Hydra effect and paradox of enrichment in discrete-time predator-prey models

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Abstract

We develop three discrete-time predator-prey models from the Nicholson-Bailey host-parasitoid framework, assuming a type II functional response and logistic prey growth in form of the Beverton-Holt map. Our models show many similarities with the continuous-time Rosenzweig-MacArthur model, not only the same equilibria and sequence of bifurcations, but also phenomena such as the hydra effect and paradox of enrichment. Our three models differ in the order of events, in which the processes of density-dependent prey regulation and predation take place. When their order is reversed, but their relative order remains the same such that only census timing is changed, we observe quantitative differences in population size, but no differences in qualitative behaviour. When a modified order of events induces delayed density dependence, we observe increased stability of population dynamics, which is somewhat contrary to conventional expectation. Overall, our models exhibit behaviour analogous to the Rosenzweig-MacArthur model and highlight the importance of the order of events in discrete-time models.

Keywords: Rosenzweig-MacArthur model, consumer-resource interactions, Nicholson-Bailey model, Neimark-Sacker bifurcation, order of events

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1. Introduction

The dynamic interaction between predators and prey is an important subject in ecology and has been investigated in many mathematical models (e.g. Kendall et al., 1999; Murdoch et al., 2003; Turchin, 2003; Barraquand et al., 2017). Mathematical models can be formulated in continuous time and discrete time. Continuous-time models have been widely used to model the dynamics of interacting species for many years (Hastings, 1997; Brauer and Castillo-Chavez, 2012), however, there are several systems with dynamics that are better captured by discrete time, for instance, species with seasonal reproduction and annual life cycle species (Begon et al., 2006). In addition, in experimental studies, data are often collected at regularly spaced intervals of time. These examples show that studying and developing not only continuous-time, but also discrete-time models can contribute to better understanding different types of systems present in nature.

Although the interest in discrete-time models has increased in the last decades, predator-prey interactions in discrete-time models remain far from being understood. One reason for that lies in the fact that most of the available discrete-time models in the literature are derived from continuous-time models, for example, through exponential-discretization (Hofbauer et al., 1987; Fan and Wang, 2002) or discretization by Euler approximation (Neubert and Kot, 1992; Wendi and Zhengyi, 1999; Liu and Xiao, 2007).

Hadeler and Gerstmann (1990) presented a discrete-time version of the widely-known continuous-time model proposed by Rosenzweig and MacArthur (1963). The authors used an Euler approximation for the derivatives and the resulting model was called "the discrete Rosenzweig model". Despite the fact that the equilibrium points were similar, their system also showed complex behaviour, such as period-doubling and even chaos, which is not observed in the continuous-time version. Besides that, two important phenomena reported

2

in the Rosenzweig-MacArthur model were not examined in that discrete-time

model, namely (i) the hydra effect, when a higher death rate in a particular species increases the size of its population (Abrams, 2002; Matsuda and Abrams, 2004; Abrams, 2009; Sieber and Hilker, 2012), and (ii) the paradox of enrichment, when there is a destabilization leading to the risk of stochastic extinction in the solutions due to an increase in the prey carrying capacity (Rosenzweig, 1971).

Moreover, unlike continuous-time models where all processes, such as birth and death, are assumed to be continuous and simultaneous in time, in discrete-time models the order in which the events occur has to be carefully examined. Different order of events may lead to different quantitative and qualitative behaviour, even in one-dimensional models (Åström et al., 1996; Jonzén and Lundberg, 1999; Hilker and Liz, 2013). Thus, it is plausible to expect significant differences in systems with more than one equation, such as predator-prey and host-parasitoid models (Wang and Gutierrez, 1980; May et al., 1981).

A well-known discrete-time model for a host-parasitoid system was developed by Nicholson and Bailey (1935), assuming that, in the absence of parasitoids, the host population grows geometrically and the fraction of hosts not being parasitized depends only on the parasitoid population. As a result, the coexistence equilibrium is always unstable. In order to make the model more realistic, modifications were proposed, including not only the effect of density dependence (Beddington et al., 1975; Hassell and Pacala, 1990; Jang, 2006) but also the use of functional responses to describe the interaction between the two species (Mills and Getz, 1996; Lane et al., 1999; Tang and Chen, 2002; Abbott and Dwyer, 2007).

In this paper we develop a discrete-time predator-prey model based on the Nicholson-Bailey framework and consider the Beverton and Holt (1957) model to represent the growth of the prey population, which is equivalent to the continuous-time logistic growth. In order to describe the effect of predation, we use a functional response of type II. In the derivation of the model, we take account of the specific order of events in both populations. Our simulations show

3

similar results to the Rosenzweig-MacArthur continuous-time model, including the same equilibria and sequence of bifurcations. Besides that, we also discuss the occurrence of the hydra effect and paradox of enrichment in our model. As far as we know it is the first time a discrete-time model has so many similarities compared to a continuous-time model without showing complex behaviour such as period doubling and chaos.

