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On the Mechanistic Derivation of Various Discrete-Time Population Models

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Abstract We present a derivation of various discrete-time population models within a single unifying mechanistic context. By systematically varying the within-year patterns of reproduction and aggression between individuals we can derive various discrete-time population models. These models include classical examples such as the Ricker model, the Beverton–Holt model, the Skellam model, the Hassell model, and others. Some of these models until now lacked a good mechanistic interpretation or have been derived in a different context. By using this mechanistic approach, the model parameters can be interpreted in terms of individual behavior.

1. Introduction

Models of ecological systems may be broadly categorized as "top-down" or "bottom-up" models (Sumpter and Broomhead, 2001). The structure of a top-down (or "phenomenological") population model can be interpreted in terms of population characteristics but typically lacks an interpretation on a more basic level. For example, a phenomenological model may contain parameters that are referred to as the "intrinsic rate of increase" or the "carrying capacity," but their relationship to characteristics of the individuals that make up the population is unclear. In contrast, bottom-up (or "mechanistic") models are derived from assumptions and processes on a more basic level such that the parameters can be interpreted in terms of the behavior of the individuals. For this reason, mechanistic approach might give better insight and ultimately may be more predictive

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(see, e.g., Sumpter and Broomhead, 2001; Johansson and Sumpter, 2003; Geritz and Kisdi, 2004).

Generally, discrete-time population models are of the form $x_{n+1} = f(x_n)$, where different values of n refer to different years. We therefore shall refer to this as the *between-year dynamics*. In a mechanistic model the function f is not merely given, but instead is derived from processes in continuous time within a year, also in this context called the *within-year dynamics*. The population density x_n is the input of the within-year dynamics (on which the initial conditions depend), and x_{n+1} is the output which is directly calculated from the state of the within-year dynamics at the end of the year.

In this paper we consider a population consisting of adults and juveniles of the same annual species. We show that by systematically varying the patterns of reproduction and aggression, various discrete-time population models can be derived. These models include classical examples such as the Ricker (1951) model, the Beverton and Holt (1957) model, the Skellam (1951) model, the Hassell (1975) model, and others. Some of the models until now lacked a good mechanistic interpretation or have been derived in a different context. However, we must emphasize that the aim of this paper is not to give realistic, as in very detailed, models. Instead, our goal is to emphasize the general relationship between the various discrete-time population models within a single context.

The basic idea is the following. Consider a population consisting of adults and juveniles of the same annual species. The population densities of adults and juveniles at the time $t \in [0, 1]$ within a year are, respectively, $u(t)$ and $v(t)$, and x_n is the amount of adults in the beginning of year $n = 0, 1, 2, \ldots$. The within-year dynamics is modelled according to the law of mass action (see, e.g., Thieme, 2003). This means that interactions occur at a rate proportional to the population density of both interacting types. Thus, adults (population density u) interact with each other at a rate proportional to u^2, juveniles (population density v) interact with adults at a rate proportional to uv, and juveniles interact with other juveniles at a rate proportional to v^2. At the end of the year ($t = 1$) all the adults die, and the population of the following year is recruited from the juveniles that survive the winter. The between-year dynamics is thus given by $x_{n+1} = \sigma v(1)$, where σ denotes the winter survival probability for the juveniles.

Within this framework, there are four basic types of aggressive interaction: adults attack other adults, adults attack juveniles, juveniles attack adults, and juveniles attack other juveniles. Concerning the timing of reproduction, we consider three different strategies, namely

(a) continuous reproduction at a constant per capita rate throughout the year,
(b) single reproductive burst at the beginning of the year, and
(c) single reproductive burst at the end of the year.

However, most of the resulting within-year systems cannot be solved explicitly, that is, no explicit expression for the between-year dynamics can be given. We ignore these cases and only consider the following six types of aggressive interaction.

(i) adults attack adults,
(ii) adults attack juveniles,

(iii) juveniles attack adults,
(iv) juveniles attack juveniles,
 (v) adults and juveniles attack juveniles, and
(vi) adults attack adults and juveniles.

This way we have 18 different combinations of the patterns of aggression and reproduction, and for all these cases we give the resulting between-year dynamics. A well-known combination is that of (b) a single reproductive burst at the beginning of the year with (ii) adults attack juveniles, which was used by Ricker (1951) to derive what is now known as the Ricker model. In this paper we derive a much larger family of models of which the Ricker model is but a specific one.

Remark 1   *In the model formulations it has been assumed that the individual who attacks does not die. Of course, it could be discussed how realistic this assumption is. In nature, aggression usually is a risk to both the individuals involved. When the individuals involved are of the same type, i.e., adults attack adults or juveniles attack juveniles, the model would still be the same, but when the types involved are different, the situation changes. In the same formulation, this would lead to a model where adults attack juveniles and juveniles attack adults. However, the resulting between-year dynamics cannot be solved explicitly, and for this reason the situation has not been considered here.*

2. Continuous reproduction

First consider the case where the reproduction happens continuously during the whole year, and let α be the constant per capita birth rate of the population. Further, let $u(t)$ and $v(t)$ denote the population densities of, respectively, adults and juveniles at time t within a year. By varying the pattern of aggression between individuals, we get the following models.

