Weak species in rock-paper-scissors models

P. P. Avelino¹-², B. F. de Oliveira³(a) and R. S. Trintin³

¹ Departamento de Física e Astronomia, Faculdade de Ciências, Universidade do Porto
Rua do Campo Alegre s/n, 4169-007 Porto, Portugal
² Instituto de Astrofísica e Ciências do Espaço, Universidade do Porto, CAUP - Rua das Estrelas, 4150-762 Porto, Portugal
³ Departamento de Física, Universidade Estadual de Maringá - 87020-900 Maringá, PR, Brazil

received 12 April 2021; accepted in final form 3 May 2021
published online 26 July 2021

Abstract – In this letter, we investigate the population dynamics in a May-Leonard formulation of the rock-paper-scissors (RPS) game in which one or two species, which we shall refer to as “weak”, have a reduced predation or reproduction probability. We show that in a non-spatial model the stationary solution where all three species coexist is always unstable, while in a spatial stochastic model coexistence is possible for a wide parameter space. We find that a reduced predation probability results in a significantly higher abundance of “weak” species, in models with either one or two “weak” species, as long as the simulation lattices are sufficiently large for coexistence to prevail. On the other hand, we show that a reduced reproduction probability has a smaller impact on the abundance of “weak” species, generally leading to a slight decrease of its population size —the increase of the population size of one of the “weak” species being more than compensated by the reduction of the other, in the two-species case. We further show that the species abundances in models where both predation and reproduction probabilities are simultaneously reduced may be accurately estimated from the results obtained considering only a reduction of either the predation or the reproduction probability.

Introduction. – Ecology is the study of the interactions of living organisms with one another and with their ecosystem. Intra-specific and inter-specific interactions are essential for the coexistence of a wide variety of species and are, therefore, also crucial for the development and sustainability of biodiversity. Evolutionary games usually seek to quantify this natural process through the simulation of the dynamics of populations with different species subject to non-hierarchical interactions.

The classic RPS model (see [1–3] for the pioneering work by Lotka and Volterra, and May and Leonard) describes the dynamics of a population of three species with cyclic predation, as well as mobility and reproduction interactions. In spatial RPS models the coexistence of all three species can be maintained in a significant parameter volume of predation, mobility and reproduction probabilities [4–7]. Corresponding biological examples have been found in Nature, including E. coli bacteria [8,9] and lizards [10].

Population dynamics in spatial stochastic RPS-type models has been investigated thoroughly in the literature considering a wide variety of models and perspectives [11–29]. Although such dynamics is usually strongly dependent on a variety of model parameters—including predation, reproduction and mobility probabilities—in most cases these are assumed to be the same for all species. However, this simplifying assumption is not expected to constitute a valid approximation in the modelling of most biological systems in Nature.

The impact of the reduction of the predation probability of a single (“weakest”) species has been investigated in the context of the spatial stochastic three-species RPS model [30–33]. It has been shown that coexistence of all three species prevails for sufficiently large simulation lattices, with the “weakest” species being the most abundant [32] —for smaller simulation lattices, large-amplitude oscillations at the initial stages of simulations with random initial conditions can lead to a significant dependence of the chance of the “weakest” species survival on the lattice size [32,33]. The crucial importance of the simulation lattice size has also been recognized in the context of public goods games with punishment [34–37].

Recent research [38] dealing with the inhibition of protein production, the digestion of genomic DNA and the rupture...
of cellular membrane with three strains of *E. coli* interacting cyclically in an asymmetric system also concluded for the dominance of the “weakest” strain.

In this letter we extend previous work on the performance of “weak” species, by investigating the dynamics of RPS models in which one or two species have their predation and/or reproduction probability reduced. We start by describing a non-spatial RPS model, showing that it does not allow for stable stationary solutions where all three species coexist. We then describe our May-Leonard implementation of the spatial stochastic RPS model and assess the performance of “weak” and “strong” species in numerical lattice simulations allowing for the coexistence of all three species. In particular, we shall highlight the dependence of the results on whether the “weak” species are characterized by a reduced predation or reproduction probability. We will also describe an approximation allowing for the estimate of the species abundances, in models where both predation and reproduction probabilities are simultaneously reduced, from the results obtained considering only a reduction of either the predation or the reproduction probability. Finally, we present the main conclusions of our work.

