PAPER

The predator-dependent replicator dynamics

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The predator-dependent replicator dynamics

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Abstract

Ecological interactions are central to understanding evolution. For example, Darwin noticed that the beautiful colours of the male peacock increase the chance of successful mating. However, the colours can be a threat because of the increased probability of being caught by predators. Eco-evolutionary dynamics takes into account environmental interactions to model the process of evolution. The selection of prey types in the presence of predators may be subjected to pressure on both reproduction and survival. Here, we analyze the evolutionary game dynamics of two types of prey in the presence of predators. We call this model *the predator-dependent replicator dynamics*. If the evolutionary time scales are different, the number of predators can be assumed constant, and the traditional replicator dynamics is recovered. However, if the time scales are the same, we end up with sixteen possible dynamics: the combinations of four reproduction's games with four predation's games. We analyze the dynamics and calculate conditions for the coexistence of prey and predator. The main result is that predators can change the equilibrium of the traditional replicator dynamics. For example, the presence of predators can induce polymorphism in prey if one type of prey is more attractive than the other, with the prey ending with a lower capture rate in this new equilibrium. Lastly, we provide two illustrations of the dynamics, which can be seen as rapid feedback responses in a predator–prey evolutionary arm's race.

S Supplementary material for this article is available online

(Some figures may appear in colour only in the online journal)

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1. Introduction

Population dynamics theory traces back to the elementary theory of rabbit growth modelled as Fibonacci sequences [1]. But it was the observation that population size would grow in geometrical progression while food supply in arithmetic progressing that drew attention to population dynamics theories [2]. The introduction of competition for limited resources, the so-called logistic term [3], improved the applicability of the models and greatly influenced the work on evolutionary theory by Charles Darwin [4]. The connection between the mechanisms of evolution proposed by Darwin and Wallace [4, 5] and the unit of selection, the gene, investigated by Mendel [6], was developed by Ronald Fisher [7]. The work of Fisher unfolded in many directions, but one is of particular interest to our work: the merging of game theory to evolutionary dynamics, done by Maynard Smith [8, 9].

The evolutionary game theory takes from game theory the concepts of strategies and payoff and maps them to phenotypes and reproductive fitness, respectively [10]. The replicator dynamics, introduced by Taylor and Jonker [11] and named by Schuster and Sigmund [12], is a simple and elegant tool to analyse the competition between types within the same species. The payoff obtained in random interactions is translated into the reproductive fitness of the types, which determines the per-capita rate of growth of the type. The idea of quasi-species is often associated with this theory because small variations of genetic content can change the phenotype, creating different individuals within the same species [13].

The replicator dynamics assumes that the environment is constant. However, feedback between environment and evolutionary dynamics is of great importance [14]. In [15], the traditional replicator equation with frequency-dependent fitness is analyzed with payoff matrix values that change in time depending on environmental factors, which also evolve in time. The environmental factors, that depend on the particular state of the population, can be the availability of resources, reproduction opportunity, or even risk-taking. In [16], the authors study a stochastic population model, where the environmental effect is captured by a time-changing parameter that influences the death's and reproduction's probability of an individual. In this framework, it is possible to model how a changing habitat modifies the optimum state of an organism characteristic. For example, plants with large seeds that stock large metabolic reserves usually establish themselves during periods of increasing competition. On the other hand, plants with smaller seeds, often produced in more quantity, have a better chance to colonize a new habitat during fast expansion [17]. Finally, in [14] the authors revised works exploring the relationship between evolutionary and ecological dynamics. The conclusion was that, in many situations, the time scales of evolutionary and ecological changes are very similar, in contrast to the common assertion that evolution occurs too slowly in comparison to ecological dynamics. They claim that there are many empirical demonstrations that ecological changes can lead to evolutionary changes. Therefore, we cannot take for granted that those processes occur in very different time scales. In fact, they propose an analogy to Dobzhansky's famous sentence, suggesting that 'nothing in evolution or ecology makes sense except in the light of the other'.

In this work, we are interested in how the interactions between predator and prey can influence the evolutionary change of prey types and how these evolutionary changes modify the ecological balance between predator and prey. The presence of predators is of great importance as an eco-evolutionary feedback [18]. For example, Darwin noticed that the beautiful colours of the male peacock increase the chance of successful mating. However, the colours can be a threat because of the increase in the probability of being caught by predators [4]. Here, we investigate the evolution of two concurrent alleles in a population of prey whose dynamics is coupled with the predator dynamics. There are only two species: the predator and the

prey, with the prey coming in two types. Our main goal is to analyse the feedback between the evolution of the two prey types and the predator abundance. Thus, we take an eco-evolutionary dynamics approach.

