# SOME TIME-DISCRETE MODELS DERIVED FROM ODE
## FOR
# SINGLE-SPECIES POPULATION DYNAMICS
## — LESLIE'S IDEA REVISITED —

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ABSTRACT. At the end of 50's, P.H. Leslie constructed and numerically analyzed a kind of time-discrete two dimensional dynamical system derived from Lotka-Volterra type of competing 2-species ordinary differential equations. Leslie's idea to derive the time-discrete model is specific, different from the usual discretization scheme for ordinal differential equation (for instance, by Euler method), and is intuitive since it significantly depends on an idea of mathematical modelling concerning to the original ODE system in part. His time-discrete system succeeds in qualitatively conserving well the characteristics of solution for the original differential dynamical system. In this paper, we consider some extensions of Leslie's idea to the more general single-species population dynamics and derive the time-discrete system which can robustly maintain the qualitative natures of original ODE system, especially focusing on the existence and the local stability of equilibria. Further, we discuss the behaviour of solution near equlibrium, too.

**1 Introduction** At the end of 50's, P.H. Leslie, who is well-known today from his pioneer works with matrix model for structured population [5, 6], constructed and numerically analyzed a kind of time-discrete two dimensional dynamical system derived from familiar Lotka-Volterra type of competing 2-species ordinary differential equations (ODE) [7, 8, 9], which is as follows:

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

where $N_i(t)$ $(i = 1, 2)$ is the population size of species $i$ at time $t$. 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 [7] consider the following time-discrete two dimensional system:

$$(2) \qquad \begin{cases} N_1(t+h) = \dfrac{1}{1 + \phi_{r_1}(h)\{b_{11}N_1(t) + b_{12}N_2(t)\}} \cdot \mathrm{e}^{r_1 h} N_1(t) \\ N_2(t+h) = \dfrac{1}{1 + \phi_{r_2}(h)\{b_{21}N_1(t) + b_{22}N_2(t)\}} \cdot \mathrm{e}^{r_2 h} N_2(t), \end{cases}$$

where

$$(3) \qquad \phi_{r_i}(h) = \dfrac{\mathrm{e}^{r_i h} - 1}{r_i} \quad (i = 1, 2),$$

and $h$ is the size of time step.

Leslie's idea to derive (2) from (1) is specific, different from the usual discretization scheme for ODE (for instance, by Euler method), and is intuitive since it significantly depends on an idea of mathematical modelling concerning to the original ODE system in part. However, the derived time-discrete system (2) qualitatively conserves the characteristics of solution for the original differential dynamical system (1), as in case of Runge-Kutta method for numerical calculations of (1). Moreover, numerical calculation of (2) seems to be rather robust to give qualitatively same results as the original ODE system (1) does, even with sufficiently large size of time step $h$. 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.

On the other hand, as mentioned above, Leslie's idea was inspired by an idea of mathematical modelling concerning to the original ODE system. This means that the derived time-discrete system could have a possibly appropriate form of mathematical model for time-discrete variation of interacting populations. Except for few models including well-known Nicholson-Bailey model [11], it have attracted so little mathematical attention what mathematical description is appropriate to describe a specific density effect in time-discrete model or how we should model a specific density effect in time-discrete model.

In this paper, we consider some extensions of Leslie's idea to the more general single-species population dynamics, and derive the time-discrete system which can robustly maintain the qualitative natures of original ODE system, especially focusing on the existence and the local stability of equilibria. Further, we discuss the behaviour of solution near equlibrium, too.

## 2    From ODE to Time-Discrete Model

### 2.1    Some exact time-discrete model derived from ODE

LOGISTIC GROWTH For the logistic equation with positive coefficient $\beta$ of intra-specific density dependency in per capita growth rate:

$$(4) \qquad \frac{dN(t)}{dt} = \{r - \beta N(t)\}\, N(t),$$

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

$$(5) \qquad N(t) = \frac{1}{1 + \phi_r(t)\beta N(0)} \cdot N(0)\mathrm{e}^{rt},$$

where $\phi_r(t)$ is defined same as (3). Making use of the exact solution (5), we can immediately obtain the corresponding exact time-discrete model as follows:

$$(6) \qquad N(t + h) = \frac{1}{1 + \phi_r(h)\beta N(t)} \cdot N(t)\mathrm{e}^{rh}.$$

This is sometimes called 'Verhurst model' or 'Beverton-Holt model'. Independently of the sign of $r$, the time-discrete model (6) can exactly trace the solution (5).