**Non-spatial RPS model.** – Here we shall consider a four-state cyclic predator-prey model, also known as a May-Leonard implementation of the RPS model. The densities of the species $i = 1, \ldots, 3$ shall be denoted by $\rho_i$. For simplicity of notation, the density associated to the additional state—denoted by a “0”—shall be referred to as the density of empty sites, even when considering a non-spatial model. The total density is normalized to unity, so that

$$\rho_0 + \sum_{i=1}^{3} \rho_i = 1. \quad (1)$$

In a non-spatial RPS model there are two possible interactions: predation ($i (i + 1) \rightarrow i$) and reproduction ($i \rightarrow i + 1$), with probabilities $p_i$ and $r_i$, respectively (we shall use modular arithmetic throughout the paper, so that the integers $i$ and $j$ represent the same species whenever $i = j \mod 3$, where mod denotes the modulo operation). With an appropriate choice of the time unit, the set of equations that represents the evolution of the densities of the different species may be written as

$$\dot{\rho}_i = r_i \rho_i \rho_0 - p_i \rho_{i-1} \rho_{i-1} \rho_i. \quad (2)$$

The stationary solutions to eq. (2) are

$$\rho_i = \frac{1}{1 + \frac{p_i r_{i-1}}{r_{i+1} + p_{i+1} r_{i+1}} + p_i r_i}, \quad (3)$$

$$\rho_0 = \frac{1}{1 + \frac{r_1}{p_3} + \frac{r_2}{p_1} + \frac{r_3}{p_2}}. \quad (4)$$

We have verified that there are no stationary solutions to eq. (2) with $\rho_i \neq 0$ for all $i = 1, 2, 3$ in which the real part of all the eigenvalues of the Jacobian matrix, defined by

$$\frac{\partial \dot{\rho}_1}{\partial \rho_1} \begin{bmatrix} \frac{\partial \dot{\rho}_1}{\partial \rho_2} \\ \frac{\partial \dot{\rho}_2}{\partial \rho_1} \\ \frac{\partial \dot{\rho}_2}{\partial \rho_2} \\ \frac{\partial \dot{\rho}_3}{\partial \rho_1} \\ \frac{\partial \dot{\rho}_3}{\partial \rho_2} \\ \frac{\partial \dot{\rho}_3}{\partial \rho_3} \end{bmatrix} = \begin{bmatrix} r_1(p_0 - p_1) - p_3 p_3 & -r_1 p_1 & -r_1 p_0 - p_3 p_3 \\ -r_1 p_1 - p_3 p_3 & r_2(p_0 - p_2) - p_1 p_1 & -r_2 p_2 \\ -r_3 p_3 & -r_3 p_3 & r_3(p_0 - p_3) - p_2 p_2 \end{bmatrix},$$

is negative. Therefore, we conclude that the stationary solutions to eq. (2), given by eqs. (3) and (4), leading to the coexistence of all three species are always unstable in a non-spatial RPS model [39].

**May-Leonard spatial stochastic RPS model.** – In this letter we shall consider a May-Leonard implementation of the spatial RPS model on a two-dimensional square lattice with $N$ sites and periodic boundary conditions. At each simulation time step, an individual (active) is randomly chosen to interact with one of its four nearest neighbors (passive)—also randomly selected. Then, one of three possible interactions (predation, reproduction, or mobility) is randomly chosen (with probabilities $p$, $m$, and $r$, respectively). In this paper we shall consider the so-called von Neumann neighbourhood (or 4-neighbourhood) composed of a central cell (the active one) and its four non-diagonal adjacent cells. Whenever mobility is selected the active individual swaps place with the passive one. On the other hand, if reproduction is selected and the passive individual is an empty site (otherwise the interaction cannot be completed, and the procedure is repeated once again), then the site becomes occupied with an individual of the same species of the active one. Finally, if predation is selected and the passive individual is a prey of the active one (otherwise the interaction cannot be completed, and the procedure is repeated once again), then the passive individual is removed from the lattice and an empty site is left at its previous position. A time step is completed whenever one interaction is carried out. A generation time (our time unit) corresponds to $N$ time steps.

Here we shall investigate the dynamical impact of a reduction of the predation or reproduction probabilities of one or two species by a factor of $P_w \in [0, 1]$ or $R_w \in [0, 1]$, respectively. We will consider the following cases: Model $P_1$: one species with reduced predation probability, $p_1 = P_w p_1$ ($p_2 = p_3 = p$); Model $R_1$: one species with reduced reproduction probability $r_1 = R_w r_1$ ($r_2 = r_3 = r$); Model $P_2$: two species with reduced predation probabilities $p_1 = p_2 = P_w p_3$ ($p_3 = p$); Model $R_2$: two species with reduced reproduction probabilities $r_1 = r_2 = R_w r_3$ ($r_3 = r$). In the models $P_1$ and $P_2$ we take $r_1 = r_2 = r_3 = r$. In the models $R_1$ and $R_2$ it is assumed that $p_1 = p_2 = p_3 = p$. We shall also consider two additional models, $(PR)_1$ and $(PR)_2$ (with one and two
Weak species in rock-paper-scissors models

Fig. 1: Scheme of predation interactions of the 3 species RPS model: (a) represents the case with a single “weak” species (models \( P_1, R_1, (PR)_1 \)); (b) represents the case with two “weak” species (models \( P_2, R_2, (PR)_2 \)). Filled and unfilled circles represent “weak” and “strong” species, respectively.

