

MATHEMATICAL OBSERVATIONS ON THE RELATION BETWEEN ECLOSION PERIODS AND THE COPULATION RATE OF CICADAS

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ABSTRACT. In many species of cicadas the peak of eclosion of males precedes that of females. In this paper, we construct a stochastic model and consider whether this sexual difference of eclosion periods works against mating or not. We also discuss the relation between the peak period of copulations and the development of population number by using this model.

1. Introduction. In many species of cicadas the peak of eclosion of males precedes that of females by about a week (e.g., [6], [9]). Though no concrete reason for this difference has been found, it is often said that it takes times to grow eggs in the females' abdomens, which causes the shift of the eclosion period. In this paper, we examine the relation between the sexual difference in eclosion period and the copulation rate of cicadas by constructing a mathematical model and running a simulation. We point out that it is difficult to find the relation by field observations. Moreover, we discuss the period when copulations are most frequent by using the mathematical model.

In the process of evolution of the eclosion schedules of insects, the male (female) schedule is determined by male (female) success, respectively, and there may exist sexual confliction between them. That is, the eclosion schedules that we can now observe are regarded as the results of the evolution procedure (stable state) with environmental influences (noises) such as fluctuation of temperature, etc. It is important to find whether the eclosion schedule observed is detrimental to the copulation rate based on fitness (performance function).

Throughout this paper we assume that female cicadas mate at most once and male cicadas can mate plural times, which is usually believed on the basis of observations (for periodical cicadas, see [1], [11]). In a previous paper [10], under this condition, the number of mating times of male cicadas was discussed by constructing a mathematical model. In this paper, we show that this sexual difference in mating behavior may emphasize the sexual shift of the eclosion period. We remark that the copulation rate of female cicadas is proportionate to the total copulation times of the population.

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Researchers have observed that in many species of butterflies eclosion of males precedes that of females ([2], [3], [4], [7]). We note that there is a large difference in mating behavior between cicadas and butterflies. For example, male butterflies often fly to females actively to mate, while male cicadas sing a calling song to attract females and females fly to the most appealing singing male to mate. However, it is not clear that this ecological difference between cicadas and butterflies works on the eclosion systems.

Fagerström and Wiklund [2] analyzed the sexual difference of the eclosion period of butterflies from the viewpoint of it being a mating strategy. Odendaal, Iwasa and Ehrlich [7] also treated the mating systems in butterflies and they showed that female availability might work on mating systems.

Iwasa and Haccou [3] constructed a mathematical model of the eclosion schedule of butterflies. They consider the expectation of logarithm of the number of matings done by a male with *p.d.f.*(probability density function) of an eclosion schedule pattern, and using Lagrange's method of indeterminate coefficients, they found the *p.d.f.* of the eclosion schedule describing the ESS (evolutionary stable strategy) (see also [4]). In this procedure, random variables are not demonstrated very clearly.

In this paper we first define random variables describing eclosion schedules, life times after eclosions and mating times in each day. We suppose that the eclosion schedules and life times after eclosions obey the normal distribution and mating times in a day with Poisson distribution, respectively. In other words, we consider realized values of the random variables to be representing each cicada individual and in analyzing the system. Then we express the copulation rate by the random variables and run a computer simulation. We found a relation between the copulation rate of female cicadas and the sexual difference of the eclosion period. This kind of approach was also used in our previous studies ([8], [10]).

In § 2 we prepare mathematical tools and in § 3 we construct the mathematical model based on the theoretical background prepared in § 2. In § 4 we show simulation results, and we discuss the results in § 5. According to the observations by Williams and Simon [11] and Mohri [6], we can assume that the sex ratio is 1 : 1. However, we also treat the case that the ratio is not equal to 1 : 1.

2. Mathematical preparation and probability distribution of mating times. On some probability space (Ω, \mathcal{F}, P) , we consider a Poisson process $\{J_t\}_{t \geq 0}$ with parameter $\lambda(> 0)$ and a normal distributed random variable $Y \sim N(m, \sigma^2)$ which is independent of $\{J_t\}_{t \geq 0}$, where $m, \sigma(> 0)$ are constants. Then we put $E(J_{Y \vee 0}) = \mu$, $Y \vee 0 \equiv \max(Y, 0)$. Now we have the following proposition.

