Populational Growth Model Proportional to Beta Densities

Sandra M. Aleixo*, J. Leonel Rocha[†] and Dinis D. Pestana**

*Inst. Sup. de Eng. de Lisboa, Math. Unit, CEAUL, 1949-014 Lisboa, sandra.aleixo@dec.isel.ipl.pt

†Inst. Sup. de Eng. de Lisboa, Math. Unit, 1949-014 Lisboa, jrocha@deq.isel.ipl.pt

**Univ. de Lisboa, FCUL, DEIO, CEAUL, 1749-016 Lisboa, dinis.pestana@fc.ul.pt

Abstract. We consider populations growth models with Allee effect, proportional to beta densities with shape parameters p and 2, where the dynamical complexity is related with the Malthusian parameter r. For p>2, these models exhibit a population dynamics with natural Allee effect. However, in the case of 1 , the proposed models do not include this effect. In order to inforce it, we present some alternative models and investigate their dynamics, presenting some important results.

Keywords: Beta Densities, Population Dynamics, Topological Entropy and Allee Effect.

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1. MOTIVATION AND PURPOSE

The families of unimodal maps are used in exhaustive numerical studies, allowing a structural and detailed theoretical description in terms of symbolic dynamics. The unimodal maps theory can be used in several contexts in the biological, economical and social sciences. In population dynamics, aiming to model the growth of a certain species, the use of those families has been frequent. The logistic map has been used with success to model the population growth for some species, but is inadequate for other.

The Verhulst Model is proportional to the Beta(2,2) density. Another models proportional to the Beta(p,2) densities, with $p \in]1,+\infty[$, presented in [1], can be interesting to model population growth in populations for whom the Verhulst Model fails. After the theoretical deduction of these models and the characterization of the respective family of unimodal maps, we analyze their behavior as a function of the considered parameters ranges, defining a variation interval to them. The universality of the Feigenbaum constant is underlined.

Two interesting questions deserve special mention: the negativity of the Schwarz derivative, for 1 , and the natural Allee effect for <math>p > 2. The negativity of the Schwarz derivative, plays an important role in unidimensional dynamics, see for example [10]. This condition is violated in a small interval of the maps domain of this family $[0,c[\cup]c,1]$, where c is the critical point of the map, when $p \in]1,2[$, but indeed it does not affect the dynamical behavior of the map. A weak point of the logistic model and of the models proportional to the Beta(p,2) densities, with $p \in]1,2[$, is the inexistence of Allee effect. We put forward three models with Allee effect, which therefore can model casual growths of some species in a more realistic way in ecological terms.

2. FAMILY OF MODELS PROPORTIONAL TO THE Beta(p,2) **DENSITIES, WITH** $p \in]1, +\infty[$

Consider that the equation which represents the population growth rate is

$$\frac{d}{dt}N(t) = r^*N(t)^{p-1}\left(1 - \frac{N(t)}{K}\right), \text{ with } p \in]1, +\infty[.$$

Doing the discretization of the model in a similar way that we made for the models proportional to the Beta(p,2) densities, with $p \in \mathbb{N} \setminus \{1,2\}$, see [1], we have

$$N(t_{n+1}) = r^* N^{p-1}(t_n) \left(1 - \frac{N(t_n)}{K} \right)$$

$$\Leftrightarrow \frac{N(t_{n+1})}{K} = r^* K^{p-2} \left(\frac{N(t_n)}{K} \right)^{p-1} \left(1 - \frac{N(t_n)}{K} \right).$$

Taking into account that $x_n = \frac{N(t_n)}{K}$ and $r = r^*K^{p-2}$, the discretized model, which is proportional to the Beta(p,2) density, with $p \in]1,+\infty[$, is given by

$$x_{n+1} = rx_n^{p-1}(1 - x_n). (2.1)$$

Let us consider the family of unimodal maps $f_{r,p}:[0,1]\to[0,1]$, with two parameters p and r, whose maximum variation intervals are given respectively by $p\in]1,p_{mc}]$ and $r\in]0,r(p_{mc})]$, defined by:

$$f_{r,p} = rx^{p-1}(1-x)$$

which satisfies the following conditions:

- $f_{r,p} \in C^3([0,1]);$
- $f'_{r,p}(x) \neq 0, \forall x \neq c$ (c is the critical point of $f_{r,p}$);
- $f'_{r,p}(c) = 0$ and $f''_{r,p}(c) < 0$ meaning that $f_{r,p}$ is strictly increasing in [0, c[and strictly decreasing in [c, 1];
- $f_{r,p}(0) = f_{r,p}(1) = 0;$
- $f_{0,p}(c) = 0$ and $f_{r(p_{mc}),p}(c) = 1$;
- $\forall x \neq c, S(f_{r,p}(x)) < 0$ where $S(f_{r,p}(x)) = \frac{f_{r,p}'''(x)}{f_{r,p}'(x)} \frac{3}{2} \left(\frac{f_{r,p}''(x)}{f_{r,p}'(x)}\right)^2$ represents the Schwarz derivative of $f_{r,p}$. Notice that $S(f_{r,p}(c)) = -\infty$.

Observe that, for the $f_{r,p}$ to be unimodal, the value of the parameter p has to be greater than one. The maximum value considered for the parameter p in this study, denoted by p_{mc} , was 20, the largest value for which the model can be realistic. In fact, the value $r(p_{mc})$ is the value of the parameter r corresponding to the full shift for $p = p_{mc}$. The two parameters r and p, associated to these unimodal maps $f_{r,p}$, are shape parameters. The parameter r is related to the height of the curve, while the parameter p is associated with its skewness. For any fixed p > 1, the value of r = 0 makes no sense because there is no curve in this case; as the value of the parameter r increases, we get higher curves,

until the value of r corresponds to the full shift, when the height of the curve attains its maximum value, 1, see the plot in Figure 1. Considering for each p the value of the parameter r for which we obtain the full shift, we conclude that the curve of the map $f_{r,p}$ can have three different patterns of skewness, as shown in Figure 2. Analyzing

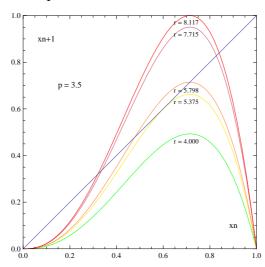


FIGURE 1. Populational growth rates using the model proportional to the Beta(3.5,2) density

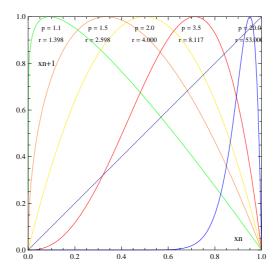


FIGURE 2. Three types of format to the populational growth rates using the model proportional to the Beta(p,2) density, with p > 1: curve skewed to the left, simmetric and skewed to the right

Figure 2, we see that the unimodal dynamics does not make sense for values of p too much close to 1, because the associated curves have an enormous skewness to the left; and also does not make sense for high values of p, since the corresponding curves become extremely skew to the right. Unimodal maps $f_{r,p}$, with these extreme values for the parameter p, hardly could model populations growths for any species. So, we consider that the maximum value is $p_{mc} = 20$, and so, with the maximum value of the parameter r = 53.001 corresponding to the full shift. Observing Figure 1, we can verify that unimodal maps $f_{r,p}$, always have the fixed point $x^* = 0$, for any r > 0 and p > 1.

However, this application has another positive fixed point besides 0, for $r > r_1$, in the case of $p \in]1,2[$. For $p \in [2,p_{mc}]$, these maps have two more fixed points besides 0, for values of $r > r_1$, where r_1 is the first value of the parameter r for which it appears an orbit of period 1. For each fixed parameter value p > 1, the critical point of the map $f_{r,p}$ is always given by $c = \frac{p-1}{p}$. The dynamical behavior of all unimodal maps $f_{r,p}$ for each fixed p > 1, always shows the same pattern: when we change the value of the parameter r we have successive bifurcations usually denoted by period doubling cascade. Associated to these cascades we have always an universal constant, denominated the Feigenbaum constant, see [1].