“weak” species, respectively), in which both the predation and reproduction probabilities are reduced.

Figure 1 displays the scheme of cyclic predator-prey interactions of the 3 species RPS models we investigate in this letter, with the filled and unfilled circles representing “weak” and “strong” species, respectively —cases (a) and (b) correspond to models with one and two “weak” species. As previously mentioned, the six models considered in this letter (three with one “weak” species and three with two “weak” species) are denoted by \( P_n, R_n \) and \( (PR)_n \), depending, respectively, on whether only the predation rate is reduced, only the reproduction rate is reduced or both are reduced — \( n \) represents the number of “weak” species (\( n = 1 \) or \( n = 2 \)). Model \( P_1 \) has also been investigated in \([32]\).

**Results.** Here we assess the performance of “weak” and “strong” species using spatial stochastic simulations of the RPS models \( P_n, R_n \) and \( (PR)_n \), with \( n = 1, 2 \).

Figure 2 shows the value of the average density of the three species and empty sites as a function of \( P_w \) for the model \( P_1 \) with a single “weak” species. \( P_w \) represents the reduction of the predation probability of the “weak” species with respect to the standard case in which the predation probability is the same for all species. The data points result from an average over the last \( 10^4 \) generations of a simulation with a time span equal to \( 1.5 \times 10^4 \) generations performed on a \( 1000^2 \) lattice, large enough to guarantee the preservation of coexistence. The results for \( P_w = 1 \) were computed starting from random initial conditions. To ensure fast convergence we used the final conditions of the simulations with \( P_w = 1 \) as initial conditions of new simulations with \( P_w = 1 - 0.01 \). The same procedure was repeated until \( P_w = 0.3 \) was reached. We verified that, with such conditions, \( 5 \times 10^2 \) generations are sufficient for \( \langle \rho \rangle \) and \( \langle w \rangle \) to attain their asymptotic value. Figure 2 shows that the “weak” species generally has an advantage, specially over its predator (the “weak” species abundance is similar to that of its prey for \( P_w \in [0.5, 1] \)). The lines represent the non-spatial stationary analytical (unstable) solution, given in eqs. (3) and (4), for the density of the species 1 (solid line), 2 and 3 and empty sites (dashed line).

Fig. 2: The average density of the species \((i = 1, 2, 3)\) and empty sites \((i = 0)\) for the spatial model \( P_1 \), as a function of \( P_w \), assuming \( m = 0.5 \) and \( p = r = 0.25 \). Notice that the “weak” species and its prey are the most abundant. The grey lines represent the stationary non-spatial solution, given in eqs. (3) and (4), for the density of the species 1 (solid line), 2 and 3 and empty sites (dashed line). Notice the significant differences between spatial and non-spatial results (this is also be verified in figs. 3, 4, and 5).

Figure 3 is analogous to fig. 2, except that in fig. 3 model \( R_1 \) is considered, with \( R_w \) representing the reduction of the predation probability of the “weak” species with respect to the standard case in which the predation probability is the same for all species. Figure 3 shows that in this case the density of the “weak” species is always smaller than the average density of the “strong” species. The relatively small advantage that the “weak” species has over its predator does not compensate the disadvantage with respect to its prey.

Figure 4 displays the results of the model \( P_2 \). In this model there are two “weak” species which have a lower predation probability. Figure 4 shows that, in this model, the two “weak” species (1 and 2, but specially species 2)
This shows that the advantage of the “weak” species found generally have advantage over the “strong” species (3). Notice that both “weak” species are more abundant than the “strong” species for $P_w \lesssim 0.6$. The grey lines represent the stationary non-spatial solution, given in eqs. (3) and (4), for the density of the species 1 and 2 (dashed line), and 3 and empty sites (solid line).

Fig. 4: The same as in fig. 2, but now for the spatial model $P_2$ with two “weak” species having a lower predation probability. Notice that both “weak” species are more abundant than the “strong” species for $P_w \lesssim 0.6$. The grey lines represent the stationary non-spatial solution, given in eqs. (3) and (4), for the density of the species 1 and 2 (dashed line), and 3 and empty sites (solid line).