The analysis of two-prey one-predator models has an extensive literature [19–23], with the focus on the ecological description of tree interacting species. Other works with more general per capita growth rates focus on the conditions for the persistence of the species. In [23], the authors proved a very general theorem that establishes conditions for persistence of three interaction species and provided interesting examples of two-prey one-predator, two-predator one-prey, and food chain dynamics where persistence is observed. In [47], the authors revised works that address the problem of coexistence of n-interacting species and provide an example where two predators coexist with one prey. However, the growth and prey capture rates in these examples are always constant. Here, we analyse the case where the reproductive and capture rates are frequency-dependent. In evolutionary game theory, we say that the prey plays two games: the reproductive and the defence against predators games. Thus, we analyse a replicator-game dynamics with a payoff matrix that depends on some environmental factor [15]. In our case, the environmental factor is the presence of predators. Because we end up with an equation analogous to the replicator equation, we called our equation *predator-dependent replicator equation.*

We provide a general analysis of the predator-dependent replication equation, illustrating the results with two interesting examples. The first one is the case of prey with two different visuals: one type is more attractive than the other for potential mates, but is also more attractive to predators. We show that polymorphic prey can be stable and that both prey types can have lower capture rates by coexisting. There is empirical evidence that polymorphism in prey can diminish predators success [24, 25]. The second example is the well-studied threshold between passive and aggressive behaviour. In contests for mates, the aggressive and passive types play Hawk–Dove game [8, 9, 26]. On the other hand, because team defence is usually much better than dispersing and trying to escape, the game that is likely to be played in interactions against predators is the stag-hunt game [27, 28]. We model this situation and find that one type can start with a tiny fraction of individuals and dominate the population, even though this is not possible in any one of the two games separately. More interesting, we show that predators can select aggressive prey by enhancing the capture rate of the passive prey, which, after all, is worse for the predators. This can be seen as a rapid feedback response in the predator–prey evolutionary arm's race.

This paper is organized as follows. In section 2, we introduce the two-prey-one-predator model. In section 3, we derive a replicator-like equation that depends on the number of predators. In section 4, we analyze the trivial cases and a general analysis to calculate the analytical conditions for the stable coexistence of both prey types and predators. In section 5, we illustrate the model with two interesting examples. Finally, conclusions are presented in section 6.

2. The model

Let us consider two types of prey of the same species interacting with predators. The assumptions of the model are

 (a) In the absence of predators and in monomorphic populations, the single prey type grows logistically.
 (b) In the absence of predators and in polymorphic populations, the growth rates are frequency-dependent.

(c) Predation reduces the prey growth at a rate that depends on the frequency of each prey type in the population.

(d) In the absence of prey, the predator abundance decreases to zero.

(e) The predator growth depends on the availability of prey and on the size of the predator population.

Let X_A, X_B be the number of prey of types A and B, respectively, and Y be the number of predators. The relative frequency of each type of prey is defined as $x_A = X_A/(X_A + X_B)$ and $x_B = X_A/(X_A + X_B)$. The system of differential equations is then given by

$$\frac{dX_A}{dt} = X_A \left[f_A(x_A, x_B) - \frac{X_A + X_B}{K} - f'_A(x_A, x_B)Y \right],$$

$$\frac{dX_B}{dt} = X_B \left[f_B(x_A, x_B) - \frac{X_A + X_B}{K} - f'_B(x_A, x_B)Y \right],$$

$$\frac{dY}{dt} = Y \left[-\beta + \gamma f'_A(x_A, x_B)X_A + \gamma f'_B(x_A, x_B)X_A \right], \qquad (1)$$

where $f^*(x_A, x_B)$ and $f'_*(x_A, x_B)$ are the growth and the capture rates, respectively (the symbol $*$ is a placeholder for the type, A or B). The carrying capacity of the environment has its order of magnitude scaled by K, β is the predator's death rate and γ is the predator's efficiency in prey consumption.

The new feature that we introduce in our model, compared to the typical two-prey one-predator models, is that the growth and the capture rates depend on the frequency of prey types. There is empirical evidence that these rates can depend on the relative fractions of the types [24–26, 42]. Notice that, if the functions f_* and f'_* are constants, the traditional two-prey one-predator system is recovered.

The functional form of the frequency-dependent rates depends on the system under consideration. If we restrict our investigation to well-mixed populations and first-order interaction terms [46], we can write the rates as

$$f_A = r + \delta(ax_A + bx_B),$$
$$f'_A = p + \delta(a'x_A + b'x_B),$$
$$f_B = r + \delta(cx_A + dx_B),$$
$$f'_B = p + \delta(c'x_A + d'x_B), \qquad (2)$$

where r is the base reproduction rate, p is the base capture rate, and δ quantifies the strength of the frequency-dependent term.

The frequency-dependent terms in equation (2) can be interpreted as payoffs coming from biological games [48]. In the reproduction game, a is the payoff coming from the encounters of type A with A, b of type A with type B, c of type B with type A, and d of type B with type A. The interpretation of the capture rate coefficients a', b', c', and d' is analogous. We must stress that even group interactions that cannot be decoupled into pair interactions can be modelled using equation (2) if the higher-order frequency-dependent interaction terms are negligible. In this case, equation (2) holds as a linear approximation to the frequency-dependent social payoffs.