The paper is organized as follows. In the next section we develop the discrete-time model considering the order of events in each population. In section 3, we present some numerical results, including stability analysis and bifurcation diagrams. We also examine the occurrence of the hydra effect and paradox of enrichment. In section 4, we develop another two models, which differ in the order of events, and then we compare the qualitative and quantitative behaviour with the model developed in section 2. Finally, in section 5 we present the discussion and conclusions.

2. Model description

We extend the well-known Nicholson-Bailey model by including logistic prey growth and a type II functional response. Besides that, we carefully study the order in which the events take place in both populations, assuming that predation occurs after prey population growth. After studying the equilibrium points and their stability, numerical results are compared with the Rosenzweig-MacArthur continuous-time model.

2.1. The model

Let X_t and Y_t be the population size of prey and predators, respectively, in generation t. We divide the time range from t to $t + 1$ as illustrated in Figure 1, where we consider different sequences of events within the generation between t and $t + 1$. The general model structure is shown in Figure 1a, such that the reproduction and intra-specific competition event (R) takes place first followed by predation (P) on the prey population. In the predator population,

4

the consumption event (C) and the predator mortality occur after predation. Figure 1b and 1c describe other orders of events and will be analysed later.
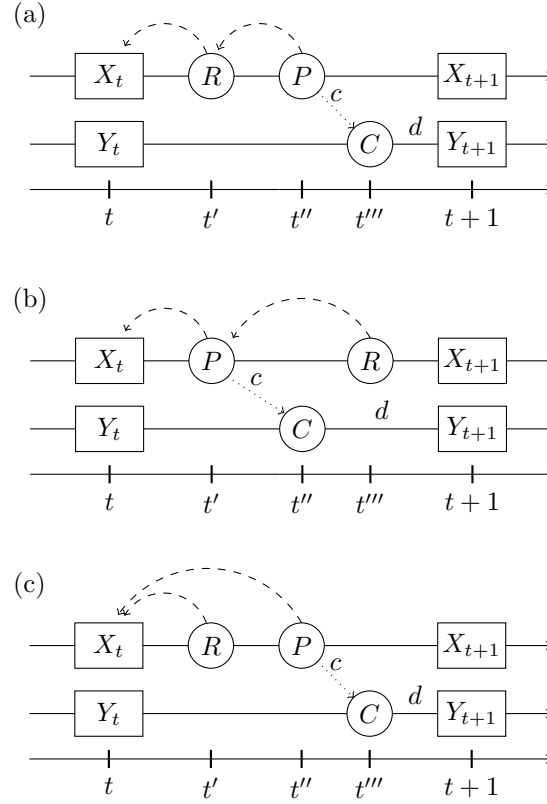

Figure 1: Sequence of events in the prey and predator populations from generation t to $t+1$: (a) reproduction and intra-specific competition followed by predation $(R \to P)$; (b) predation followed by reproduction and intra-specific competition $(P \to R)$; (c) reproduction and intra-specific competition followed by predation, but the last event depends on the prey population size prior to R $(R \to P_D)$. Dashed lines indicate the previous event on which a process depends. Dotted lines represent biomass conversion. Variables explained in the main text.

90   The prey reproduction event R at $t = t'$ represents the reproduction and intra-specific competition of the prey population according to a function $f(X_t)$, the factor of per-capita growth in the prey population. At this instant, while

the prey population changes, the predator population remains the same, so that

$$
\begin{aligned}
X_{t'} &= X_t f(X_t), \\
Y_{t'} &= Y_t.
\end{aligned}
\tag{1}
$$

At $t = t''$ the predation event P occurs. A fraction of $X_{t'}$, the newborns and survivors from R, is preyed upon by $Y_{t'}$ predators, such that only a fraction $g(X_{t'}, Y_{t'})$ survives. The predator population also remains the same during this event:

$$
\begin{aligned}
X_{t''} &= X_{t'} g(X_{t'}, Y_{t'}), \\
Y_{t''} &= Y_{t'}.
\end{aligned}
\tag{2}
$$

At $t = t'''$ the consumption event C takes place. The fraction of prey that has been preyed upon is converted into new predators with a factor $c > 0$, the conversion efficiency. Here, the prey population remains the same,

$$
\begin{aligned}
X_{t'''} &= X_{t''}, \\
Y_{t'''} &= c X_{t'} \left[1 - g(X_{t'}, Y_{t'}) \right].
\end{aligned}
\tag{3}
$$

At $t = t+1$, the prey population is the same as at the previous event, while the predator population is composed of the predators that have survived from natural deaths,

$$
\begin{aligned}
X_{t+1} &= X_{t'''}, \\
Y_{t+1} &= d Y_{t'''},
\end{aligned}
\tag{4}
$$

where d is the predator survival probability, $d \in [0, 1]$. The general model, considering the order of events where R is followed by P (from now on also referred to as $R \to P$ model), can be written using the equations (1)-(4) as

$$
\begin{aligned}
X_{t+1} &= X_t f(X_t) g(X_t f(X_t), Y_t), \\
Y_{t+1} &= c d X_t f(X_t) \left[1 - g(X_t f(X_t), Y_t) \right].
\end{aligned}
\tag{5}
$$

In this paper, we use the Beverton-Holt model to describe the prey per-capita growth

$$
f(X) = \frac{\lambda}{1 + (\lambda - 1) X / K},
\tag{6}
$$

where $\lambda > 1$ is the factor of intrinsic per-capita growth and $K > 0$ is the carrying capacity.