Proposition 1. *We have*

$$\mu = \lambda m \cdot \Phi\left(\frac{m}{\sigma}\right) + \frac{\lambda \sigma}{\sqrt{2\pi}} e^{-\frac{m^2}{2\sigma^2}},$$

where $\Phi(x)$ is the distribution function of standard normal distribution $N(0, 1)$.

Proof. For $k > 0$, we have

$$\begin{aligned} P(J_{Y \vee 0} = k) &= P(J_Y = k, Y > 0) \\ &= \int_0^\infty P(J_t = k) \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \int_0^\infty \frac{(\lambda t)^k}{k!} e^{-\lambda t} \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(t-m)^2}{2\sigma^2}} dt \end{aligned}$$

and using the monotone convergence theorem, we have

$$\begin{aligned} \mu = E(J_{Y \vee 0}) &= \sum_{k=0}^\infty k P(J_{Y \vee 0} = k) \\ &= \int_0^\infty k \sum_{k=1}^\infty \frac{(\lambda t)^k}{k!} e^{-\lambda t} \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \int_0^\infty \sum_{k=1}^\infty \frac{(\lambda t)^{k-1}}{(k-1)!} \cdot \lambda t \cdot e^{-\lambda t} \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \int_0^\infty \lambda t \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \lambda \cdot \frac{1}{\sqrt{2\pi\sigma}} \int_0^\infty t e^{-\frac{(t-m)^2}{2\sigma^2}} dt. \end{aligned}$$

Setting

$$I =: \frac{1}{\sqrt{2\pi\sigma}} \int_0^\infty t e^{-\frac{(t-m)^2}{2\sigma^2}} dt,$$

we have

$$\begin{aligned} I &= \frac{1}{\sqrt{2\pi\sigma}} \int_0^\infty (t-m) e^{-\frac{(t-m)^2}{2\sigma^2}} dt + \frac{m}{\sqrt{2\pi\sigma}} \int_0^\infty e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \frac{1}{\sqrt{2\pi\sigma}} [-\sigma^2 e^{-\frac{(t-m)^2}{2\sigma^2}}]_0^\infty + \frac{m}{\sqrt{2\pi\sigma}} \int_0^\infty e^{-\frac{(t-m)^2}{2\sigma^2}} dt \\ &= \frac{\sigma}{\sqrt{2\pi}} e^{-\frac{m^2}{2\sigma^2}} + \frac{m}{\sqrt{2\pi\sigma}} \int_{-m}^\infty e^{-\frac{u^2}{2\sigma^2}} du \\ &= \frac{\sigma}{\sqrt{2\pi}} e^{-\frac{m^2}{2\sigma^2}} + m \cdot \Phi\left(\frac{m}{\sigma}\right). \end{aligned}$$

Therefore we consequently have

$$\mu = \lambda m \cdot \Phi\left(\frac{m}{\sigma}\right) + \frac{\lambda\sigma}{\sqrt{2\pi}} e^{-\frac{m^2}{2\sigma^2}}.$$

□

Example. When $\mu = 1$, $m = 21$ and $\sigma = 8$, we have $\Phi\left(\frac{m}{\sigma}\right) \simeq 0.9957$, which yields $\lambda \simeq 0.0415$.

Remark 1. For sufficiently large m , we have $\mu \simeq \lambda m$.

