

A discrete prey-predator model preserving the dynamics of a structurally unstable Lotka-Volterra model

Hiromi SENO

Department of Mathematical and Life Sciences, Graduate School of Science,
Hiroshima University, Higashi-hiroshima 739-8526, JAPAN

(May 21, 2007)

P.H. Leslie's method to construct a discrete two dimensional dynamical system dynamically consistent with the Lotka-Volterra type of competing two species ordinary differential equations is applied in a newly extended manner for the Lotka-Volterra prey-predator system which is structurally unstable. We show that, independently of the time step size, the derived discrete prey-predator system is dynamically consistent with the continuous counterpart, keeping the nature of neutrally stable periodic orbit. Further, we show that the extended method to construct the discrete prey-predator system can provide a dynamically consistent model also for the logistic Lotka-Volterra one.

Keywords: Lotka-Volterra system; prey-predator model; dynamically consistent; neutrally stable; population dynamics

1 Introduction

At the end of 50's, P.H. Leslie, who is well-known from his pioneer works of the matrix model for the structured population [3,4], constructed and numerically analyzed a kind of discrete two dimensional dynamical system derived from the familiar Lotka-Volterra type of competing two species ordinary differential equations (ODE) [5-7]:

$$\begin{cases} \frac{dN_1(t)}{dt} = \{r_1 - b_{11}N_1(t) - b_{12}N_2(t)\} N_1(t); \\ \frac{dN_2(t)}{dt} = \{r_2 - b_{21}N_1(t) - b_{22}N_2(t)\} N_2(t), \end{cases} \quad (1)$$

where $N_i(t)$ ($i = 1, 2$) is the population size of species i . Parameters r_i , b_{ij} ($i, j = 1, 2$) are all positive. r_i ($i = 1, 2$) is the intrinsic growth rate of species i ,

b_{ii} ($i = 1, 2$) the *intra*-specific density effect of species i , and b_{ij} ($i, j = 1, 2; i \neq j$) the *inter*-specific density effect, that is, the competition effect from species j to species i . For the ODE system (1), Leslie [5] considered the following discrete two dimensional system:

$$\begin{cases} N_1(t+h) = \frac{1}{1 + \phi_1(h) \{b_{11}N_1(t) + b_{12}N_2(t)\}} \cdot e^{r_1 h} N_1(t); \\ N_2(t+h) = \frac{1}{1 + \phi_2(h) \{b_{21}N_1(t) + b_{22}N_2(t)\}} \cdot e^{r_2 h} N_2(t), \end{cases} \quad (2)$$

where

$$\phi_i(h) = \frac{e^{r_i h} - 1}{r_i} \quad (i = 1, 2),$$

and h is the size of time step.

Surprisingly, his discrete system (2) qualitatively conserves the characteristics of the solution of the original ODE system (1) even with sufficiently large time step size h , that is, (2) is a *dynamically consistent* discrete system for the ODE system (1) [2, 8–10, 12, 13]. Therefore, Leslie’s idea to construct the difference equations from the ODEs might serve as an alternative and satisfactory numerical scheme for numerical investigation about nonlinear ODE system.

Different from the usual discretization scheme for ODE (for instance, by Euler method), Leslie’s idea to derive (2) from (1) is specific and intuitive since it significantly depends on the idea of mathematical modelling concerning to the original ODE system. His idea is originally inspired by the relationship between the logistic equation and its exactly corresponding difference equation. For the logistic equation with positive coefficient β of intra-specific density effect on the per capita growth rate:

$$\frac{dN(t)}{dt} = \{r - \beta N(t)\} N(t), \quad (3)$$

we can easily obtain the following exact solution with the initial population size $N(0)$:

$$N(t) = \frac{1}{1 + \phi(t)\beta N(0)} \cdot N(0)e^{rt}, \quad (4)$$

where $\phi(t) = (e^{rt} - 1)/r$. Making use of the exact solution (4), we can immediately obtain the corresponding exact discrete model with an arbitrary time

step size h as follows ($k = 0, 1, 2, \dots$):

$$N_{k+1} = \frac{e^{rh} N_k}{1 + \phi(h)\beta N_k} \tag{5}$$

with $N_0 = N(0)$. This is a discrete model sometimes called ‘Verhulst model’ or ‘Beverton-Holt model’. Independently of the sign of r , the exact discrete model (5) can exactly trace the solution (4) with same parameter values, independently of the time step size h .

Seno [14] has investigated the Leslie’s idea from the viewpoint of the dynamical consistency with respect to the general single-species model given by the following ODE and the counterpart difference equation:

$$\begin{aligned} \frac{dN(t)}{dt} &= \{r - Q(N(t))\}N(t); \\ N_{k+1} &= \frac{e^{rh} N_k}{1 + \phi(h)Q(N_k)}, \end{aligned} \tag{6}$$

where the parameter r is positive, and the function Q is assumed to be non-negative and sufficiently smooth. It was shown that, independently of the time step size h , the qualitative behavior around trivial equilibria is consistent between them, and, if

$$0 < \left. \frac{d[\log Q(N)]}{d[\log N]} \right|_{N=N^*} \leq 1, \tag{7}$$

so is that around the non-trivial equilibrium.

Although Leslie’s idea was inspired by the idea of mathematical modelling concerning to the original ODE system, the derived discrete system could provide a possibly appropriate form as a mathematical model for a generational variation of interacting populations. Except for few models including well-known Nicholson-Bailey model [11], it have attracted little mathematical attention what mathematical description would be appropriate to describe a density effect or an intra/inter-specific reaction in a time step (generation) specified in the discrete model. Especially with respect to the multi species system, the relationship between the ODE model and the discrete model has been considered much little.

In this paper, in contrast to previous researches about such discrete systems dynamically consistent with the continuous counterpart from the viewpoint of some nonstandard *discretization* method (for example, [2,8–10,12,13]), we consider an extension of Leslie’s idea for the Lotka-Volterra prey-predator model, and present a new discrete prey-predator system dynamically consistent with

the original ODE model, even when the original one is structurally unstable.

2 From ODE to time-discrete model

The following Lotka-Volterra prey-predator model is well-known from its structurally unstable nature (e.g. see [1]):

$$\begin{cases} \frac{dH(t)}{dt} = rH(t) - bH(t)P(t); \\ \frac{dP(t)}{dt} = cbH(t)P(t) - \delta P(t), \end{cases} \quad (8)$$

where $H(t)$ and $P(t)$ are respectively population sizes of prey and predator. r is the intrinsic (malthusian) growth rate of prey, δ the natural death rate of predator. b is the predation coefficient, c the energy conversion rate from the predation to the predator's reproduction.