6

We assume a functional response of type II to describe the fraction of prey that escapes predation. The function $g(X, Y)$ is given as follows

$$g(X, Y) = \exp\left(\frac{-AY}{1 + HX}\right), \tag{7}$$

where A is the average number of encounters per prey between prey and predators leading to predation, and H is the handling time of predators per prey. (Hassell, 2000).

Replacing (6) and (7) into the equations in (5), our model can now be written as

$$
\begin{aligned}
X_{t+1} &= X_t f(X_t) \exp\left(\frac{-AY_t}{1 + HX_t f(X_t)}\right), \\
Y_{t+1} &= B X_t f(X_t) \left[1 - \exp\left(\frac{-AY_t}{1 + HX_t f(X_t)}\right)\right],
\end{aligned}
\tag{8}
$$

where $B = cd > 0$.

In this model, in the absence of predators, the prey population grows according to the Beverton-Holt model, i.e., for every non-zero initial condition, the population approaches its carrying capacity. On the other hand, in the absence of prey, the predator population goes extinct at the next iteration. These characteristics and the choices of $f(X)$ and $g(X, Y)$ make the behaviour of model (8) similar to the continuous-time Rosenzweig-MacArthur model, as we will show later on.

The model equations can be simplified by introducing dimensionless variables. Choosing

$$N_t = HX_t \quad \text{and} \quad P_t = AY_t \tag{9}$$

for the prey and predator populations, respectively, we obtain the non-dimensional predator-prey model

$$
\begin{aligned}
N_{t+1} &= N_t F(N_t) \exp\left(\frac{-P_t}{1 + N_t F(N_t)}\right), \\
P_{t+1} &= b N_t F(N_t) \left[1 - \exp\left(\frac{-P_t}{1 + N_t F(N_t)}\right)\right],
\end{aligned}
\tag{10}
$$

where $k = HK$ and $b = AB/H$ are the new dimensionless parameters, also referred to in the following sections as *prey carrying capacity* and *predator growth factor*, respectively. The function $F(N_t)$ is given by

$$F(N_t) = \frac{\lambda}{1 + (\lambda - 1)N_t/k}, \tag{11}$$

7

which is obtained by replacing K by k in (6).

2.2. Equilibria and stability analysis

System (10) has three possible equilibrium points: *extinction*, *prey-only* and *coexistence equilibrium*, namely

$$E_0 = (0,0), \quad E_N = (k,0) \quad \text{and} \quad E_{NP} = (N^*, P^*), \tag{12}$$

respectively, where N^* is the positive solution of a transcendental equation (see Appendix A) and

$$P^* = bN^* \left(F(N^*) - 1 \right). \tag{13}$$

If the coexistence equilibrium exists, it is unique; see the proof in Appendix A.

For the equilibrium points E_0 and E_N, linear stability analysis (see Appendix B) shows that the extinction equilibrium is always unstable while the prey-only equilibrium is stable if and only if the condition

$$b < \frac{1+k}{k} \tag{14}$$

holds. Inequality (14) gives a condition under which predators will go extinct. For predators to survive, their growth factor needs to be larger than a critical value that depends on the availability of prey, given by the (scaled) prey carrying capacity k.

For the coexistence equilibrium, since there is no closed form for N^* we investigate its stability numerically in the next section.

3. Results for the $R \rightarrow P$ model

The aim of this section is to present numerical simulations for the discrete-time predator-prey model (10) and compare some of the results with the continuous-time Rosenzweig-MacArthur model. First, we obtain the nullclines and discuss the stability of the coexistence equilibrium and the different qualitative behaviours as a function of the predator growth factor b. Furthermore, we

8

examine the bifurcation diagram and the occurrence of the hydra effect. Finally, we investigate the paradox of enrichment as the prey carrying capacity k is increased.