The mathematical analysis can be simplified by noticing that

$$f_A = r + \delta(ax_A + bx_B) = (r + \delta a)x_A + (r + \delta b)x_B,$$

so that the parameters r, p and δ are absorbed into the payoff matrix by making the changes $(r + \delta a) \to a$, $(r + \delta b) \to b$, $(p + \delta a') \to a'$, $(p + \delta b') \to b'$, $(r + \delta c) \to c$, $(r + \delta d) \to d$, $(p + \delta c') \to c'$ and $(p + \delta d') \to d'$. Thus, the system of differential equations in equation (1) can be written in terms of the number of prey and predators and the transformed payoff matrix values as

$$\frac{dX_A}{dt} = X_A \left[\frac{aX_A + bX_B}{X_A + X_B} - \frac{X_A + X_B}{K} - \frac{a'X_A + b'X_B}{X_A + X_B}Y \right],$$

$$\frac{dX_B}{dt} = X_B \left[\frac{cX_A + dX_B}{X_A + X_B} - \frac{X_A + X_B}{K} - \frac{c'X_A + d'X_B}{X_A + X_B}Y \right],$$

$$\frac{dY}{dt} = Y \left[-\beta + \gamma \frac{a'X_A + b'X_B}{X_A + X_B}X_A + \gamma \frac{c'X_A + d'X_B}{X_A + X_B}X_B \right]. \tag{3}$$

3. The predator-dependent replicator equation

The system of differential equations in equation (3) describes the time evolution of the number of prey types and predators. To analyze the competition between the prey types, we can look at the projection of the orbits on the simplex $x_A + x_B = 1$. To obtain the dynamics on the simplex, we just have to change the variables in equation (3) from X_A and X_B to x_A and x_B.

First, the equation (3) can be simplified if we notice that f_* and f'_* can be combined into a single term $\tilde{f}_*$ corresponding to the effective rate for each type:

$$\tilde{f}_A = \frac{(a - a'Y)X_A + (b - b'Y)X_B}{X_A + X_B}, \tag{4}$$

$$\tilde{f}_B = \frac{(c - c'Y)X_A + (d - d'Y)X_B}{X_A + X_B}.$$

Defining $\tilde{a} = a - a'Y$, $\tilde{b} = b - b'Y$, $\tilde{c} = c - c'Y$ and $\tilde{d} = d - d'Y$, we obtain

$$\tilde{f}_A = \tilde{a}x_A + \tilde{b}x_B, \tag{5}$$

$$\tilde{f}_B = \tilde{c}x_A + \tilde{d}x_B.$$

The evolution of the relative fractions x_A and x_B can then be written as

$$\frac{dx_A}{dt} = x_A(\tilde{f}_A - \phi), \tag{6}$$

$$\frac{dx_B}{dt} = x_B(\tilde{f}_B - \phi),$$

where $\phi = x_A\tilde{f}_A + x_B\tilde{f}_B$ is the average effective fitness of the population of prey. Because $x_B = 1 - x_A$, we can define $x = x_A$ so that we have to work only with the equation

$$\frac{dx}{dt} = x(1 - x)\left[\left(\tilde{a} - \tilde{b} - \tilde{c} + \tilde{d}\right)x + \tilde{b} - \tilde{d}\right], \tag{7}$$

which is the *predator-dependent replicator* equation (see a detailed deduction in the supplementary material (https://stacks.iop.org/JPA/55/025601/mmedia)). The form of equation (7) is

analogous to the traditional replicator equation with payoff matrix given by

$$\begin{pmatrix} \tilde{a} & \tilde{b} \\ \tilde{c} & \tilde{d} \end{pmatrix} = \begin{pmatrix} a - a'Y & b - b'Y \\ c - c'Y & d - d'Y \end{pmatrix}. \tag{8}$$

The difference to the traditional replicator equation is that the elements of the payoff matrix are not constant, but depends on the number of predators. If there are no predators, that is, if $Y = 0$, the traditional replicator dynamics is recovered [48].

4. Analysis

The focus of this work is to analyze how different types of prey co-evolve in the presence of predators. The information on the competition between the prey types is contained in the dynamics of the predator-dependent replicator equation, which shows clearly that the presence of predators affects the competition by the possibility of changing the game class of the payoff matrix in equation (8).

4.1. Trivial cases

There are four trivial cases for which the analysis reduces to the analysis of the traditional replicator equation. Let us, first, recall the analysis of the traditional replicator equation. The traditional replicator equation has the same form of equation (7), but with constant coefficients, that is, $\tilde{a}$, $\tilde{b}$, $\tilde{c}$, and $\tilde{d}$ are constant values. In this case, if $\tilde{a} > \tilde{c}$ and $\tilde{b} > \tilde{d}$, the point $x = 1$ is a global attractor, that is, type A dominates the population (prisoner's dilemma game, with B being the cooperative type). If $\tilde{a} > \tilde{c}$ and $\tilde{b} < \tilde{d}$, there is an unstable internal equilibrium with orbits converging to either $x = 0$ or $x = 1$ and we say that there is codominance (stag-hunt game). If $\tilde{a} < \tilde{c}$ and $\tilde{b} > \tilde{d}$, the points $x = 0$ and $x = 1$ are unstable and the point $x^* = (\tilde{d} - \tilde{b})/(\tilde{a} - \tilde{b} - \tilde{c} + \tilde{d})$ is an internal stable equilibrium if $0 < x^* < 1$ (hawk-or-dove game) and we say that there is coexistence. Last, if $\tilde{a} < \tilde{c}$ and $\tilde{b} < \tilde{d}$, the point $x = 0$ is a global attractor, that is, type B dominates the population (harmony game).