3. DETERMINISTIC POPULATIONAL GROWTH MODELS WITH ALLEE EFFECT. HEURISTIC APPROACH

The essence of the heuristic approach, in which the deterministic models used to model populations growths of species that exhibit Allee effect are based, date back at least to Odum and Allee (1954), see [15]. The *per capita* growth rate, dependent on the expected or observed population size, is modeled by a suitable function. We shall consider only one population, whose growth in a homogeneous environment is described by the ordinary differential equation

$$\frac{dN(t)}{dt} = N(t) g(N(t))$$
(3.1)

or by the difference equation

$$N_{t+1} - N_t = N_t g(N_t). (3.2)$$

In both cases N is the population size and g(N) denote the *per capita* growth rate dependent of the size N, which is negative for decreasing populations and positive for increasing populations.

In this work, we consider the cases where the Allee effect occurs at small population sizes; the examples where the Allee effect occurs at large population sizes are few, see for example [12]. The per capita growth rate g(N) that describe the Allee effect is an unimodal function, with a long tail; the maximum rate is obtained for only one positive dimension, N = C > 0. Below this "optimal" population size, positive effects of the presence of individuals of the same species prevail and g(N) is increasing, while above this "optimal" population size, the negative dependence of the population size dominates and so the per capita growth rate, g(N) is decreasing. Most of the models include overcapacity and avoid the indefinite growth by assuming a negative per capita growth rate, g(N) < 0, for a population size sufficiently large. In the aim of analyzing the stability, the values of the per capita growth rate g(N) should have small oscillations near the equilibrium point (slightly increasing until the equilibrium point, and slightly decreasing soon after this value), and should be a continuous function for other values of the population size N, as in the two proposed models, (3.1) and (3.2), see [4]. In the difference equations, (3.2), the per capita growth rate should satisfy as well the condition $g(N_t) \ge -1$ to have always $N_t > 0$.

In these heuristic population growth models, (3.1) e (3.2), three basic settings can occur, see [4]:

Unconditional-Extinction (UE): if the Allee effect is too much strong, the *per capita* growth rate g(N) is negative for all the population size N and the populations will inevitably become extinct, whatever the value of its initial size;

Extinction-Survival (ES): at moderate levels of the Allee effect, the *per capita* growth rate g(N) is positive for intermediate values of the population size N, but is negative for very low or very high values of the population size N. Two equilibrium values exist: the smaller one, which is unstable, denoted by E^i , and the larger E^s which is locally stable. The population size at the instant 0, denoted by E^0 , that is locally stable, is called trivial equilibrium. The populations whose dimension at 0 is smaller than the value E^i will become extint, while those with dimension at 0 is greater than the value E^i stabilize at the value E^s :

Unconditional-Survival (US): when the Allee effect gets weaker, the unstable equilibrium E^i vanishes, the trivial equilibrium E^0 becomes unstable every time the *per capita* growth rate g(N) is positive for all the population size N>0, and the population stabilizes in E^s , even though its *per capita* growth rate is still increasing with N at low populations sizes.

The setting ES is the most familiar consequence of the Allee effect, and the issue of extinction or survival of the population, is of utmost practical relevance, see [4].

4. MODELS BASED ON MAPS PROPORTIONAL TO THE Beta(p,2) DENSITIES, WITH $p \in]1,2[$ AND ALLEE EFFECT

As it happens in the classical logistic model, and also for the models proportional to Beta(p,2) densities, with 1 , the inexistence of a rarefaction critical dimension <math>E, and consequent inexistence of the Allee effect is a drawback that can be corrected, as done usually in the logistic model, described below.