3.1. Nullcline investigation and bifurcation analysis

Since the coexistence equilibrium can not be expressed in an analytical form, we investigate its stability through numerical simulations. To this end, we first consider the non-trivial nullcline equations for model (10) as follows:

$$
\begin{aligned}
&\text{prey nullcline}: \quad N = NF(N)\exp\left(\tfrac{-P}{1+NF(N)}\right), \\
&\text{predator nullcline}: \quad P = bN\left[1 - \exp\left(\tfrac{-P}{1+NF(N)}\right)\right].
\end{aligned}
\tag{15}
$$

In order to examine the different qualitative behaviours as the predator growth factor increases, we fix values of λ and k and consider different values of the predator growth factor b. Figure 2 shows the orbits in the phase plane and the respective nullclines for each set of parameters.

Figure 2a shows a solution reaching the equilibrium E_N, where the predators go extinct and the prey population is at carrying capacity. In this case the value of b is such that condition (14) holds, which means E_N is stable.

Where condition (14) is reversed, there is a transcritical bifurcation, i.e., the coexistence equilibrium E_{NP} becomes feasible and exchanges stability with E_N. Initially, E_{NP} is a stable node but becomes a stable spiral when b is increased (Fig. 2b). For even larger values of b, Figure 2c shows an attracting invariant circle generated by a Neimark-Sacker bifurcation, which is the discrete-time analogue of a Hopf bifurcation (Elaydi, 2000; Hale and Koçak, 2012). This sequence of bifurcations and changes of equilibrium type can also be seen in the bifurcation diagram in Figure 3.

In comparison to the continuous-time Rosenzweig-MacArthur model, despite the fact that the shape of the predator nullcline is slightly different, our model has not only equivalent equilibrium points (extinction, prey only and coexistence equilibrium), but also the same sequence of bifurcations when we increase
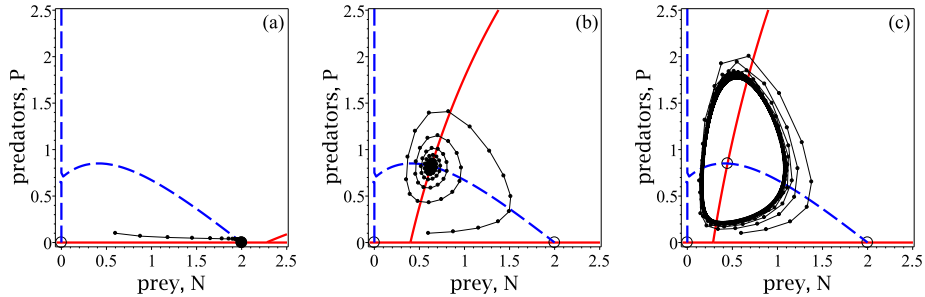
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Figure 2: Solutions of model (10) in the phase plane with the prey and predator nullclines showing different qualitative behaviour of the solutions as the predator growth factor b increases: (a) stable prey-only state, for $b = 1.47$; (b) stable coexistence equilibrium, for $b = 2.5$; (c) oscillatory coexistence on an invariant curve, for $b = 3$. The solid lines (red) represent the predator nullclines and the dashed lines (blue) the prey nullclines. The equilibrium points E_0, E_N and E_{NP} are represented by circles, according to their stability: empty circles when the equilibrium point is unstable and filled circle if it is stable. Black line connects orbits. Initial condition: $(N_0, P_0) = (0.6, 0.1)$, $k = 2$ and $\lambda = 2$.

the predator's growth factor b: transcritical bifurcation and Neimark-Sacker bifurcation. Moreover, the equilibrium type of coexistence state for b increasing is also similar to the continuous case, i.e., first non-feasible, then stable node, then stable spiral and finally an unstable spiral with an invariant circle.

3.2. Hydra effect and bifurcation diagrams

We now investigate the effect that the mean predator population size increases as its survival factor decreases. This non-intuitive phenomenon, known as hydra effect, has been the subject of many theoretical and experimental studies and has important implications for pest and resource management (Schröder et al., 2014).

Figure 3 shows the bifurcation diagram and the mean population size of system (10) as function of the parameter b, which decreases as the predator mortality increases. Thus, we can see an increase in the mean predator population size as we decrease the value of b, provided the dynamic is unstable (here $b > 2.8$). This demonstrates the occurrence of the hydra effect in our model.
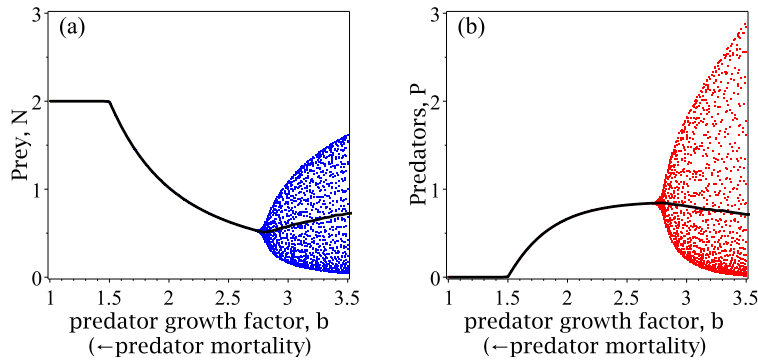
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Figure 3: Bifurcation diagram of system (10) and mean population size (solid black line) for each value of b showing the final 50 points after 1500 iterations for (a) prey (blue points), (b) predators (red points). The mean populations size was evaluated over the final 500 iterations. At stable equilibria, the mean population size curve coincides with the equilibria values. $\lambda = 2$, $k = 2$ and random initial condition.