From (8), we can easily find that the following function of populations H and P , which value is kept constant independently of time [1]:

$$V(H, P) = cbH - \delta \log H + bP - r \log P. \quad (9)$$

The constant value is determined by the initial state $(H(0), P(0))$. Indeed, the ODE system (8) has the infinite number of periodic orbits depending on the initial state, and each periodic orbit in the phase space is given by $V(H, P) = V(H(0), P(0))$ (see Fig. 1).

Now, we present the following discrete system dynamically consistent with the original ODE system (8) as we will show in the subsequent analysis:

$$\begin{cases} H_{k+1} = \frac{e^{rh} H_k}{1 + \phi_H(h) b P_k}; \\ P_k = \frac{e^{\delta h} P_{k+1}}{1 + \phi_P(h) c b H_{k+1}}, \end{cases} \quad (10)$$

where

$$\phi_H(h) = \frac{e^{rh} - 1}{r}; \quad \phi_P(h) = \frac{e^{\delta h} - 1}{\delta}$$

and h is the time step size.

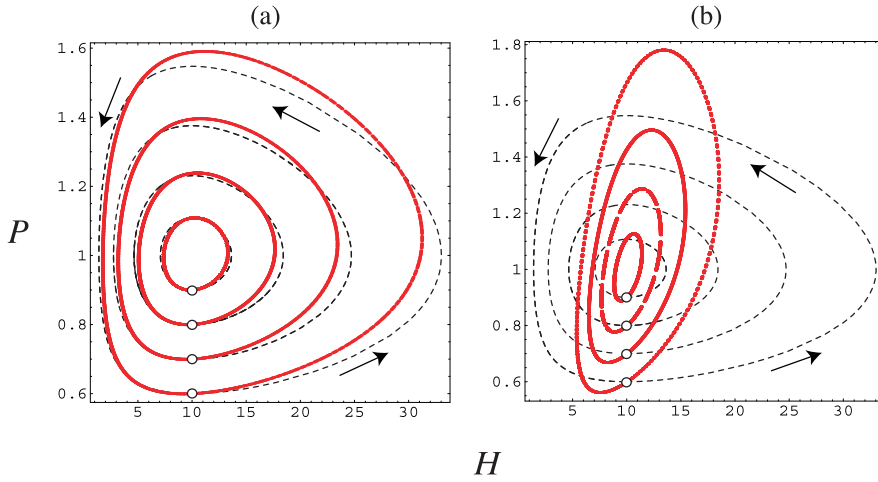


Figure 1. Numerically obtained trajectories in the phase plane (H, P) for the ODE system (8) and the discrete system (11). Trajectories from some different initial points (white circles) are drawn. Dashed thin curves are for (8) and the darker thick plots for (11). (a) $h = 0.5$ to the 1500 th step; (b) $h = 20.0$ to the 3000 th step. $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$.

The first equation for the prey in (10) is built along the method of Leslie [5–7]. In contrast, the second equation for the predator in (10) is built with our method newly extended from the Leslie’s idea: The equation for the predator in the ODE system (8) can be written as follows:

$$\frac{dP(t)}{d[-t]} = \delta P(t) - cbH(t)P(t).$$

The form in the right side of this equation corresponds to that in the right side of the equation for the prey in (8), and is adoptable for the Leslie’s method of building the corresponding discrete equation, except for the variables H and P of $-t$ instead of t . Since the use of $-t$ indicates the temporal inversion as t increases, we put the temporal relation inverse as shown by the second equation in (10), applying the Leslie’s method to build the corresponding discrete equation. Similarly as in Leslie’s case, this extension of the method to build a discrete equation corresponding to an ODE is still intuitive. However, it surprisingly works well as we will show in the following analysis.

Now the system (10) can be rewritten as follows:

$$\begin{cases} H_{k+1} = e^{r_h} H_k \{1 - \Pi_h(P_k)\}; \\ P_{k+1} = e^{-\delta h} \left\{ P_k + c \frac{\phi_P(h)}{\phi_H(h)} \cdot e^{r_h} H_k \cdot \Pi_h(P_k) \right\}, \end{cases} \quad (11)$$

where

$$\Pi_h(P_k) = \frac{\phi_H(h)bP_k}{1 + \phi_H(h)bP_k}. \quad (12)$$

We can easily find that the discrete system (11) converges to the ODE system (8) as $h \rightarrow 0$.

We can regard (11) as the discrete prey-predator system characterized by the predation probability Π_h per prey in the time interval h , given by (12), and the corresponding energy conversion rate from the predation to the predator's reproduction, given by $c\phi_P(h)/\phi_H(h)$.

Since $\phi_H(h)/h \rightarrow 1$ as $h \rightarrow 0$, $\Pi_h(P_k)/h$ converges to bP_k . Therefore, the predation probability Π_h given by (12) can be regarded as providing the predation effect appropriately corresponding to the predation term in the ODE system (8). The energy conversion rate in the discrete model (11) converges to c as $h \rightarrow 0$, which exactly corresponds to that in the ODE model (8), too.

These features of the discrete model (11) is very interesting from the viewpoint of mathematical modelling for the time-discrete variation of population size. The predation probability Π_h is a rational function of bP , which is monotonically increasing in terms of bP with the upper bound 1. Hence the ratio of predated prey population is not proportional to the predator population size in the time-discrete model. In contrast, in the ODE model (8), the momental predation rate is proportional to the predator population size at each moment, because of the mass-action type of predation term. In fact, such mass-action type of predation term in the ODE model does not mean the linear relationship of the decrease of prey population size due to the predation. It results in a non-linear characteristics of the decrease of prey population size. In our derivation of a dynamically consistent discrete prey-predator model, we can regard that such non-linearity of the decrease of prey population size due to the predation would be reflected to the form of rational function for the predation probability Π_h .

2.1 Existence and stability of equilibria

It is easily shown that the systems of (8) and (11) have the common equilibria: $(0, 0)$ and $(\delta/\alpha, r/b)$. No other equilibrium exists. As for the trivial equilibrium $(0, 0)$, the eigenvalues for (8) are r and $-\delta$ while e^{rh} and $e^{-\delta h}$ for (11). Therefore, for both systems of (8) and (11), the equilibrium $(0, 0)$ is unstable as a saddle point, independently of the time step size h .