2.1. Adults attack adults: The "log-model"

Suppose that adults attack other adults with the constant per unit rate γ. Using the principle of mass action, the dynamics of the population in year n are given by the following pair of differential equations, where $\dot{u}$ and $\dot{v}$ denote the derivatives of the population densities with respect to time.

$$\begin{cases} \dot{u} = -\dfrac{1}{2}\gamma u^2, & u(0) = x_n \\ \dot{v} = \alpha u, & v(0) = 0 \end{cases} \tag{1}$$

which has the solution

$$\begin{cases} u(t) = \dfrac{x_n}{\dfrac{1}{2}\gamma x_n t + 1} \\ v(t) = \dfrac{2\alpha}{\gamma} \log\left(\dfrac{1}{2}\gamma x_n t + 1\right). \end{cases} \tag{2}$$
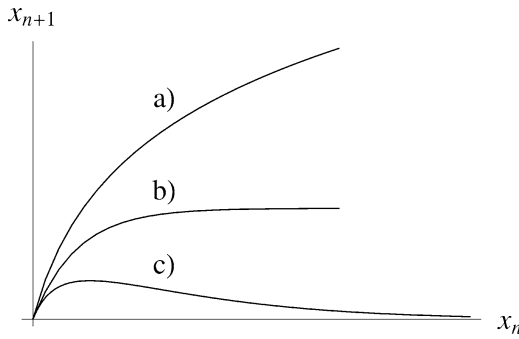
x_{n+1}

Fig. 1 Type of the between-year dynamics of the derived models, with a) x_{n+1} monotonously increasing function of x_n with unbounded increase, b) x_{n+1} monotonously increasing function of x_n, but with asymptotical approach to a finite value, and c) overcompensation. Curves a) and b) give monotonic growth or decline to an equilibrium, whereas c) can also give cycles or even chaotic between-year dynamics.

Assuming a unit year length, the population for the following year then becomes

$$x_{n+1} = \frac{a}{b} \log (bx_n + 1), \tag{3}$$

where $a = \sigma\alpha$ and $b = \frac{1}{2}\gamma$.

Denote now $x_{n+1} = f(x_n)$. One readily verifies that $f'(x) > 0$ and $f''(x) < 0$ for all $x \geq 0$, and thus x_{n+1} is a monotonously increasing and concave function of x_n (Fig. 1a). If $f'(0) = a \leq 1$, then $\hat{x} = 0$ is a globally attracting equilibrium, so the population will go extinct, and when $a > 1$ there exists a positive, globally attracting equilibrium $\hat{x}$, but it cannot be calculated explicitly.

We call this model the *log-model*, where "log" refers to the natural logarithm and which is not to be confused with the logistic model.

2.2. Adults attack juveniles: The Skellam model

Suppose now that adults attack juveniles with the constant per unit rate β. The dynamics of the population in year n are given by the following.

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\beta u v + \alpha u, & v(0) = 0 \end{cases} \tag{4}$$

Because there is no change in the amount of adults during the year, we have $u(t) = x_n$ for all t. With this we can directly solve

$$v(t) = \frac{\alpha}{\beta}(1 - e^{-\beta x_n t}), \tag{5}$$

and the population for the following year becomes

$$x_{n+1} = a(1 - e^{-bx_n}) \tag{6}$$

for $x_n \geq 0$ and with $a = \frac{\sigma\alpha}{\beta}$ and $b = \beta$. We have recovered the model of Skellam (1951). However, Skellam derived the model in a totally different context, namely for annual plants with competition for germination sites and Poisson-distributed seed numbers per site.

2.3. Juveniles attack either adults or juveniles: The "tanh-model"

The following model can be recovered from two different patterns of aggression, namely if juveniles attack either adults or other juveniles.

Mechanism 1 Assume first that juveniles attack adults with the constant per unit rate ε. Then the dynamics of the population in year n are given by the following pair of differential equations.

$$\begin{cases} \dot{u} = -\varepsilon u v, & u(0) = x_n \\ \dot{v} = \alpha u, & v(0) = 0 \end{cases} \tag{7}$$

The details of the solution can be found in Appendix A. For now it suffices to say that we find for the juveniles

$$v(t) = \sqrt{\frac{2\alpha x_n}{\varepsilon}} \tanh\left(t\sqrt{\frac{\alpha \varepsilon x_n}{2}}\right), \tag{8}$$

and the population for the following year thus becomes

$$x_{n+1} = \frac{a}{b}\sqrt{x_n} \tanh\left(b\sqrt{x_n}\right), \tag{9}$$

where $a = \sigma\alpha$ and $b = \sqrt{\frac{1}{2}\alpha\varepsilon}$.

Like in the case of the log-model, denote $x_{n+1} = f(x_n)$. Because $f'(x) > 0$ and $f''(x) < 0$ for all $x \geq 0$, x_{n+1} is a monotonously increasing and concave function of x_n (Fig. 1a), and $\lim_{x\to 0} f'(x) = a$. For the existence of a positive equilibrium, we must have $a > 1$, and in this case the positive equilibrium is globally stable, but it cannot be calculated explicitly. If $a \leq 1$, then $\hat{x} = 0$ is a globally attracting equilibrium and the population will go extinct.

