Persistence of Population
with Age-dependent Sex Reversal

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3   t

a a' $v(a,t)$ $w(a',t)$

a a' $c(a,a',t)$

$v_e(a,t)$ $w_e(a',t)$

(1)   (2)

δ_v, δ_w

$M(a)(= 0 \text{ for } a < a_c; m \text{ for } a_c \leq a)$ $M(a) = 0$

$M(a) > 0$

a_c

$\delta_v + \delta_w$ D S

S

λ β

(6-8)

a_c

$X(t)$

$V(t)$ $W(t)$ $C(t)$

(6 -8)   4   (21-24) $X(t)$

(22) $v(a_c,t)$ (6-8)

(25)

(27-29)

δ_v δ_w

2

1

(40-42)

Fig. 3(a) (δ_v, δ_w)

Fig. 3(a)

(40-42)

(17)
(21-24)

(51)

(51) a_c

a_c

m a_c $\delta_w < (1 - \beta)\lambda$

Fig. 7(a)

a_c

$\delta_w > (1 - \beta)\lambda$

Fig. 7(b)

a_c

a_c

a_c
a_c

$m \to \infty$

2

m a_c a_c

Fig. 8 a_c m

m

Fig. 9

$d_w < (1-\beta)\lambda$

Fig. 10(a) $d_w > (1-\beta)\lambda$

Fig. 10(b)

r a_c $\delta_w < (1-\beta)\lambda$

Fig. 11(a)

$d_w > (1-\beta)\lambda$

Fig. 11(b)

(V^*, X^*, W^*, C^*) a_c

$\delta_w < (1-\beta)\lambda$

Fig. 12

Fig. 12(b)

$d_w > (1-\beta)\lambda$

Fig. 13

Fig. 13(b)

1 Assumptions and Modelling

1.1 Dynamics of age distribution

We denote the age distribution function of male age a and that of female age a' at time t by $v(a,t)$ and $w(a,t)$ respectively. In addition, $c(a,a',t)$ gives the density of reproductive couple which consists of male with age a and female with age a' at time t.

We assume that the changes of $v(a,t)$ and $w(a,t)$ are occurred by the natural death and the sex reversal *from male to female*. On the other hand, the change of $c(a,a',t)$ is due to the separating and the coupling. The former occurs by the death of male or female of couple, or by the alive separation of them.

Now, we define the constant separating rate D and the density-dependent coupling rate S for reproductive couple. We assume that the coupling rate S depends on the densities v_e and w_e of single male and female, defined by

$$v_e(a,t) \quad = \quad v(a,t) - \int_0^\infty c(a,a',t)da' \qquad (1)$$

$$w_e(a',t) \quad = \quad w(a',t) - \int_0^\infty c(a,a',t)da. \qquad (2)$$

The integral of right side of (1) means the density of coupled male of age a at time t, and that of (2) does the density of coupled female of age a' at time t.

With these assumptions, our modelling for the changes of $v(a,t)$, $w(a,t)$ and $c(a,a',t)$ in sufficiently small period h are given by

$$v(a+h,t+h) - v(a,t)$$
$$= -\delta_v h \cdot v(a,t) - M(a)h \cdot v(a,t) + o(h^2) \qquad (3)$$

$$w(a'+h,t+h) - w(a',t)$$
$$= -\delta_w h \cdot w(a',t) + M(a')h \cdot v(a',t) + o(h^2) \qquad (4)$$

$$c(a+h,a'+h,t+h) - c(a,a',t)$$
$$= -(\delta_v h + \delta_w h) \cdot c(a,a',w) - Dh \cdot c(a,a',w)$$
$$+ S(a,a';v_e,w_e)h + o(h^2), \qquad (5)$$

where δ_v and δ_w are the constant natural death rates for male and female respectively, and $M(a)$ the *age-dependent* sex reversal rate from male to female at age a.

From (3), (4), and (5), we can derive the following partial differential equations to give the dynamics of age distributions $v(a,t)$, $w(a,t)$ and $c(a,a',t)$, as shown in Appendix A:

$$\frac{\partial v(a,t)}{\partial t} + \frac{\partial v(a,t)}{\partial a} \quad = \quad -\delta_v v(a,t) - M(a)v(a,t) \qquad (6)$$

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$$\frac{\partial w(a',t)}{\partial t} + \frac{\partial w(a',t)}{\partial a'} = -\delta_w w(a',t) + M(a')v(a',t) \quad (7)$$

$$\frac{\partial c(a,a',t)}{\partial t} + \frac{\partial c(a,a',t)}{\partial a} + \frac{\partial c(a,a',t)}{\partial a'}$$

$$= -(\delta_v + \delta_w)c(a,a',t) - Dc(a,a',t) + S(a,a';v_e,w_e) \quad (8)$$

We assume that the initial age distributions for $v(a,t)$ and $w(a',t)$ are not everywhere zero, denoted by $v(a,0) = v_0(a), w(a',0) = w_0(a')$, whereas that for $c(a,a',t)$ is everywhere zero, $c(a,a',0) = 0$ ($0 \le a < \infty; 0 \le a' < \infty$).