As for the non-trivial equilibrium $(\delta/\alpha, r/b)$, the eigenvalues for (8) is given by $\pm i\sqrt{r\delta}$. So the equilibrium $(\delta/\alpha, r/b)$ has the neutral stability for (8). In comparison, the eigenvalue λ for the equilibrium $(\delta/\alpha, r/b)$ of (11) is given by

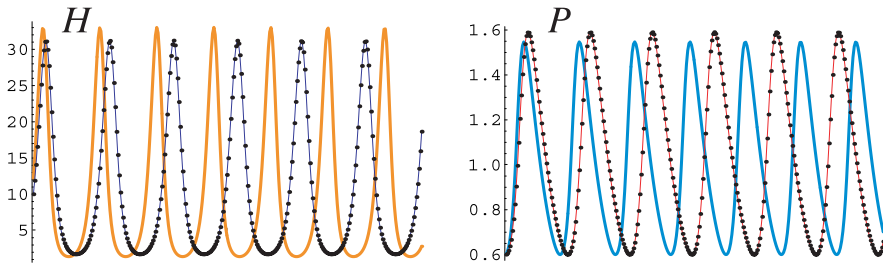


Figure 2. Numerically obtained variation of H and P to the 300 th step. Thick curve is for the ODE system (8), and the thin with black plots is for the discrete system (11). $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$; $h = 0.5$; $H(0) = H_0 = 10.0$; $P(0) = P_0 = 0.6$.

the roots of the following characteristic equation:

$$\lambda^2 - \left(1 + e^{-rh} + e^{-\delta h} - e^{-rh}e^{-\delta h}\right)\lambda + 1 = 0. \tag{13}$$

Since the discriminant for this equation is given by

$$-\left(1 - e^{-rh}\right)\left(1 - e^{-\delta h}\right)\left(3 + e^{-rh} + e^{-\delta h} - e^{-rh}e^{-\delta h}\right) < 0,$$

the eigenvalues are always complex. Further from the characteristic equation (13), we can easily find that the absolute value of the eigenvalue is 1. The unity of the absolute value of the eigenvalue means that the stability of the equilibrium $(\delta/\alpha, r/b)$ of (11) is neutral as that of (8), again independently of the time step size h .

As indicated by the numerical calculation of trajectories in the phase plane (H, P) in Fig. 1, the sequence of points given by (11) is on a closed curve determined by the initial point in the phase plane. This can be regarded as a nature dynamically consistent with the original ODE system (8) which has the periodic orbit $V(H, P) = V(H(0), P(0))$ defined by (9).

On the other hand, from a mathematical viewpoint, the discrete system (11) shows a sort of chaotic variation. Although Fig. 2 might be quasi-periodic, it does not, because the trajectory in the phase plane appears dense on a closed curve as shown in Fig. 1. However, the numerically estimated Lyapunov exponent results in nearly zero instead of positive.

2.2 Numerical estimation of the difference from the ODE counterpart

In this section, we numerically investigate the quantitative difference between the behaviors of the discrete system (11) and the ODE one (8). Although we have seen the qualitative correspondence between them in the previous section,

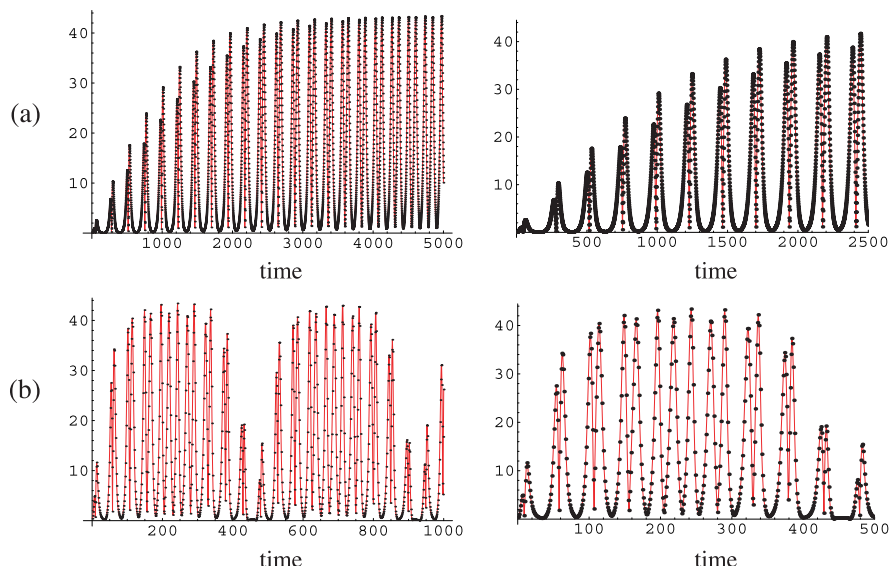


Figure 3. Numerically obtained variation of the distance between points of (8) and (11) in the phase plane (H, P) . (a) $h = 0.1$; (b) $h = 0.5$. Commonly, $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$; $H(0) = H_0 = 10.0$; $P(0) = P_0 = 0.5$.

the quantitative difference between them could be relevant, for instance, as a nonstandard discretization method for the ODE system (8).

As seen in Fig. 2, the variation of population sizes for (8) and (11) is quantitatively different from each other in terms of their values at each moment, whereas the qualitative nature is consistent as shown in the previous section. In fact, as shown in Fig. 3, the distance between points of (8) and (11) in the phase plane (H, P) appears oscillatory. Numerical results imply that the actual velocity of moving on a closed curve in the phase plane is different about these two system even with the same parameter values. We can see that the velocity is higher for the discrete system (11) than for the ODE system (8).

To investigate numerically the h -dependence of the difference in terms of the distance between points of (8) and (11) in the phase plane (H, P) , we consider the following time-averaged difference of the distance:

$$\widehat{E}_d = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{k=1}^n \sqrt{\{H_k - H(kh)\}^2 + \{P_k - P(kh)\}^2}. \quad (14)$$

Numerically estimated value of \widehat{E}_d is shown in Fig. 5. Our numerical calculations indicate that the value of \widehat{E}_d tends to increase in terms of h . This means that the trajectory of the discrete system (11) becomes quantitatively more different from the trajectory of the ODE system (8) with the same initial state.