The difference scheme derived from (4) by Euler method with positive $r$:

$$(7) \qquad \widetilde{N}(t + h) = \left\{1 + rh - \beta h \widetilde{N}(t)\right\} \widetilde{N}(t)$$

is well-known as to show a pitch-fork bifurcation toward chaos as $h$ gets larger. Only when $h < 2/r$, $\widetilde{N}$ asymptotically converges to the equilibrium value same with that for (4):

$\widetilde{N}(t) \to r/\beta$ as $t \to \infty$. However, in case of $1/r < h < 2/r$, $\widetilde{N}$ asymptotically converges to the equilibrium value with a dumping oscillation, although the solution $N(t)$ of (4) monotonically does. In this sense, only $\widetilde{N}$ with $h \leq 1/r$ realizes the qualitatively same behaviour as the solution $N(t)$ of (4) does. When $h > 2/r$, $\widetilde{N}(t)$ asymptotically converges to a periodic variation as $t \to \infty$, or behaves chaotic.

**TIME-INVERSED LOGISTIC EQUATION** In this section, we consider the equation (4) substituted $\beta = -\gamma < 0$ and $r = -\rho < 0$:

$$(8) \qquad \frac{dN(t)}{dt} = \{\gamma N(t) - \rho\} N(t).$$

This is mathematically equivalent to the equation (4) substituted $-t$ for time $t$, that is, with the inversion of time. The exact solution for (8) can be formally given by (5) with parameters' substitutions of $\beta = -\gamma$ and $r = -\rho$. As a mathematical model for population dynamics, (8) can be regarded as a model to have the meaning such that the population has per capita natural growth rate proportional to the population size $N$ and a constant natural death rate $\rho$.

According to (8), $N(t)$ monotonically converges to zero as $t \to \infty$ for $N(0) \leq \rho/\gamma$, whereas it infinitely diverges for $N(0) > \rho/\gamma$ at a finite time $t = t_c$:

$$t_c = -\frac{1}{r} \ln \left\{ 1 - \frac{\rho/\gamma}{N(0)} \right\}.$$

The corresponding time-discrete model can be derived directly from the exact solution for (8):

$$(9) \qquad N(t+h) = \frac{1}{1 - \phi_{-\rho}(h)\gamma N(t)} \cdot N(t)\mathrm{e}^{-\rho h}.$$

Also for the time-discrete model (9) with $N(0) \leq \rho/\gamma$, $N(t)$ monotonically converges to zero as $t \to \infty$, too. In contrast, with $N(0) > \rho/\gamma$, the behaviour of (9) is different from that of the solution for (8) even though (9) is derived from the exact solution without any approximation. For $N(0) > 1/(\phi_{-\rho}(h)\gamma)$, $N(1)$ is negative, and subsequent values of $N$ become all negative, which are monotonically and asymptotically converging to zero. For $\rho/\gamma < N(0) < 1/(\phi_{-\rho}(h)\gamma)$, the value of $N$ is positive and increasing in a finite number of time steps, and subsequently becomes $1/(\phi_{-\rho}(h)\gamma)$ or beyond it. Once it becomes $1/(\phi_{-\rho}(h)\gamma)$ at a time step, $N$ then becomes indefinite, because

$$\lim_{N(t) \to 1/(\phi_{-\rho}(h)\gamma)-0} N(t+h) = +\infty$$

and

$$\lim_{N(t) \to 1/(\phi_{-\rho}(h)\gamma)+0} N(t+h) = -\infty.$$

These cases can be regarded as corresponding to the case of positive divergence for the ODE model (8) at a finite time $t = t_c$ given above. Once the value becomes beyond $1/(\phi_{-\rho}(h)\gamma)$ at a time step, $N$ becomes negative at any subsequent time step. The appearance of negative value for $N$ in (9) can be regarded mathematically as an overshoot of its trajectory compared to the trajectory for (8), due to the temporal discretization.

From the viewpoint of mathematical model for population dynamics, any negative value of $N$ indicates its breakdown for the role of 'model'. So the time-discrete model (9) can have the role of 'model' only when the value of $N$ is well-defined and non-negative, which is for any time step if $N(0) \leq \rho/\gamma$ and for a finite number of time steps if $\rho/\gamma < N(0) < 1/(\phi_{-\rho}(h)\gamma)$.

