_i(m),\ i=1, 2, 3] = \sum_{i=1}^{2} n_i(m)\, p_{ij}(m, m+1)[1-p_{ij}(m, m+1)], \quad j=1, 1, 2, 3. \tag{6}$$

DATA ANALYSIS

The applicability of the present stochastic model is examined through analyzing the available experimental results. For illustration, the data reported by Dowse *et al.* (1986) are adopted. The mating experiment was conducted with one strain of female and one strain of male *Drosophila* flies. Their experimental data along with the values predicted by the present stochastic model are presented in Figs. 1 through 3. Also shown in these figures is an approximate 95% confidence interval, calculated by $E[.]\pm 1.96\mathrm{Var}[.]^{1/2}$. The estimation of the values of the adjustable parameters k_1 and k_2 are based on equation (5). The least sum of error squares criterion is adopted.

DISCUSSION

Note that the time scale in a Markov chain model is discrete. If the mating behavior under consideration is expressed in a deterministic manner, we have

$$n_1(m+1)=n_1(m)-k_1\, n_1(m)\, n_F(m)\Delta t \tag{7}$$

$$n_2(m+1)=n_2(m)+k_1\, n_1(m)\, n_F(m)\Delta t - k_2\, n_2(m)\Delta t \tag{8}$$

$$n_3(m+1)=n_3(m)+k_2\, n_2(m)\Delta t \tag{9}$$

where $n_F=F_0-M_0+n_1$. In the limit as $\Delta t\to 0$ equations (7) through (9) reduce to the following differential equations:

$$\frac{dn_1}{dt}=-k_1n_1n_F \tag{10}$$

$$\frac{dn_2}{dt}=k_1n_1n_F-k_2n_2 \tag{11}$$

$$\frac{dn_3}{dt}=k_2n_2 \tag{12}$$

Thus the deterministic counterpart of the present stochastic model is equivalent to that proposed by Hsu and Tseng (1988). This is also justified by the variation of the mean of the number of mated pairs illustrated in Figs. 1 through 3. The present stochastic model is capable of providing more detailed information about the dynamic system. For instance, the variation of the number of flies, which is necessary in constructing the confidence bands shown in Figs. 1 through 3. It should be pointed out that n_F is a random variable, and therefore, its value at an arbitrary time $m\Delta t$ can not be determined except at $m=0$. Hence in evaluating the values of the elements in the transition probability matrix defined by equation (4), n_F is replaced by its mean or expected value $E[n_F]$. This procedure has the effect of reducing the magnitude of the variances of the number of flies. The confidence interval shown in Figs. 1 through 3 should thus be viewed as a lower bound, i.e., the actual bands can be much wider than those presented.