Fig. 5: The same as in fig. 3, but now for the spatial model $R_2$. In this case one weak species is the most abundant and the other is the least abundant. The grey lines represent the stationary non-spatial solution, given in eqs. (3) and (4), for the density of the species 1 and 3 (solid line), and 2 and empty sites (dashed line).

on the dynamics of population networks. It is this spatial structure which is responsible for the stability of the population of three species in sufficiently large spatial simulations, in sharp contrast with the instability associated to the non-spatial stationary solutions.

Figure 6 displays the results of the model $(PR)_1$ with one “weak” species (1). These results were obtained using the same procedure followed in fig. 2 and fig. 3 for models $P_1$ and $R_1$, respectively, but now reducing both the predation and reproduction of the “weak” species (1) by the same amount ($(PR)_w = P_w = R_w$). Figure 6 shows that, in this case, one of the strong species, the species (2), is the most abundant followed by the “weak” species (1). The “weak” species is therefore not the most abundant, but its population is always larger than that of its predator.

Motivated by the fact that, for fixed $p$, $r$ and $m$, and $1-P_w \ll 1$ and $1-R_w \ll 1$

\begin{align}
\rho(P_w, R_w) &\sim \rho(1,1) + \frac{\partial \rho}{\partial P_w} \bigg|_{(1,1)} (P_w - 1) \\
&+ \frac{\partial \rho}{\partial R_w} \bigg|_{(1,1)} (R_w - 1) \\
&\sim \rho(P_w,1) + \rho(1,R_w) - \rho(1,1), \tag{5}
\end{align}

we consider the following approximation, allowing for the estimation of the abundances of the species and empty sites in models where both predation and reproduction probabilities are simultaneously reduced from the results obtained considering only a reduction of either the predation or the reproduction probability:

\begin{align}
\rho^{\text{approx}}_{P_w}(P_w, R_w) &= \rho(1,1) + \rho(P_w,1) + \rho(1,R_w) - \rho(1,1), \tag{6} \\
\rho^{\text{approx}}_{R_w}(P_w, R_w) &= \rho(1,1) + \rho(P_w,1) + \rho(1,R_w) - \rho(1,1). \tag{7}
\end{align}

The lines in fig. 6 show the results obtained using the approximation given in eqs. (6) and (7) (i.e., summing the
results of models $P_1$ and $R_1$ for the corresponding values of $(P)_w$ and $(R)_w$ and then subtracting either $\langle P_1((PR)_w = 1) \rangle = 0.3$ (species 1, 2 and 3) or $\langle P_0((PR)_w = 1) \rangle = 0.1$ (empty sites)). The quality of the approximation is remarkable, especially for $(PR)_w > 0.6$, thus showing that an accurate estimate of the model $(PR)_1$ results may be obtained directly from those found for models $P_1$ and $R_1$. The more significant differences observed for $(PR)_w < 0.6$ are a further demonstration of the non-linear behaviour of these systems.

Figure 7 is similar to fig. 6, but now for the model $(PR)_2$ (in this model the predation and reproduction probabilities are reduced by the same amount for species 1 and 2). Figure 7 shows that, in this case, one of the “weak” species (2) is the most abundant followed by the “strong” species (3), with the remaining “weak” species (1) being the least abundant. Again, it is possible to verify that the approximate solution, obtained using eqs. (6) and (7) in combination with the results of models $P_2$ and $R_2$, provides an excellent fit to the results of model $(PR)_2$. We have also verified that the accuracy of this approximation is, in general, much better than 20% for models with reduced predation and reproduction probabilities (not necessarily by the same amount) in the range $1 \leq P_w + R_w \leq 2$.

**Conclusions.** – In this letter we investigated the performance of “weak” and “strong” species in a May-Leonard formulation of a three-species cyclic predator-prey model. We generalized previous work by considering cases with two “weak” species and by extending the definition of “weak” species to also include species with a reduced reproduction rate. We have shown that the spatial dynamics is essential for coexistence, with stationary solutions in which all three species coexist being always unstable in non-spatial models. On the other hand, we have found that, for sufficiently large simulation lattices, all three species may naturally coexist for a wide range of parameters. We have shown that the significantly higher abundance of “weak” species found in spatial stochastic RPS models with a single “weak” species also occurs in models with two “weak” species. However, we have shown that the predominance of the “weak” species does not generally hold if the “weak” species have a reduced reproduction rate. We have also developed a simple approximation which allows for an accurate estimation of the species abundances in models where both predation and reproduction probabilities of “weak” species are simultaneously reduced from the results obtained considering only a reduction of either the predation or the reproduction probability.