Since we assume that the reproduction is possible only by couples, the recruitment as the boundary conditions are given by

$$v(0,t) = \beta\lambda C(t) \quad (9)$$

$$w(0,t) = (1-\beta)\lambda C(t), \quad (10)$$

where $C(t)$ is the total number of couples at time t, defined by

$$C(t) \equiv \int_0^\infty \int_0^\infty c(a,a',t)dada', \quad (11)$$

and λ is the birth rate per couple, β the male ratio at birth. Hence, $\beta\lambda$ and $(1-\beta)\lambda$ indicate the number of male newborns per couple, and that of female. We assume that both λ and β are constant independently of time and parent's age. Besides, we assume that the newborn with age 0 cannot be coupled, so that

$$c(a,0,t) = c(0,a',t) = 0. \quad (12)$$

Additional boundary conditions can be new given by

$$v(\infty,t) = 0 \quad (13)$$
$$w(\infty,t) = 0 \quad (14)$$
$$c(\infty,a',t) = 0 \quad (15)$$
$$c(a,\infty,t) = 0, \quad (16)$$

since any individual cannot live forever.

1.2 Sex reversal rate

In this paper, we assume the following age-dependent sex reversal rate $M(a)$:

$$M(a) = \begin{cases} 0 & (0 \le a < a_c) \\ m & (a_c \le a < \infty). \end{cases} \quad (17)$$

After the critical age a_c, the sex reversal from male to female occurs at randam with a constant rate, m. If $a_c \to 0$, the sex reversal occurs at any age. On the other hand, if $a_c \to \infty$, it is the case without sex reversal at any age.

1.3 Coupling rate

In this paper, we assume that $S(a, a'; v_e, w_e) = r \cdot v_e w_e$, where r is a positive constant. This is the assumption of mass action between female and male to couple, that is, the coupling is assumed to occur under the complete mixing of females and males to give the random occurrence of coupling.

1.4 Dynamics of population size

From the age distribution functions, $v(a, t)$, $w(a, t)$ and $c(a, a', t)$, we can define the population size of male, $V(t)$, and that of female, $W(t)$:

$$V(t) \equiv \int_0^\infty v(a, t) da \tag{18}$$

$$W(t) \equiv \int_0^\infty w(a', t) da'. \tag{19}$$

Besides, for mathematical convenience, we define here the subpopulation size of male younger than age a_c:

$$X(t) \equiv \int_0^{a_c} v(a, t) da. \tag{20}$$

Integrating (6), (7) and (8), we can derive the following dynamical system of ordinary differential equations that govern the temporal variations of population sizes defined by (11), (18), (19) and (20) (see Appendix B):

$$\frac{dV(t)}{dt} = -\delta_v V(t) + \beta \lambda C(t) - m\{V(t) - X(t)\} \tag{21}$$

$$\frac{dX(t)}{dt} = \beta \lambda C(t) - \delta_v X(t) - v(a_c, t) \tag{22}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + (1 - \beta)\lambda C(t) + m\{V(t) - X(t)\} \tag{23}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{24}$$

As for $v(a_c, t)$ appeared in (22), we can derive the following result with the method of characteristic curve for (6) (Appendix C):

$$v(a_c, t) = \begin{cases} \beta \lambda C(t - a_c) e^{-\delta_v a_c} & (t > a_c) \\ v_0(a_c - t) e^{-\delta_v t} & (t \le a_c). \end{cases} \tag{25}$$

We assume that the initial population sizes $V(0)$, $X(0)$ and $W(0)$ are positive:

$$V(0) = \int_0^\infty v_0(a) da > 0$$

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$$X(0) = \int_0^{a_c} v_0(a)da > 0$$

$$W(0) = \int_0^{\infty} w_0(a)da > 0.$$

On the other hand, since $c(a, a', 0) = 0$,

$$C(0) = \int_0^{\infty} \int_0^{\infty} c(a, a', 0)dada' = 0.$$

1.5 The condition for the population size

In our modelling, both population size of male and female are to be larger than that of couple:

$$\begin{cases} C^* < V^* \\ C^* < W^*. \end{cases} \tag{26}$$

2 Analysis

As the first step of our mathematical study, we separately consider three cases in terms of the value of the critical age a_c: 0, ∞, and finite positive.

2.1 $a_c \to \infty$

2.1.1 Dynamics of population sizes

Since this is the case when the sex reversal does not occur, the dynamics of population sizes can be written as the following three dimensional dynamical system derived from (21), (23) and (24):

$$\frac{dV(t)}{dt} = -\delta_v V(t) + \beta\lambda C(t) \tag{27}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + (1-\beta)\lambda C(t) \tag{28}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{29}$$

2.1.2 Extinction state at three-dimensional differential equations

The extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ is always locally stable. This can be easily shown by the eigenvalue analysis for it. Indeed, the characteristic equation about the extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_v)(\alpha + \delta_w)(\alpha + \delta_v + \delta_w + D) = 0, \tag{30}$$

where α is eigenvalue. Hence, $\alpha = -\delta_v$, δ_w and $-(\delta_v + \delta_w + D)$, that is, all are negative real.

2.1.3 Non-trivial equilibrium state

From (27), (28) and (29), we can see that at most one non-trivial equilibrium state exists:

$$(V^*, W^*, C^*) = \left(\frac{\beta\lambda}{\delta_v}C^*, \frac{(1-\beta)\lambda}{\delta_w}C^*, \frac{\delta_v\delta_w(\delta_v + \delta_w + D)}{r(\beta\lambda - \delta_v)\{(1-\beta)\lambda - \delta_w\}} \right) \quad (31)$$

From the condition (26) and the positiveness for (31), we can get the following condition for the existence of non-trivial equilibrium state (31):

$$\begin{cases} \beta\lambda & > \delta_v \\ (1-\beta)\lambda & > \delta_w. \end{cases} \quad (32)$$

This means that the non-trivial positive equilibrium state (31) exists if and only if the sex-specified birth rate of each sex is larger than the natural death rate.