3.3. Paradox of Enrichment

The paradox of enrichment, first mentioned by Rosenzweig (1971) in continuous-time predator-prey models, is characterized by a destabilization of the coexistence equilibrium point via a Hopf bifurcation (Freedman, 1976). As the carrying capacity is increased, the limit circles move closer to one or both axes in the phase plane, thus making stochastic extinction more likely.

For illustration, we first present solutions of system (10) reaching the stable coexistence equilibrium in Figures 4a and 4b. When the carrying capacity is increased, the coexistence equilibrium loses stability and the solutions oscillate, which generates an invariant circle that can come close to the axes in the phase plane (see Fig. 4c and 4d).

The bifurcation diagrams for varying carrying capacities are shown in Figure 4e and 4f. There is a Neimark-Sacker bifurcation at $k \approx 1.8$, above which the amplitude of oscillations increases and the population sizes vary from near zero to high values, when the system becomes enriched (large values of k).
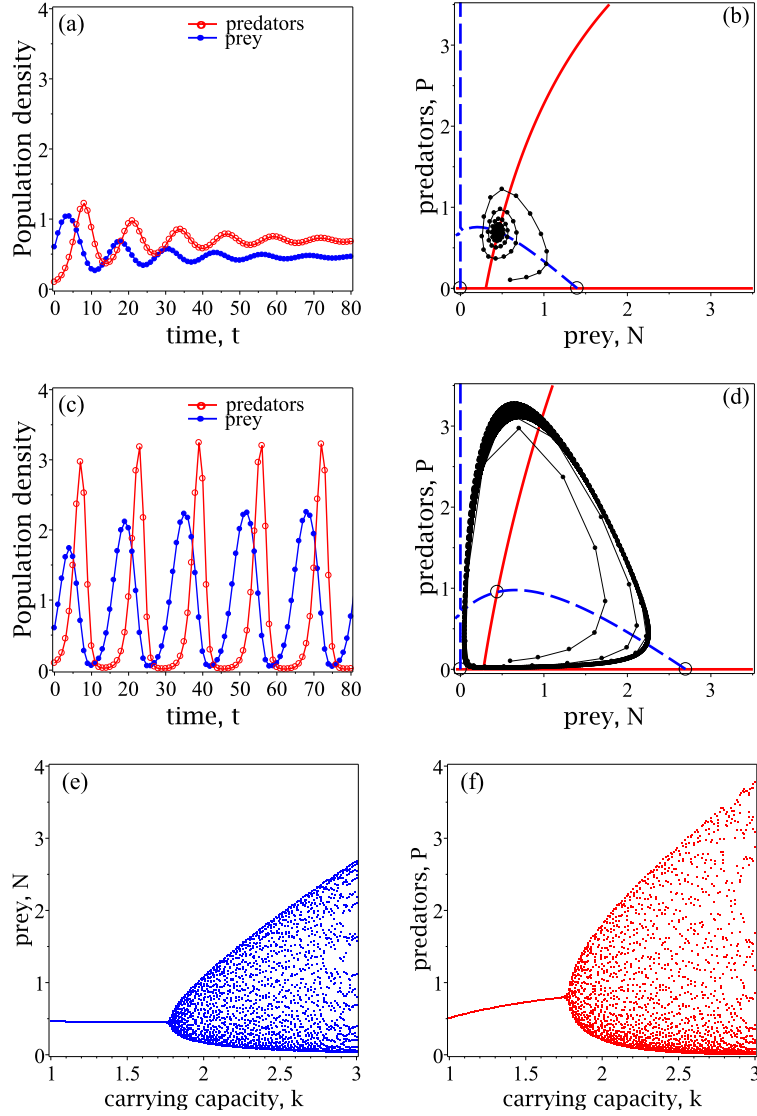
11

Figure 4: Solutions of model (10) in time and in the phase plane showing different qualitative behaviours as the carrying capacity increases: (a)-(b) stable coexistence equilibrium, for $k = 1.4$; (c)-(d) oscillatory coexistence on an invariant circle, for $k = 2.7$. In (b) and (d) the solid line (red) represents the predator nullcline and the dashed line (blue) the prey nullcline. The empty circles in Figures (b) and (d) represent unstable equilibrium points. Figures (e) and (f) show the bifurcation diagram of system (10) as function of k for prey and predators population, respectively. $\lambda = 2$ and $b = 3$.