We call this model the *tanh-model*, where "tanh" refers to the hyperbolic tangent function.

Mechanism 2 Assume now that juveniles attack other juveniles with the constant per unit rate δ, and the dynamics of the population on year n are given by

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\frac{1}{2}\delta v^2 + \alpha u, & v(0) = 0 \end{cases} \tag{10}$$

This can easily be solved, and the population for the following year again becomes

$$x_{n+1} = \frac{a}{b}\sqrt{x_n}\tanh\left(b\sqrt{x_n}\right), \tag{11}$$

where $a = \sigma\alpha$ and $b = \sqrt{\frac{1}{2}\alpha\delta}$.

Both of these models have the same kind of dynamics, but notice that the interpretation of the parameters on the individual level is different.

2.4. Adults and juveniles attack juveniles: The "tanh-arctanh-model"

Assume now that adults attack juveniles with the constant per unit rate β and juveniles attack other juveniles with the constant per unit rate δ. The dynamics of the population in year n are given by the following differential equations.

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\beta uv - \frac{1}{2}\delta v^2 + \alpha u, & v(0) = 0 \end{cases} \tag{12}$$

Like in the case that lead to the Skellam model, there is no change in the amount of adults during the year and we have $u(t) = x_n$ for all t. With this we can solve the equation for the juveniles, which gives

$$v(t) = \frac{-\beta x_n + \sqrt{x_n\left(\beta^2 x_n + 2\alpha\delta\right)}\tanh\left(\frac{1}{2}(t+2c)\sqrt{x_n\left(\beta^2 x_n + 2\alpha\delta\right)}\right)}{\delta}, \tag{13}$$

where c is the constant of integration. From the initial condition $v(0) = 0$ we find

$$c = \frac{\operatorname{arctanh}\left(\frac{\beta x_n}{\sqrt{x_n(\beta^2 x_n + 2\alpha\delta)}}\right)}{\sqrt{x_n(\beta^2 x_n + 2\alpha\delta)}}. \tag{14}$$

The between-year dynamics thus becomes

$$x_{n+1} = \frac{\sigma}{\delta}\left(-\beta x_n + \sqrt{x_n\left(\beta^2 x_n + 2\alpha\delta\right)}\right)$$

$$\tanh\left(\frac{1}{2}\sqrt{x_n\left(\beta^2 x_n + 2\alpha\delta\right)} + \operatorname{arctanh}\left(\frac{\beta x_n}{\sqrt{x_n\left(\beta^2 x_n + 2\alpha\delta\right)}}\right)\right), \tag{15}$$

and we refer to this model as the *tanh-arctanh-model*.

In its basic form, this model looks somewhat intimidating. However, if we denote $\xi_n := \beta x_n$, $\eta := \frac{\sigma}{\delta}$ and $\theta := \frac{2\alpha\delta}{\beta}$, it becomes clear that we have essentially a

two-parameter model with

$$\xi_{n+1} = \eta(-\xi_n + \sqrt{\xi_n(\xi_n + \theta)}) \tag{16}$$

$$\tanh\left(\frac{1}{2}\sqrt{\xi_n(\xi_n + \theta)} + \operatorname{arctanh}\left(\frac{\xi_n}{\sqrt{\xi_n(\xi_n + \theta)}}\right)\right). \tag{17}$$

We don't pursue a full analysis of the tanh-arctanh-model in this paper, but some numerical results are presented in Appendix B. Numerically it appears that ξ_{n+1} is a concave and monotonously increasing function of ξ_n for all positive θ and η (Fig. 1a). Assuming this, we can deduce that if $\frac{1}{2}\eta(2 + \theta) < 1$ there exists a positive equilibrium and it is stable. In case $\frac{1}{2}\eta(2 + \theta) \geq 1$ there exists no positive equilibrium and value $\hat{\xi} = 0$ is stable, so the population will go extinct.

2.5. Adults attack adults and juveniles: The "modified Beverton–Holt model"

Suppose that adults attack other adults with the constant per unit rate γ and juveniles with the constant per unit rate β. The dynamics of the population in year n are given by the following.

$$\begin{cases} \dot{u} = -\frac{1}{2}\gamma u^2, & u(0) = x_n \\ \dot{v} = -\beta uv + \alpha u, & v(0) = 0 \end{cases} \tag{18}$$

which has as solution

$$\begin{cases} u(t) = \dfrac{x_n}{\frac{1}{2}\gamma x_n t + 1} \\ v(t) = \dfrac{\alpha}{\beta}\left(1 - \left(\dfrac{1}{2}\gamma x_n t + 1\right)^{-2\beta/\gamma}\right). \end{cases} \tag{19}$$

Hence, the population in the beginning of the following year becomes

$$x_{n+1} = a\left(1 - \frac{1}{(bx_n + 1)^c}\right), \tag{20}$$

where $a = \frac{\sigma\alpha}{\beta}$, $b = \frac{1}{2}\gamma$ and $c = \frac{2\beta}{\gamma}$.