2.1.4 Asymptotic sex ratio

If $\delta_v = \delta_w = \delta$, we can get the following from (27) and (28):

$$\frac{d}{dt}\{(1-\beta)V(t) - \beta W(t)\} = -\delta\{(1-\beta)V(t) - \beta W(t)\}. \quad (33)$$

Therefore, we can get immediately the following:

$$(1-\beta)V(t) - \beta W(t) = \{(1-\beta)V(0) - \beta W(0)\}e^{-\delta t}. \quad (34)$$

This means that, as $t \to \infty$, the sex ratio asymptotically converges to that at birth:

$$\frac{V(t)}{W(t)} \to \frac{\beta}{1-\beta} \quad (t \to \infty). \quad (35)$$

2.1.5 Asymptotic dynamics

From the above result about the asymptotic behavior of sex ratio, let us consider the following two dimensional dynamical system for $\delta_v = \delta_w = \delta$ instead of three dimensional one described by (27), (28) and (29) for $t \gg 1$:

$$\frac{dW(t)}{dt} = -\delta W(t) + (1-\beta)\lambda C(t) \quad (36)$$

$$\frac{dC(t)}{dt} = -(2\delta + D)C(t) + r\left\{ \frac{\beta}{1-\beta}W(t) - C(t) \right\}\{W(t) - C(t)\}. \quad (37)$$

This system corresponds to that given by (28) and (29) with $V(t) \equiv \beta W(t)/(1-\beta)$ and $\delta_v = \delta_w = \delta$. Asymptotic behavior of the system given by (36) and (37)

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asymptotically coincides with that of (C, W) of the system given by (27), (28) and (29).

In our analysis for the case when $a_c \to \infty$, in order to consider the asymptotic behavior as $t \to \infty$, we now focus the two dimensional system given by (36) and (37) when $\delta_v = \delta_w = \delta$.

Equilibrium state for the asymptotic two-dimensional system The extinction state $(C^*, W^*) = (0, 0)$ is always locally stable. This can be easily shown as described in the section 2.1.2. As for the non-trivial equilibrium state, from (36) and (37), we can see that at most one exists:

$$(C^*, W^*) = \left(\frac{\delta^2 (2\delta + D)}{(\delta - \beta\lambda)\{\delta - (1 - \beta)\lambda\}}, \frac{\delta(2\delta + D)(1 - \beta)\lambda}{(\delta - \beta\lambda)\{\delta - (1 - \beta)\lambda\}} \right). \qquad (38)$$

From the condition (26) and the positiveness for (38), we can get the condition for the existence of non-trivial equilibrium state (38), substituting $\delta_v = \delta_w = \delta$ in (32): $\min\{\beta\lambda, (1 - \beta)\lambda\} > \delta$.

On the other hand, the eigenvalue analysis proves that the non-trivial equilibrium state (38) exists unstable as a saddle point. Indeed, its characteristic equation can be written as follows:

$$\alpha^2 + \left[\frac{(2\delta + D)\{-\delta^2 + \beta(1 - \beta)\lambda^2\}}{(\delta - \beta\lambda)\{\delta - (1 - \beta)\lambda\}} + \delta \right] \alpha - \delta(2\delta + D) = 0, \qquad (39)$$

where α is eigenvalue. From (39), we can see that, since the sum and the product of two roots for (39) are both negative, two eigenvalues are real with different signs. Fig. 1 shows some trajectories of (C, W) when the non-trivial equilibrium state (38) exists.

Since the population goes extinct or infinite, depending on the initial state as shown in Fig. 1 when the non-trivial equilibirium state exists, we now consider the separatrix which corresponds to the stable manifold for the non-trivial equilibrium state. Although the stable manifold could not be analytically obtained, we can numerically draw it as shown in Fig. 2. Numerical result indicates the followings:

1. When both $C(0)$ and $W(0)$ are sufficiently small, the population goes extinct.

2. When $C(0)$ has an intermediate value, there is such a case that only some intermediate value of $W(0)$ causes the extinction of population, and too small or too large $W(0)$ does the growth.

Supposing that the coupling dynamics is sufficiently faster than the temporal variation of male and female populations, we put $dC(t)/dt \approx 0$ as an approximation for the dynamics given by (27), (28) and (29), and get an approximated two-dimensional differential equations about V and W. For the approximated dynamical system, we can carry out the same analysis about the asymptotic states considered above, and get the qualitatively same result.

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2.2 $a_c \rightarrow 0$

2.2.1   Dynamics of population size

Since this is the case when the sex reversal always occurs, the dynamics of population size can be written as follows from (21), (23) and (24):

$$\frac{dV(t)}{dt} = -\delta_v V(t) - mV(t) + \beta\lambda C(t) \tag{40}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + mV(t) + (1-\beta)\lambda C(t) \tag{41}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{42}$$

2.2.2   Extinction state

Extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ is always locally stable. This can be easily shown by the eigenvalue analysis for it. Indeed, the characteristic equation about the extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_w)(\alpha + \delta_v + m)(\alpha + \delta_v + \delta_w + D) = 0$$

, where α is eigenvalue. From this equation, $\alpha = -\delta_w, -(\delta_v + m)$, and $-(\delta_v + \delta_w + D)$, so that three eigenvalues are all negative real.