12

4. Different order of events

In the previous sections we studied a discrete-time predator-prey model in which the events of reproduction and intra-specific competition act first, followed by predation. In this section, we investigate two other models by considering different orders of events. The first one considers predation acting first, followed by the effect of reproduction and intra-specific competition ($P \to R$ model). The second one assumes delayed density dependence and is developed considering that, after reproduction and intra-specific competition, the fraction of prey that escapes predation depends on the number of prey prior to this stage ($R \to P_D$ model). After that, we discuss the quantitative and qualitative differences and similarities of the models.

4.1. Model formulation for different orders of events

For the $P \to R$ model, we follow analogous steps as in the previous sections to develop the model equations. In other words, we assume that the fraction of prey that reproduce and survive from intra-specific competition is composed of the fraction that has escaped predation. This scheme is illustrated in Figure 1b. Using the same notation of the previous sections, the general equations are given by

$$
\begin{aligned}
X_{t+1} &= X_t g(X_t, Y_t) f(X_t g(X_t, Y_t)), \\
Y_{t+1} &= B X_t \left(1 - g(X_t, Y_t)\right).
\end{aligned}
\tag{16}
$$

For the $R \to P_D$ model, we consider the same order of events as in $R \to P$, but with delayed density dependence. This delayed density dependence comes from the assumption that, after the event R, the fraction of prey which is preyed upon by P_t predators depends on the prey population prior to R. May et al. (1981) called this case "not the most obvious way of introducing density dependence into the host life cycle", in the case of host-parasitoid systems, but also pointed out that it may correspond to some natural situations, such as the larvae of the winter moth (*Operophtera brumata*), which is attacked by a parasitoid fly (*Cyzenis albican*) at Wytham Woods (U.K.).

13

Thus, the general equations for the $R \to P_D$ model are given by

$$
\begin{aligned}
X_{t+1} &= X_t f(X_t) g(X_t, Y_t), \\
Y_{t+1} &= B X_t \left(1 - g(X_t, Y_t)\right).
\end{aligned}
\tag{17}
$$

Unlike model (8), the fraction of prey that escapes predation depends only on Y_t and X_t. It is also possible, but analogous, to examine this model by considering that predation acts first, so that those individuals that escape predation will reproduce and may die due to intra-specific competition, but at a level dependent on the population prior to P.

4.2. Results for different orders of events

In order to compare the models developed in this section ($P \to R$ and $R \to P_D$) to the first model ($R \to P$), we choose the same functions $f(X)$ and $g(X, Y)$ as in (6) and (7), respectively (see Appendix C). We observe that both $P \to R$ and $R \to P_D$ models show the same types of equilibrium points, namely, the extinction of both species, prey-only and the coexistence equilibrium, as well as the same sequence of bifurcations described in section 3.1 and illustrated in Figure 2. Furthermore, the hydra effect and the paradox of enrichment are also observed in both $P \to R$ and $R \to P_D$ models.

Here, we focus on the different quantitative and qualitative behaviour of the models. For this sake we show in Figure 5 the bifurcation diagrams as function of the predator growth factor b for both the prey and predator population.

First, let us compare the models $R \to P$ and $P \to R$. In these models, the order of events in the prey population is different, however, the relative temporal order is the same (Åström et al., 1996). Thus, the only difference between them is the time of measurement of population size. Therefore, it is obvious that the prey coexistence equilibrium in the model $R \to P$ (when the prey population is measured after predation) is smaller than the prey coexistence equilibrium in the model $P \to R$ (when it is measured after reproduction). This different quantitative behaviour is shown in Figure 5a. On the other hand, Figure 5b shows the same quantitative behaviour for the predator population for both
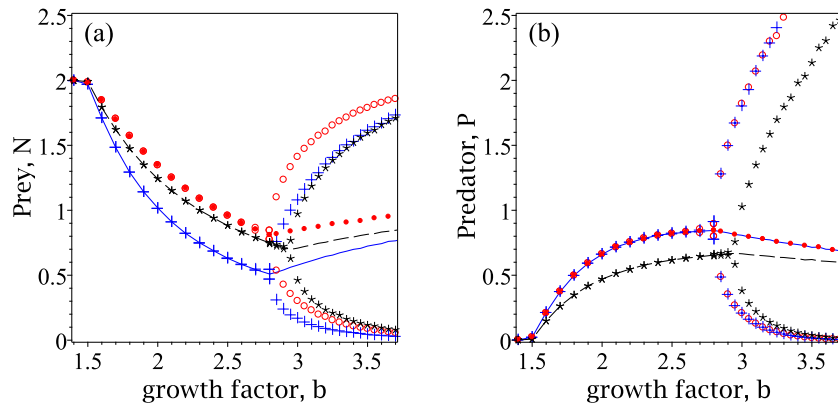
14

Figure 5: Bifurcation diagrams (symbols) and mean population sizes (lines) for the models $R \rightarrow P$ (blue crosses and solid line), $P \rightarrow R$ (red circles and dotted line) and $R \rightarrow P_D$ (black stars and dashed line) as function of the predator growth factor b. The diagrams show the maximum and the minimum value reached by the solutions. For stable equilibrium points these values coincide, whereas after the Neimark-Sacker bifurcation they correspond to the maximum and minimum value reached by the corresponding invariant limit circle. $\lambda = 2$, $k = 2$ and random initial conditions.