Denote again $x_{n+1} = f(x_n)$. One can verify that $f'(x) > 0$ and $f''(x) < 0$ for all $x \geq 0$, and thus x_{n+1} is a concave monotonously increasing function of x_n, but now x_{n+1} is asymptotically approaching value $\frac{\sigma\alpha}{\beta}$ as $x_n \to \infty$ (Fig. 1b). If $f'(0) = a > 1$, there exists a single positive equilibrium which is globally stable, but it cannot be solved explicitly. If $a \leq 1$, there exists no positive equilibrium and the population goes extinct.

If we set $c = 1$, the model reduces to the model of Beverton and Holt (1957). Also, for values c greater or smaller than one, the dynamics of the model are

very much like that of the Beverton-Holt model. Therefore, we refer to this model as the *modified Beverton–Holt model.* Brännström and Sumpter (2005) have also given a derivation of the model, but in a different context, namely for negative binomially distributed individuals and contest competition for resource sites.

3. Reproductive burst at the beginning of the year

Consider now the case where the reproduction happens in a single reproductive burst at the beginning of the year, and let α be the amount of juveniles produced by a single adult. With this pattern of reproduction, we only get four meaningful population models by varying the pattern of aggression between the individuals. The reason is that if we consider the cases where juveniles are not being attacked, neither by adults nor by other juveniles, there is no change in the amount of juveniles during the year. Hence, the between-year dynamics becomes $x_{n+1} = \sigma\alpha x_n$, which cannot be a stable situation, so we ignore these cases.

3.1. Adults attack juveniles: The Ricker model

Assume that adults attack juveniles with the constant per unit rate β. The dynamics of the population on year n are given by the following pair of differential equations, where $\dot{u}$ and $\dot{v}$ still denote the time derivatives of the population densities of adults and juveniles, respectively.

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\beta uv, & v(0) = \alpha x_n \end{cases} \tag{21}$$

There is no change in the amount of adults during the year, so we have $u(t) = x_n$ for all t. Thus, we can directly solve

$$v(t) = \alpha x_n e^{-\beta x_n t}, \tag{22}$$

and the population for the following year becomes

$$x_{n+1} = a x_n e^{-bx_n} \tag{23}$$

for $x_n \geq 0$ and with $a = \sigma\alpha$ and $b = \beta$, which is the model of Ricker (1951).

Note that the same aggression pattern but with continuous reproduction produces the Skellam model (see Section 2.2). The mechanism that Ricker (1951) himself proposed is the same as presented in here. Geritz and Kisdi (2004) have given another mechanistic underpinning of the Ricker model in a totally different context, namely using a resource-consumer within-year dynamics.

3.2. Juveniles attack juveniles: The Beverton–Holt model

Assume that juveniles attack other juveniles with the constant per unit rate δ. The dynamics of the population on year n are now given by the following.

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\frac{1}{2}\delta v^2, & v(0) = \alpha x_n \end{cases} \tag{24}$$

There is no interaction between adults and juveniles after reproduction, and we can directly solve

$$v(t) = \frac{\alpha x_n}{\frac{1}{2}\delta\alpha x_n t + 1}, \tag{25}$$

so the population in the beginning of the following year becomes

$$x_{n+1} = \frac{ax_n}{bx_n + 1} \tag{26}$$

for $x_n \geq 0$ and with $a = \sigma\alpha$ and $b = \frac{\delta\alpha}{2}$, which is the model of Beverton and Holt (1957). In fact, Beverton and Holt derived the model in essentially the same way, but with competitive interaction. Furthermore, Geritz and Kisdi (2004) and Brännström and Sumpter (2005) have given derivations different from the one represented in here.

3.3. Adults and juveniles attack juveniles: The "modified Ricker model"

Assume that adults attack juveniles with the constant per unit rate β and juveniles attack other juveniles with the constant per unit rate δ. The dynamics of the population on year n are given by the following pair of differential equations.

$$\begin{cases} \dot{u} = 0, & u(0) = x_n \\ \dot{v} = -\beta uv - \frac{1}{2}\delta v^2, & v(0) = \alpha x_n \end{cases} \tag{27}$$

There is no change in the amount of adults during the year, so we have $u(t) = x_n$ for all t. Hence, after simplification we get for the juveniles

$$v(t) = \frac{\alpha\beta x_n e^{-\beta x_n}}{1 + \frac{\alpha\delta}{2\beta}\left(1 - e^{-\beta x_n t}\right)}. \tag{28}$$

Furthermore, the population in the beginning of next year becomes

$$x_{n+1} = \frac{ax_n e^{-bx_n}}{1 + c\left(1 - e^{-bx_n}\right)} \tag{29}$$

for $x_n \geq 0$ and with $a = \sigma\alpha\beta$, $b = \beta$ and $c = \frac{\alpha\delta}{2\beta}$.

Now x_{n+1} is not a monotonously increasing function of x_n, but instead we have overcompensation in our model, i.e., x_{n+1} becomes a decreasing function of x_n for large values of x_n (Fig. 1c). If we reduce the number of parameters in the equilibrium equation by denoting $\mu := \frac{\alpha\delta}{2\beta}$ and $\hat{\xi} := \beta\hat{x}$, we can solve the possible equilibria $\hat{\xi} = 0$ and $\hat{\xi} = \log\frac{\mu+\sigma\alpha}{1+\mu}$. We present some numerical results for the stability of the equilibria in Appendix D, but we don't pursue a full analysis in this paper. For now, it suffices to say that the model shows signs of very interesting dynamics.