Remark 2. Suppose that J_1, J_2, \dots, J_n is a sequence of *i.i.d.* (independently identical distributed) random variables on (Ω, \mathcal{F}, P) and J_1 obeys Poisson distribution with parameter λ (we abbreviate it to $J_1 \sim \mathcal{P}(\lambda)$) for some constant $\lambda(> 0)$. Then it is well known that $\sum_{k=1}^n J_k \sim \mathcal{P}(n\lambda)$. On the other hand, the number of mating times of a male cicada in a day can be consider obeying Poisson distribution with parameter λ for some constant $\lambda(> 0)$ (see [10]). We also note that for *Drosophila sp.*, the number of mating times is known to obey Poisson distribution ([5]). Thus, if we assume that matings of male cicadas in a population are independent, mating times of the population in a day obeys Poisson distribution $\mathcal{P}(n\lambda)$ when the number of living mature males is equal to n .

3. Construction of the mathematical model. Let the population size of male and female cicadas in a season be n_m and n_f respectively and set

$$\mathbf{X}'_m := \{X'_{m,1}, X'_{m,2}, \dots, X'_{m,n_m}\}, \quad \mathbf{X}'_f := \{X'_{f,1}, X'_{f,2}, \dots, X'_{f,n_f}\},$$

where $X'_{m,1}, X'_{m,2}, \dots, X'_{m,n_m}$ is a sequence of *i.i.d.* random variables with $X'_{m,1} \sim N(\mu_m, \sigma_m^2)$ and $X'_{f,1}, X'_{f,2}, \dots, X'_{f,n_f}$ is a sequence of *i.i.d.* random variables with $X'_{f,1} \sim N(\mu_f, \sigma_f^2)$. We assume that \mathbf{X}'_m and \mathbf{X}'_f are independent. Here, μ_m, μ_f, σ_m and σ_f are positive constants.

If we put

$$X_{m,k} := \text{round}(\max(X'_{m,k}, 0)), \quad X_{f,k} := \text{round}(\max(X'_{f,k}, 0)), \quad k = 1, 2, \dots,$$

we can recognize that

$$\mathbf{X}_m = \{X_{m,1}, X_{m,2}, \dots, X_{m,n_m}\}, \quad \mathbf{X}_f = \{X_{f,1}, X_{f,2}, \dots, X_{f,n_f}\}$$

are the lists of eclosion dates of male and female cicadas respectively. Here $\text{round}(x)$ describes the nearest integer of x .

Next, we put

$$\mathbf{Y}'_m := \{Y'_{m,1}, Y'_{m,2}, \dots, Y'_{m,n_m}\}, \quad \mathbf{Y}'_f := \{Y'_{f,1}, Y'_{f,2}, \dots, Y'_{f,n_f}\}.$$

Here, $Y'_{m,1}, Y'_{m,2}, \dots, Y'_{m,n_m}$ is a sequence of *i.i.d.* random variables with $Y'_{m,1} \sim N(\mu'_m, s_m^2)$ and $Y'_{f,1}, Y'_{f,2}, \dots, Y'_{f,n_f}$ is a sequence of *i.i.d.* random variables with $Y'_{f,1} \sim N(\mu'_f, s_f^2)$. We assume that \mathbf{Y}'_m and \mathbf{Y}'_f are independent and we also assume that $\mathbf{X}' = \{\mathbf{X}'_m, \mathbf{X}'_f\}$ and $\mathbf{Y}' = \{\mathbf{Y}'_m, \mathbf{Y}'_f\}$ are independent. Here, μ'_m, μ'_f, s_m and s_f are positive constants.

If we put

$$Y_{m,k} := \text{round}(\max(Y'_{m,k}, 0)), \quad Y_{f,k} := \text{round}(\max(Y'_{f,k}, 0)), \quad k = 1, 2, \dots,$$

we can recognize that

$$\mathbf{Y}_m = \{Y_{m,1}, Y_{m,2}, \dots, Y_{m,n_m}\}, \quad \mathbf{Y}_f = \{Y_{f,1}, Y_{f,2}, \dots, Y_{f,n_f}\}$$

are lists of life times after eclosions of male and female cicadas respectively.

Let $\Lambda_m := \{1, 2, \dots, n_m\}$, $\Lambda_f := \{1, 2, \dots, n_f\}$ be the indexes of male and female cicadas of the population eclose in the season respectively.