$R \rightarrow P$ and $P \rightarrow R$ models. This is due to the fact that in both models there is only one event (consumption) in the predator population within generation t and $t + 1$, such that the event P is always preceded by the prey reproduction, i.e., the relative temporal order is again the same.

270   Furthermore, the models $R \rightarrow P$ and $P \rightarrow R$ have the same qualitative behaviour. The possible reason for that is the fact that the functions $f(X)$ and $g(X, Y)$ are one-to-one, which makes systems (5) and (16) topologically conjugated. If we had chosen one of the functions for f or g to be non-surjective, for example, the qualitative behaviour of the systems could have showed significant
275   differences (Hilker and Liz, 2013).

Let us now compare models $R \rightarrow P$ and $R \rightarrow P_D$. The delayed density dependence is responsible for the different quantitative and qualitative behaviour, as shown in Figure 5. In particular, the parameter range where the coexistence equilibrium is stable has been extended. Hence, interestingly, the delayed
280   density dependence in this case has a stabilizing effect. This seems interest-

15

ing because delayed density dependence is often associated with destabilizing effects (May, 1973, 1974) and the appearance of alternative attractors (Franco and Hilker, 2014).

5. Discussion and Conclusions

We studied a discrete-time predator-prey model by including logistic prey growth and a type II functional response in the Nicholson-Bailey framework. We developed three different discrete-time predator-prey models by considering distinct orders of events in the prey population. First, reproduction followed by predation, second, predation followed by reproduction, and third with delayed density dependence.

In our first model we observed similar behaviour to the Rosenzweig-MacArthur continuous-time model. To be more precise, it exhibits the hydra effect when increasing predator mortality and it also shows the paradox of enrichment when increasing prey carrying capacity. It has the same three equilibrium points, and their stability properties appear to be analogous to those in the Rosenzweig-MacArthur model. In particular, we observed the same sequence of bifurcations and equilibrium types when varying the predators growth factor.

The Rosenzweig-MacArthur model is widely used in theoretical ecology and has gained almost iconic importance. It serves as a building block in constructing food web models (Yodzis, 1989; Pimm, 2002; Loreau, 2010). There has been tremendous interest in discrete-time versions of this model. Yet, existing discrete-time predator-prey models frequently show dynamics very different from it. For example, many of the discrete-time predator-prey models show cycles and chaos. One reason for this more complex behaviour is the derivation of the discrete-time model. There have been approaches to discretize the Rosenzweig-MacArthur model by Euler approximation (Hadeler and Gerstmann, 1990) or by piece-wise constant arguments (Fan and Wang, 2002). Those discretizations, however, introduce time delays causing complex dynamics not existing in the original model. This is most obviously evidenced by the prey dy-

16

namics in the absence of predators. In many discrete-time predator-prey models, prey growth follows the quadratic (Hadeler and Gerstmann, 1990; Neubert and Kot, 1992; Liu and Xiao, 2007) or Ricker map (Beddington et al., 1975; Lane et al., 1999), which by themselves show period-doubling bifurcations leading to chaos even in the absence of predators. In our model, in contrast, in the absence of predators, the prey grow logistically according to the Beverton-Holt equation.

Our model also shows some minor differences to the Rosenzweig-MacArthur model: the predator nullcline is not a vertical line and there is a lack of a closed solution for the coexistence equilibrium. Even though we do not want to claim our model is *the* discrete-time version of the Rosenzweig-MacArthur, its behaviour is very similar to the continuous-time case.

While discrete-time models assume a certain order of events, in continuous-time models all processes take place simultaneously. We also compared the qualitative and quantitative behaviour of models with different orders of events. For instance, we considered a model with delayed density dependence and observed not only qualitative and quantitative behaviour, but also a non-intuitive stabilizing effect, where the parameter range in which the equilibrium is stable was extended.

Here we investigated a model based on the Nicholson-Bailey framework with an average encounter rate between predators and prey following a type II functional response, preceded or followed by logistic prey growth. There may be other discrete-time models showing similarly analogous behaviour to the Rosenzweig-MacArthur model. It is our hope that this paper may contribute to increasing attention to the intricacies of modelling predator-prey dynamics in discrete time.

Appendix A: Proof of the uniquiness of the coexistence equilibrium

For the coexistence equilibrium, N^* is the positive solution of the transcendental equation

$$(1 + N^* F(N^*)) \ln(F(N^*)) = bN^* (F(N^*) - 1), \qquad (18)$$

17

and P^* is given by

$$P^* = bN^* \left(F(N^*) - 1 \right). \tag{19}$$

It is feasible if $N^*, P^* > 0$, which implies $F(N^*) > 1$. Thus, from equation (11), we obtain $N^* < k$.