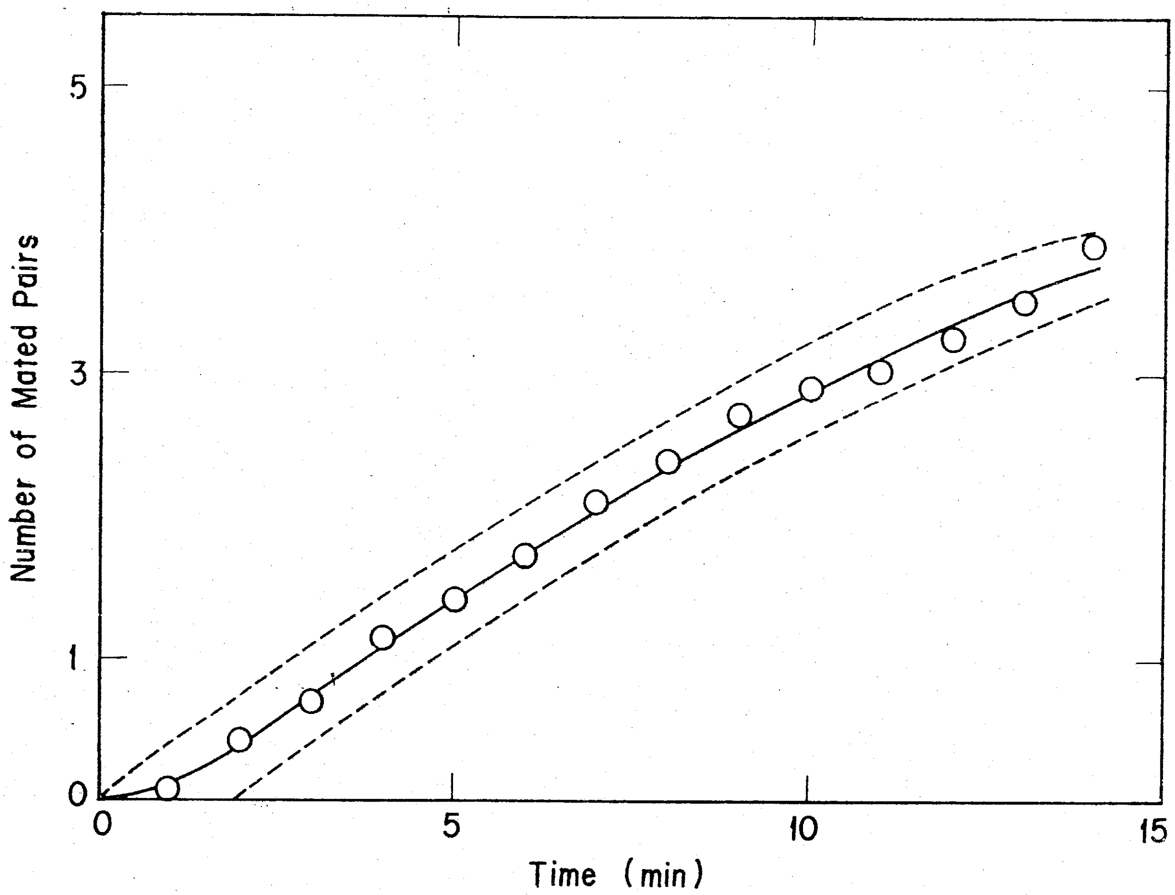

Fig. 1. Experimental data of mating of *D. simulans* with $M_0=8$ and $F_0=16$ (Dowse *et al.*, 1986) along with the predicted results by the present model, $k_1=3.688\times10^{-3}$/min, $k_2=6.6237\times10^{-1}$/min. ——: mean number of mated pairs; - - -: approximated 95% confidence interval.

The present stochastic model can be generalized without much difficuly if the mating of flies occurs in an open environment. Let us consider the case if flies are allowed to enter or leave a specified volume in space. Suppose that the rate of fly leaving this volume is proportional to its number in the volume. Then the transition probability matrix takes the following form:

$$P(m, m+1)=\begin{array}{c} \\ 1\\2\\3\\4\end{array}\begin{array}{c}\begin{array}{cccc}1 & 2 & 3 & 4\end{array}\\ \begin{bmatrix} 1-[k_1 n_F(m)+k_3]\Delta t & k_1 n_F(m)\Delta t & 0 & k_3\Delta t \\ 0 & 1-[k_2+k_4]\Delta t & k_2\Delta t & k_4\Delta t \\ 0 & 0 & 1-k_5\Delta t & k_5\Delta t \\ 0 & 0 & 0 & 1 \end{bmatrix}\end{array} \quad (13)$$

where k_3, k_4, and k_5 are constant. A fly or fly pair in state 4 denotes it leaves the volume. Let $N_i(m)$ be the rate of flies in state i entering the volume at time $m\Delta t$. The conditional mean and the variance of n_j at $(m+1)\Delta t$, given the values of n_i and N_i at time $m\Delta t$, $i, j=1, 2, 3$, are, respectively,