It is known that cicadas do not mate in a few days after eclosion. It is usually said that it is because it costs a few days to harden their timbals and sexual organs ([11]). According to this fact, we suppose that the male (female) cicadas needs τ_m (τ_f) days to mature after eclosion, where τ_m, τ_f are positive integers. That is, the cicadas do not mate up to $\tau_m - 1$ ($\tau_f - 1$) days after eclosion. Then

$$\mathcal{E}_m(t) := \{k \in \Lambda_m : X_{m,k} = t\}, \quad \mathcal{E}_f(t) := \{k \in \Lambda_f : X_{f,k} = t\}, \quad t = 1, 2, \dots$$

describe the set of indexes of male and female cicadas eclose in the day t respectively. Furthermore,

$$\begin{aligned} N_m(t) &:= \{k \in \Lambda_m : X_{m,k} \leq t - \tau_m, X_{m,k} + Y_{m,k} \geq t\}, \quad t = \tau_m, \tau_m + 1, \dots, \\ N_f(t) &:= \{k \in \Lambda_f : X_{f,k} \leq t - \tau_f, X_{f,k} + Y_{f,k} \geq t\}, \quad t = \tau_f, \tau_f + 1, \dots \end{aligned}$$

describe the set of indexes of mature male and female cicadas living in the day t respectively and

$$\tilde{V}_f(t) := \{k \in \Lambda_f : X_{f,k} + \tau_f = t, X_{f,k} + Y_{f,k} \geq t\}, \quad t = 1, 2, \dots$$

is the set of female cicadas matures in the very day t .

Suppose that the number of mating times of a male cicada up to s days after mature is J_s and $\{J_s\}_{s \geq 0}$ is a Poisson process with parameter λ . If Y is the life time after mature, we have $Y \stackrel{d}{=} \text{round}(\max(Y_{m,1} - \tau_m, 0))$ and the number of mating times of this cicada is given by J_Y , where $\stackrel{d}{=}$ means equality in distribution. Therefore, the expectation of mating times μ of a male cicada is given by $\mu = E(J_Y)$. If $n_m = n_f$, we can assume $\mu = 1$ (see [10]) and Proposition 1 implies

$$\lambda \simeq \left\{ (\mu'_m - \tau_m) \cdot \Phi\left(\frac{\mu'_m - \tau_m}{s_m}\right) + \frac{s_m}{\sqrt{2\pi}} e^{-\frac{(\mu'_m - \tau_m)^2}{2s_m^2}} \right\}^{-1}.$$

Now let \tilde{M}_n be a random variable obeying Poisson distribution $\mathcal{P}(\lambda n)$ which is independent of $\{\mathbf{X}_m, \mathbf{X}_f, \mathbf{Y}_m, \mathbf{Y}_f\}$ and set $m(t) := \min(\tilde{M}_{\#N_m(t)}, \#N_f(t))$, where $\#A$ describes the number of elements of a set A . Then by Remark 2, $m(t)$ is the number of mating times of the population in the day t . In our model, mating times in each day depends on the population size of mature cicadas living in the day.

Remark 3. As we see in Remark 2, we have

$$P(\tilde{M}_{\#N_m(t)} = k | \#N_m(t) = n) = \frac{(\lambda n)^k}{k!} e^{-\lambda n}, \quad k = 0, 1, 2, \dots, \quad n = 1, 2, \dots$$

Remembering the mating of female cicadas is at most once, we define the set $V(t)$ of mature virgin female cicadas living in the day t and the set $M(t)$ of female mating in the day t by

$$\begin{cases} V(1) = V(2) = \dots = V(\tau_f) = \emptyset, \\ M(1) = M(2) = \dots = M(\tau_f) = \emptyset, \\ V(t) = \{V(t-1) \cap (M(t-1))^c \cap N_f(t)\} \cup \tilde{V}_f(t), \quad t = \tau_f + 1, \tau_f + 2, \dots \\ M(t) = \text{the subset of size } m(t) \text{ randomly chosen from } V(t) \\ \quad \text{with equal probability.} \end{cases}$$

As stated above, the total number of mating times of the population in the day t is $m(t) = \#M(t)$; the number of mature virgin females living in the day t is $v(t) := \#V(t)$; the number of female mate during the occurrence period $t = 1, 2, \dots, T$ (which is equal to all mating times of the population in the period of emergence) is given by $\sum_{t=1}^T m(t)$ and the copulation rate of female cicadas is given by $r := \sum_{t=1}^T m(t)/n_f$.