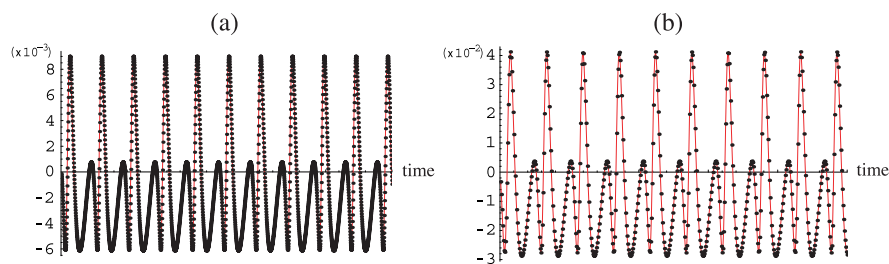


Figure 4. Numerically obtained variation of the difference of the value of function $V(H, P)$, defined by (9), for the discrete system (11). The value of $\{V(H_k, P_k) - V(H_0, P_0)\}/V(H_0, P_0)$ is plotted. (a) $h = 0.1$ to the 2500 th step; (b) $h = 0.5$ to the 500 step. Commonly, $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$; $H_0 = 10.0$; $P_0 = 0.5$.

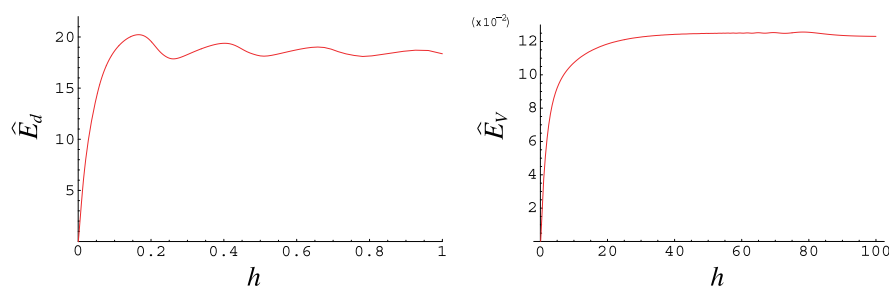


Figure 5. Numerically obtained h -dependence of the averaged difference \widehat{E}_d and \widehat{E}_V , respectively defined by (14) and (15), between the ODE system (8) and the discrete one (11), according to the trajectory in the phase plane (H, P) . $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$; $H_0 = 10.0$; $P_0 = 0.5$.

This can be seen also in Fig. 2. It is natural that the value \widehat{E}_d also depends on the initial state (H_0, P_0) . Besides, since each trajectory is on a closed curve, the averaged difference \widehat{E}_d is bounded.

As another comparison between them, we investigate the temporal variation in the value of the function $V(H, P)$ defined by (9), since it temporally keeps a constant value $V(H(0), P(0))$ determined by the initial state in case of the ODE system (8). As shown in Fig. 4, its variation is oscillatory for the discrete system (11), too, and however has relatively small values in its temporal variation. As we can see in Fig. 1(a), the closed curve on which the trajectory of the discrete system (11) for a small h (even though still relatively large from the viewpoint of numerical calculation approximating the ODE system (8)) has a little difference from that of the ODE system (8), while the difference becomes greater as the time step size h gets larger.

To investigate numerically the h -dependence of the difference of the value of $V(H, P)$ for the discrete system (11), we consider the following time-averaged

difference of the value of $V(H, P)$:

$$\widehat{E}_V = \lim_{n \rightarrow \infty} \frac{1}{V(H_0, P_0)} \sqrt{\frac{1}{n} \sum_{k=1}^n \{V(H_k, P_k) - V(H_0, P_0)\}^2}. \quad (15)$$

Numerically estimated value of \widehat{E}_V is shown in Fig. 5. Our numerical calculations indicate that the value of \widehat{E}_V is monotonically increasing in terms of h . This means that the closed curve on which the trajectory of the discrete system (11) is located is more different from the closed orbit of the ODE system (8) with the same initial state as the time step size h gets larger. This can be seen also in Fig. 1. It is natural that the value \widehat{E}_V also depends on the initial state (H_0, P_0) . Besides, since each trajectory is on a closed curve, the averaged difference \widehat{E}_V is bounded.

2.3 General form of the discrete 1 prey-1 predator model

From the discrete system (11), we can derive the following general form of the discrete 1 prey-1 predator model:

$$\begin{cases} X_{k+1} = R \left(X_k - \frac{X_k Y_k}{1 + Y_k} \right); \\ Y_{k+1} = D Y_k + \frac{X_k Y_k}{1 + Y_k}. \end{cases} \quad (16)$$

Parameters R and D are positive with $D < 1$. This system can be derived from (11) with the following transformation of variables and parameters: $X_k = cb\phi_P(h)e^{rh}H_k$; $X_{k+1} = cb\phi_P(h)e^{rh}H_{k+1}$; $Y_k = \phi_H(h)bP_k$; $Y_{k+1} = \phi_H(h)bP_{k+1}$; $R = e^{rh}$; $D = e^{-\delta h}$. Although these parameters are not independent of each other in terms of h , we here consider more generally the case when these parameters R and D are independent.

The confinement of $D < 1$ is a modelling requirement. As a dynamics of predator population growth, the predator population can grow only with the predation. If $D > 1$, $Y_k \rightarrow \infty$ as $k \rightarrow \infty$ even without the prey, since $Y_{k+1} > Y_k$ for any k . Now the parameter D means the natural death rate for the predator, so that we assume hereafter that $D < 1$.

The system (16) has only two equilibria: $(0, 0)$ and $(R(1 - D), R - 1)$. The non-trivial POSITIVE equilibrium $(R(1 - D), R - 1)$ exists if and only if $D < 1$ and $R > 1$. If $R < 1$ and $D < 1$, the trivial equilibrium $(0, 0)$ is locally stable. As in case of the discrete system (11), even in this general case of (16), the stability of the non-trivial positive equilibrium is neutral whenever it exists.

Numerical calculations show that the trajectory for (16) is always on a closed curve, as in case of (11), independently of parameter values. Therefore, the general form of discrete population dynamics given by (16) can be regarded as dynamically consistent with the Lotka-Volterra prey-predator system (8).

Consequently, we can regard the model of the prey-predator population dynamics given by (16) as a time-discrete version corresponding to the Lotka-Volterra prey-predator model (8). Further, we could regard the prey-predator reaction term given by a rational function in (16) as a temporally integrated (over the period of the discrete time step) mass-action type of prey-predator reaction, because of the correspondence with the mass-action term in the ODE model (8).

