Allee effect in models of interacting species

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Abstract: *The search for more realistic models for interacting species has produced many adaptations of the original Lotka -Volterra equations, such as the inclusion of the Allee effect and the different Holling's types of functional response. In the present work we show that a correct implementation of both ideas together requires a careful formulation. We focus our work in the fact that a density dependent carrying capacity, combined with the Allee effect, can lead to meaningless effects. We illustrate the difficulties in predator- prey and two-species competition models, together with our proposed solution of the careful inclusion of the corresponding cubic terms.*

1. INTRODUCTION

In his work published in the 1930s [1] , W. C. Allee suggested the possibility that individuals in a population might benefit from the presence of conspecifics, implying that, in some cases, instead of intra-competition there could be a positive feedback. The phenomenon, that was later called Allee effect, does not have a clear definition and has been ambiguously used in many examples [2,3] . In most cases, the Allee effect accounts for a positive correlation between population density and individual fitness. One of the most usual interpretations is that individuals may experience a difficulty mating when the population density drops below a certain level.

There are many scenarios where the Allee effect can be observed [4] . The situations in which the benefits of conspecific presence may be relevant include dilution or saturation of predators, surveillance and defense, cooperative predation, social thermoregulation, etc. While the general rule is that the Allee effect occurs in small or scattered populations, examples of its occurrence at high population densities have been reported for some species [5].

The positive relationship between fitness and population size may be associated with a variety of mechanisms that affect repro- duction and survival. As mentioned above, a well-established but not exclusive example is the limitation to find a mate, which can reduce the birth rate and lead to a population collapse in species with sexual reproduction. If reproduction, feeding and protection are cooperative to some extent, they will become more efficient in larger groups, with ensuing greater reproductive success or survival [6].

There exist still other situations where there are not cooperative behaviors, yet the presence of conspecific individuals is beneficial. For example, the risk of per capita predation is lower in larger prey populations than in smaller ones [7, 8]. This effect can be included as a saturation in the predation term.

The ubiquity of different situations liable to be related to the Allee effect, as well as the lack of an accurate definition, has led to the considerations of two versions of the effect, defined by Stephens et al. [2] as the component Allee effect and the demo- graphic Allee effect. The difference between them is that, in the former, the increase of the population affects some particular components of the fitness of an individual; in the latter, the effect manifests at the level of total fitness. These definitions clearly imply that the demographic Allee effect requires the existence of at least one component Allee effect, while the reciprocal is not true.

Summarizing the previous ideas, it is possible to say that the Allee effect is a positive association between absolute average individual aptitude and population size. Such a positive association may result in a critical population size below which the population cannot persist [2]. When the Allee effect is responsible for the existence of such a threshold it is called strong, otherwise, it is called weak.

2. The Nagumo equation and the Allee effect

One way to capture both flairs of the Allee effect in a dynamical model of a single population is by means of the following simple equation, which unlike the logistic has two stable equilibria. One of them is analogous to the stable equilibrium of the logistic equa- tion, associated with saturation, while the other one corresponds to the possibility of extinction of below-threshold populations:

$$dx/dt = r\, x\,(x - a)(1 - x /K) \qquad (1)$$

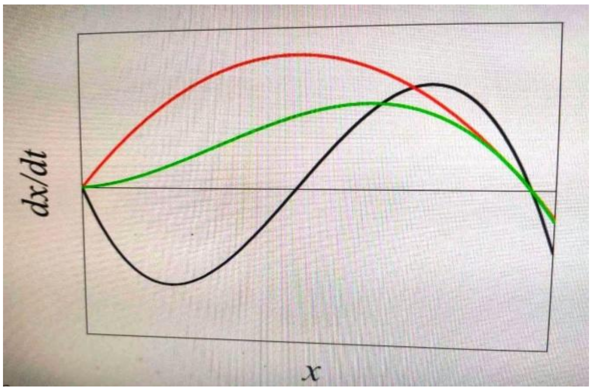


Fig. 1. Comparison between the logistic (red), weak Allee ($a < 0$, green) and strong Allee ($0 < a < K$, black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This equation is analogous to the voltage equation proposed by Nagumo [9] for the active transmission of a pulse along a nerve axon, and we will call it “Nagumo model”henceforth. It has three equilibria, $x = 0$, $x = K$and $x = a$. If we plot the expression on the right-hand side of Eq. (1) we can see that, when $0 < a < K$, the first two equilibria are stable, while the third one is unstable. This corresponds to the strong Allee effect: a population smaller than a becomes extinct. In this case, a is a critical value, a threshold be- low which the population cannot persist. Extinction, unlike what happens with the logistic equation, is a stable situation. On the other hand, negative values of a add an equilibrium for negative x, which is irrelevant in the context of populations. However, this case serves to model the weak Allee effect, which is reflected in a slight departure from the logistic case, with a decrease in the growth rate for small values of x, but without stabilizing the extinction. Figure 1 shows a comparison between the behavior of the right-hand side of Eq. (1) for both positive and negative values of a and the logistic case.

There is extensive use of the Nagumo equation to study the Allee effect in the literature. An example is given in [6] where the authors, with the objective of mathematically characterizing the Allee effect, propose a Nagumo-like equation. They associate this effect with a situation in which a small population tends to extinc- tion due to a positive relationship between population growth rate and density. In [10], the authors present a study of a predator-prey system with a strong Allee effect in the population of the prey. The core of the model is based on a Nagumo-like equation accounting for the Allee effect. An interesting study of pattern formation in a system associated to the Allee effect and the Nagumo equation can be found in [11]. Also the formation of patterns can be affected by non-local effects as shown by Clerc et al. in [12]. The latter shows an interesting implementation of the Nagumo equation in the case where the cubic term, associated with self-competition, is nonlo- cal. Although the results are compelling, it is not clear that the equation represents adequately a population dynamics scenario in each of the cases. It would be of further interest to understand these matters based on what we propose in the present work.

All those effort s and more have produced an increase of our understanding on the range and the relevance of the Allee effect, as well as its possible link with the formation of patterns observed in nature. However, at the core of these models resides a Nagumo- like equation that can lead to ecologically meaningless scenarios if its use is not limited within a proper boundary of validity?

There is no doubt that, for a wide range of values of the thresh- old and the carrying capacity, the Nagumo model can adequately describe the Allee effect in many situations. Suppose, instead, that we face a situation when, while modeling our system by means of Eq. (1) , we have $a > K$. The associated dynamical system is well behaved but the results are ecologically meaningless. What if, for example (as in [13]), the carrying capacity has its own dynamics? Such a case can arise in a predator-prey model where the carrying capacity of the predator is determined by the abundance of the prey. The Nagumo model for the predators would read:

$$\dot{x} = r x (x - a)(1 - x / K (y)) \qquad (2)$$

where the threshold a is a characteristic feature of the species x and is constant, but the carrying capacity K(y) is defined by the population of the prey, y . For the model to have the biological meaning that we expect, we need a < K(y), implying that the carrying capacity must be larger than the critical value of the pop- ulation to survive. Inasmuch as y is a variable with its own dynamics, this relation cannot be assured. If K(y) were to become smaller than a , the dynamics described by the Eq. (2) turns nonsensical: the population should get extinct (since the carrying ca- pacity is smaller than the threshold), but at K(y) = a the system suffers a transcritical bifurcation, the equilibria interchange stabil- ity, and x = a becomes the new stable equilibrium. In such a scenario, the whole equation loses its original biological meaning. An interesting example of such scenario is presented in [14] , where the Allee effect is analyzed in the presence of a stochastic dynamics that can lead to the extinction of very low-density populations and that includes a reference to a real case. An analogous situation occurs when the competition of two species feeding on the same resource alters the carrying capacity of the environment relative to each species in a dynamical way depending on the abundance of the competitor. In such a case, a simple model for each species and with Allee effect is (see [15]):