4.1. Logistic map modified with Allee effect

The logistic model is frequently used to model the population growth of certain species. However, several criticisms have been made, namely the fact that this model doesn't implement the Allee effect. In fact, the logistic equation assumes that the population always increases, even when its dimension is low; besides, in this case (small population size), this model assumes a fast population increase. At first sight, this could seem acceptable because the environment resources are abundant to the few individuals in the population. However, this assumption is questionable, since for many populations there is a minimal population size (rarefaction critical density), denoted by E, required for reproduction. Below E, the probability that individuals of opposite sexes effectively meet for reproduction is so small that the population can not recover its dimension in order to substitute those who die, and finally becomes extinct. In this case, the instantaneous growth rate r is negative. Above E, the probability of the individuals

meetting mates for reproduction is enough for the population to grow until its carrying capacity K. In this situation, the instantaneous growth rate r is positive. This minimal population size E corresponds to a null growth rate, which allows that the population maintains exactly its dimension at a fixed value. At this density E, the population is incapable to grow up and maintains its equilibrium value, until some disturbance happens, leading either to extintion or to growth.

Obviously the rarefaction critical density E is smaller than the carrying capacity K. Between E and K there is a variety of populations dimensions for which the instantaneous growth rate is positive.

The inexistence of a rarefaction critical density E, and consequent inexistence of the Allee effect in the logistic model is a drawback that can be corrected. Several investigators discussed this issue (see for example the ones mentioned by [4]), suggesting various models for the *per capita* growth rate. The basic idea is to introduce a term in the classic logistic model, T(N(t)), forcing the rate g(N(t)) to be negative as soon as the population size N(t) is smaller than the rarefaction critical density E:

$$g\left(N(t)\right) = \frac{dN(t)}{dt} \frac{1}{N(t)} = r\left(1 - \frac{N(t)}{K}\right) T\left(N(t)\right).$$

4.2. Models based on maps proportional to Beta(p,2) densities, with $p \in]1,2[$ and Allee effect

Using a similar procedure to the one used for correct the logistic model, we are going to deduce three new models for the *per capita* growth rate. So, the basic idea is to introduce in the models proportional to Beta(p,2) densities, with 1 , a new term <math>T(N(t)), in such a way that this rate, $g^*(N(t))$, is negative as soon as the population size N(t) gets smaller than the rarefaction critical density E:

$$g^{*}(N(t)) = \frac{dN(t)}{dt} \frac{1}{N(t)} = rN(t)^{p-2} \left(1 - \frac{N(t)}{K}\right) T(N(t)).$$

Therefore, using the same three terms T(N(t)) suggested by several authors for the logistic model, see [4], we obtain the three maps to model the *per capita* growth rate of a population.

1. Using the term
$$T(N(t)) = \left(1 - \frac{E}{N(t)}\right) = \frac{N(t) - E}{N(t)}$$

suggested in [16, 7, 8, 9, 5] to inforce the Allee effect in the logistic model, we obtain the following function for the *per capita* growth rate

$$g_1^*(N(t)) = r^* N(t)^{p-2} \left(1 - \frac{N(t)}{K} \right) \left(1 - \frac{E}{N(t)} \right)$$
 (4.1)

and consequently, the corresponding population growth rate is given by

$$f_1^*(N(t)) = N(t) \ g_1^*(N(t)) = r^*N(t)^{p-1} \left(1 - \frac{N(t)}{K}\right) \left(1 - \frac{E}{N(t)}\right). \tag{4.2}$$

The model (4.2) can be discretized, in order to have the properties allowing its study using the symbolic dynamic methods. Two important points: the signal of the Schwarz derivative it is not always negative, for 1 , and for certain instantaneous growth rates <math>r the discreet maps that represent the growth rate with Allee effect take values out of the invariant interval, suggesting the need to study Cantor sets. The discretized model, designated by Model 1, can be obtained from the differential equation (4.2), considering that $x_n = \frac{N(t_n)}{K}$ and $r = r^*K^{p-2}$, in the following way:

$$N(t_{n+1}) = f_1^* \left(N(t_n) \right) \Leftrightarrow x_{n+1} = r x_n^{p-2} \left(1 - x_n \right) \left(x_n - \frac{E}{K} \right).$$

