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On the Predator-Prey Dynamics Considering the Age-dependent Outlivability of the Prey

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Abstract: A mathematical model is presented to simulate how the population dynamics of a predator-prey system depends on the prey outlivability distribution due to age difference. The prey population is described by a Lotka-Volterra equation govering the time evolution of the age density; the equation is so formulated as to take account of the age-dependent divergence in the birth/death potential and in the level of predation by the predator. The time evolution of the predator population is modelled by a logistic equation. Numerical simulation reveals that the system given an initial condition far from the equilibrium (EQ) arrives at the EQ via two restoration stages; in the one which finishes almost in a short time approximate to the maximum life span of the prey species, the density of prey age tends to assume a profile analogous to that at the EQ though the total population is still greatly distant from the EQ value, and in the other stage, for both species the total population approaches its EQ exponentially with a time constant greater than that of the preceding stage.

1 Introduction

The population dynamics of a predator-prey system or a binary competitive ecosystem is often modelled by combined *logistic* equations which describe the time evolution of the total populations in terms of the intrinsic birthrate and two kinds of deathrates, one being inherent to each species and the other related to the existence of the opponents; the combining coefficients of these rates are treated as the system constants[1].

In general, however, the childbirth potential of organisms such as animals is lower and the deathrate is higher for younger and older. The predation pressure, the rate at which an animal is predated by the predator depends on its age. The competitive potential also differs with ages. These should affect how the system behaves when perturbed from its equilibrium and then left free. But, any analysis considering such problems seems so far not to have been reported.

We discuss here the population dynamics of a predator-prey system introducing the age distribution of the prey animals as well as the dependency of the prey ecological parameters on age. Our analysis will point out that the system given any prey age-construction approaches fi-

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nally the equilibrium via two distinguishable stages; in the earlier stage, the prey age-distribution restores fast its equilibrium constitution and, in the later stage, the total population restores slowly its equilibrium both for the prey and for the predator.

2 Underlying Equations

Suppose a system of two animal species one of which may be a food source for the other, and name the species to be predated the *prey* and the other the *predator*. Let the age of a *prey* be denoted by x, and the time variable by t. Other major variables used here are listed below:

$n_1(x,t)$: the number density of x-aged *prey*.
$N_1(t)$: the *prey* (total) population.
$N_2(t)$: the *predator* (total) population.
$\beta(x)$: the rate of childbirth by an x-aged *prey*.
β_2 : the mean *predator* birthrate.
$\delta(x)$: the deathrate of an x-aged *prey*.
$p(x)$: the predation pressure to an x-aged *prey*.
x_M : the maximum life span of the *prey*.

We assume the time evolution of the density $n_1(x,t)$ to be governed by

$$\frac{\partial n_1}{\partial t} = -\frac{\partial n_1}{\partial x} - (\delta + pN_2)n_1 \tag{1}$$

for $x > 0$, where the first term in the right-hand expression is the change rate of n_1 due to ageing[1] and the second due to death. The death rate comprises δn_1 intrinsic to the *prey* and pN_2n_1 caused by predation. The total population N_1 of the *prey* should also obey a usual multiplication law, so that

$$\frac{1}{N_1}\frac{dN_1}{dt} = \bar{\beta} - (\bar{\delta} + N_2\bar{p}) \ , \tag{2}$$

where $\bar{\beta}$ is the mean birthrate and $\bar{\delta} + N_2\bar{p}$ is the average deathrate; the related notations are defined as follows:

$$N_1(t) \equiv \int_0^{x_M} n_1(x,t)dx \ , \tag{3}$$

$$\bar{\beta}(t) \equiv \frac{1}{N_1}\int_0^{x_M} \beta(x)n_1(x,t)dx \ , \tag{4a}$$

$$\bar{\delta}(t) \equiv \frac{1}{N_1}\int_0^{x_M} \delta(x)n_1(x,t)dx \ , \tag{4b}$$

and

$$\bar{p}(t) \equiv \frac{1}{N_1}\int_0^{x_M} p(x)n_1(x,t)dx \ . \tag{4c}$$

We have further to consider the boundary condition at $x = 0$ as follows:

$$\left(\frac{\partial n_1}{\partial t}\right)_{x=0} = \bar{\beta} - (\bar{\delta} + N_2\bar{p}) \ . \tag{5}$$

To describe how the *predator* population N_2 is changed, on the other hand, we assume a *logistic* equation

$$\frac{dN_2}{dt} = \beta_2\left(1 - \frac{N_2}{K_0 + \kappa N_1\bar{p}_1}\right)N_2 \ . \tag{6}$$

The *logistic* term, the second in the brackets above, takes into account two kinds of food sources for the *predator*, that is, the *prey* noted here ($\kappa N_1\bar{p}_1$), and other organisms excepting it (K_0).