$$\dot{x} = r_i x_i (t_i - x_i)(1 - xi /Ki - aij\, xi/Ki) \qquad (3)$$

where i = 1 , 2 identifies the competing species, and ti is the survival threshold for xi. These equations present no conflict provided that (1 - aijxj /Ki) > ti. But the same argument as in the case of the predator holds: what would happen if the carrying capacity associated with xi is reduced by the abundance of the competitor xj, to values below its survival threshold? The model (3) would no longer describe the real dynamics of the system, introducing new unrealistic stable equilibrium. Furthermore, the exchange of stability between the equilibria associated with the carrying capacity and survival thresholds can induce artificial oscillations of both competing populations, as will be shown below. This problem is correctly captured by other ways of modeling the Allee effect by Wang et al. in [16], with a set of equations that cannot avoid a mobile threshold and with a less straightforward interpretation of the Allee effect. In order to deal with all these issues rooted in a flawed formulation of the equations describing the dynamics, we propose here a proper formalism that not only leads to correct results but also encompasses a sensible interpretation of the ecological reality.

3. ALLEE MODEL FOR A DYNAMICAL CARYING CAPACITY

Here we present an alternative mathematical formulation, one that preserves the spirit of the Allee effect in the context of a dynamically changing carrying capacity. Observe again Eq. (2). What we need, in order to solve the mentioned problem, is that in- stead of a transcritical bifurcation when K = a, a saddle-node bifurcation occurs. If so, the stable equilibrium x = K and the unstable one, x = a, collide and disappear. Meanwhile, the other equilibrium, x = 0, must persist, remain stable and attract the flow. This is the expected behavior: when the carrying capacity becomes smaller than the extinction threshold, the population should get extinct.

We propose the following normal form that satisfies the required conditions:

$$\dot{x} = \frac{x}{K}((K-a)|K-a| - (2x-a-K)^2) \qquad (4)$$

The polynomial on the r.h.s. has three roots:

$$x_1 = 0$$

$$x_2 = {}^1/_2\,(a + K - \sqrt{K-a}\sqrt{|a-K|})$$

$$x_3 = {}^1/_2\,(a + K + \sqrt{K-a}\sqrt{|a-K|})$$

When a < K the three roots are real: $x_1 = 0$, $x_2 = a$, $x_3 = K$, while when a > K only $x_1 = 0$ is real. Figure 2 shows three examples of the polynomial behavior for Ka . It also shows the behavior of the r.h.s of Eq. (1), that differs from Eq. (4) when K < a.

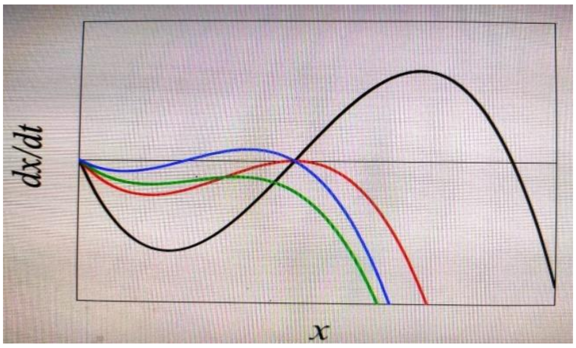


Fig. 2. Examples of the behavior of the r.h.s. of Eqs. (4) and (1) . For K > a (black) and K = a (red), both give the same behavior. But for K < a, Eq. (4) gives the green curve, while Eq. (1) gives the blue one. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In order to assess the relevance and the advantages of this consistent scheme for the Allee effect, we will compare its behavior with the one displayed by analogous models where only the logistic form is considered.