The first trivial case is when there are no predators, $Y = 0$. In this case, the payoff matrix depends only on the reproduction coefficients, which are constants, and the analysis is the same as in the traditional replicator equation analysis.

The second trivial case is when there is only the reproduction game, with the predation rate not depending on the frequency. This is equivalent to have $a' = b' = c' = d'$. In this case, the same quantity Y is added to the entries of the payoff matrix in equation (8), which is known not to affect the equilibrium analysis of the replicator dynamics. Thus, the outcomes of the traditional replication dynamics are recovered.

The third trivial case is when there is only the predation game, which is equivalent to have $a = b = c = d$. The analysis is analogous to the second trivial case, but with the inequalities interchanged, since predation payoffs negatively affect the prey's effective fitness.

The fourth trivial case is when the number of predators is constant, which can happen, for example, if the predators depend only weakly on the two prey types. In this case, the coefficients of the payoff matrix 8 are all constant, and the traditional replication dynamics is once more recovered. Interestingly, the simple presence of predators can change the class of the game. For example, in the absence of predators, type B may not invade if the reproductive payoff matrix is of the prisoner's dilemma type. However, if type B teams up so the cooperative behaviour in the defence against the predators compensate

for the reproductive disadvantage, the type B may invade depending on the number of predators.

4.2. General case

In the general case, the population of predators co-evolves with the population of prey because the payoff matrix in equation (8) has a time dependence on the number of predators. Thus, during the evolution, the effective game defined in equation (8) may change. For example, suppose the reproduction game is a prisoner's dilemma game and the predation game is a harmony game. If the number of predators is small, the dynamics is mainly driven by the prisoner's dilemma dynamics, with the type A having the advantage. On the other hand, if the number of predators is large, the dynamics is mainly driven by the harmony game, with type B having the advantage. Thus, the fate of the prey type evolution depends on the coupling with the predator dynamics.

Because there are four classes of games for reproduction and four for predation, there are sixteen different combinations of reproductive and predation games, as shown in figure 1. Although each class of game tries to push the system to its game equilibrium (A dominates, co-dominance, coexistence, or B dominates), it is the combination of the reproduction and the predation games, as two competing forces, that will ultimately determine the prey composition in the population.

The simplest combinations are the ones where both the reproduction and predation games are of the same class, as in cases 1, 6, 11 and 16 in figure 1. In these cases, the class of the effective payoff matrix in equation (8) does not change. For example, in case 1, the type A dominates because both the reproduction and the predation games are games where type A dominates. This can be seen from a simple analysis of equation (7): the state $x = 1$ is a global attractor for any value of Y. Because only one type dominates in cases 1, 6, and 16, the dominated type will be eventually eliminated, reducing the system to the simple one-prey-one-predator dynamics. In case 11, because both the reproduction and the predation games yield coexistence, the combination also yields coexistence.

In the other cases, the class of the effective game with the payoff matrix in equation (8) can change during the system evolution, and the analysis is not trivial. Hence, the main question is about the conditions of persistence of the two types of prey along with the predator. The dynamical systems that we are analysing here is an instance of the general Kolmogorov equations, for which conditions for persistence can be derived [23], as shown in the appendix A and further detailed in our supplementary material. For our system, the conditions of persistence are given by

$$\text{(i) } (bd' - b'd)\gamma K + (b'/d' - 1)\beta > 0 \tag{9}$$

$$\text{(ii) } (ca' - c'a)\gamma K + (c'/a' - 1)\beta > 0. \tag{10}$$

That is, to have the coexistence of both types of prey, both conditions must be satisfied. We stress that these conditions are just sufficient, not necessary ones. Condition (i) guarantees that type A is not extinct and (ii) guarantees the same for type B. If the carrying capacity is large enough, we can simplify the conditions to

$$\text{(i) } (bd' - b'd)\gamma K > 0$$

$$\text{(ii) } (ca' - c'a)\gamma K > 0. \tag{11}$$

In fact, given the payoff matrix values, we can always choose K sufficiently large so that the full conditions and the reduced ones are equivalent. Analyzing the reduced conditions, we can

	Conditions can not be satisfied	Conditions can be satisfied	Conditions are always satisfied	

Predation / Reproduction	A dominates $a' < c'$ $b' < d'$	Codominance $a' < c'$ $b' > d'$	Coexistence $a' > c'$ $b' < d'$	B dominates $a' > c'$ $b' > d'$
A dominates $a > c$ $b > d$	A dominates 1	2	3	4
Codominance $a > c$ $b < d$	5	Codominance 6	7	8
Coexistence $a < c$ $b > d$	9	10	Coexistence 11	12
B dominates $a < c$ $b < d$	13	14	15	B dominates 16