Therefore, Model 1 corrected with Allee effect is a map $h_1^* : [0,1] \to \mathbb{R}$, defined by:

$$h_1^*(x) = rx^{p-2} (1-x) \left(x - \frac{E}{K}\right).$$

2. If we use the term $T(N(t)) = \left(\frac{N(t)}{K} - \frac{E}{K}\right) = \frac{N(t) - E}{K}$

presented in [14, 2, 3, 13] to correct the inexistence of the Allee effect in the classical logistic model, we have

$$g_2^*(N(t)) = r^*N(t)^{p-2} \left(1 - \frac{N(t)}{K}\right) \left(\frac{N(t)}{K} - \frac{E}{K}\right)$$
 (4.3)

and therefore, the corresponding population growth rate is given by

$$f_2^*(N(t)) = N(t) \ g_2^*(N(t)) = r^*N(t)^{p-1} \left(1 - \frac{N(t)}{K}\right) \left(\frac{N(t)}{K} - \frac{E}{K}\right). \tag{4.4}$$

The discretized model, designated by Model 2, can be obtained from (4.4) as in the previous model:

$$N(t_{n+1}) = f_2^* \left(N(t_n) \right) \Leftrightarrow x_{n+1} = r x_n^{p-1} \left(1 - x_n \right) \left(x_n - \frac{E}{K} \right).$$

So, Model 2 corrected with Allee effect is a map $h_2^* : [0,1] \to \mathbb{R}$, defined by:

$$h_2^*(x) = rx^{p-1} (1-x) \left(x - \frac{E}{K}\right).$$

3. In an alternative way, if we use the term $T(N(t)) = \left(\frac{N(t)}{E} - 1\right) = \frac{N(t) - E}{E}$

suggested in [11, 6], we get the following function to the *per capita* growth rate

$$g_3^*(N(t)) = r^* N(t)^{p-2} \left(1 - \frac{N(t)}{K} \right) \left(\frac{N(t)}{E} - 1 \right)$$
 (4.5)

and so, the corresponding population growth rate is given by

$$f_3^*(N(t)) = N(t) \ g_3^*(N(t)) = r^*N(t)^{p-1} \left(1 - \frac{N(t)}{K}\right) \left(\frac{N(t)}{E} - 1\right). \tag{4.6}$$

The discretized model, designated by Model 3, obtained from (4.6), is given by:

$$N(t_{n+1}) = f_3(N(t_n)) \Leftrightarrow x_{n+1} = rx_n^{p-1} (1 - x_n) \left(\frac{K}{E}x_n - 1\right).$$

So, Model 3 corrected with Allee effect is a map $h_3^* : [0,1] \to \mathbb{R}$, defined by:

$$h_3^*(x) = rx^{p-1} (1-x) \left(\frac{K}{E}x - 1\right).$$

5. CHARACTERIZATION OF THE NEW MODELS

We should remark some aspects in what concerns to the new models presented above. So, in this section we established two propositions, and state some important notes about the characteristics of these models.

Proposition 1. The models based on the maps proportional to the Beta(p,2) densities, with $p \in]1,2[$, modified with the Allee effect, h_i^* , with i = 1,2,3, verify the following propositions:

- 1. The conditions of the setting *ES* (Extinction-Survival), which is the more usual consequence of the Allee effect, are satisfied by all the models presented.
- 2. The conditions of the setting *US* (Unconditional-Survival), are satisfied by the Models 1 and 2, but not by the Model 3.
- 3. None of these models satisfies the conditions of the setting UE (Unconditional-Extinction).
- *Proof.* 1. Having in mind the conditions of the setting ES, we have, for 1 , that the*per capita*growth rates pertaining to any of these models, given respectively by <math>(4.1), (4.3) and (4.5), are positive if and only if

$$(0 < E < K) \land [(r < 0) \land ((0 < N(t) < E) \lor (N(t) > K))] \lor [(r > 0) \land (E < N(t) < K)].$$