4. Numerical computations. In this section, we give numerical computations made with Mathematica (Wolfram Research, Inc.) using parameters on eclosion based on observations by Mohri [6]. Throughout this section, we suppose $T = 80$.

4.1. The sexual difference of eclosion period and the copulation rate r of cicadas. In this subsection, we study the change of the copulation rate $r = r(t_d)$ of female cicadas in $t_d := E(X'_{m,1}) - E(X'_{f,1}) = \mu_m - \mu_f$. For each case, graph represents the mean value of 50 times calculations for each t_d .

(a) Here we set $n_m = n_f = 10000$ (the sex ratio is 1 : 1), $\mu_m = 20$ and $\sigma_m = \sigma_f = 5$ in common (Figures 1-5).

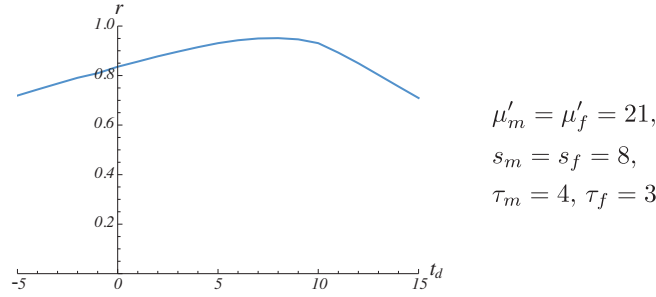


FIGURE 1. In the standard settings of (a).

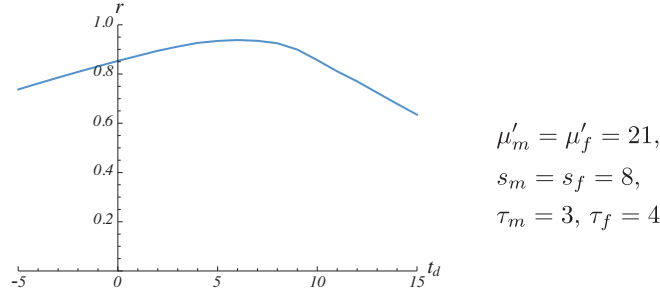


FIGURE 2. (a) In the case $\tau_m < \tau_f$.