For both small and large values of x_n, the dynamics of this new model is very much like that of the model of Ricker (1951). Therefore, we refer to it as the *modified Ricker model*.

3.4. Adults attack adults and juveniles: The Hassell model

Assume that adults attack other adults with the constant per unit rate γ and juveniles with the constant per unit rate β. The dynamics of the population on year n are given by the following pair of differential equations.

$$\begin{cases} \dot{u} = -\frac{1}{2}\gamma u^2, & u(0) = x_n \\ \dot{v} = -\beta u v, & v(0) = \alpha x_n \end{cases} \tag{30}$$

We can solve

$$\begin{cases} u(t) = \dfrac{x_n}{\frac{1}{2}\gamma x_n t + 1} \\ v(t) = \dfrac{\alpha x_n}{\left(\frac{1}{2}\gamma x_n t + 1\right)^{2\beta/\gamma}} \end{cases} \tag{31}$$

and the population in the beginning of the following year becomes

$$x_{n+1} = \frac{ax_n}{(bx_n + 1)^c} \tag{32}$$

for $x_n \geq 0$ and with $a = \sigma\alpha$, $b = \gamma/2$ and $c = \frac{2\beta}{\gamma}$.

Thus, we have recovered the model of Hassell (1975). Hassell himself introduced the model without mechanistic derivation. Derivations based on different mechanisms from the one shown here have been given by Geritz and Kisdi (2004) and Brännström and Sumpter (2005). Notice that if $c = 1$, the model reduces to the model of Beverton and Holt (1957).

4. Reproductive burst at the end of the year

Assume that the reproduction happens in a single reproductive burst at the end of the year, and let α again be the amount of juveniles produced by a single adult. However, this kind of framework always leads to exponential growth for

the between-year dynamics except if adults attack other adults, in which case we recover the Beverton–Holt model, as shown below.

4.1. The Beverton–Holt model

Suppose now that adults attack other adults with the constant per unit rate γ. The dynamics of the population in year n are thus given by the following.

$$
\begin{aligned}
\dot{u} &= -\frac{1}{2}\gamma u^2 \text{ with initial condition } u(0) = x_n, \quad \text{and} \\
v(t) &= \begin{cases} 0 \text{ for } t \in [0, 1), \quad \text{and} \\ \alpha u(1) \text{ at } t = 1. \end{cases}
\end{aligned} \tag{33}
$$

which has as solution

$$
\begin{aligned}
u(t) &= \frac{x_n}{\frac{1}{2}\gamma x_n t + 1} \\
v(t) &= \begin{cases} 0 \text{ for } t \in [0, 1), \quad \text{and} \\ \dfrac{\alpha x_n}{\frac{1}{2}\gamma x_n + 1} \text{ at } t = 1. \end{cases}
\end{aligned} \tag{34}
$$

The population for the following year becomes

$$
x_{n+1} = \frac{a x_n}{b x_n + 1} \tag{35}
$$

for $x_n \geq 0$ and with $a = \sigma \alpha$ and $b = \frac{\delta \alpha}{2}$. Thus, like in the case of a reproductive burst at the beginning of the year and with juveniles attacking other juveniles, we have recovered the model of Beverton and Holt (1957).

5. Conclusions

In this paper we presented a single ecological context for the derivation of various discrete-time population models. These include a number of well-known models such as the Ricker (1951) model, the Beverton and Holt (1957) model, the Skellam (1951) model, and the Hassell (1975) model, but also several new models that we have not seen elsewhere (see Table 1). The derivation of the Ricker model in this paper is identical to that given by Ricker (1951) himself. However, here we embedded the Ricker model in a larger family of models. An advantage of this approach is that it shows how the different models are related to one another, and how their parameters can be interpreted within the same ecological setting.

Some of the models derived here can also be derived in different and unrelated contexts. For example, Geritz and Kisdi (2004) derived the Ricker (1951) model, the Beverton and Holt (1957) model, and the Hassell (1975) model (and others) from within-year dynamics featuring resource–consumer interactions.

Table 1 Summary of the resulting models for specific combinations of timing of reproduction and type of aggressive interaction. In addition, the combination of a reproductive burst at the end of the year and adults attacking adults leads to the Beverton and Holt (1957) model