Figure 1. Combinations of reproduction and predation games. In the rows (columns), we show the four possible reproduction (predation) games. Each class of game, taken separately, has its dynamics: type *A* dominates; co-dominance, which is the case where either *A* or *B* dominates depending on the initial conditions; coexistence; and type *B* dominates. The cases in the main diagonal have both reproduction and predation games in the same class, and the dynamics reflect the common class's dynamics. For the other combinations, there can be coexistence of the prey with the predator depending on whether conditions 9 and 10 are satisfied. The combinations in which no coexistence is possible are shown in grey, the ones in which there are payoff values for which coexistence is possible is shown in light blue, and the single one in which coexistence always happens is shown in dark blue.

see that there can be persistence in all cases where one game is a coexistence game (cases 3, 7, 15 and 9, 10 and 12) and also in the two cases where each type has total dominance in one of the games (cases 4 and 13), as shown in figure 1. In particular, only in case 11, where both games are of the coexistence class, the conditions 9 and 10 are always satisfied.

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5. Examples

In this section, we illustrate the dynamics with biological examples. The mapping between the game framework and the actual payoffs coming from the biological interactions is not a trivial task. The social component of the rates can be a non-linear function of the frequencies of the types. The replicator dynamics looks only at first-order interaction terms [46], describing the rates as a constant base value plus a linear frequency-dependent term. The theoretical insights coming from the simplicity of evolutionary game theory are of great value and often come before the phenomena' empirical investigation. For example, oscillations in 'rock-scissors-paper' games were first viewed as theoretical issues, that were later observed in nature [42, 49].

The replicator dynamics assumes asexual reproduction, which may sound rather unnatural if applied to sexually reproductive species. However, the essential features of the simple sexual models are preserved in the more complex sexual reproduction models [50–52]. The power of the replication equation lies in the fact that it looks at the competition between phenotypes relative to the average fitness of the population, which is the core of selective processes. Hence, the replicator equation can be seen as a mathematical model of gross variables: the frequency of phenotypes.

5.1. Attractiveness

Colour, ornaments, extravagant behaviour and other attractive features are often associated with a greater reproduction success [29–31]. However, at the same time, they can increase the risk of predation [32–34]. More specifically, we can define two types, *A* and *B*, with type *A* being the more attractive. If the reproductive and the predation rates are frequency-dependent, both can be modelled as dominance games: type *A* is dominant in the reproduction and type *B* in avoiding predators. This is an example of case 4 in figure 1.

In the absence of predators, type *A* dominates. The replicator dynamics gives no chance for type *B*. For example, if all males are equally attractive, a mutation yielding a less attractive male would have no chance against the attractive type and would be readily eliminated. However, if predators are present, the less attractive type can coexist with the more attractive type if conditions 9 and 10 are satisfied, which is the case illustrated in figure 2. Notice that, in this example, both games—reproduction and capture—are dominance games. However, because conditions 9 and 10 are satisfied, there is coexistence. Consequently, if there are two types of colours, one that is more attractive for reproduction and the other that is better to avoid predators, there can be a coexistence of polymorphic prey. In addition, both prey types in this example have a lower capture rate if the other type is present. So, in this case, the stable colour polymorphism can diminish predators success. Empirical work has shown that colour polymorphism can reduce predation risk [24, 25].

5.2. Aggressive behaviour

Aggressive behaviour can be a double-edged sword. In the competition for mates, aggressive types have an advantage over passive types [27, 28, 35]. However, when facing predators, a solitary fight against a group of predators may not be as good as trying to escape. For large animals, team defence is usually more effective than dispersing [36]. The interaction between gnus, also known as wildebeests, and African wild dogs illustrates the point. Gnus can either run away from the wild dogs or fight them. In the latter case, the best option is to form a two-individual formation where each gnu protects one side of the formation. If both gnus are more aggressive, they make the two-individual formation, and survival chances are higher. However,