3 Application for a more general structurally unstable system of prey-predator type

In this section, we consider a family of general prey-predator ODE system given by

$$\begin{cases} \frac{dX(t)}{dt} = rX(t) - f(Y(t))X(t) \\ \frac{dY(t)}{dt} = g(X(t))Y(t) - \delta Y(t), \end{cases} \tag{17}$$

where functions f and g are assumed to be sufficiently smooth and satisfy that $f(x) \geq 0$ and $g(x) \geq 0$ for any $x > 0$ with $f(0) = g(0) = 0$.

Our method to construct the corresponding discrete system gives the following:

$$\begin{cases} X_{k+1} = \frac{e^{rh} X_k}{1 + \phi_H(h)f(Y_k)}; \\ Y_k = \frac{e^{\delta h} Y_{k+1}}{1 + \phi_P(h)g(X_{k+1})}, \end{cases}$$

that is,

$$\begin{cases} X_{k+1} = e^{rh} X(t) \{1 - \Pi_h(Y_k)\}; \\ Y_{k+1} = e^{-\delta h} \{Y_k + \phi_P(h)g(X_{k+1})Y_k\}, \end{cases} \tag{18}$$

where

$$\Pi_h(Y_k) = \frac{\phi_H(h)f(Y_k)}{1 + \phi_H(h)f(Y_k)}.$$

Existence and stability of equilibria. It can be easily seen that the ODE prey-predator system (17) and the discrete system (18) have the following common equilibria and does not have any other: $(0, 0)$ and (X^*, Y^*) , where the coexistent equilibrium (X^*, Y^*) can exist if and only if the following equations have positive roots:

$$\begin{cases} f(Y^*) = r; \\ g(X^*) = \delta. \end{cases}$$

As for the trivial equilibrium $(0, 0)$, the eigenvalues for (17) are r and $-\delta$ while e^{rh} and $e^{-\delta h}$ for (18). Therefore, for both systems of (17) and (18), the equilibrium $(0, 0)$ is unstable as a saddle point, independently of the time step size h .

Next, let us consider the case when a non-trivial equilibrium (X^*, Y^*) exists. In this case, the eigenvalues for the ODE system (17) are given by $\pm\sqrt{-f'(Y^*)g'(X^*)X^*Y^*}$. Therefore, for the ODE system (17), the coexistent equilibrium (X^*, Y^*) is unstable if $f'(Y^*)g'(X^*) < 0$ as a saddle, while neutrally stable with purely imaginary eigenvalues if $f'(Y^*)g'(X^*) > 0$.

As for the discrete system (18), the eigenvalue λ for the coexistent equilibrium (X^*, Y^*) is given by the root of the following characteristic equation:

$$\lambda^2 - (2 - AB)\lambda + 1 = (\lambda - 1)^2 - AB\lambda = 0,$$

where

$$A = e^{-rh}\phi_H(h)f'(Y^*)X^*; \quad B = e^{-\delta h}\phi_P(h)g'(X^*)Y^*.$$

From the above characteristic equation, we can find that the coexistent equilibrium (X^*, Y^*) of the discrete system (18) is unstable if $f'(Y^*)g'(X^*) < 0$ as a saddle with positive eigenvalues, one of which is less than 1 and the other more than 1. When $f'(Y^*)g'(X^*) > 0$, if

$$f'(Y^*)g'(X^*)X^*Y^* < \Psi(h) = \frac{4e^{(r+\delta)h}}{\phi_H(h)\phi_P(h)}, \tag{19}$$

the eigenvalues are complex with the absolute value 1, so that the equilibrium is neutrally stable. In contrast, when $f'(Y^*)g'(X^*) > 0$, if $f'(Y^*)g'(X^*)X^*Y^* >$

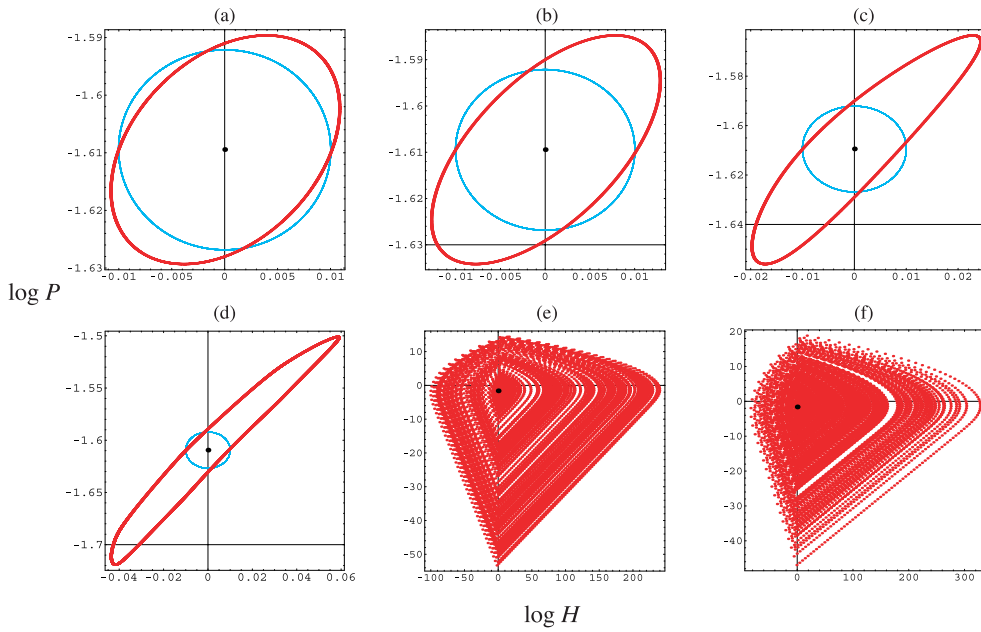


Figure 6. Numerically obtained trajectories in the phase plane (H, P) for the ODE system (17) and the discrete one (18) with (20). Uniquely determined coexistent equilibrium is indicated by a black point. The lighter curve is for (17) and the darker plots to the ten thousandth step for (18). (a) $h = 0.5$; (b) $h = 1.0$; (c) $h = 2.0$; (d) $h = 2.5$; (e) $h = 2.65$; (f) $h = 5.0$. Commonly, $r = 1.0$; $\delta = 0.5$; $H_0 = 0.99$; $P_0 = 0.25$.