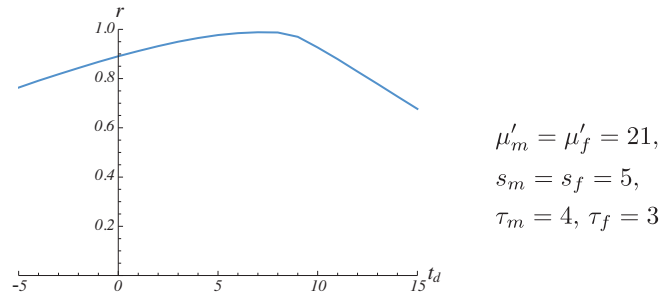
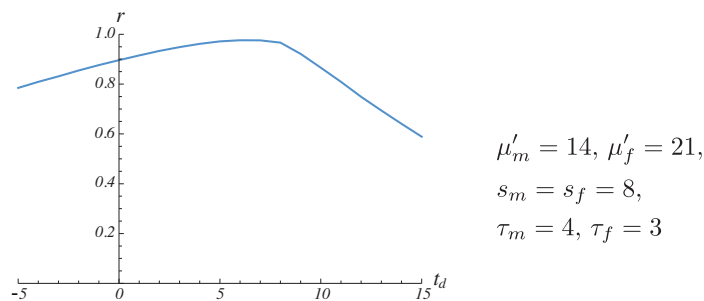
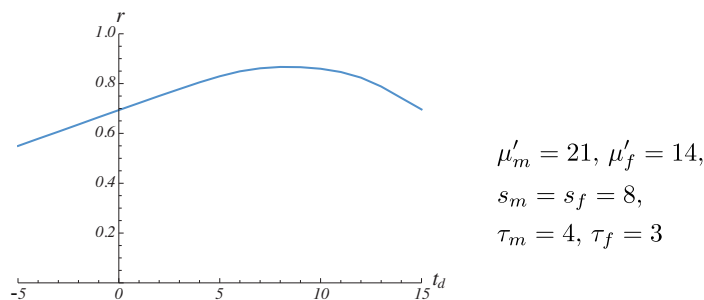
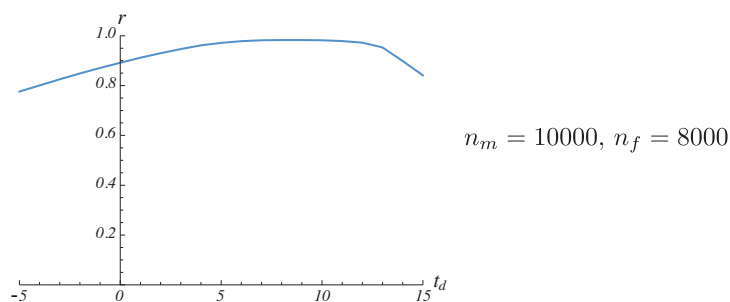
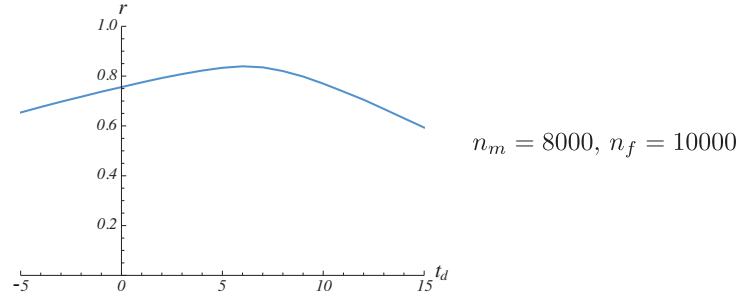


FIGURE 3. (a) In the case that s_m and s_f are smaller.

FIGURE 4. (a) In the case $\mu'_m < \mu'_f$ (males are short-lived).FIGURE 5. (a) In the case $\mu'_m > \mu'_f$ (females are short-lived).

(b) Here, we treat the cases that the sex ratio is not equal to one ($n_m \neq n_f$) and $\mu_m = 20$, $\mu'_m = \mu'_f = 21$, $\sigma_m = \sigma_f = 5$, $s_m = s_f = 8$, $\tau_m = 4$ and $\tau_f = 3$ (Figures 6-7).

FIGURE 6. (b) In the case $n_m > n_f$.

FIGURE 7. (b) In the case $n_m < n_f$.

4.2. The increase and decrease of total mating times in the occurrence period. In this subsection we study the development of the total number of mating times in the population and that of the number of living mature cicadas at t_d^* (t_d which maximizes the copulation rate r of female cicadas in §4.1). We remark that as is stated in §5.1 again, t_d^* is nearly coincident with the difference of average emergence timing in field observations. That is to say, the computations in this subsection can be regarded as the simulations of the mating behavior in the field.

In each figure (Figure 8-14), the left graphs represent the population size of living mature males (blue line), females (red dashed line) and the right graph shows the change of mating times in the population.

(a) Here we set $n_m = n_f = 100000$ (the sex ratio is 1 : 1), $\mu_m = 20$ and $\sigma_m = \sigma_f = 5$ in common (Figures 8-12).