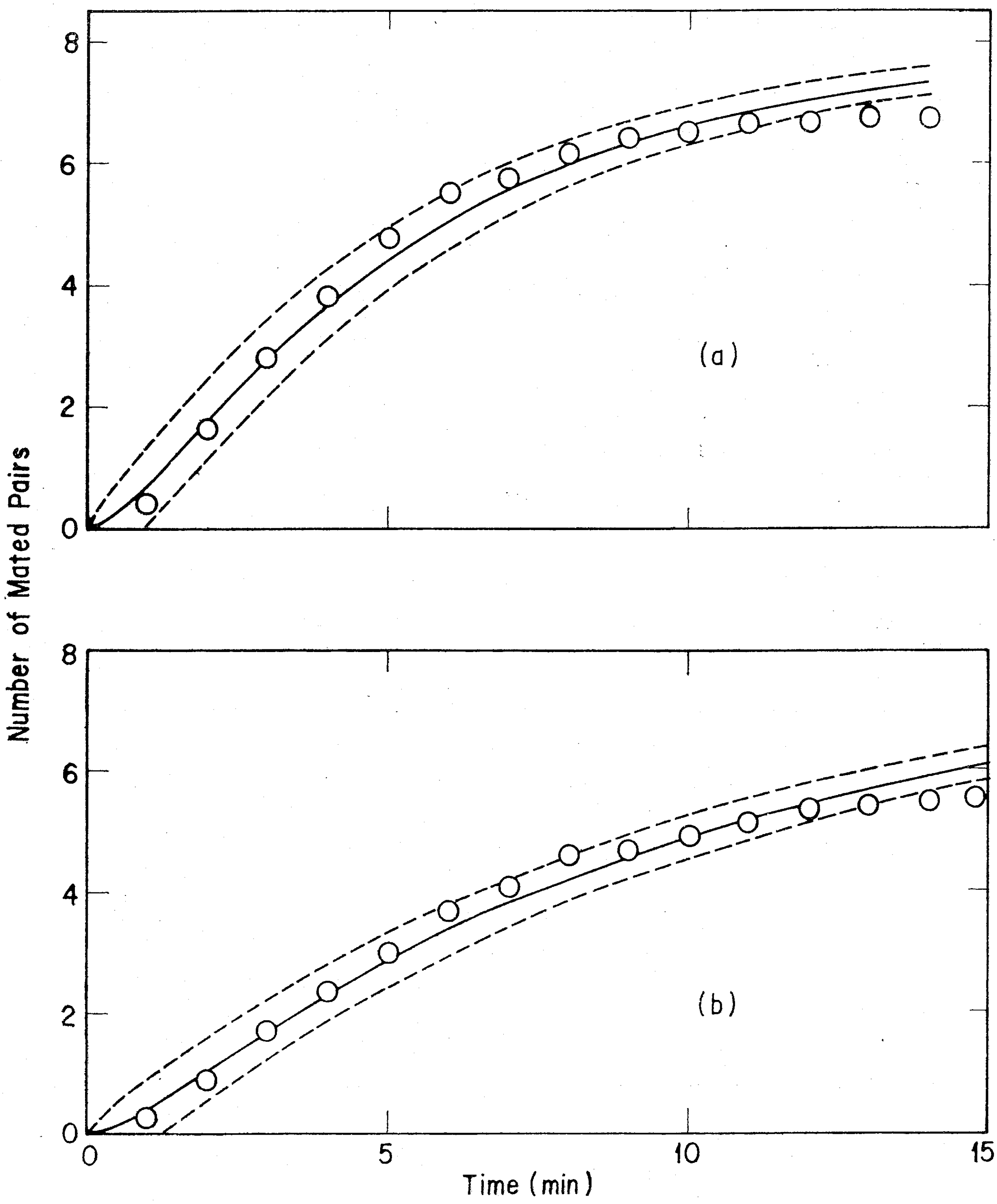

Fig. 2. Experimental data of mating of wild-type *D. melanogaster* (a) $M_0=8$, $F_0=32$; (b) $M_0=32$, $F_0=8$ (Dowse *et al.*, 1986) along with the predicted results by the present model: $k_1=5.2429\times10^{-2}$/min, $k_2=1.8793\times10^{-1}$/min in case (a); $k_1=5.8271\times10^{-2}$/min, $k_2=1.0095\times10^{-1}$/min in case (b). ——: mean number of mated pairs; - - -: approximated 95% confidence interval.