Aggression	Continuous reproduction	Reproductive burst at the beginning of the year
Adults attack adults	log-model $x_{n+1} = a \log(bx_n + 1)$	Exponential growth $x_{n+1} = ax_n$
Adults attack juveniles	Skellam model $x_{n+1} = a(1 - e^{-bx_n})$	Ricker model $x_{n+1} = ax_n e^{-bx_n}$
Juveniles attack adults	tanh-model $x_{n+1} = \frac{a}{b}\sqrt{x_n}\tanh(b\sqrt{x_n})$	Exponential growth $x_{n+1} = ax_n$
Juveniles attack juveniles	tanh-model $x_{n+1} = \frac{a}{b}\sqrt{x_n}\tanh(b\sqrt{x_n})$	Beverton–Holt model $x_{n+1} = \frac{ax_n}{bx_n+1}$
Adults and juveniles attack juveniles	tanh-arctanh-model $\xi_{n+1} = \eta(-\xi_n + \sqrt{\xi_n(\xi_n+\theta)})$ $\tanh\left(\frac{1}{2}\sqrt{\xi_n(\xi_n+\theta)} + \text{arctanh}\left(\frac{\xi_n}{\sqrt{\xi_n(\xi_n+\theta)}}\right)\right)$ with $\xi_n := bx_n$	Modified Ricker model $x_{n+1} = \frac{ax_n e^{-bx_n}}{1+c(1-e^{-bx_n})}$
Adults attack adults and juveniles	Modified Beverton–Holt model $x_{n+1} = a[1 - (bx_n+1)^{-c}]$	Hassell model $x_{n+1} = \frac{ax_n}{(bx_n+1)^c}$

Skellam (1951) used a site-based approach to derive his model. Sumpter and Broomhead (2001) also used a site-based approach to derive the Ricker (1951) model. Brännström and Sumpter (2005) extended the site-based framework proposed by Sumpter and Broomhead (2001) and Johansson and Sumpter (2003) and derived the Ricker (1951) model, the Hassell (1975) model, both the modified and original Beverton and Holt (1957) models and the Skellam (1951) model (and others) by varying the type of competition and the spatial clustering of the individuals. Thieme (2003, p. 237) derived the Beverton and Holt (1957) model, and the Hassell (1975) model (and others) as variations on the derivation by the Ricker (1951) model by changing the (stochastic) duration of the juvenile period to cannibalism by the adults.

   Of course, the different derivations for the models don't take anything away from each other. Instead, when dealing with real population data, the availability of mechanistic underpinnings for different models in different ecological settings may eventually enable the choice of an appropriate model based on the biological background of the system at hand.

Acknowledgement

Appendix

A Solving the model for continuous reproduction and juveniles attacking adults

Here we give the detailed calculations for solving the model given by

$$
\begin{cases}
\dfrac{du}{dt} = -\varepsilon u v, & u(0) = x_n \\[2mm]
\dfrac{dv}{dt} = \alpha u, & v(0) = 0
\end{cases}
$$

in Section 2.3.

   First, in order to solve the dynamics of the adults, we write

$$
\frac{\mathrm{d}u}{\mathrm{d}v} = -\frac{\varepsilon}{\alpha} v,
\tag{A.1}
$$

which leads to

$$
u(v) = -\frac{\varepsilon}{2\alpha} v^2 + C,
\tag{A.2}
$$

where C is the constant of integration. From the initial condition $u(v(0)) = u(0) = x_n$ we can solve $C = x_n$, so

$$u(v) = x_n - \frac{\varepsilon}{2\alpha} v^2. \tag{A.3}$$

Because the amount of adults must always be positive, i.e., $u > 0$, we also have condition $v^2 < \frac{2\alpha x_n}{\varepsilon}$. As a consequence of this, when we solve the differential equation

$$\frac{\mathrm{d}v}{\mathrm{d}t} = \alpha u(v) = \alpha x_n - \frac{\varepsilon}{2} v^2 \tag{A.4}$$

using the separation of variables we get the solution

$$v(t) = \sqrt{\frac{2\alpha x_n}{\varepsilon}} \tanh \left(t \sqrt{\frac{\alpha \varepsilon x_n}{2}} \right). \tag{A.5}$$

B Numerical analysis of the dynamics of the tanh-arctanh-model

In Section 2.4 we concluded that the tanh-arctanh-model can be written as a two-parameter model

$$\xi_{n+1} = \eta(-\xi_n + \sqrt{\xi_n (\xi_n + \theta)}) \tag{B.1}$$

$$\tanh \left(\frac{1}{2} \sqrt{\xi_n (\xi_n + \theta)} + \operatorname{arctanh} \left(\frac{\xi_n}{\sqrt{\xi_n (\xi_n + \theta)}} \right) \right), \tag{B.2}$$

where $\xi_n := \beta x_n$, $\eta := \frac{\sigma}{\delta}$ and $\theta := \frac{2\alpha\delta}{\beta}$, and moreover η is only a scaling parameter.

The value of ξ_{n+1} is plotted as a function of ξ_n and θ and with $\eta = 1$ in Fig. B.1. Numerically it seems that ξ_{n+1} is monotonically increasing and concave, but we
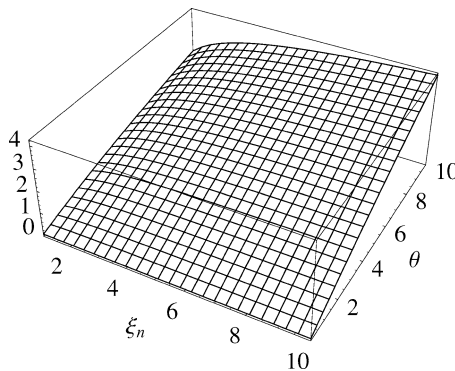