For $N(0) > 1/(\phi_{-\rho}(h)\gamma)$, it is nonsense as a mathematical model for population dynamics, whereas the original ODE model (8) has no dependence on the initial value $N(0)$. As for a specific case of $N(0) = 1/(\phi_{-\rho}(h)\gamma)$, the time-discrete model (9) cannot be mathematically well-defined. Consequently, only with the confinement for the initial value $N(0) < 1/(\phi_{-\rho}(h)\gamma)$, the time-discrete model (9) can be regarded as a well-defined model for population dynamics.

**2.2　General self-density dependent per capita growth rate** In this section, we consider a general extension of Leslie's idea to construct a time-discrete model from ODE. At the beginning, let us consider the following autonomous ODE model with per capita growth rate $f(N(t))$:

$$(10) \qquad \frac{dN(t)}{dt} = f(N(t))N(t),$$

where $f(N)$ is a function of non-negative $N$. In this paper, we assume $f(N)$ such as

- $0 < r = \sup_{N \geq 0} f(N) < +\infty$;

- having at least one positive $N^*$ such that $f(N^*) = 0$;

- differentiable at $N = 0$ and $N = N^*$;

- $|f(0)| < +\infty$;

- $|f'(0)| < +\infty$.

Depending on the nonlinearity of $f(N)$, the ODE model (10) may not be able to be solved to give any explicit form of its exact solution, so that any exact time-discrete model can be hardly derived in such case.

Now we construct and consider a time-discrete model from the ODE model (10), inspired from (6) for the logistic equation (4), as P.H. Leslie and J.C. Gower did for two-species competition or prey-predator system at the end of 50's [7, 8, 9]. For this purpose, we rewrite (10) as follows:

$$(11) \qquad \frac{dN(t)}{dt} = \{r - R(N(t))\} N(t),$$

where $R(N) = r - f(N) = \sup_{z \geq 0} f(z) - f(N)$, satisfying the following natures:

- non-negative;

- having at least one positive $N^*$ such that $R(N^*) = r$;

- differentiable at $N = 0$ and $N = N^*$;

- $|R(0)| < +\infty$;

- $|R'(0)| < +\infty$.

We can regard $r$ as the intrinsic growth rate, and the function $R(N)$ as a density dependent self-regulation function for per capita growth rate. In case of logistic equation (4), $R(N) = \beta N$.

According to (11), we consider the following time-discrete model:

$$(12) \qquad N(t + h) = F_h(N(t)) = \frac{1}{1 + \phi_r(h)R(N(t))} \cdot N(t)\mathrm{e}^{rh},$$

where $\phi_r(h)$ is defined as (3). As Leslie and Gower did, our intuition is from the fact that the self-regulation term is introduced into the denominator of rational form in the exact time-discrete model (6) corresponding to the logistic equation (4).

**EXISTENCE OF EQUILIBRIUM**  We can easily find that the time-discrete model (12) has the equilibria same with those of ODE model (11), and does not have any other. Now we focus the local stability of those equilibria for (12), compared to that for (11).

**LOCAL STABILITY OF TRIVIAL EQUILIBRIUM**  At first, let us consider the local stability of trivial equilibrium $N = 0$. As for the ODE model (10), the local stability of equilibrium $N = 0$ is determined by the sign of $f(0)$, because its linearized equation around $N = 0$ is

$$\frac{dn(t)}{dt} = f(0)n(t),$$

where $n(t)$ is the perturbation from $N = 0$. For the ODE model (10), the equilibrium $N = 0$ is locally stable if $f(0) < 0$ and is unstable if $f(0) > 0$.

In contrast, as for the time-discrete model (12), the equilibrium $N = 0$ for (12) is locally stable if $|F_h'(0)| < 1$, where

$$F_h'(0) = \frac{\mathrm{e}^{rh}}{1 + \phi_r(h)R(0)}.$$

Since $R$ is non-negative and $\phi_r(h) > 0$, always $F_h'(0) > 0$. Therefore the local stability condition for $N = 0$ of (12) is given by $F_h'(0) < 1$, so that $R(0) > r$, that is, $f(0) < 0$. So we conclude the following result:

> **Theorem 1** *Local stability of the trivial equilibrium $N = 0$ for the time-discrete model (12) is always identical to that for the ODE model (10).*

**LOCAL STABILITY OF NON-TRIVIAL EQUILIBRIUM**  Next, as for the non-trivial equilibrium $N = N^* > 0$, it is locally stable if $f'(N^*) < 0$ and is unstable if $f'(N^*) > 0$ for the ODE model (10). As for the time-discrete model (12), the local stability is determined by $|F_h'(N^*)|$ where

$$F_h'(N^*) = 1 + \phi_r(-h)N^* R'(N^*) = 1 - \phi_r(-h)N^* f'(N^*).$$

Since $\phi_r(-h) < 0$, the non-trivial equilibrium is unstable if $f'(N^*) > 0$ because $F_h'(N^*) > 1$. This coincides with the stability condition of non-trivial equilibrium for the ODE model (10).