2.2.3   Non-trivial equilibrium state

From (40), (41) and (42), we can see that at most one non-trivial equilibrium state could exist:

$$
\begin{cases}
V^* &= \dfrac{\beta\lambda}{\delta_v + m}C^* \\[2ex]
W^* &= \dfrac{1}{\delta_w}\left\{\dfrac{m\beta\lambda}{d_{11} + m} + (1-\beta)\lambda\right\}C^* \\[2ex]
C^* &= \dfrac{\delta_v + \delta_w + D}{r\left\{\frac{\beta\lambda}{\delta_v+m} - 1\right\}\left[\frac{1}{\delta_w}\left\{\frac{m\beta\lambda}{\delta_v+m} + (1-\beta)\lambda\right\} - 1\right]}.
\end{cases}
\tag{43}
$$

From the condition (26) and the positiveness for (43), we can get the following condition for the existence of non-trivial equilibrium state (43):

$$
\begin{cases}
\beta\lambda &> \delta_v + \dfrac{m}{\delta_v + m}\beta\lambda \\[2ex]
\dfrac{m}{\delta_v + m}\beta\lambda + (1-\beta)\lambda &> \delta_w.
\end{cases}
\tag{44}
$$

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The first inequality of (44) means the condition such that the male birth is larger than the decrease caused by the natural death and the sex reversal. The second means the corresponding condition for female population such that the increase caused by the new born and the sex reversal is larger than the natural death. If and only if these two conditions are satisfied at the same time, the non-trivial equilibrium state (43) exists. Fig. 3(a) shows the condition for the existence of non-trivial equilibrium state (43). Figs. 4(a, b) that whether the population goes extinct or growth depends on the initial condition.

Analyzing the characteric equation for the non-trivial eqilibrium state (43) of the system given by (40-42), we can obtain the condition for the local stability (see Appendix D).

2.2.4 Approximation with two-timing method

Now, we apply the two-timing method for the dynamics governed by (40-42) in order to consider its characteristic nature in detail. Supposing that the change of coupling dynamics is sufficiently faster than those of male and female populations, we put $dC(t)/dt \approx 0$ as an approximation for this dynamics given by (40-42). With $dC(t)/dt = 0$ at (42), we can get the followings from (40) and (41):

$$\frac{dV(t)}{dt} = -\delta_v V(t) - mV(t) + \frac{\beta\lambda}{2}\{rV(t) + rW(t) + g\}$$

$$-\frac{\beta\lambda}{2r}\sqrt{f(V(t), W(t))} \qquad (45)$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + mV(t) + \frac{(1-\beta)\lambda}{2}\{rV(t) + rW(t) + g\}$$

$$-\frac{(1-\beta)\lambda}{2r}\sqrt{f(V(t), W(t))}, \qquad (46)$$

where

$$f(V(t), W(t)) = r^2\{V(t) + W(t) + g\}^2 - 4r^2V(t)W(t)$$

$$= r^2[\{V(t) - W(t) + g\}^2 + 4W(t)g] > 0 \qquad (47)$$

and

$$g = \frac{\delta_v + \delta_w + D}{r}. \qquad (48)$$

Since the population goes extinct or infinite depending on the initial condition as shown in Fig. 5 when the non-trivial equilibirium state exists, we again consider the separatrix. We can numerically draw it as shown in Fig. 6. Numerical result indicates the followings:

1. When $V(0)$ and $W(0)$ are sufficiently small, the population goes extinct and when $V(0)$ and $W(0)$ are sufficiently large, the population will diverge.

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2. When $W(0)$ has an intermediate value, there is such a case that sufficiently small value of $V(0)$ causes the extinction of population, and sufficiently large $V(0)$ does the growth.

Analyzing the characteric equation for the non-trivial equilibrium state which is given by (45) and (46), we can obtain the condition for the local stability (see Appendix E).

2.3 $0 < a_c < \infty$

This is the case when the sex reversal occurs at random with a constant rate after a given age a_c as shown in (17). Population dynamics is given by (21-24).

2.3.1   Extinction state

The extinction state $(V^*, X^*, W^*, C^*) = (0, 0, 0, 0)$ is always locally stable. The characteristic equation about the extinction state $(V^*, X^*, W^*, C^*) = (0, 0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_v)(\alpha + \delta_w)(\alpha + \delta_v + m)(\alpha + \delta_v + \delta_w + D) = 0, \tag{49}$$

where α is eigenvalue. Hence, $\alpha = -\delta_v, -\delta_w, -(\delta_v + m)$, and $-(\delta_v + \delta_w + D)$, that is, four eigenvalues are all negative real.

2.3.2   Non-trivial equilibrium state

From (21-24), we can see that at most one non-trivial equilibrium state could exist as follows:

$$
\begin{cases}
X^* &= \dfrac{\beta\lambda(1 - e^{-\delta_v a_c})}{\delta_v} C^* \\[2mm]
V^* &= \dfrac{\beta\lambda\{m(1 - e^{-\delta_v a_c}) + \delta_v\}}{\delta_v(\delta_v + m)} C^* \\[2mm]
W^* &= \dfrac{1}{\delta_w}\left\{ \dfrac{m\beta\lambda\{m(1 - e^{-\delta_v a_c}) + \delta_v\}}{\delta_v(\delta_v + m)} - \dfrac{m\beta\lambda(1 - e^{-\delta_v a_c})}{\delta_v} + (1 - \beta)\lambda \right\} C^* \\[2mm]
C^* &= \dfrac{\delta_v + \delta_w + D}{r\left(\frac{V^*}{C^*} - 1\right)\left(\frac{W^*}{C^*} - 1\right)}.
\end{cases}
\tag{50}
$$

From the condition (26) and the positiveness for (50), we can get the following condition for the existence of non-trivial equilibrium state (50):

$$
\begin{cases}
\beta\lambda &> \quad \delta_v + \dfrac{m}{\delta_v + m}\beta\lambda e^{-\delta_v a_c} \\[2mm]
(1 - \beta)\lambda + \dfrac{m}{\delta_v + m}\beta\lambda e^{-\delta_v a_c} &> \quad \delta_w.
\end{cases}
\tag{51}
$$

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The first inequality of (51) means the condition such that the male birth is larger than the decrease caused by the natural death and the sex reversal which follows the age-dependent function (17). The second means the corresponding condition for female population such that the increase caused by the new born and the sex reversal which follows the age-dependent function (17) is larger than the natural death. If and only if these two conditions are satisfied at the same time, the non-trivial equilibrium state (50) exists. Fig. 3(b) shows the condition for the existence of non-trivial equilibrium state (50).