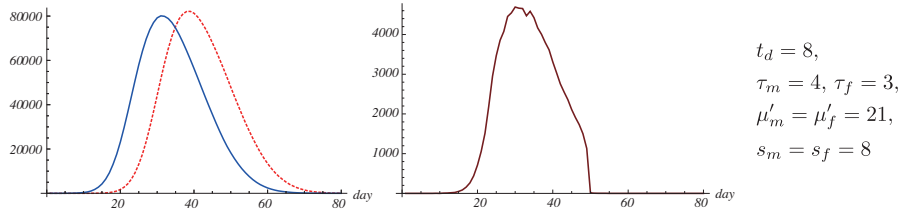
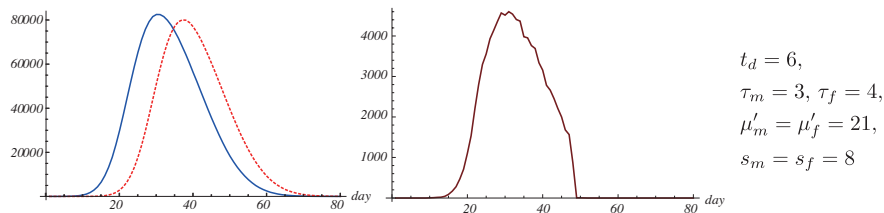
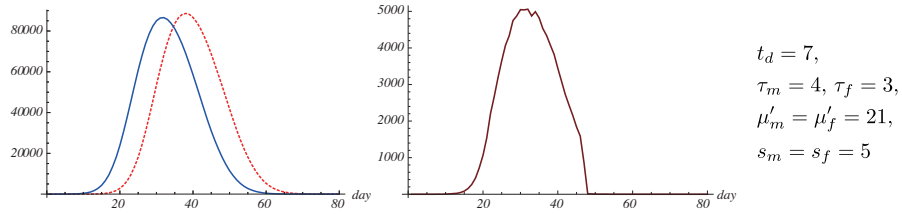
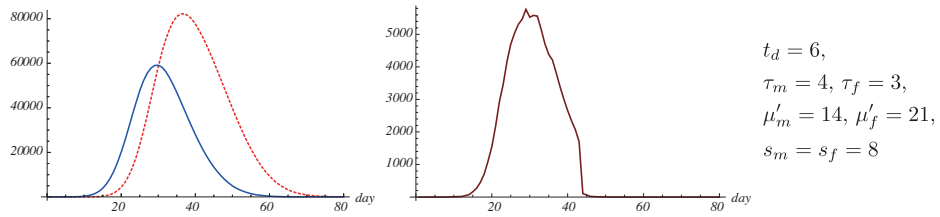
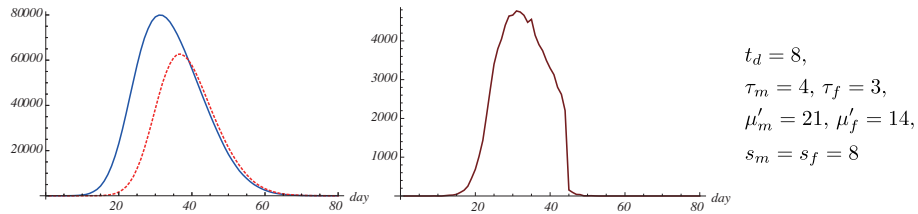
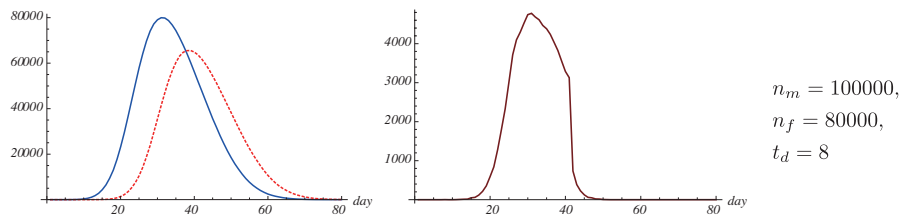


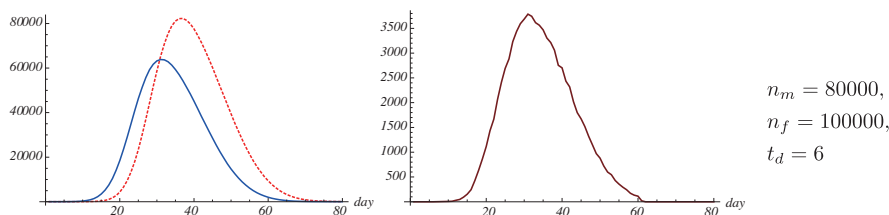
FIGURE 8. (a) In the standard settings of (a).