In case of $f'(N^*) < 0$, it is clear that $F_h'(N^*) < 1$. Inverse is true, too. Since the non-trivial equilibrium $N = N^*$ for (12) is unstable if $F_h'(N^*) < -1$, let us consider the condition $F_h'(N^*) > -1$ for the locally stable equilibrium $N = N^*$, which is now

$$2 - \phi_r(-h)N^* f'(N^*) > 0,$$

that is,

$$(13) \qquad\qquad \mathrm{e}^{-rh} > 1 + \frac{2r}{N^* f'(N^*)}.$$

Since the *left*hand side of (13) is positive and less than 1, the satisfaction of (13) is sufficient to satisfy $f'(N^*) < 0$. Besides, if $f'(N^*) \geq 0$, the condition (13) cannot be satisfied. Lastly we can get the following result:

> **Theorem 2** *If the condition (13) is satisfied with the non-trivial equilibrium $N = N^*$ for the time-discrete model (12), it is locally stable, and otherwise unstable.*

Therefore, as for the dependency of local stability on the time step size $h$, we can get the following result: If $f'(N^*) < 0$ and the following condition for the time step size $h$ is satisfied, the non-trivial equilibrium $N = N^*$ for the time-discrete model (12) is locally stable, and otherwise unstable:

$$(14) \qquad h < -\frac{1}{r}\ln\left\{1 + \frac{2r}{N^*f'(N^*)}\right\}.$$

Moreover, since the lefthand side of (13) is positive, we can get the following corollary about a sufficient condition for the local stability of the non-trivial equilibrium $N = N^*$ for the time-discrete model (12):

> **Corollary 2.1** *If the following condition is satisfied for the non-trivial equilibrium $N = N^*$ for the time-discrete model (12), it is locally stable independently of time step size $h$:*
>
> $$(15) \qquad\qquad -2r \leq N^*f'(N^*) < 0.$$

BEHAVIOUR OF SOLUTION NEAR EQUILIBRIUM  When the equilibrium $N = N^*$ is locally stable for the ODE model (10), the trajectory with the initial value sufficiently near the equilibrium monotonically converges to $N^*$ as $t \to \infty$. In other words, the trajectory with the initial value sufficiently near and less (or more) than the equilibrium $N^*$ monotonically increases (or decreases) to converge to $N^*$ as $t \to \infty$.

As for the trivial equilibrium $N = 0$, our analysis in the previous section shows that the local stability for the time-discrete model (12) and for the ODE model (11) always coincides with each other. Moreover, in locally stable case, the monotonicity of trajectory approaching the equilibrium is always assured for the time-discrete model (12), too, because always $0 < F_h'(0) < 1$ in this case. Consequently we get the following:

> **Theorem 3** *Behaviour of solution near the trivial equilibrium $N = 0$ for the time-discrete model (12) always equivalent to that for the ODE model (10).*

In contrast, even when the non-trivial equilibrium $N = N^*$ is locally stable for the time-discrete model (12), that is, even when the condition (13) is satisfied, such monotonicity of trajectory approaching the equilibrium is not always assured. Indeed, if $-1 < F_h'(N^*) < 0$, the non-trivial equilibrium $N = N^*$ is locally stable, and the trajectory with the initial value sufficiently near the equilibrium shows a dumping oscillation to converge to $N^*$ in asymptotic manner as time steps go by. If $0 < F_h'(N^*) < 1$, the trajectory monotonically converges to $N^*$ in asymptotic manner as time steps go by. Hence, only when $0 < F'(N^*) < 1$, the behaviour of trajectory with the initial value sufficiently near the equilibrium $N = N^*$ for the time-discrete model (12) qualitatively corresponds to that for the ODE model (11). The condition $0 < F_h'(N^*) < 1$ leads to