Making use of numerical calculations, we get the results given by Fig. 7 about the parameter dependence of population extinction. From Fig. 7(a), we can result in the followings:

- When the sex reversal does not occur so often, the population does not go extinct even if the critical age a_c is rather small.

- As the sex reversal rate m gets larger, the population does not go extinct when a_c is larger than a critical value.

- Population goes extinct with sufficiently large sex reversal rate m when a_c is smaller than a critical value.

- When a_c is larger than critical value, the population does not go extinct for any m.

From Fig. 7(b),

- Population goes extinct when the age a_c is too small or too large, that is, too early or too late.

- Even if the age a_c has an intermediate value, the population goes extinct when the sex reversal rate m is too small, while it does not when m is larger than a critical value.

- When the age a_c is larger than a critical value and smaller than another critical age, the population would not go extinct with any sex reversal rate m.

- When the age a_c is smaller than a critical value, the population would go extinct except in case of having small sex reversal rate m.

From Figs. 4, we can see that different initial condition causes the dynamics diffrent.

From Figs. 8, we can see that too small and too large critical age causes the population goes extinct. From Figs. 9, we can see that too large sex reversal rate causes the population goes extinct.

2.3.3 Coupling and sex reversal rates

From our numerical calculations shown in Figs. 10(a, b), we can see the followings:

- As the coupling coefficient r gets larger, the population does not go extinct if the sex reversal rate m is sufficiently small.

- Even if r is rather large, the population goes extinct when the sex reversal occurs so often.

- For the population persistence, the coupling coefficient r has to be sufficiently large. With too small r, the population goes extinct.

2.3.4 Coupling coefficient the critical age a_c

As shown in Fig. 11(a), we can see the followings:

- As the coupling rare r gets larger, the population does not go extinct with the age a_c larger than a critical value.

- Population goes extinct when the coupling coefficient r is smaller than a critical value.

- When the age a_c is earlier than a critical, any coupling coefficient r causes the population extinct.

From Fig. 11(b),

- As the coupling coefficient r gets larger, the population does not go extinct when the age a_c has an intermediate value.

- Population goes extinct when r is smaller than a critical value. In this case, the critical value for r would be determined by m.

- When the age a_c is smaller than a critical value, the population goes extinct for any coupling coefficient r.

- When the age a_c is larger than a critical value, the population goes extinct for any coupling coefficient r.

2.3.5 Effect of the critical age on the equilibrium population sizes

Fig. 12 shows the case when $\delta_w < (1 - \beta)\lambda$, which means that the female's population persistence is possible. As shown in Fig. 12(a), we can see that, if the critical age a_c is sufficiently small for the case when the non-trivial equilibrium exists, the non-trivial equilibrium population sizes are so large that the region of initial points to go extinct is much wide. Since the non-trivial equilibrium point is saddle with a separatrix for the region of initial points to go extinct, the possibility of population persistence can be regarded as rather low in such case (also see Figs. 1, 2, 5, 6, and Fig. 12(b)). The later the critical age a_c is, the population persistence is feasible. Further, from Fig. 12(b), we can see that such the unique and intermediate critical age exists as to make the equilibrium point the nearest to the origin so that it makes the population persistence the most possible.

On the other hand, Fig. 13 shows the case when $\delta_w > (1 - \beta)\lambda$, which means that the female's population persistence is difficult. As shown in Fig. 13(a), we can see that, if the critical age a_c is too small or too large for the case when the non-trivial equilibrium exists, the non-trivial equilibrium population sizes are so large that the region of initial points to go extinct is much wide. Hence, in such case, the possibility of population persistence can be regarded as rather low (also see Fig. 13(b)). Lastly, an intermediate range of the critical age a_c could make the possibility of population persistence the higher. Further, from Fig. 13(b), we can see again that such the unique and intermediate critical age exists as to make the equilibrium point the nearest to the origin so that it makes the population persistence the most possible.

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References

[1]   , 1995.   .

[2]   ,   , 1975   17
                     .

Appendix A

For sufficiently short period h, we calculate the Taylor series expansion of $v(a + h, t + h)$ as follows:

$$v(a + h, t + h) \;=\; v(a,t) + \frac{\partial v(a,t)}{\partial t}h + \frac{\partial v(a,t)}{\partial a}h + o(h^2). \tag{52}$$

Hence, substituting (52) to (3), we can obtain the following:

$$\frac{v(a + h, t + h) - v(a,t)}{h} \;=\; \frac{\partial v(a,t)}{\partial t} + \frac{\partial v(a,t)}{\partial a} + \frac{o(h^2)}{h}$$

$$\;=\; -\delta_v v(a,t) - M(a)v(a,t) + \frac{o(h^2)}{h}. \tag{53}$$

As $h \to 0$ for (53), we can get (6).