Equation (18) can be rewritten as

$$h_1(N^*) = h_2(N^*), \tag{20}$$

where

$$h_1(x) = \ln(F(x)) = \ln\left(\frac{\lambda}{1 + ax} \right) \tag{21}$$

and

$$h_2(x) = \frac{bx \left(F(x) - 1 \right)}{1 + xF(x)} = \frac{bx(\lambda - 1 - ax)}{1 + (a + \lambda)x}, \tag{22}$$

where $a = \frac{\lambda - 1}{k} > 0$.

Function h_1 is such that $h_1(0) = \ln(\lambda) > 0$, $h_1(k) = 0$, and it is a monotonically decreasing function since $h_1'(x) = -\frac{a}{ax+1} < 0$ for any $x > 0$. On the other hand, function h_2 has two roots $x = 0$ and $x = k$; its graph is concave down because $h_2''(x) = -\frac{2b\lambda(a+\lambda-1)}{[(a+\lambda)x+1]^3} < 0$ for any $x > 0$, since $a, b > 0$ and $\lambda > 1$.

A solution of equation (20) is $x = k$. Combining this solution with equation (19), we obtain the equilibrium $E_N = (k, 0)$.

Therefore, we conclude that there is up to one solution $N^* \in (0, k)$ which satisfies equation (20). Thus, the coexistence equilibrium E_{NP}, when it exists, is unique.

Appendix B. Linear stability analysis

Stability analysis of the equilibrium points of model (10):

- $E_0 = (0, 0)$. The extinction equilibrium point is always unstable. The eigenvalues of the Jacobian Matrix are

$$\mu_1 = \lambda > 1, \quad \mu_2 = 0. \tag{23}$$

18

- $E_N = (k, 0)$ with eigenvalues

$$\mu_1 = \frac{1}{\lambda} < 1, \quad \mu_2 = \frac{bk}{1+k}. \tag{24}$$

Since $|\mu_1| < 1$ for every value of $\lambda > 1$, the prey-only equilibrium is stable if and only if $|\mu_2| < 1$, which leads to condition (14) for the stability of E_N.

- $E_{NP} = (N^*, P^*)$, where N^* is the positive solution (if there is one) of (18)

According to the Jury conditions, E_{NP} is stable if and only if

$$|\mathrm{tr}(J(E_{NP})| < 1 + \det(J(E_{NP})) < 2. \tag{25}$$

Appendix C: Models $P \to R$ and $R \to P_D$

Here, we present the non-dimensional version of the models $P \to R$ and $R \to P_D$ discussed in the main text.

Model $P \to R$

Choosing the same functions $f(X)$ and $g(X, Y)$ given by equations (6) and (7), respectively, we can write the non-dimensional $P \to R$ system as

$$
\begin{aligned}
N_{t+1} &= \frac{\lambda N_t G(N_t, P_t)}{1 + (\lambda - 1)G(N_t, P_t)/k}, \\
P_{t+1} &= bN_t \left[1 - G(N_t, P_t)\right],
\end{aligned}
\tag{26}
$$

where $G(N_t, P_t)$ is given by

$$G(N_t, P_t) = \exp\left(\frac{-P_t}{1 + N_t}\right). \tag{27}$$

System (26) has three equilibrium points, $E_0 = (0, 0)$, $E_N = (k, 0)$ and $E_{NP} = (N^*, P^*)$, where N^* is the positive solution (if there is one) of

$$(1 + N^*)\ln\left(\lambda - \frac{(\lambda - 1)N^*}{k}\right) = bN^*\left(1 - \frac{1}{\lambda - (\lambda - 1)N^*/k}\right), \tag{28}$$

and P^* is given by

$$P^* = bN^*\left(1 - \frac{1}{\lambda - (\lambda - 1)N^*/k}\right). \tag{29}$$

19

Model $R \to P_D$

Analogously, the non-dimensional $R \to P_D$ system is given by

$$N_{t+1} = N_t F(N_t) G(N_t, P_t),$$
$$P_{t+1} = b N_t [1 - G(N_t, P_t)]. \tag{30}$$

System (30) has three equilibrium points, $E_0 = (0, 0)$, $E_N = (k, 0)$ and $E_{NP} = (N^*, P^*)$, where N^* is the positive solution (if there is one) of

$$b N^* \left(1 - \frac{1}{F(N^*)} \right) = (1 + N^*) \ln(F(N^*)), \tag{31}$$

and P^* is given by

$$P^* = b N^* \left(1 - \frac{1}{F(N^*)} \right). \tag{32}$$

Stability analysis of the equilibrium points, in both $P \to R$ and $R \to P_D$ models, leads to equations (23)-(25).

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22

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