$\Psi(h)$, the eigenvalues are negative, one of which is less than -1 and the other more than -1 , so that it is a saddle again. In this case, the dynamical consistency breaks down between (17) and (18). Since $\Psi(h)$ is monotonically decreasing in terms of h and $\lim_{h \rightarrow 0} \Psi(h) = \infty$, this inconsistency can not occur for sufficiently small time step size h but could do for relatively large time step size h , depending on the characteristics of functions f and g . For example, the following f and g give an example for such a case of the dynamical consistency breaking down (see Fig. 6):

$$\begin{aligned}
 f(y) &= 5y; \\
 g(x) &= \frac{x^{12}}{1 + x^{12}}.
 \end{aligned}
 \tag{20}$$

In this case, the discrete system (18) shows a chaotic oscillation for sufficiently large time step size h .

Since $\Psi(h)$ further satisfies that $\lim_{h \rightarrow \infty} \Psi(h) = r\delta$, if $f'(Y^*)g'(X^*)X^*Y^* \leq$

$r\delta = f(Y^*)g(X^*)$, that is, if

$$\left. \frac{d[\log f(y)]}{d[\log y]} \right|_{y=Y^*} \cdot \left. \frac{d[\log g(x)]}{d[\log x]} \right|_{x=X^*} \leq 1, \tag{21}$$

then the condition (19) is always satisfied so that the coexistent equilibrium (X^*, Y^*) is neutrally stable, independently of the value of time step h , when $f'(Y^*)g'(X^*) > 0$. The condition (21) appears the extension of the corresponding (7) for the one-dimensional case (6) discussed by Seno [14]. Lastly, if the condition (21) is satisfied for every equilibrium, then the discrete system (18) is dynamically consistent with the ODE system (17) according to the existence and the local stability of equilibria.

4 Application for the Lotka-Volterra prey-predator system with logistically growing prey

In this section, as a natural extended ODE model from (8), we consider the following ODE system with logistically growing prey:

$$\begin{cases} \frac{dH(t)}{dt} = \{r - \beta H(t)\} H(t) - bH(t)P(t); \\ \frac{dP(t)}{dt} = cbH(t)P(t) - \delta P(t). \end{cases} \tag{22}$$

Analogously to the discrete system (10), we now present the following discrete system a corresponding discrete model:

$$\begin{cases} H_{k+1} = \frac{e^{rh} H_k}{1 + \phi_H(h) \{\beta H_k + bP_k\}}; \\ P_k = \frac{e^{\delta h} P_{k+1}}{1 + \phi_P(h) cbH_{k+1}}, \end{cases}$$

that is,

$$\begin{cases} H_{k+1} = e^{rh} H_k \{1 - \Gamma_h(H_k, P_k) - \Pi_h(H_k, P_k)\}; \\ P_{k+1} = e^{-\delta h} \left\{ P_k + c \frac{\phi_P(h)}{\phi_H(h)} \cdot e^{rh} H_k \cdot \Pi_h(H_k, P_k) \right\}, \end{cases} \tag{23}$$

where

$$\Gamma_h(H_k, P_k) = \frac{\phi_H(h)\beta H_k}{1 + \phi_H(h)\beta H_k + \phi_H(h)bP_k}; \tag{24}$$

$$\Pi_h(H_k, P_k) = \frac{\phi_H(h)bP_k}{1 + \phi_H(h)\beta H_k + \phi_H(h)bP_k}. \tag{25}$$

From the obtained form of the discrete system (23), we can see that the function Γ_h represents the contribution of the logistic density effect on the prey population growth in the period h , and the function Π_h does that of the predation. Differently from the predation probability (12) in the previous discrete model (11), the function Π_h of (25) depends also on the prey population size H_k . We can consider that this would be an effect of the logistic density effect on the predation efficiency since the reduction of prey density is reflected to the net growth rate through the density effect while the predation to reduce the prey density depends on the prey density itself. Simultaneously the density effect function Γ_h of (24) depends on the predator population size. This can be regarded as to reflect the effect of predation which decreases the prey density and then reduces the density effect in the period h .

Existence and stability of equilibria. It can be easily seen that the ODE system (22) and the discrete system (23) have the following common three equilibria: $(0, 0)$, $(r/\beta, 0)$, and $(\delta/(cb), (rcb - \beta\delta)/(cb^2))$.

The extinction equilibrium $(0, 0)$ is unstable as a saddle point for both systems because the eigenvalues are r and $-\delta$ for the ODE system (22) while e^{rh} and $e^{-\delta h}$ for the discrete system (23).

As for the predator extinction equilibrium $(r/\beta, 0)$, the eigenvalues are $-r$ and $rcb/\beta - \delta$ for the ODE system (22) while e^{-rh} and

$$(1 - e^{-\delta h})\frac{rcb}{\beta\delta} + e^{-\delta h}$$

for the discrete system (23). In both cases, we find that the equilibrium is a locally stable node if $\beta\delta/rcb > 1$. If $\beta\delta/rcb < 1$, it is a saddle in both cases. Hence, also as for the stability of the predator extinction equilibrium $(r/\beta, 0)$, the discrete system (23) is dynamically consistent with the ODE system (22).

As for the coexistent equilibrium $(\delta/(cb), (rcb - \beta\delta)/(cb^2))$, we consider its stability under the following condition for its positiveness: $\beta\delta/rcb < 1$. If this positiveness condition is satisfied, the predator extinction equilibrium $(r/\beta, 0)$ is always unstable, that is, if the coexistent equilibrium exists, the predator extinction equilibrium is not feasible.