Appendix B

By integrating the left side of (6) from 0 to ∞ in terms of a and using (9), (13) and (18), supposing that the exchange between the integration in terms of a and the differentiation in terms of t is possible, we can get the following.

$$\int_0^\infty \frac{\partial v(a,t)}{\partial t}da + \int_0^\infty \frac{\partial v(a,t)}{\partial a}da \;=\; \frac{\partial}{\partial t}\int_0^\infty v(a,t)da + v(\infty,t) - v(0,t)$$

$$\;=\; \frac{dV(t)}{dt} - \beta\lambda C(t). \tag{54}$$

By integrating the right side of (6) from 0 to ∞ in terms of a, using (17) and (18), we can get the following:

$$-\delta_v \int_0^\infty v(a,t)da - \int_0^\infty M(a)v(a,t)da$$

$$= -\delta_v V(t) - \left\{ 0 \cdot \int_0^{a_c} v(a,t)da + m \cdot \int_{a_c}^\infty v(a,t)da \right\}$$

$$= -\delta_v V(t) - m\left\{ \int_0^\infty v(a,t)da - \int_0^{a_c} v(a,t)da \right\}$$

$$= -\delta_v V(t) - m\{V(t) - X(t)\}. \tag{55}$$

From (54) and (55), we can get (21). Similarly, (23) can be derived from (7), (10), (14), (17) and (19).

By integrating the left side of (6) from 0 to a_c in terms of a, using (9) and (20), we can get the following:

$$\int_0^{a_c} \left(\frac{\partial v}{\partial a} + \frac{\partial v}{\partial t}\right) da = v(a_c, t) - v(0, t) + \frac{\partial}{\partial t} \int_0^{a_c} v(a, t) da$$

$$= v(a_c, t) - \beta \lambda C(t) + \frac{dX(t)}{dt}. \tag{56}$$

By integrating the right side of (6) from 0 to a_c in terms of a, using (17) and (20),

$$-\delta_v \int_0^{a_c} v(a, t) da - \int_0^{a_c} M(a) v(a, t) da = -\delta_v X(t). \tag{57}$$

From (56) and (57), we can get (22).

By integrating (6) and (7) from 0 to ∞ in terms of a and a', using (11), (18) and (19), we can get the followings:

$$\int_0^{\infty} v_e(a, t) da = \int_0^{\infty} v(a, t) da - \int_0^{\infty} \int_0^{\infty} c(a, a', t) da da'$$

$$= V(t) - C(t), \tag{58}$$

$$\int_0^{\infty} w_e(a', t) da = \int_0^{\infty} w(a', t) da - \int_0^{\infty} \int_0^{\infty} c(a, a', t) da da'$$

$$= W(t) - C(t). \tag{59}$$

By integrating the left side of (8) from 0 to ∞ in terms of both a and a', using (11), (12), (15) and (16), we can get the following:

$$\int_0^{\infty} \int_0^{\infty} \left(\frac{\partial c}{\partial a} + \frac{\partial c}{\partial a'} + \frac{\partial c}{\partial t}\right) da da'$$

$$= \int_0^{\infty} \int_0^{\infty} \frac{\partial c}{\partial a} da da' + \int_0^{\infty} \int_0^{\infty} \frac{\partial c}{\partial a'} da da' + \int_0^{\infty} \int_0^{\infty} \frac{\partial c}{\partial t} da da'$$

$$= \frac{d}{dt} \int_0^{\infty} \int_0^{\infty} c(a, a', t) da da'$$

$$= \frac{dC(t)}{dt}. \tag{60}$$

By integrating the right side of (8) from 0 to ∞ in terms of a and a', we can get the following, using (11), (58) and (59):

$$-(\delta_v + \delta_w + D) \int_0^{\infty} \int_0^{\infty} c(a, a', t) da da' + e \int_0^{\infty} v_e(a, t) da \int_0^{\infty} w_e(a', t) da'$$

$$= -(\delta_v + \delta_w + D) C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{61}$$

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From (60) and (61), we can get (24).

Appendix C

Now, $v(a_c, t)$ corresponds to the density of male with age a_c at time t. If $t \geq a_c$, it originates with the density $v(0, t - a_c)$ of male newborn at time $t - a_c$. This is because age increases by the same increment as time does, so that $v(a_c, t)$ originates with the density $v(a_c - p, t - p)$ for any p such that $0 < p \leq a_c$. Let us put $F(p) \equiv v(a_c - p, t - p)$ $(0 < p \leq a_c)$ for any fixed $t \geq a_c$, then the function $F(p)$ is assumed to be continuous and sufficiently smooth.

From our modelling, since any male younger than age a_c does not make the sex reversal, the temporal variation of density $v(a_c - p, t - p)$ from time $t - p$ to $t - p + h$ is only due to the natural death. Therefore, for sufficiently small period h,

$$v(a_c - p + h, t - p + h) - v(a_c - p, t - p) = -\delta_v h \cdot v(a_c - p, t - p) + o(h^2),$$

that is,

$$\frac{F(p - h) - F(p)}{h} = -\delta_v \cdot F(p) + \frac{o(h^2)}{h}.$$

As $t \to 0$, we can get the following linear differential equation about $F(p)$:

$$\frac{dF(p)}{dp} = \delta_v \cdot F(p) \quad (0 < p \leq a_c). \tag{62}$$

As the boundary condition for (62), we use the below, derived from (9):

$$F(a_c) = v(0, t - a_c) = \beta \lambda C(t - a_c). \tag{63}$$

The differential equation (62) of $F(p)$ with the condition (63) can be easily solved and the solution becomes

$$F(p) = v(a_c - p, t - p) = \beta \lambda C(t - a_c) e^{\delta_v (p - a_c)} \quad (0 < p \leq a_c),$$

thus lastly, with $p \to 0$,

$$v(a_c, t) = \beta \lambda C(t - a_c) e^{-\delta_v a_c} \quad (t \geq a_c). \tag{64}$$

On the other hand, if $t < a_c$, $v(a_c, t)$ originates with the density of male with age $a_c - t$ at time 0. Hence, with $v(a_c - t, 0) = v_0(a_c - t)$ for any fixed $t < a_c$, in the similar way as above for the case when $t \geq a_c$, we can obtain the following:

$$v(a_c, t) = v_0(a_c - t) e^{-\delta_v a_c} \quad (t < a_c). \tag{65}$$

These results (64) and (65) give $v(a_c, t)$ of (25).