2. (a) In what concerns Model 1 *per capita* growth rate $g_1^*(N(t))$, given by expression (4.1), considering E = N(0) = 0, we get

$$g_1^*(N(t)) = r^*N(t)^{p-2} \left(1 - \frac{N(t)}{K}\right).$$

For $1 , as <math>0 \le E \le K$ and $0 \le N(t) \le K$, we have $N(t)^p - 2 \ge 0$ and $0 \le \frac{N(t)}{K} \le 1$, so $1 - \frac{N(t)}{K} \ge 0$ and considering r*>0, we have $g_1^*(N(t)) \ge 0$.

(b) In what concerns Model 2 *per capita* growth rate $g_2^*(N(t))$, given by expression (4.3), if E = N(0) = 0, then we have

$$g_2^*(N(t)) = r^*N(t)^{p-2} \left(1 - \frac{N(t)}{K}\right) \left(\frac{N(t)}{K}\right).$$

For $1 , as <math>0 \le E \le K$ and $0 \le N(t) \le K$, then $N(t)^p - 2 \ge 0$ and $0 \le \frac{N(t)}{K} \le 1$, therefore $1 - \frac{N(t)}{K} \ge 0$ and having in mind that r*>0, we have $g_2^*(N(t)) \ge 0$.

- (c) In what concerns Model 3 *per capita* growth rate $g_3^*(N(t))$, given by (4.5), for 1 , considering <math>E = N(0) = 0, the expression of $g_3^*(N(t))$ makes no sense because it includes the ratio $\frac{N(t)}{E}$ which as no meaning. So, the Model 3 does not satisfy the conditions for the setting *US*.
- 3. For any of the three models, the *per capita* growth rate $g_i^*(N(t))$, with i = 1, 2, 3, is not negative for all the population sizes N(t). In fact, $g_i^*(N(t)) < 0$, for 1 , if and only if

$$(0 < E < K) \land \\ \big[[(r < 0) \land (E < N(t) < K)] \lor [(r > 0) \land ((N(t) > K) \lor (0 < N(t) < E))] \big].$$

The condition (N(t) > K) is impossible, because K corresponds to the carrying capacity. So, if r > 0 then $g_i^*(N(t))$ is negative only if 0 < N(t) < E, and therefore it is not negative to any N(t). If r < 0 then $g_i^*(N(t))$ is negative only if E < N(t) < K and not in all the interval range of N(t). Therefore, none of the presented models satisfy the setting UE.

So, we can state that Models 1 and 2 for the *per capita* growth rate are more flexible than Model 3, because this one only satisfies the conditions of one setting while the other two models satisfy the conditions of two settings. The Schwarz derivatives of these models verify the following result:

Proposition 2. The Schwarz derivatives of the Models h_i^* , with i = 1, 2, 3, do not depend on the value of the Malthusian parameter r and satisfy $S_{h_2^*}(x) = S_{h_3^*}(x)$.

Proof. Having in mind the expressions of the Schwarz derivatives for these models, which are given by:

$$S_{h_{1}^{*}}(x) = -\frac{-2EK(-2+p)px(3+4p(-1+x)+p^{2}(-1+x)^{2}+4x-x^{2})}{2x^{2}(K(1+p(-1+x))x+E(-2+p+x-px))^{2}}$$

$$-\frac{E^{2}(2-3p+p^{2})(6+p^{2}(-1+x)^{2}-p(5-6x+x^{2}))}{2x^{2}(K(1+p(-1+x))x+E(-2+p+x-px))^{2}}$$

$$-\frac{K^{2}(-1+p)px^{2}(2+p^{2}(-1+x)^{2}+4x+p(-3+2x+x^{2}))}{2x^{2}(K(1+p(-1+x))x+E(-2+p+x-px))^{2}}$$