The coefficient κ represents how the *predator* life depends on the *prey* as a food source. If the *prey* does not exist, *i.e.*, $\kappa = 0$, then the equilibrium *predator* population will equal K_0. We call hence K_0 the *basic environmental capacity* or the *basic carrying capacity* for the *predator.*

3 Equilibrium Solutions

The equilibrium solutions of Equations 1, 5, and 6, denoted as ${n_1}^*(x)$, ${N_1}^*$, and ${N_2}^*$, can be determined by the following relations:

$$ {n_1}^*(x) = {n_1}^*(0)\nu^*(x) \quad \text{for } x > 0 \,, \tag{7} $$

$$ {N_1}^* = {n_1}^*(0) \int_0^{x_M} \nu^*(x)dx \,, \tag{8} $$

$$ {N_2}^* = K_0 + \kappa {N_1}^* \bar{p}^* = \frac{\bar{\beta}^* - \bar{\delta}^*}{\bar{p}^*} \,, \tag{9} $$

where the function $\nu^*(x)$ is defined by

$$ \nu^*(x) \equiv \exp\left\{ -\int_0^x [\delta(\xi) + {N_2}^* p(\xi)]d\xi \right\} \,, \tag{10} $$

and $\bar{\beta}^*$, $\bar{\delta}^*$, and $\bar{p}^*$ are the averages of β, δ, and p which are taken with respect to the equilibrium distribution ${n_1}^*(x)$ (see Equation 4).

4 Models for Calculation

To simplify numerical analysis, we scale time t by x_M, the maximum life span of the *prey*, *i.e.*, put $x_M = 1$.

We take the following model for the birthrate $\beta(x)$ (Fig. 1) to express how the childbirth potential depends on age:

$$ \beta(x) = B_M \exp\left[-\frac{(x - x_b)^2}{2{s_b}^2} \right] \,, \tag{11} $$

where x_b is the age of the maximum birthrate, B_M and s_b are positive constants; giving s_b a smaller (greater) value will make the age range having appreciable potential narrower (wider).

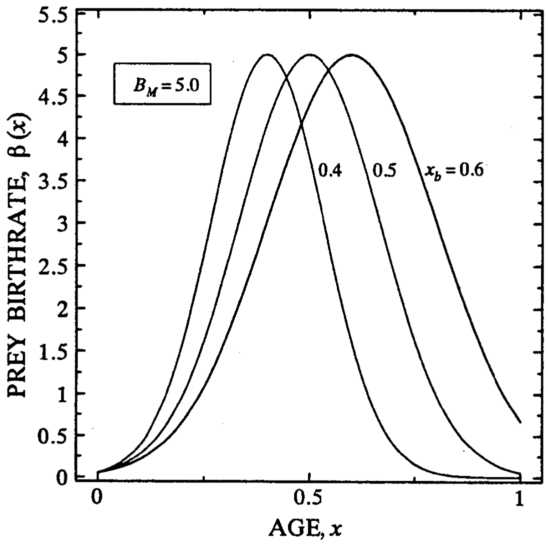


Fig. 1 Model birthrate function.

To simulate the age-dependent deathrate $\delta(x)$, we take the expression

$$ \delta(x) = \begin{cases} D_m \left[1 + d_0 \left(\dfrac{x_d - x}{x_d} \right)^6 \right] & \text{if } 0 \le x < x_d \\ D_m \left[1 + d_1 \left(\dfrac{x - x_d}{1 - x_d} \right)^6 \right] & \text{if } x_d \le x \le 1 \,; \end{cases} \tag{12} $$

where d_0, d_1, x_d, and D_m are all positive free parameters. This model can consider higher deathrates for *preys* infant and aged, as illustrated in Fig. 2.