Appendix D

We can get the following characteristic equation for the non-trivial equilibrium state (43) of the system given by (40-42):

$$\alpha^3 \quad + \quad \{2(\delta_v + \delta_w) + A + B + m + D\}\alpha^2$$

$$+ \quad [(\delta_v + \delta_w + m)\{A + B + \delta_v + \delta_w + D\} + \delta_w(\delta_v + m) - (1 - \beta)\lambda A - \beta\lambda B]\alpha$$

$$+ \quad \delta_w(\delta_v + m)\{A + B + \delta_v + \delta_w + D\}$$

$$-\{(1 - \beta)\lambda(\delta_v + m) + m\beta\lambda\}A - \delta_w\beta\lambda B = 0, \qquad (66)$$

where $A = r(V^* - C^*)$, $B = r(W^* - C^*)$. V^*, W^* and C^* satisfy (43). From (66), we can formally get the condition for stability, making use of the Routh-Hurwitz criterion:

$$\left\{ \begin{array}{l} \delta_w(\delta_v + m)\{A + B + \delta_v + \delta_w + D\} - \{(1 - \beta)\lambda(\delta_v + m) + m\beta\lambda\}A - \delta_w\beta\lambda B > 0 \\[2mm] \{2(\delta_v + \delta_w) + A + B + m + D\} \\[2mm] \times[(\delta_v + \delta_w + m)\{A + B + \delta_v + \delta_w + D\} + \delta_w(\delta_v + m) - (1 - \beta)\lambda A - \beta\lambda B] \\[2mm] -\delta_w(\delta_v + m)\{A + B + \delta_v + \delta_w + D\} - \{(1 - \beta)\lambda(\delta_v + m) + m\beta\lambda\}A - \delta_w\beta\lambda B > 0. \end{array} \right.$$

Appendix E

We can get the following characteristic equation for the non-trivial equilibrium state given by (45-46):

$$\alpha^2 + \left[-(\delta_v + \delta_w + m) + \frac{1}{2}\{\beta\lambda A + (1 - \beta)\lambda B\}\right]\alpha$$

$$+ \left\{\frac{\beta\lambda}{2}A - (\delta_v + m)\right\}\left\{\frac{(1 - \beta)\lambda}{2}B - \delta_w\right\}$$

$$-\frac{\beta\lambda}{2}B\left\{m + \frac{(1 - \beta)\lambda}{2}A\right\} = 0, \quad (67)$$

where

$$\left\{ \begin{array}{l} A = 1 - \dfrac{2r(V^* - W^*) + 2(\delta_v + \delta_w + D)}{\sqrt{(\delta_v + \delta_w + D + rV^* + rW^*)^2 - 4r^2V^*W^*}} \\[5mm] B = 1 - \dfrac{2r(W^* - V^*) + 2(\delta_v + \delta_w + D)}{\sqrt{(\delta_v + \delta_w + D + rV^* + rW^*)^2 - 4r^2V^*W^*}}. \end{array} \right.$$

V^*, W^* and C^* satisfy (43). From (67), we can get the condition for the local stability:

$$
\begin{cases}
-(\delta_v + \delta_w + m) + \dfrac{1}{2}\{\beta\lambda A + (1-\beta)\lambda B\} < 0 \\[2mm]
\left\{\dfrac{\beta\lambda}{2}A - (\delta_v + m)\right\}\left\{\dfrac{(1-\beta)\lambda}{2}B - \delta_w\right\} - \dfrac{\beta\lambda}{2}B\left\{m + \dfrac{(1-\beta)\lambda}{2}A\right\} > 0.
\end{cases}
$$

Figure Captions

Fig. 1

Numerical trajectories for the two dimensional system given by (33) and (34). $\beta = 0.4; \lambda = 1.0; \delta = 0.3; D = 0.0; r = 1.0$.

Fig. 2

Manifolds for the non-trivial equilibrium (C^*, W^*) about the two dimensional system given by (33) and (34). Numerically obtained. $\beta = 0.4; \lambda = 1.0; \delta = 0.3; D = 0.0; r = 1.0$.

Fig. 3

(δ_v, δ_w)-dependence of the existence of non-trivial equilibrium. (a)Region A is for the case when $a_c \to 0$, and B for $a_c \to +\infty$. (b)For the case when $0 < a_c < +\infty$. p shows the value for δ_v which satisfies the equation $(\delta_v + m)(\delta_v - \beta\lambda) = -\beta\lambda m e^{-\delta_v a_c}$.

Fig. 4

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$. (a) $(V(0), X(0), W(0), C(0)) = (1.0, 0.865, 1.0, 0.0)$; (b) $(V(0), X(0), W(0), C(0)) = (1.0, 0.865, 0.3, 0.0)$. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.3; \delta_w = 0.2; D = 0.0; r = 1.0; m = 0.2; a_c = 2.0$.

Fig. 5

Numerical trajectories for the two dimensional system given by (46) and (47). $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.5; D = 0.0; r = 1.0; m = 0.1$.