$$(16) \qquad\qquad \mathrm{e}^{-rh} > 1 + \frac{r}{N^*f'(N^*)}.$$
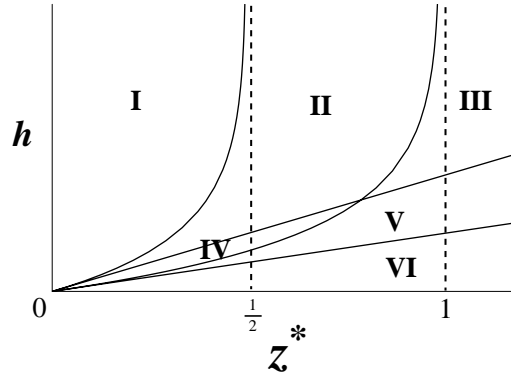
Now we can obtain the following result:

**Figure 1:** $h$-dependence of the local stability of non-trivial equilibrium $N = N^*$ ($> 0$) for the time-discrete model (12) and for the Euler scheme (18), when the equilibrium $N = N^*$ for the ODE model (10) is locally stable. $z^* = r/\{N^*f'(N^*)\}$. With $h$ of the region I, it is unstable for both (12) and (18). With any $h$ out of the region I, it is locally stable for (12), whereas it is locally stable for (18) only in the regions VI, V and VI. With $h$ of the regions III, V and VI, the trajectory of (12) with the initial value sufficiently near the equilibrium $N = N^*$ monotonically converges to $N^*$ in asymptotic manner as time steps go by, whereas, only with $h$ of the region VI, the trajectory of (18) does. Trajectory shows a dumping oscillation with $h$ of the regions II and IV for (12) and with $h$ of the regions IV and V for (18).

**Theorem 4** *If the condition (16) is satisfied with the non-trivial equilibrium $N = N^*$ for the time-discrete model (12), it is locally stable, while the trajectory with the initial value sufficiently near the equilibrium $N = N^*$ monotonically converges to $N^*$ in asymptotic manner as time steps go by.*

Moreover, we can obtain the following corollary about a sufficient condition for the behaviour of solution near the non-trivial equilibrium $N = N^*$:

**Corollary 4.1** *If the following condition is satisfied with the non-trivial equilibrium $N = N^*$ for the time-discrete model (12), it is locally stable independently of time step size $h$, while the trajectory with the initial value sufficiently near the equilibrium $N = N^*$ monotonically converges to $N^*$ in asymptotic manner as time steps go by:*

$$(17) \qquad\qquad -r \leq N^*f'(N^*) < 0.$$

COMPARISON TO THE EULER SCHEME Here we compare the time-discrete model (12) with the Euler scheme for the ODE (10) given by

$$(18) \qquad\qquad N(t+h) = N(t) + f(N(t))N(t)h.$$

As for the existence of equilibria, (18) coincides with the ODE (10). Besides, the local stability of trivial equilibrium $N = 0$ is common between them, as between (10) and (12), whereas the local stability of non-trivial equilibrium $N = N^* > 0$ for (18) requires the following condition:

$$(19) \qquad\qquad h < -\frac{2}{N^*f'(N^*)}.$$

We can easily find that, for any function $f$ satisfying our assumptions, the righthand side of condition (14) is always greater than that of (19) when $f'(N^*) < 0$. This means that the time-discrete model (12) can qualitatively approximate the solution of ODE (10) for wider range of time step size $h$ than the Euler scheme given by (18) can (see Fig.1).

IN CASE OF $f(N) = r - \beta N^\alpha$ $(\alpha > 0)$: As a specific case, we consider the case of $f(N) = r - \beta N^\alpha$ $(\alpha > 0)$. Parameters $r$ and $\beta$ are positive. In this case, the unique and always stable non-trivial positive equilibrium is $N = N^* = (r/\beta)^{1/\alpha}$.

The ODE model (10) of this type has been studied by Gilpin and Ayala [3]. Moreover, the time-discrete model (12) of this type has also been studied by Maynard Smith and Slatkin [10] and by Bellows [1].