We also postulate the age-dependent predation pressure $p(x)$ as

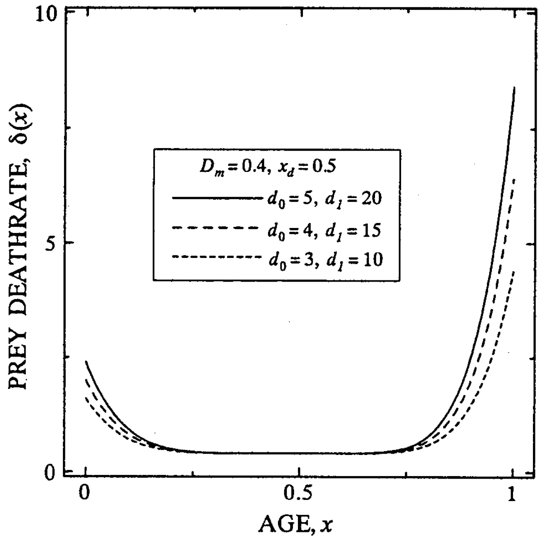


Fig. 2 Model deathrate function.

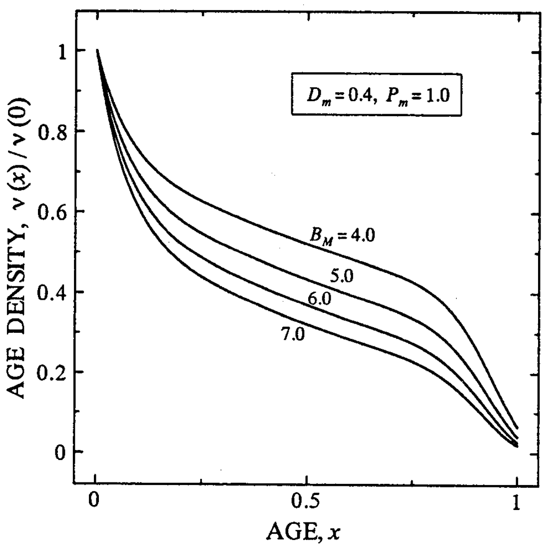


Fig. 3 Equilibrium age distribution.

$$p(x) = \begin{cases} P_m \left[1 + p_0 \left(\dfrac{x_p - x}{x_p} \right)^4 \right] & \text{if } 0 \le x < x_p \\ P_m \left[1 + p_1 \left(\dfrac{x - x_p}{1 - x_p} \right)^4 \right] & \text{if } x_p \le x \le 1 \ ; \end{cases} \tag{13}$$

where p_0, p_1, x_p, and P_m are all positive free parameters. The profile of $p(x)$ curve is similar to that of $\delta(x)$ illustrated in Fig. 2. Fig. 3 shows equilibrium solutions, $\nu^*(x)$, which were calculated based on these models with differently specified parameters.

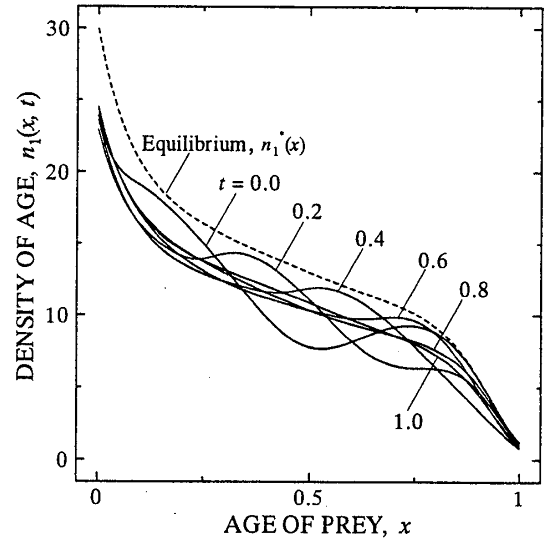


Fig. 4 Prey age density in an early time.