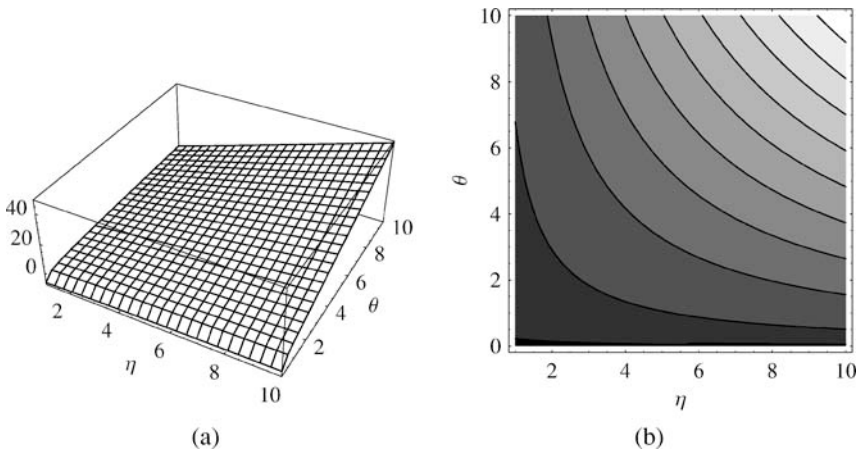**Fig. B.1** The scaled between-year dynamics of the tanh-arctanh-model.

Fig. B.2 **a** Equilibrium values for the tanh-arctanh-model. **b** The tanh-arctanh-model equilibrium contour lines as a function of η and θ. The value of the function increases as the color gets lighter.

don't pursue to show this analytically in this paper. The equilibrium value $\hat{\xi}$ is numerically plotted in Fig. B.2a as a function of η and θ, and the contours of this equilibrium are shown in Fig. B.2b.

Actually, if we denote $\xi_{n+1} = f(\xi_n)$ and assume that f is monotonically increasing and concave, we can say more about these equilibria. First, we can calculate that $f(\xi) \to \eta\theta/2 = \sigma\alpha/\beta$ as $\xi \to \infty$, and the derivative

$$f'(\xi) \to \frac{1}{2}\eta(2 + \theta) = \frac{\sigma}{\delta} + \frac{\sigma\alpha}{\beta} \tag{B.3}$$

as $\xi \to 0$. So, if $\frac{1}{2}\eta(2 + \theta) > 1$ we know that a positive equilibrium $\hat{\xi}$ exists and it is stable. On the other hand, if $\frac{1}{2}\eta(2 + \theta) < 1$, then a positive equilibrium doesn't exist and $\hat{\xi} = 0$ is stable, so the population goes extinct.

C Numerical analysis of the dynamics of the modified Beverton–Holt model

In Section 2.5 we had the result that the between-year dynamics of the modified Beverton–Holt model is given by

$$x_{n+1} = a \left(1 - \frac{1}{(bx_n + 1)^c}\right), \tag{C.1}$$

where $a = \frac{\sigma\alpha}{\beta}$, $b = \frac{1}{2}\gamma$ and $c = \frac{2\beta}{\gamma}$. We also concluded that x_{n+1} is a monotonously increasing and concave function of x_n, and x_{n+1} is asymptotically approaching value $\frac{\sigma\alpha}{\beta}$ as the value of x_n increases.
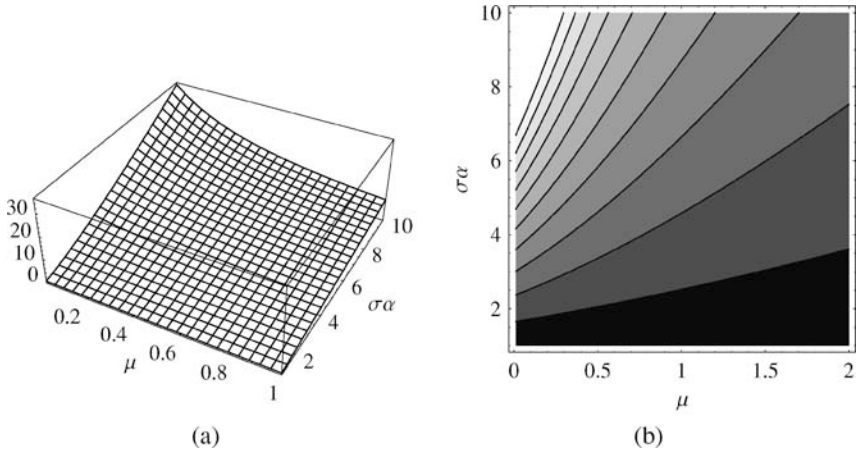
Fig. C.1 **a** Equilibrium values for the modified Beverton–Holt model. **b** The modified Beverton–Holt model equilibrium contour lines as a function of μ and $\sigma\alpha$. The value of the function increases as the color gets lighter.