For the time-discrete model (12), from Theorem 2, the non-trivial equilibrium is locally stable, if the following condition is satisfied:

$$\mathrm{e}^{-rh} > 1 - \frac{2}{\alpha}.$$

When $\alpha \leq 2$, from Corollary 2.1, the non-trivial equilibrium is locally stable independently of the time step size $h$. When $\alpha > 2$, from (14), the non-trivial equilibrium is locally stable if the time step size $h$ satisfies the following condition:

$$h < -\frac{1}{r} \ln\left(1 - \frac{2}{\alpha}\right).$$

Further, from Theorem 4, the non-trivial equilibrium is locally stable and the trajectory with the initial value sufficiently near the equilibrium $N = N^*$ monotonically converges to $N^*$ in asymptotic manner as time steps go by, if the following condition is satisfied:

$$\mathrm{e}^{-rh} > 1 - \frac{1}{\alpha}.$$

Then, from Corollary 4.1, if $\alpha \leq 1$, such nature of the non-trivial equilibrium is independent of the time step size $h$.

From these results, we can say that not only in the case of logistic equation, that is, of $\alpha = 1$, but also in any case of $\alpha \leq 1$, the time-discrete model (12) has the qualitatively equivalent local stability of equilibria to that for the ODE model (10).

Time-discrete model (12) is just a sort of time-discretized equation for the ODE model (10). Indeed, in case of $f(N) = r - \beta N^\alpha$ $(\alpha > 0)$, the ODE (11) is of so-to-called Bernoulli type and can be solved directly:

$$N(t) = \frac{1}{[1 + \phi_{\alpha r}(t)\alpha\beta\{N(0)\}^\alpha]^{1/\alpha}} \cdot N(0)\mathrm{e}^{rt}.$$

From this exact solution, the corresponding exact time-discrete model can be directly derived as follows:

$$(20) \qquad N(t+h) = \frac{1}{[1 + \phi_{\alpha r}(h)\beta\{N(t)\}^\alpha]^{1/\alpha}} \cdot N(t)\mathrm{e}^{rh}.$$

It is clear that the time-discrete model (12) cannot coincide with (20) for (11), except for the case of $\alpha = 1$. Hassell [4] has studied a mathematical model equivalent to (20).

**3 Conclusion** In this paper, we constructed some time-discrete models of single-species population dynamics, making use of Leslie's idea which was inspired from well-known logistic equation of ODE and Verhurst model of difference equation. Our results indicate that, if we consider the density effect in time-discrete population dynamics, which is corresponding to the density effect in an ODE model of time-continuous population dynamics, the form of density effect in time-discrete model is not trivial even in case of some simple form of density effect function in the ODE model. Mathematical relationship of our constructed time-discrete model (12) to the original ODE model (10), including why and to what extent (12) could have the mathematically equivalent nature with (10), has not been yet revealed well, and remained some mathematical open problems.

We know some well-known time-discrete models with difference equation(s) and time-continuous ones with ODE(s). However, we have been paying little attention to the relationship between them from the viewpoint of mathematical modelling for population dynamics, instead of the sense of numerical approximation for continuous time to discrete time steps. Indeed, especially in population dynamics of biological phenomena, lots of events occur in discrete time. Moreover, usually, biological research could get the data only in time-discrete manner, e.g. in year, in day, in one hour or in every few minutes. This means that we see lots of natural biological events in time-discrete unit.

One way to study such data is to consider them as snap-shots of the observed event. That is, the data is regarding as giving us an approximated view to the observed biological event. In most popular mathematical modelling, this corresponds to the modelling with time-continuous ODE(s). The ODE(s) can be regarded as a model for the observed time-continuous event behind the obtained time-discrete data.

Alternative way is to consider the data as the observed event itself. In this sense, the observed event is regarded as essentially time-discrete. In most popular mathematical modelling, this corresponds to the modelling with time-discrete difference equation(s).

In history, for instance, in case of some insect population dynamics with non-overlapping generations, the mathematical model has been constructed with time-discrete difference equation(s), as Nicholson-Bailey model for host-parasite relationship [11]. On the other hand, except for well-developed field of matrix model about plant population dynamics (for instance, see [2]), most of mathematical models for population dynamics with overlapping generations have been constructed with ODE(s), even if the reproduction is restricted within a period of each year.

Time-continuous ODE models have been successful in explaining or describing the observed biological phenomena, and in giving perspectives to a number of biological researches. Since we know, as mentioned above, that any of time-continuous ODE models can be regarded as approximated modelling to time-discrete event in population dynamics, there must be some relationship between ODE models and time-discrete difference equation models from the viewpoint of mathematical modelling. Studying such relationship is expected to serve to give some practical or perspective insights to develop some new or more sophisticated mathematical modellings in time-discrete population dynamics.

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