Predator/prey population over time
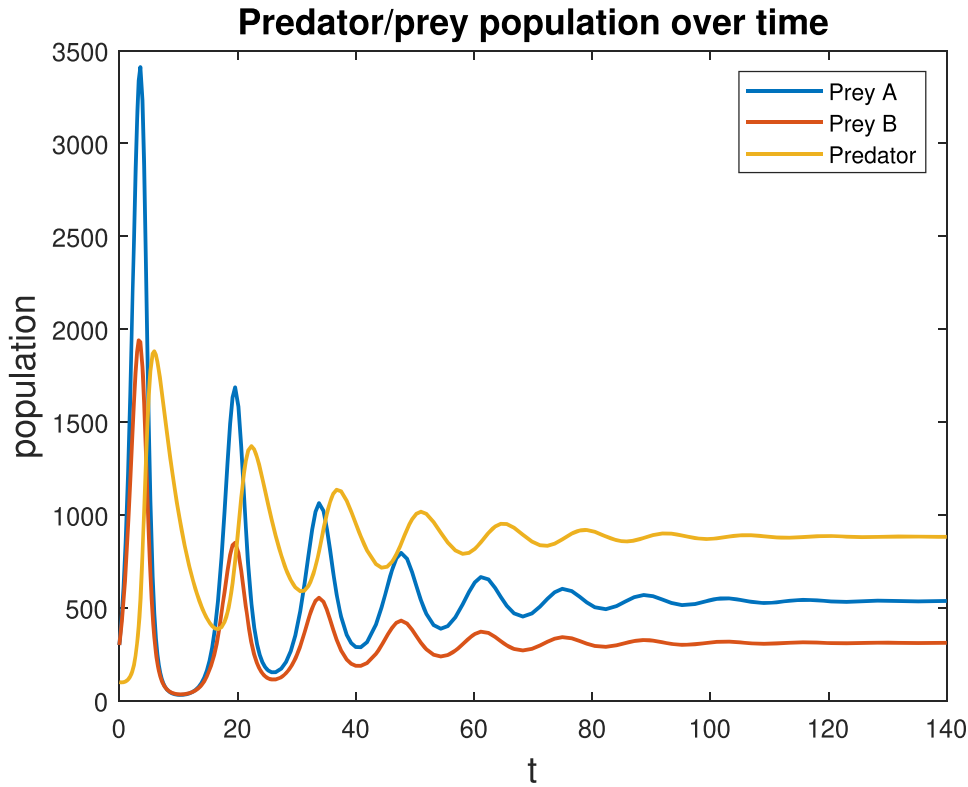
Figure 2. Polymorphic prey. Although the two games are dominance games, in the presence of predators both types of prey coexist because conditions (i) and (ii) are satisfied. Furthermore, the rate of capture in the presence of both types of prey is lower than if there was only one type of prey. Parameters are $a = b = 1.2$, $c = d = 1$, $a' = 0.0013$, $b' = 0.0012$, $c' = 0.001$, $d' = 0.0011$, $\gamma = \beta = 0.2$ and $K = 10\,000$. Here we are in case 4 shown in figure 1.

if one is more passive and prefer to escape, the chance to survive is reduced for both and, for the one that stays, it would be better if it had tried to escape. This situation can be represented as a stag-hunt predation defence game. On the other hand, aggressive gnus may have an advantage in the competition for mates. The Hawk–Dove game can represent this situation: the aggressive type is better off than the passive one, but can be severely injured in the fight against another aggressive type [8, 9, 26].

The wild dogs vs wildebeests interaction is an interesting illustration of reproduction determined by the Hawk–Dove game and predation defence determined by stag-hunt game, which is the case 10 in figure 1, with type A being the more aggressive type. Type *A* can never invade and dominate the population if just one of the two games is played. This can happen if they play Hawk–Dove in the reproduction game and have equal capture rates or stag-hunt in the predation game and have equal reproduction rates. Recall that, in Hawk–Dove games, there is an internal equilibrium that is a global attractor, and, in stag-hunt games, the type *B* is locally stable. However, type *A* may dominate the population when both reproduction and predation defence games are played. The theorem shows that, if type *A* dominates, the persistence conditions cannot be satisfied. Notice that the theorem does not guarantee that
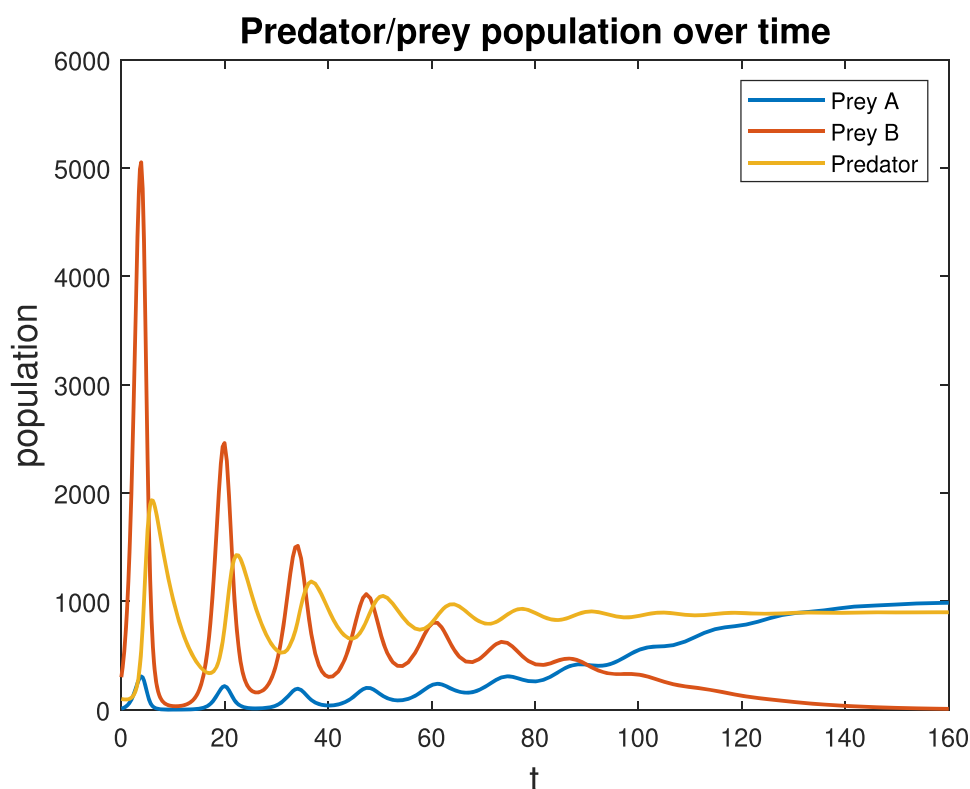
Figure 3. Aggressive type dominance. The prey type *A* can invade and dominate the population, even though this not being possible in any one of the two games separately. Initial conditions are $X_A(0) = 10$, $X_B(0) = 300$, $Y(0) = 100$, and parameters are $a = 1$, $b = 1.4$, $c = 1.1$, $d = 1.2$, $a' = 0.001$, $b' = 0.0015$, $c' = 0.0012$, $d' = 0.0013$, $K = 10\,000$ and $\beta = \gamma = 0.2$. Here we are in case 10 shown in figure 1.