3.1. PREDATOR – PREY MODEL

Let us consider a two-species system with one prey, y, and one predator, x. For the prey, we propose a logistic demography and a predation term with saturation, as in [15]. Further, we assume that the dynamics of the predator presents the Allee effect, with a threshold of critical population, x_t , and a carrying capacity proportional to the prey population, K_x = cAy . This last term accounts for the fact that the resources that the predator can obtain from the environment depend both on its ability to predate and on prey abundance. The equations read:

$$\dot{y} = ry\left(1 - \frac{y}{K}\right) - A\frac{xy}{y+B} \qquad (5a)$$

$$\dot{x} = \frac{x}{4cAy}\left((cAy - x_t)|cAy - x_t| - (2x - x_t - cAy)^2\right) \qquad (5b)$$

where A , B , c, K, rand s are positive constants. When $x_t < y$ the equations become:

$$\dot{y} = ry\left(1 - \frac{y}{K}\right) - A\frac{xy}{y+B} \qquad (6a)$$

$$\dot{x} = sx(x - x_t)\left(1 - \frac{x}{cAy}\right) \qquad (6b)$$

where the predator equation has the Nagumo form, and when xt > y we have:

$$\dot{y} = ry\left(1 - \frac{y}{K}\right) - A\frac{xy}{y+B} \qquad (7a)$$

$$\dot{x} = -s\frac{x}{2cAy}\left((x - x_t)^2 + ((cAy - x)^2)\right) \qquad (7b)$$

While a deconstruction of the polynomial expression of Eq. (7b) in terms of biological processes can be hard, it is interesting to notice that its functional form presents sensible features. Once the carrying capacity of the environment falls below the critical population size, the predator population should evolve towards extinction. In fact, this is what happens, as the derivative is always negative. But interestingly, there is still a ghost behavior remembering the existence of a critical size, as it is usual in saddle-node transitions. The speed towards extinction is not constant and depends on x . The rate of extinction is minimum when the population is at the critical size, and it increases for larger or smaller populations.

ig. 3. Two examples of different behaviors displayed by the Nagumo (black) and the Allee (red) predator-prey models under the same conditions. Each panel shows the phase space, with a stream plot of the velocity field and four sets of initial con- ditions and the corresponding trajectories, as described in the text. Top: b = 0 . 15 , v t = 0 . 2 ; bottom: b = 0 . 25 , v t = 0 . 3 ; both: a = σ= 1 . (For interpretation of the ref- erences to color in this figure legend, the reader is referred to the web version of this article.)

Let us rewrite Eq. (5) in dimensionless form with the following change of variables and parameters:

$$u(\tau) = \frac{y(t)}{K}, v(t) = \frac{x(t)}{cAK} \quad \tau = rt.$$

$a = cA^2/r$, $b = B/K$

$v_{t = x_t/cAK}, \quad \sigma = scAK/r$

Equations (5) becomes

$$\dot{u} = u(1 - \dot{u}) - a\frac{uv}{u+b} \qquad (8a)$$

$$\dot{v} = \frac{\sigma v}{4u}\left((u - v_t)|u - v_t| - (2v - v_{t-u})^2\right)$$
(8b)

When u > vt, these are analogous to Murray's realistic predator- prey models studied in [15]:

$$\dot{u} = u(1 - \dot{u}) - a\frac{uv}{u+b} \qquad (9a)$$

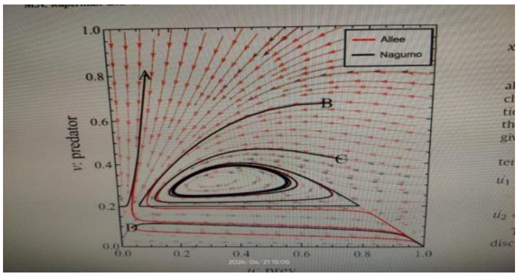
$$\dot{v} = \sigma v(1 - \frac{v}{u}) \qquad (9b)$$

Where the existence of a limit cycle is verified when:

$$\sigma < (a - Q)\frac{1+a+b-Q}{2a}$$

with $Q = ((1 - a - b)^2 + 4b)^{1/2}$.