**REFERENCES**

[1] Lotka A. J., Proc. Natl. Acad. Sci. U.S.A., 6 (1920) 410.
[2] Volterra V., Nature, 118 (1926) 558.
[3] May R. and Leonard W., SIAM J. Appl. Math., 29 (1975) 243.
[4] Reichenbach T., Mobilia M. and Frey E., Phys. Rev. E, 74 (2006) 051907.
[5] Perc M. c. v., Szolnoki A. and Szabó G., Phys. Rev. E, 75 (2007) 052102.
[6] Reichenbach T., Mobilia M. and Frey E., Nature, 448 (2007) 1046.
[7] Reichenbach T., Mobilia M. and Frey E., Phys. Rev. Lett., 99 (2007) 238105.
[8] Kerr B., Riley M. A., Feldman M. W. and Bohannan B. J. M., Nature, 418 (2002) 171.
[9] Kirkup B. C. and Riley M. A., Nature, 428 (2004) 412.
[10] Sinervo B. and Lively C. M., Nature, 380 (1996) 240.
[11] Szabó G., Szolnoki A. and Borsos I., Phys. Rev. E, 77 (2008) 041919.
[12] Allesina S. and Levine J. M., Proc. Natl. Acad. Sci. U.S.A., 108 (2011) 5638.
[13] Avelino P. P., Bazeia D., Losano L. and Menezes J., Phys. Rev. E, 86 (2012) 031119.
[14] Avelino P. P., Bazeia D., Losano L., Menezes J. and Oliveira B. F., Phys. Rev. E, 86 (2012) 036112.
[15] Li Y., Dong L. and Yang G., Phys. A: Stat. Mech. Appl., 391 (2012) 125.
[16] Roman A., Konrad D. and Pleimling M., J. Stat. Mech.: Theory Exp., 2012 (2012) P07014.
[17] Lütz A. F., Risau-Gusman S. and Arenzon J. J., J. Theor. Biol., 317 (2013) 286.
[18] Roman A., Dasgupta D. and Pleimling M., Phys. Rev. E, 87 (2013) 032148.
[19] Cheng H., Yao N., Huang Z.-G., Park J., Do Y. and Lai Y.-C., Sci. Rep., 4 (2014) 7486.
[20] Szolnoki A., Mobilia M., Jiang L.-L., Szczesny B., Rucklidge A. M. and Perc M., J. R. Soc. Interface, 11 (2014) 20140735.
[21] Kang Y., Pan Q., Wang X. and He M., Entropy, 18 (2016) 284.
[22] Roman A., Dasgupta D. and Pleimling M., J. Theor. Biol., 403 (2016) 10.
[23] Brown B. L. and Pleimling M., Phys. Rev. E, 96 (2017) 012147.
[24] Park J., Do Y., Jang B. and Lai Y.-C., Sci. Rep., 7 (2017) 7465.
[25] Bazeia, D., Menezes, J., de Oliveira, B. F. and Ramos, J. G. G. S., EPL, 119 (2017) 58003.
[26] Souza-Filho C. A., Bazeia D. and Ramos J. G. G. S., Phys. Rev. E, 95 (2017) 062411.
[27] Esmaeili S., Brown B. L. and Pleimling M., Phys. Rev. E, 98 (2018) 062105.
[28] Avelino P. P., Menezes J., de Oliveira B. F. and Pereira T. A., Phys. Rev. E, 99 (2019) 052310.
[29] Szolnoki A., de Oliveira B. F. and Bazeia D., EPL, 131 (2020) 68001.
[30] Frean M. and Abraham E. R., Proc. R. Soc. Lond. B, 268 (2001) 1323.
[31] Berr M., Reichenbach T., Schottenloher M. and Frey E., Phys. Rev. Lett., 102 (2009) 048102.
[32] Avelino P. P., de Oliveira B. F. and Trintin R. S., Phys. Rev. E, 100 (2019) 042209.
[33] Menezes J., Moura B. and Pereira T. A., EPL, 126 (2019) 18003.
[34] Szolnoki A. and Perc M., Phys. Rev. X, 3 (2013) 041021.
[35] Szolnoki A. and Perc M. c. v., Phys. Rev. X, 7 (2017) 041027.
[36] Szolnoki A., Perc M. c. v. and Szabó G., Phys. Rev. Lett., 109 (2012) 078701.
[37] Szolnoki A. and Perc M., New J. Phys., 18 (2016) 083021.
[38] Liao M. J., Miano A., Nguyen C. B., Chao L. and Hasty J., Nat. Commun., 11 (2020) 6055.
[39] Hofbauer J. and Sigmund K., Evolutionary Games and Population Dynamics (Cambridge University Press) 1998.