type *A* dominates, but is delimits the parameter region where type *A* domination may happen. One way to fail the conditions is to have condition 9 satisfied and 10 not satisfied. In this case, the condition 9 guarantees that type *A* can emerge and the failure of condition 10 keeps open the possibility of extinction of type *B*. Figure 3 shows the orbit for a specific set of parameters for which type *A* ends up dominating the population. We stress that, in this case, type *A* can invade and dominate the population, even if type *A* starts with a tiny fraction of individuals.

The interaction between agonistic behaviour and team defence can have an interesting effect on the population equilibrium. Suppose that the initial population of gnus is mainly composed of passive types and that conditions 9 and 10 are not satisfied. An example of this situation is shown in figure 4, where the aggressive prey cannot invade the population. Recall that d' quantifies the effect of the interaction between passive types on the rate of capture. Suppose that, due to some evolutionary mechanism, the capture rate d' increases so that the condition 9 starts to be satisfied. In this case, the type *A*, which is more aggressive, may have a chance to invade and dominate, as shown in figure 3. Then, for the predators, the unwanted consequence of an increase in the capture rate of passive prey is the selection of the aggressive prey. For the parameters in figures 3 and 4, the equilibrium number of predators is approximately 10%
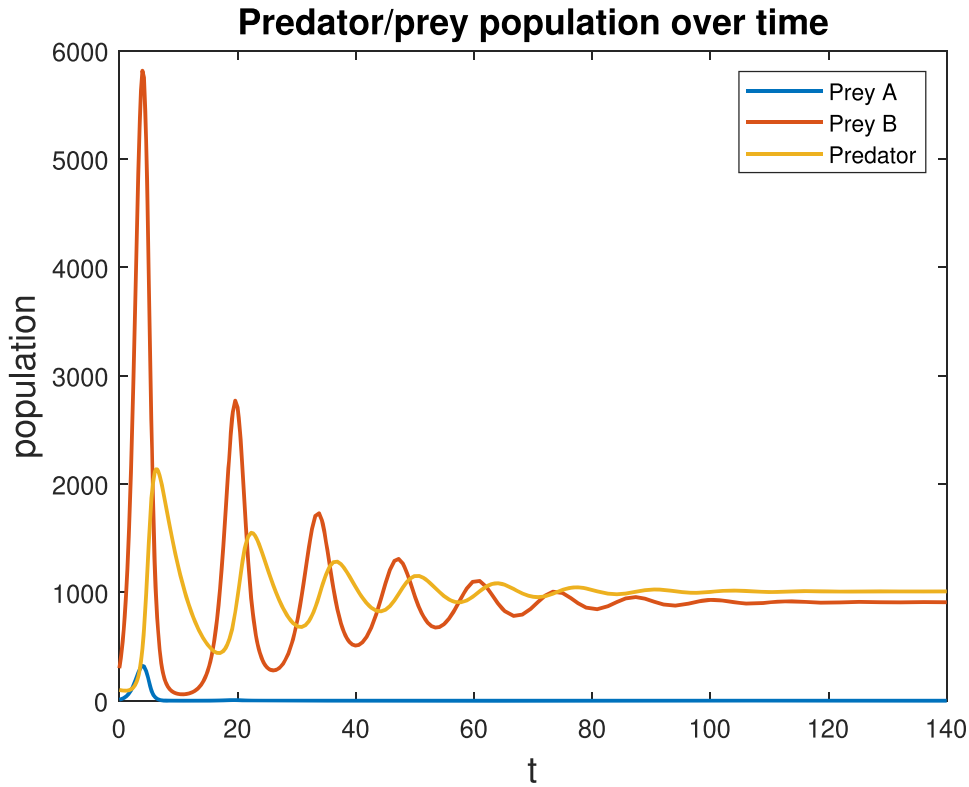
Figure 4. Aggressive type cannot invade. In this figure the parameters differ from those in figure 3 only by d'. The consequence of this small change is that prey B can resist against prey A invasion. Note that predators do better in this case, living with the passive type, even having less available prey. Initial conditions are $X_A(0) = 10$, $X_B(0) = 300$, $Y(0) = 100$, and parameters are $a = 1$, $b = 1.4$, $c = 1.1$, $d = 1.2$, $a' = 0.001$, $b' = 0.0015$, $c' = 0.0012$, $d' = 0.0011$, $K = 10\,000$ and $\beta = \gamma = 0.2$. Here we are in case 10 shown in figure 1.

lower if predators live with aggressive type than if living with the passive type, even having more available prey. This can be seen as an arm's race evolutionary feedback.