$$\begin{split} S_{h_2^*}(x) &= S_{h_3^*}(x) = -\frac{-2EK(-1+p^2)x\left(p^2(-1+x)^2 + 6x + 2p(-1+x^2)\right)}{2x^2\left(Kx\left(p(-1+x) + x\right) + E\left(-1 + p - px\right)\right)^2} \\ &- \frac{E^2(-1+p)p\left(2 + p^2(-1+x)^2 + 4x + p(-3 + 2x + x^2)\right)}{2x^2\left(Kx\left(p(-1+x) + x\right) + E\left(-1 + p - px\right)\right)^2} \\ &- \frac{K^2p(1+p)x^2\left(p^2(-1+x)^2 + 2x(2+x) + p(-1-2x + 3x^2)\right)}{2x^2\left(Kx\left(p(-1+x) + x\right) + E\left(-1 + p - px\right)\right)^2} \end{split}$$

in fact we verify that none of them depend on r and $S_{h_2^*}(x) = S_{h_3^*}(x)$.

Remark 5.1. For any of the models h_i^* , with i = 1, 2, 3, the negativity of the Schwarz derivative is not verified in all the interval [0, 1]. This unimodal maps property is not satisfied in a subinterval $[0, x_{di}] \subset [0, 1]$.

This positivity of the Schwarz derivative near the origin is due to the fact that the first three derivatives of each one of the models h_i^* , with i = 1, 2, 3, go to ∞ when x goes to 0.

Moreover, the value of the point x_{di} depends on the model h_i^* , which is associated to a parameter $p \in]1,2[$, and it also depends on the values of E and K.

REFERENCES

- Sandra M. Aleixo, J. Leonel Rocha and Dinis D. Pestana, "Populational Growth Models in the Light of Symbolic Dynamics", in 30th International Conference on Information Technology Interfaces, edited by V. Luzar-Stiffler, V. Dobric and Z. Bekic, Proceedings of the ITI 2008, Univ. Zagreb, Dubrovnik, 2008, pp. 311–316.
- 2. P. Amarasekare, Am. Nat., 152, pp. 298–302 (1998a).
- 3. P. Amarasekare, *Theor. Popul. Biol.*, **53**, pp. 44–59 (1998b).
- 4. D. S. Boukal and L. Berec, J. Theor. Biol., 218, pp. 375–394 (2002).
- 5. C. E. Brassil, *Ecol. Model*, **143**, pp. 9–13 (2001).
- 6. F. Courchamp, T. H. Clutton-Brock and B. Grenfell, **14**, pp. 405–410 (1999a).
- 7. F. Courchamp, B. Grenfell and T. H. Clutton-Brock, *Proc. R. Soc. London B*, **266**, pp. 557–563 (1999b).
- 8. F. Courchamp, T. H. Clutton-Brock and B. Grenfell, *Animal conservation*, 3, pp. 277–285 (2000a).
- 9. F. Courchamp, B. Grenfell and T. H. Clutton-Brock, Oikos, 91, pp. 311–322 (2000b).
- 10. J. Graczyk, G. Swiatek and D. Sands, C. R. Acad. Sci. Paris, 332, série I, pp. 329-332 (2001).
- 11. Y. Gruntfest, R. Arditi and Y. Dombrovsky, J. Theor. Biol., 185, pp. 539–547 (1997).
- 12. H. Kokko and W. J. Sutherland, Evol. Ecol. Res., 3, pp. 537–551 (2001).
- 13. T. H. Keitt, M. A. Lewis and R. D. Holt, *Am. Nat.*, **157**, pp. 203–216 (2001).
- 14. M. A. Lewis and P. Kareiva, *Theor. Popul. Biol.*, **43**, pp. 141–158 (1993).
- 15. H. T. Odum and W. C. Allee, *Ecology*, **35**, pp. 95–97 (1954).
- 16. E. O. Wilson and W. H. Bossert, *A Primer of Population Biology*, Sinauer Associates Sunderland, MA, U.S.A., 1971.