The eigenvalue λ of the coexistent equilibrium for the ODE system (22) is

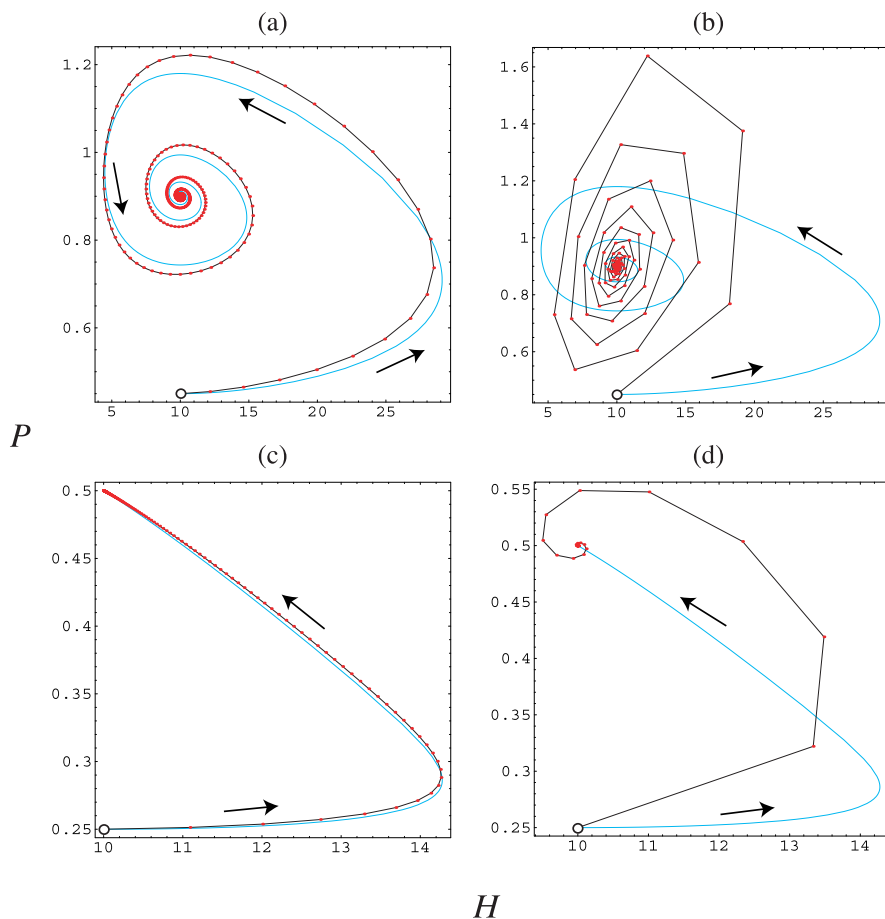


Figure 7. Numerically obtained trajectories in the phase plane (H, P) for the ODE system (22) and the discrete system (23). Lighter curves are for (22) and the darker thick plots (connected with thin black lines) for (23). (a) $\beta = 0.01$ and $h = 0.5$; (b) $\beta = 0.01$ and $h = 20.0$; (c) $\beta = 0.05$ and $h = 0.5$; (d) $\beta = 0.05$ and $h = 20.0$. Commonly, $r = 1.0$; $b = 1.0$; $c = 0.01$; $\delta = 0.1$.

given by the following characteristic equation:

$$\lambda^2 + \frac{\beta\delta}{cb}\lambda + r\delta\left(1 - \frac{\beta\delta}{rcb}\right) = 0.$$

We can easily find that the coexistent equilibrium $(\delta/(cb), (rcb - \beta\delta)/(cb^2))$ for the ODE system (22) is locally stable whenever it exists (see Fig. 7). Further, from the above characteristic equation, we find that, if

$$\frac{\beta\delta}{rcb} < \frac{2}{1 + \sqrt{1 + r/\delta}},$$

the coexistent equilibrium $(\delta/(cb), (rcb - \beta\delta)/(cb^2))$ is a stable focus (Fig. 7(a, b)), while, if

$$\frac{2}{1 + \sqrt{1 + r/\delta}} \leq \frac{\beta\delta}{rcb} < 1,$$

it is a stable node (Fig. 7(c, d)).

In contrast, the eigenvalue λ of the coexistent equilibrium for the discrete system (23) is given by the following characteristic equation:

$$g(\lambda) = \lambda^2 - B\lambda + 1 - \frac{\beta\delta}{rcb}(1 - e^{-rh}) = 0,$$

where

$$B = \left\{ 1 - \frac{\beta\delta}{rcb}(1 - e^{-rh}) \right\} e^{-\delta h} + \left\{ 1 + (1 - e^{-\delta h})e^{-rh} \right\}.$$

For $\beta\delta/rcb < 1$ when the coexistence equilibrium exists, $0 < g(0) < 1$, $g(1) > 0$ and $0 < B < 2$. Hence we can easily see that the root of above characteristic equation always satisfies that $|\lambda| < 1$. This means that the coexistent equilibrium for the discrete system (23) is locally stable if it exists (Fig. 7).

Further analysis shows that every eigenvalue for the coexistent equilibrium for the discrete system (23) is positive less than 1 if the following condition is satisfied:

$$q(h) < \frac{\beta\delta}{rcb} < 1,$$

where

$$q(h) = 1 - \frac{1 - e^{-rh}}{\left\{ \sqrt{1 - e^{-\delta h}} + \sqrt{1 - e^{-(r+\delta)h}} \right\}^2}.$$

In this case, the coexistence equilibrium of the discrete system (23) is a stable node. If $\beta\delta/rcb < q(h)$, every eigenvalue is complex with its absolute value less than 1, so that the coexistence equilibrium of the discrete system (23) is a stable focus. We can easily find that $q(h) \rightarrow 2/(1 + \sqrt{1 + r/\delta})$ as $h \rightarrow 0$, and $q(h) \rightarrow 3/4$ as $h \rightarrow \infty$.

From these results, although the dynamical behaviors of the ODE system (22) and the discrete one (23) are mostly consistent, the subtle nature of the bifurcation with respect to the stability of coexistent equilibrium is affected