6. Conclusions

We analyze a two-prey one-predator system with frequency-dependent rates of reproduction and predation. We show that a replicator-like dynamics, which we called the predator-dependent replicator equation, describes the projection of the orbit on the simplex in the prey space. The analysis of the predator-dependent replicator dynamics is more complex than the analysis of the traditional replicator equation because the game class can change during evolution. Nevertheless, it is possible to obtain analytical conditions to predict the coexistence of both prey and predator.

   We illustrate the model with two interesting examples. In the first one, we show that predators can lead to the coexistence of polymorphic prey if one of the prey types has higher reproduction's and predation's rates. Interestingly, this coexistence can lead to lower capture

rates for both prey types. In the second example, we show that predators can help a type of prey, initially rare, to take over the population by improving its capture rate, an example of the evolutionary feedback of arm's race.

Theoretical models are powerful tools to replicate qualitative features and shed light on various non-trivial phenomena. For example: the selfish nature of individuals that can lead to worse outcomes in the population level [37]; the great height achieved by trees in environments where the Sun is the main limiting factor [38]; the one-to-one sex ratio in species where the majority of males never reproduces [39], as in elephant seals [40]; the limit of escalating aggression in animal contests for food [41] or in contests stuck by male for reproduction [8, 26]; the polymorphic stability of three types of males side-blotched lizards (*Uta stansburiana*) due to rock-paper-scissors game dynamics [42]; the widely spread phenomenon of cooperation in structured populations, seemingly paradoxical, but that can emerge if there is some spatial restriction [43–45]. Following this list, our model provides valuable theoretical insights on the evolution of animals in the presence of predators.

The framework developed here can be easily extended to the analysis of more complex ecological interaction, for example, models of *n*-prey and *m*-predators. Our results show that the simple predator-dependent replicator equation can explain newsworthy examples of predators evolutionary-game dynamics.

Acknowledgments

Data availability statement

No new data were created or analysed in this study.

Appendix A. Appendix: mathematical analysis

Our system is a special case of the following three interacting populations Kolmogorov system [23]:

$$\frac{\mathrm{d}X_A}{\mathrm{d}t} = X_A F_A(X_A, X_B, Y)$$

$$\frac{\mathrm{d}X_B}{\mathrm{d}t} = X_B F_B(X_A, X_B, Y)$$

$$\frac{\mathrm{d}Y}{\mathrm{d}t} = Y G(X_A, X_B, Y) \tag{A.1}$$

with $X_A(0) > 0$, $X_B(0) > 0$, and $Y(0) > 0$; F_A, F_B, and G are continuously differentiable. To connect to our model, we interpreted the first two equations as determining the dynamics of the abundance of the two prey types and the third one determining the dynamics of the predators.

Let E_0 be the origin, E_A be the prey's A equilibrium in the absence of predators and prey B, and E_B be the prey's B equilibrium in the absence of predators and prey A. As proven in [23], the general conditions of persistence of the types, that is, for the long-run coexistence of the three types, are given by the following theorem.

Theorem 1. *The system* (A.1) *persist if the following conditions are satisfied:*

(H1) F_A, F_B, G *are* C^1 *in* (X_A, X_B, Y).

(*H2*) *All solutions of the system (with nonnegative initial conditions) are bounded in forward time.*

(*H3*) E_A, *and* E_B *(if it exists) are hyperbolic equilibrium points.*

(*H4*) *Interior to each positive coordinate plane there is at most one equilibrium, which if it exists is unstable in the positive direction orthogonal to that plane, and around which there are no periodic orbits.*

(*H5*) *The origin* $E_0 = (0,0,0)$ *are unstable in the direction of the prey and asymptotically stable in the direction of predators.*

We show in the supplementary material that our system satisfies all conditions. In particular, the hypothesis (H4) is satisfied in our model if:

$$\text{(i) } (bd' - b'd)\gamma K + (b'/d' - 1)\beta > 0 \tag{A.2}$$

$$\text{(ii) } (ca' - c'a)\gamma K + (c'/a' - 1)\beta > 0. \tag{A.3}$$

These two inequalities follow from the analysis of the equilibrium of the predator with just one of the prey types (remember that, in this analysis, we are dealing with parameters that can maintain a predator's population). The conditions (A.2) and (A.3) guarantees that type *A* and type *B* are not extinct, respectively. If both are satisfied, then the system persists.

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