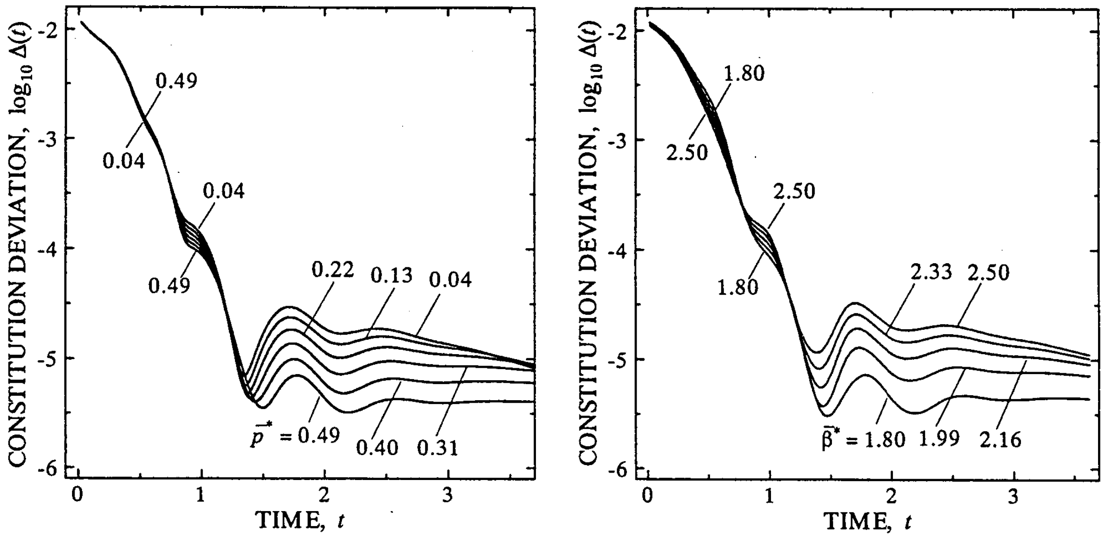
5 Constitution Restoration

Fig. 4 depicts the time evolution of *prey* density n_1 in an early stage up to $t = 1$ ($= x_M$, the maximum life span of the *prey*) for a given initial age construction. They suggest that the density assumes a profile analogous to the equilibrium one in a short time. To ascertain this quantitatively, we introduce a measure to express how distant the density profile at an instant is from the equilibrium:

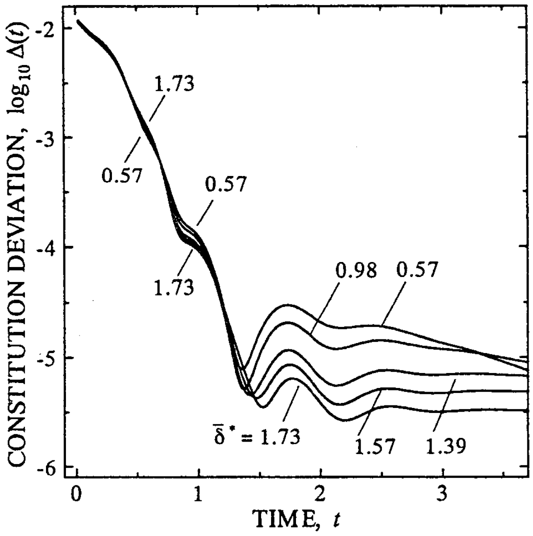
$$\Delta(t) \equiv \sqrt{\int_0^{x_M} \left[\frac{n_1(x,t)}{N_1(t)} - \frac{n_1{}^*(x)}{N_1{}^*} \right]^2 dx} \ . \tag{14}$$

Function $\Delta(t)$, named *constitution deviation*, approaches zero if the normalized densities of age come close, even though the total populations $N_1(t)$ is far from the equilibrium value $N_1{}^*$.

Fig. 5 depicts $\log \Delta$ versus t; the dependency on the birthrate (a), on the death rate (b), and on the predation pressure (c). These figures confirm the conjecture stated above and further suggest that the constitution deviation Δ decays roughly exponentially in the range of $t \approx 0.2$ to 1.2 though weak kink appears near $t \approx 0.5$ and 0.8, and the decay time constant seems to depend little on any of the averages of p, β, and δ. Let this early process of decay in constitution deviation Δ be called the stage of *constitution restoration.*



(a) Dependency on birthrate. **(b) Dependency on deathrate.**



(c) Dependency on predation pressure.

Fig. 5 Constitution restoration.