Fig. 6

Manifolds for the non-trivial equilibrium (V^*, W^*) for the two-dimensional system given by (46) and (47). Numerically obtained. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.5; D = 0.0; r = 1.0; m = 0.1$.

Fig. 7

(m, a_c)-dependence of population extinction. Black points indicate the parameter set to cause the extinction, estimated by numerical calculations. $\lambda = 1.0; D = 0.0; r = 1.0; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$; (a) $\delta_w < (1 - \beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$;(b) $\delta_w > (1 - \beta)\lambda; \beta = 0.7; \delta_v = 0.1; \delta_w = 0.4$.

Fig. 8

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$ for $m = 5.0$. (a) $a_c = 2.0$; (b) $a_c = 5.0$; (c) $a_c = 10.0$. $\beta = 0.6; \lambda = 1.0; \delta_v = 0.2; \delta_w = 0.1; D = 0.0; r = 1.0$.

Fig. 9

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$ for $a_c = 1.5$. (a) $m = 0.5$; (b) $m = 5.0$; (c) $m = 10.0$. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.4; D = 0.0; r = 1.0$.

Fig. 10

(r, m)-dependence of population extinction. $\lambda = 1.0; D = 0.0; a_c = 1.0; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$. (a) $\delta_w < (1 - \beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$; (b) $\delta_w > (1 - \beta)\lambda; \beta = 0.78; \delta_v = \delta_w = 0.23$.

Fig. 11

(r, a_c)-dependence of population extinction. $\lambda = 1.0; D = 0.0; m = 1.5; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$. (a) $\delta_w < (1 - \beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$; (b) $\delta_w > (1 - \beta)\lambda; \beta = 0.7; \delta_v = 0.1; \delta_w = 0.4$.

Fig. 12

(a)a_c-dependence of the non-trivial equilibrium population sizes $V^*, X^*, W^*, C^*, V^* + W^*$. (b)$a_c$-dependence of the distance of equilibrium point from the origin. For $\delta_w < (1 - \beta)\lambda; \beta = 0.5; \lambda = 1.0; \delta_v = 0.2; \delta_w = 0.3; r = 1.0; D = 0.0; m = 2.0$. The non-trivial equilibrium can exist for $2.0776 < ac$.

Fig. 13

(a)a_c-dependence of the non-trivial equilibrium population sizes $V^*, X^*, W^*, C^*, V^* + W^*$. (b)$a_c$-dependence of the distance of equilibrium point from the origin. For $\delta_w > (1 - \beta)\lambda; \beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.4; r = 4.0; D = 0.0; m = 1.5$. The non-trivial equilibrium can exist for $0.8961 < ac < 18.8167$.

W

dW/dt=0

W=C

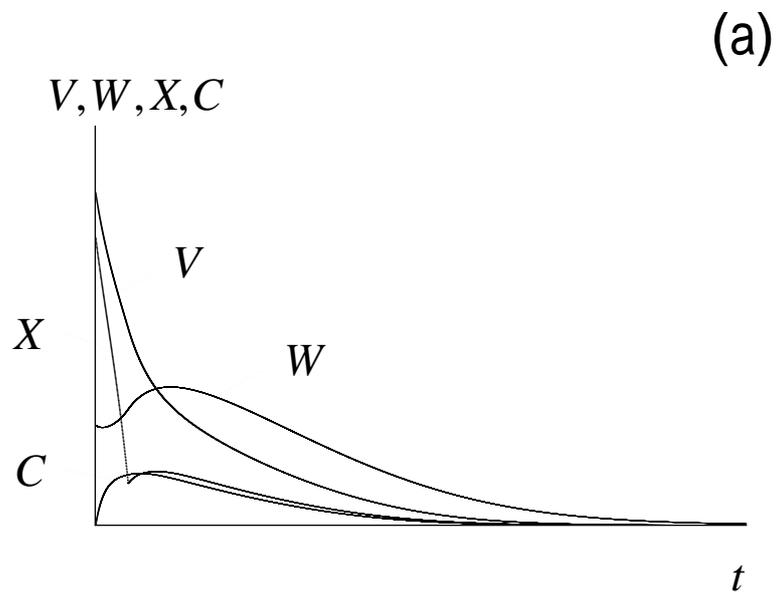dC/dt=0

C

-1   1   2   3   4

8

6

4

2

-2

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7(a)

(b)

a_c

$-\frac{1}{\delta_v}\ln\left(\frac{\delta_w-(1-\beta)\lambda}{\beta\lambda}\right)$

20

15

10

5

$-\frac{1}{\delta_v}\ln\left(\frac{\beta\lambda-\delta_v}{\beta\lambda}\right)$

$\frac{\delta_v\{\delta_w-(1-\beta)\lambda\}}{\lambda-\delta}$

$\beta\lambda^-\delta$

2   4   6   8

m

Fig. 7(b)

(a)

V,W,X,C

W

V

X

C

t

(b)

V,W,X,C

V

X

W

C

t

(c)

V,W,X,C

V

X   *W*   *C*

t

Fig. 8

(a)

V,W,X,C

X

V

W

C

t

(b)

V,W,X,C

W

V

X

C

t

(c)

V,W,X,C

W

V

X

C

t

Fig. 9

(a)

(b)

Fig. 10

Fig. 11

Fig. 12

(a)

$X^*, V^*, W^*, C^*, V^* + W^*$

$V^* + W^*$

X^* V^*

a_c

W^* C^*

(b)

$\sqrt{V^{*2} + W^{*2} + X^{*2} + C^{*2}}$

a_c

Fig. 13