For the existence of a positive equilibrium we need to have $\sigma\alpha > 1$ again, otherwise the population will go extinct. The equilibrium is given by

$$\hat{x} = \frac{\sigma\alpha}{\beta}\left(1 - \left(\frac{1}{2}\gamma\hat{x} + 1\right)^{-2\beta/\gamma}\right), \tag{C.2}$$

but $\hat{x}$ cannot be calculated analytically. For the numerical calculation of the equilibrium we first scale the population size by factor $\frac{\gamma}{2}$. So, if we denote $\mu := \frac{2\beta}{\gamma}$ and $\hat{\xi} := \frac{\gamma}{2\hat{x}}$, after substitution our equilibrium equation becomes

$$\hat{\xi} = \frac{\sigma\alpha}{\mu}(1 - (\hat{\xi} + 1)^{-\mu}). \tag{C.3}$$

This new equilibrium $\hat{\xi}$ is plotted in Fig. C.1a as a function of μ and $\sigma\alpha$, and the contours of the equilibrium are shown in Fig. C.1b. Because x_{n+1} is a monotonously increasing and concave function of x_n, as we concluded in Section 2.5, the equilibrium is globally stable for $\sigma\alpha > 1$.

D Numerical analysis of the dynamics of the modified Ricker model

In Section 3.3 we concluded that the between-year dynamics of the modified Ricker model is given by

$$x_{n+1} = \frac{ax_n e^{-bx_n}}{1 + c\left(1 - e^{-bx_n}\right)} \tag{D.1}$$
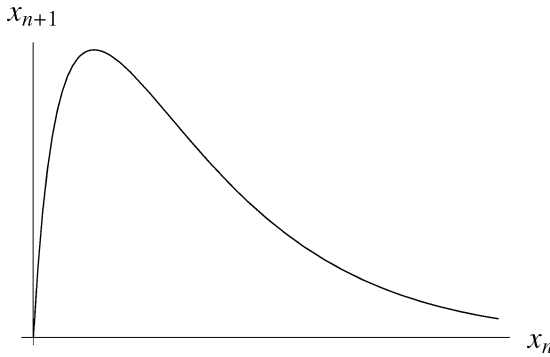
Fig. D.1   Between-year dynamics of the modified Ricker model.
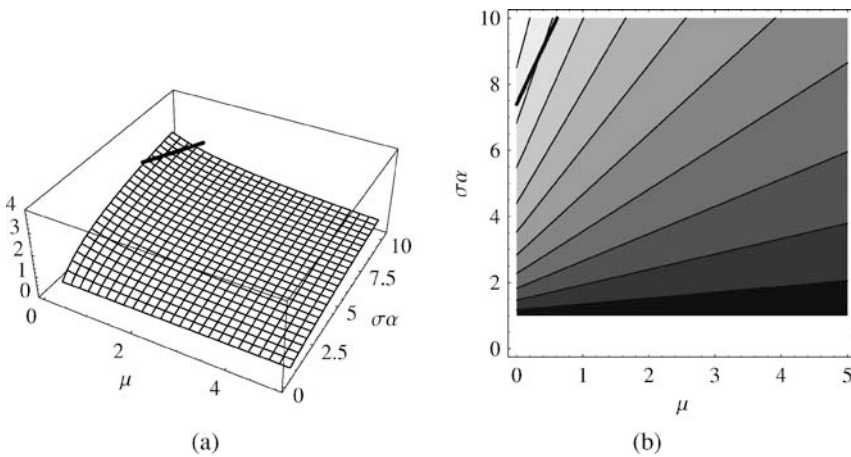

(a)   (b)

Fig. D.2   **a** Equilibrium values for the modified Ricker model. **b** The modified Ricker model equilibrium contour lines as a function of μ and $\sigma\alpha$. The value of the function increases as the color gets lighter. The equilibrium becomes unstable in the upper left-hand corner in both of the figures.

for $x_n \geq 0$ and with $a = \sigma\alpha\beta$, $b = \beta$ and $c = \frac{\alpha\delta}{2\beta}$, and a typical case of x_{n+1} as a function of x_n is shown in Fig. D.1. As mentioned in Section 3.3, we have overcompensation in this model. Now we see numerically how the equilibrium behaves depending on the parameters.

The equilibrium is given by

$$\hat{x} = \frac{\sigma\alpha\beta\hat{x}e^{-\beta\hat{x}}}{1 + \frac{1}{2}\frac{\alpha\delta}{\beta}\left(1 - e^{-\beta\hat{x}}\right)}. \tag{D.2}$$

If we reduce the number of parameters in the equilibrium equation by denoting $\mu := \frac{\alpha\delta}{2\beta}$ and $\hat{\xi} := \beta\hat{x}$, we have after substitution

$$\hat{\xi} = \frac{\sigma\alpha\hat{\xi}e^{-\hat{\xi}}}{1 + \mu(1 - e^{-\hat{\xi}})}. \tag{D.3}$$

This has solutions $\hat{\xi} = 0$ and $\hat{\xi} = \log \frac{\mu + \sigma\alpha}{1+\mu}$, which are plotted in Fig. D.2a as a function of μ and $\sigma\alpha$, and the contours of the equilibrium are shown in Fig. D.2b. A positive equilibrium only exists if $\sigma\alpha > 1$, so the range $\sigma\alpha < 1$ is left out from the figures. Moreover, the curve that separates the area of a stable equilibrium was calculated numerically and plotted in the figures. The equilibrium loses its stability in the upper left-hand corner in both of the figures.

Even though this model shows signs of very interesting dynamics, we are not going to pursue the details in this paper.

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