6 Total Restoration

Fig. 6 depicts temporal changes in n_1, N_1, and N_2 for a given starting age distribution. This suggests that the total populations N_1 and N_2 approach their equilibrium values $N_1{}^*$ and $N_2{}^*$ keeping almost the same prey-age-density profile. Let this process be called the stage of *total restoration.* In this stage, the density $n_1(x,t)$ may be factorized into the product of the equilibrium solution $n_1{}^*(x)$ and a function only of time t. Using this, we can examine how the system behaves when weak perturbation is given to the equilibrium state, as follows.

6.1 Linear Stability

For the reason stated just above, we may approximately factorize $n_1(x,t)$ near the equilibrium state, into

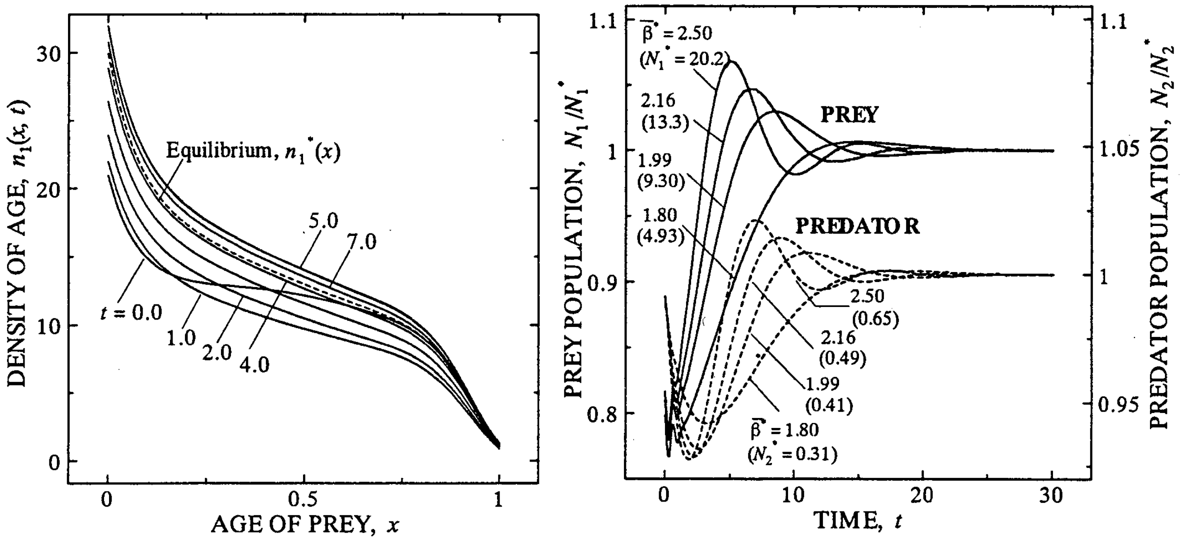
$$n_1(x,t) \equiv n_1{}^*(x)[1+\epsilon_1(t)] \ , \tag{15}$$

where $\epsilon_1(t)$ is a small perturbation. Integrating this with respect to x leads to

$$N_1(t) = N_1{}^*[1+\epsilon_1(t)] \ . \tag{16}$$

For the *predator* population disturbed infinitesimally, we assume

$$N_2(t) \equiv N_2{}^*[1+\epsilon_2(t)] \ . \tag{17}$$



(a) Prey age density in the later stage. **(b) Total population.**

Fig. 6 Time evolution of the total population.

Linearizing Equation 2 upon these suppositions leads to

$$\frac{d\epsilon_1}{dt} = \alpha_{11}\epsilon_1 - \alpha_{12}\epsilon_2 \ , \tag{18}$$

where α_{11} and α_{12} are defined by

$$\alpha_{11} \equiv \bar{\beta}^* - (\bar{\delta}^* + N_2{}^*\bar{p}^*) \quad \text{and} \quad \alpha_{12} \equiv N_2{}^*\bar{p}^* \ . \tag{19}$$

Equation 6 is linearized into

$$\frac{d\epsilon_2}{dt} = \alpha_{21}\epsilon_1 - \alpha_{22}\epsilon_2 \ , \tag{20}$$

where α_{21} and α_{22} are defined by

$$\alpha_{21} \equiv \frac{kN_1{}^*\bar{p}^*}{K_0 + kN_1{}^*\bar{p}^*}\beta_2 \quad \text{and} \quad \alpha_{22} \equiv \beta_2 \ . \tag{21}$$