FIGURE 9. (a) In the case $\tau_m < \tau_f$.

FIGURE 10. (a) In the case that s_m and s_f are smaller.FIGURE 11. (a) In the case $\mu'_m < \mu'_f$ (males are short-lived).FIGURE 12. (a) In the case $\mu'_m > \mu'_f$ (females are short-lived).

(b) Here, we treat the cases that the sex ratio is not equal to one ($n_m \neq n_f$) and $\mu_m = 20, \mu'_m = \mu'_f = 21, \sigma_m = \sigma_f = 5, s_m = s_f = 8, \tau_m = 4$ and $\tau_f = 3$ (Figures 13-14).

FIGURE 13. (b) In the case $n_m > n_f$.

FIGURE 14. (b) In the case $n_m < n_f$.

5. Discussion.

5.1. The sexual difference t_d of eclosion period and the copulation rate.

We first point out that t_d^* ($= t_d$ which maximizes r) found in §4.1 is nearly coincident with the observed difference of average emergence timing between male and female (see [6], [9]).

We also find in §4.1 that the copulation rate $r = r(t_d)$ of female cicadas attains the maximum value at positive t_d and the change of r is not symmetrical in t_d (i.e., $r(t_d) \neq r(-t_d)$) under any values of parameters of eclosion dates, life times after eclosions or days necessary for maturity (Figures 1-5). In our mathematical model, we find that the sexual difference of mating behavior is the only cause of this asymmetry. That is, under the assumption that female cicadas mate at most once and male cicadas can mate plural times, the delay in eclosion by females is advantageous for the copulation rate. Though this result does not mean that the copulation rate is the only reason for the existence of the sexual drift of eclosion, it does show that the delay of eclosion of females promotes an increased copulation rate or the total copulation times of the population.

As is stated in Introduction, there is a large difference in mating behavior between cicadas and butterflies. Furthermore it is known that in many species of butterfly females can mate plural times and it is empirically observed that the eclosion of males also precedes that of females. Therefore, it is suggested that these differences of mating behavior do not play essential roles in the shift of eclosion period and the copulation rate of females may not be the only reason for the delay of eclosion of females (see [2]).

According to Williams and Simon [11] and Mohri [6], though there may be temporary biases, we can suppose that the sex ratio $r_s := n_m/n_f$ is equal to one. Setting $r_s = 0.8$ or 1.25 , we find that the phenomenon is essentially the same as in the case of $r_s = 1$. However, when $r_s = 1.25$, the variational range of the copulation rate r of females in t_d is smaller than that in the case of $r_s = 1$ (Figures 6-7).

5.2. The increase and decrease of total mating times in the occurrence period.

The numerical computations given in §4.2 show that the peak date of the change of mating times in the population coincides with that of the population size of living mature male cicadas when t_d attains the maximal value of copulation rate r of female cicadas, regardless of the parameters of eclosion dates, living dates and life times after eclosion and days necessary for maturity (Figures 8-14). This fact essentially does not change even when the sex ratio r_s is not equal to one (Figures 13-14). It appears that mating times depend strongly on the number of mature males, because the mating time of each female is at most once.

5.3. Future problem. Characteristics of organism have established through evolution, where a new rare mutant increases its frequency in a population comprising the resident type and we should focus on a success of the mutant type in the resident population. If the resident can suppress invasions of any mutant types, it is regarded as an ESS. From this viewpoint, we can study whether the states obtained in §4.1 are the ESSs or not using our mathematical model and computations. This simulation is very interesting and important but we will leave it for a future work.

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