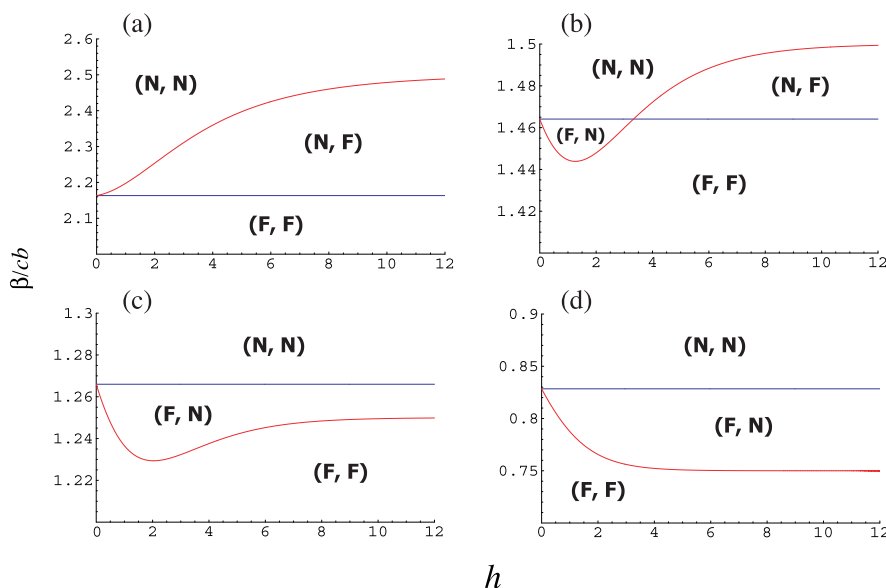


Figure 8. A numerical example of the h -dependence of the bifurcation between the stable node and the stable focus according to the coexistent equilibrium of (22) and (23). Region (F, F) indicates that both the ODE and the discrete systems show the stable focus, and (N, F) does that the ODE system shows the stable node while the discrete one does the stable focus. The other symbols are similarly defined. (a) $b = 0.3$; (b) $b = 0.5$; (c) $b = 0.6$; (d) $b = 1.0$. Commonly $r = 1.0$.

by the value of time step size h (see Figs. 7(d) and 8). However, since $q(h)$ has a finite limit of the value $3/4$ as shown in the above, surprisingly the difference of the bifurcation boundary is bounded for any time step size h (Fig. 8). In this sense, the dynamical consistency between the ODE system (22) and the discrete one (23) would be regarded as rather robust against the time step size h .

5 Conclusion and future directions

Our method to construct a discrete prey-predator system from the ODE model successfully provides a dynamically consistent model which could have a structure explicitly translatable in ecological meanings from the viewpoint of mathematical modelling. Although our method is somehow intuitive as Leslie's, the mathematical formulas in the constructed model would be appropriate expression of the intra/inter-specific density effect on the population dynamics in a discrete time step. For further example, some numerical and mathematical analyses show that our method would be valid also for the Kermack-McKendrick SIR model, which we did not describe in this paper.

In history, lots of ODE models have been successful to explain or describe

biological phenomena even when those phenomena are fundamentally composed of time-discrete or temporally discontinuous events. Generally we could have any data in a discrete time step or analyze only such a sequence of data. In these reasons, some successful ODE models would be expected to provide some informations useful to find an appropriate structure of time-discrete model which explain or describe the biological phenomena. Especially in the theory of population dynamics, the essential structure of mathematical model depends on the expression of intra/inter-specific interaction. Hence it is very important how the density effect is involved in the model. However, we have had little knowledge or discussion about the appropriate formulas of some density effect in the discrete model, although some discrete model derived from the ODE counterpart model with a discretization method have been successful. We expect that our result would be helpful to develop some theory or discussion about this subject.

As another aspect, since our method to construct a discrete system from the ODE counterpart is newly discussed here, it would be helpful for some discussion about some nonstandard discretization method which could robustly dynamically consistent with the original ODE system. Recently some works have been done on the nonstandard discretization of the Lotka-Volterra prey-predator model that also preserves the unstable structure of the original ODE system [2, 8–10, 12, 13]. Those works have focused the algorithmic way of the dynamically consistent discretization for the ODE system with the polynomial (especially mass-action) type of reaction terms. Roeger [13] discussed the generalization of the dynamically consistent discretization originally proposed by Mickens [9] for the Lotka-Volterra system, though there was no discussion about the meanings or the perspectives as the discrete model of population dynamics with some specific density effect. In her paper, the discrete prey-predator system corresponding to ours, (11) with (12), appears as a specific case, although there was a difference about the contribution of the time step size h in the discrete system. Moreover her and the other previous works did not mention the idea and the intuitive way of discretization by Leslie and Gower [5–7], and independently discussed the dynamically consistent discretization.

Since the aim of this paper is to discuss the structure of a discrete *model* corresponding to the Lotka-Volterra prey-predator model, we do not discuss in this paper any more the further generalization of our method to construct a discrete system. It is very interesting to extend our method, for instance, to a multi-species (more than one prey or predator) system or to a more general family of 1 prey-1 predator system. It is one of the next steps of our work.

References

- [1] Britton, N.F., 2003, *Essential Mathematical Biology*, Springer-Verlag, London.
- [2] Cushing, J.M., Leverage, S., Chitnis, N. and Henson, S.M., 2004, Some discrete competition models and the competitive exclusion principle, *J. Diff. Eq. Appl.*, **10**, 1139–1151.
- [3] Leslie, P.H., 1945, On the use of matrices in certain population mathematics, *Biometrika*, **33**, 183–212.
- [4] Leslie, P.H., 1948, Some further notes on the use of matrices in population mathematics, *Biometrika*, **35**, 213–245.
- [5] Leslie, P.H., 1958, A stochastic model for studying the properties of certain biological systems by numerical methods, *Biometrika*, **45**, 16–31.
- [6] Leslie, P.H. and Gower, J.C., 1958, The properties of a stochastic model for two competing species, *Biometrika*, **45**, 316–330.
- [7] Leslie, P.H. and Gower, J.C., 1960, The properties of a stochastic model for the prey-predator type of interaction between two species, *Biometrika*, **47**, 219–234.
- [8] Liu, P. and Elaydi, S.N., 2001, Discrete competitive and cooperative models of Lotka-Volterra type, *Ecology*, **54**, 384–391.
- [9] Mickens, R.E., 2003, A nonstandard finite-difference scheme for the Lotka-Volterra system, *Appl. Num. Math.*, **45**, 309–314.
- [10] Mounim, A.S. and de Dormale, B., 2004, A note on Mickens's finite-difference scheme for the Lotka-Volterra system, *Appl. Num. Math.*, **51**, 341–344.
- [11] Nicholson, A.J. and Bailey, V.A., 1935, The balance of animal populations. part I, *Proc. Zool. Soc. Lond.*, **1935**(3), 551–598.
- [12] Roeger, L.-I.W., 2005, A nonstandard discretization method for Lotka-Volterra models that preserves periodic solutions, *J. Diff. Eq. Appl.*, **11**, 721–733.
- [13] Roeger, L.-I.W., 2006, Nonstandard finite-difference schemes for the Lotka-Volterra systems: generalization of Mickens's method, *J. Diff. Eq. Appl.*, **12**, 937–948.
- [14] Seno, H., 2003, Some time-discrete models derived from ODE for single-species population dynamics: Leslie's idea revisited, *Scientiae Mathematicae Japonicae*, **58**, 389–398.