Let the symbol D be further introduced for the later use, by

$$D \equiv (\alpha_{11} - \alpha_{22})^2 - 4(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}) \ . \tag{22}$$

We can check the stability of the equilibrium state by examining the *eigen* values of the coefficient matrix $[\alpha_{ij}]$, and present here the results explicitly only for two stable cases:

If $D < 0$ and $\alpha_{11} < \alpha_{22}$ (*case* 1), then ϵ_i falls to zero with oscillating; the decay time constant τ and the vibrating period T are given by

$$\tau = \frac{2}{\alpha_{22} - \alpha_{11}} \quad \text{and} \quad T = \frac{4\pi}{\sqrt{-D}} \ . \tag{23}$$

If $D > 0$ and $\alpha_{22} - \alpha_{11} > \sqrt{D}$ (*case* 2), then ϵ_i decreases exponentially in two modes; the decay time constants are given by

$$\tau_{\pm} = \frac{2}{(\alpha_{22} - \alpha_{11}) \pm \sqrt{D}} \ . \tag{24}$$

The system is unstable under any other condition; that is, one or two modes diverging exponentially are excited however weak disturbance may be. We will discuss elsewhere as to such cases and here restrict our interest to the stable ones.

6.2 Numerical Check

Fig. 7 gives two examples of the numerical solutions of N_1 in the total restoration stage; the solid curve corresponds to *case* 1 and the dashed one to *case* 2. We can expect from the analysis above that the late stage behaviors of N_i are expressed as follows:

For *case* 1,

$$N_i(t) \approx a_i e^{-t/\tau} \cos\left(2\pi \frac{t}{T} + c_i\right) + N_i{}^* \quad (i = 1,\ 2)\ , \tag{25}$$

where a_i, τ, and T are positive constants, and c_i is a constant.

For *case* 2,

$$N_i(t) \approx a_{i+} e^{-t/\tau_+} + a_{i-} e^{-t/\tau_-} + N_i{}^* \quad (i = 1,\ 2)\ , \tag{26}$$

where $a_{i\pm}$ are constants and $\tau_\pm$ are positive constants.

Fig. 8a depicts the maxima of $\log|N_1(t) - N_1{}^*|$ plotted against the corresponding t for a few examples of *case* 1, which shows the dependency being nearly linear except early time. Table 1a lists a few examples of the decay time τ and oscillation period T; τ was estimated from the least-squares-mean slope of each plot, and T from the time intervals between adjacent peaks of $N_1(t)$. They seem to agree well with their evaluations by Equation 23, listed in the same table.

To check the validity of the linear stability analysis above for damped modes without oscillation, we have to determine four unknown quantities $a_{i\pm}$ and $\tau_\pm$ in Equation 24 from the calculated $N_i(t)$. We may however expect that the mode having greater one of two decay constants $\tau_\pm$, *i.e.*, τ_-, becomes dominant in the later stage, since the mode with the smaller decay constant will die out faster and finally contributes