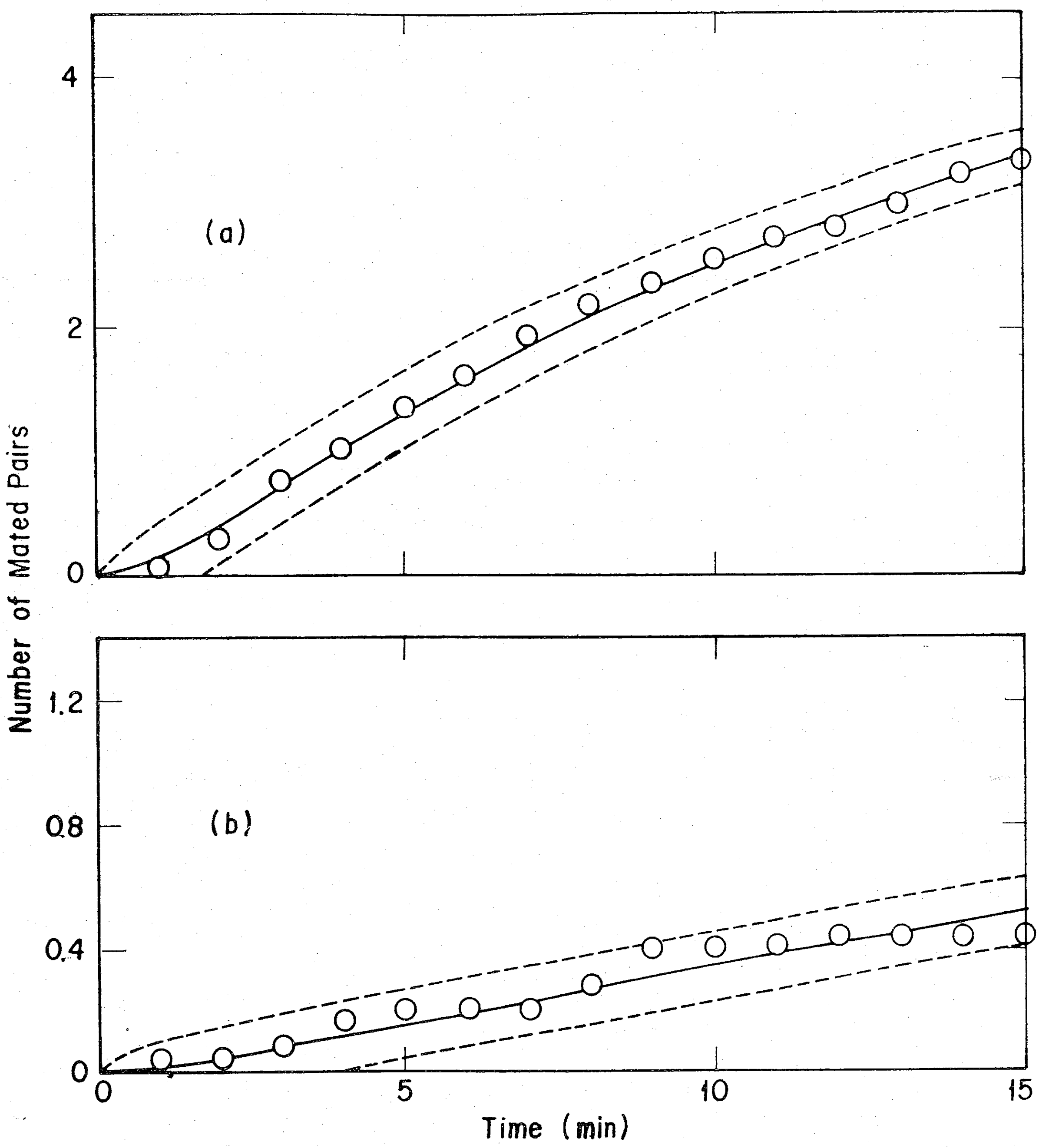

Fig. 3. (a) and (b) show the experimental data of mating of *D. simulans* and *D. melanogaster vg* males when $M_0=F_0=8$ (Dowse *et al.*, 1986) along with the predicted results by the present model: $k_1=6.4407\times10^{-3}$/min, $k_2=8.6517\times10^{-1}$/min in case (a); $k_1=6.2025\times10^{-4}$/min, $k_2=9.5079\times10^{-1}$/min in case (b). ——: mean number of mated pairs; - - -: approximated 95% confidence interval.

$$E[n_j(m+1)\,|\,n_i(m),\ N_i(m),\ i=1,\ 2,\ 3] = \sum_{i=1}^{3} n_i(m)\,p_{ij}(m,\ m+1)+N_j(m), \quad j=1,\ 2,\ 3. \tag{14}$$

and

$$\mathrm{Var}[n_j(m+1)\,|\,n_i(m),\ N_i(m),\ i=1,\ 2,\ 3] = \sum_{i=1}^{3} n_i(m)\,p_{ij}(m,\ m+1)[1-p_{ij}(m,\ m+1)], \quad j=1,\ 2,\ 3. \tag{15}$$

where $N_i(m)$, $i=1,2,3$, is assumed to be deterministic. If $N_i(m)$ is also randomly distributed with $n_i(m)$ and $N_i(m)$ uncorrelated, $i,j=1,2,3$, equations (14) and (15) should be modified as

$$E[n_j(m+1)\,|\,n_i(m),\ N_i(m),\ i=1,\ 2,\ 3] = \sum_{i=1}^{3} n_i(m)\,p_{ij}(m,\ m+1)+E[N_j(m)], \quad j=1,\ 2,\ 3. \tag{16}$$

and

$$\mathrm{Var}[n_j(m+1)\,|\,n_i(m),\ N_i(m),\ i=1,\ 2,\ 3] = \sum_{i=1}^{3} n_i(m)\,p_{ij}(m,\ m+1)[1-p_{ij}(m,\ m+1)]+\mathrm{Var}[N_j(m)] \quad j=1,\ 2,\ 3. \tag{17}$$

where $E[N_i(m)]$ and $\mathrm{Var}[N_i(m)]$ denote, respectively, the mean of $N_i(m)$ and the variance of $N_i(m)$.

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以馬哥夫鏈模型描述果蠅之交配行爲

曹琇瑱　　徐治平

本文以馬哥夫鏈模型描述果蠅在封閉系統以及開放系統中之動態交配情形。所提出之隨機模式除了能够描述系統內之平均交配對數隨時間之變化關係外亦能估計相對之不準度。文獻中之實驗數據分析結果顯示，所推導之模式適用於描述所考慮之現象。