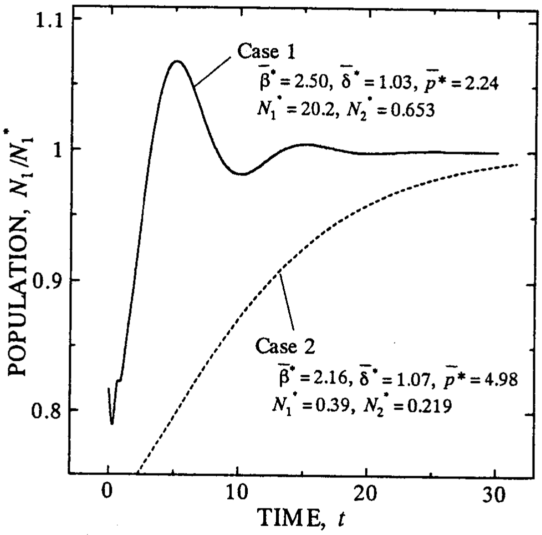
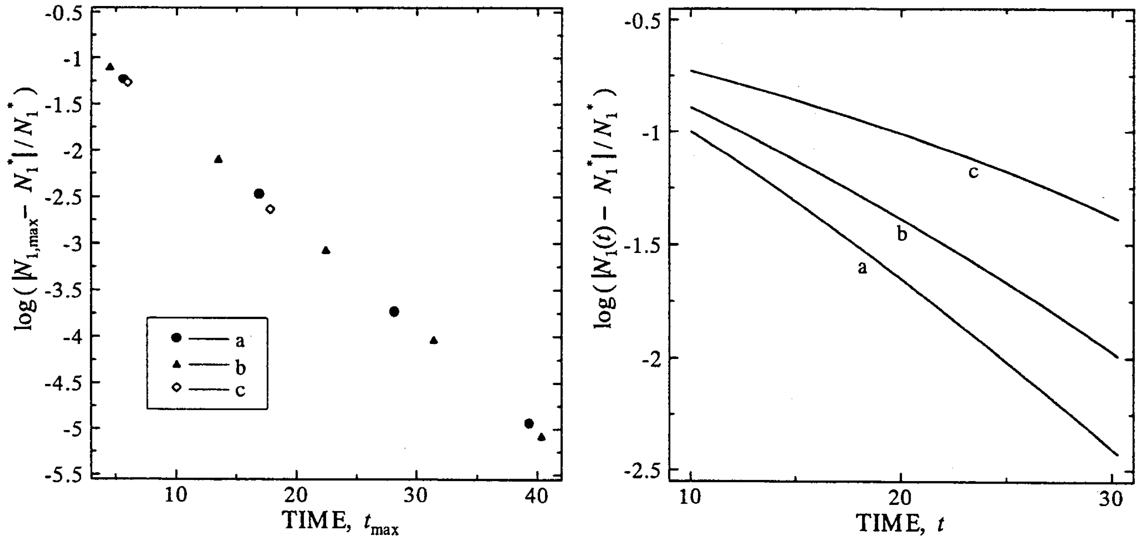


Fig. 7 Modes of the total restoration.



(a) *Case* 1. (b) *Case* 2.

Fig. 8 Evaluating the total-restoration time constant for the *prey*.

Table 1 Total-restoration time constant.

(a) *Case* 1

	$\bar{\beta}^*$	$\bar{\delta}^*$	$\bar{p}^*$	$N_1{}^*$	$N_2{}^*$	τ	τ^{LSA}	T	T^{LSA}
a	2.33	1.05	2.23	16.9	0.576	3.99	4.00	11.2	10.5
b	2.14	0.434	2.27	24.2	0.749	3.99	4.00	8.96	8.39
c	2.16	0.950	2.22	15.4	0.543	3.99	4.00	11.8	11.1

(b) *Case* 2

	$\bar{\beta}^*$	$\bar{\delta}^*$	$\bar{p}^*$	$N_1{}^*$	$N_2{}^*$	τ_-	τ_-^{LSA}
a	2.16	1.07	5.20	0.195	0.210	16.7	16.1
b	2.18	1.63	2.17	2.49	0.254	5.39	5.15
c	1.65	1.16	2.18	1.14	0.225	16.2	15.9

Note: τ, T, and τ_- were estimated based on the calculated values of N_1. τ^{LSA}, T^{LSA}, and τ_-^{LSA} were calculated by the linear stability analysis, see Equations 23 and 24. The ecological parameters were set for all cases as $K_0 = 0.2$, $\kappa = 0.01$, and $\beta_2 = 0.5$.

little. So, we compare τ_- evaluated by Equation 24 with the decay time which is estimated from the final gradient of $\log|N_1(t) - N_1{}^*|$-t dependence as illustrated in Fig. 8b, and give the results in Table 1b. The linear stability analysis is seen to work well also for *case* 2.

7 Conclusion

We have simulated using a mathematical model how the population dynamics of a predator-prey system is affected by the prey outlivability distribution due to age difference. The results suggest that the system perturbed far from the equilibrium and then left free follows two restoration stages before arrives at the final state; in the one (named the constitution restoration) which finishes almost in a time approximate to the maximum life span of the prey species, the prey restores nearly the same relative age constitution as that at the equilibrium, and in the other stage (named the total restoration) which lasts for ten or more times the former period, the total populations of the two species restore slowly their equilibrium values. It was also found that the speed of constitution restoration has only weak dependency on the ecological parameters such as childbirth rate, deathrate, and predation pressure but the total restoration process is significantly influenced by these parameters. As to the latter fact, however, further systematic case study is necessary for clarifying the details.

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