We show in Fig. 3 phase portraits of typical scenarios where the two models (with Nagumo in black and Allee in red) have different behaviors. Each panel shows stream plots, to help visualize the flow, as well as four selected trajectories, to show the disparity of the basins of attraction. Observe, for example, the top panel, which corresponds to a set of parameters where a limit cycle exists for both models. The initial condition A corresponds to a situation where the Nagumo model drives the prey to extinction, and the predator persists. This is clearly an unrealistic situation, which arises from the interchange of stability of the equilibria (as explained in the Introduction), and the proper Allee model solves it. The initial condition B is in the basin of attraction of the cycle for the Nagumo model, but for the Allee one, it also goes to the



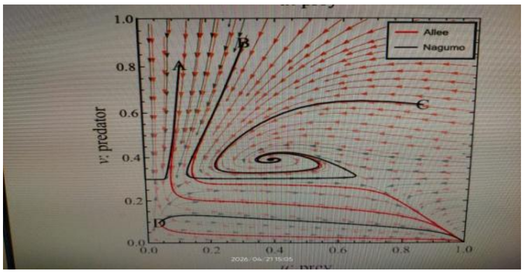


Fig. 3. Two examples of different behaviors displayed by the Nagumo (black) and the Allee (red) predator-prey models under the same conditions. Each panel shows the phase space, with a stream plot of the velocity field and four sets of initial con- ditions and the corresponding trajectories, as described in the text. Top: b = 0 . 15 , v t = 0 . 2 ; bottom: b = 0 . 25 , v t = 0 . 3 ; both: a = σ= 1 . (For interpretation of the ref- erences to color in this figure legend, the reader is referred to the web version of this article.)

extinction of the predator. Condition C, instead, goes to the cycle in both models (observe that the trajectories of both models are almost indistinguishable in this scenario). The initial condition D, finally, has both models driving the predator to extinction, with different transients. The bottom panel shows the equivalent picture for another set of parameters, one where we see a stable spiral of coexistence instead of the limit cycle (related to it by a Hopf bifurcation). We also see the same general behavior: the two models differ in the nature and stability of equilibria, as well as in their basins of attraction.

3.2. COMPETITIVE INTERACTION

We will focus now on a competitive interaction between two species. The usual equations for the dynamics of the population of two competing species x1 and x2 are [15]:

Here Ki is the carrying capacity associated to each species in the absence of competitive interactions. The effect of competition is included by means of the non linear term that couples both equa- tions and that lead to a lower effective carrying capacity due to the presence of a competitor. The strength of the competition is given by aij.

With a proper change of variables these equations can be written as

$$\dot{x}_1 = (1 - u_1 - \alpha_{12} u_2)$$

$$\dot{x}_2 = \rho (1 - u_2 - \alpha_{21} u_1)$$

These equations have four equilibria, whose stability will be discussed in the Appendix:

Equation (11) can be adapted to include the Allee effect, but this should be done with care. Direct inclusion of a multiplying monomial to account for the Allee effect, as in Eq. (3), and a proper non-dimensionalization of the system will leave us with:

$$u_1 = u_1 (1 - u_1 - \alpha_{12} u_2)(u_1 - t_1)$$

$$u_2 = \rho u_2 (1 - u_2 - \alpha_{21} u_1)(u_2 - t_2),$$

where now ti is the survival threshold for species ui. However, these equations do not contemplate the situation when the depletion of the carrying capacity of the environment due to the presence of the competing species can lead one of them below its survival threshold. The consequences of this fact will be discussed later. A correct way to include the Allee effect is, again, by reformu- lating the equations as:

As in the predator-prey model, the derivative in this last case is al- ways negative, leading to the extinction of the species, as it should. In both cases, Eqs. (12) and (13) , the consideration of the Allee effect affecting two com petitive species adds five new equilibria to the ones already present in Eq. (11) . These five equilibria are:

We start by discussing the differences between Eqs. (11) and (12) and (13) regarding the common equilibria. As shown in [15] , (0,0) is an unstable equilibrium of Eq. (11). Due to the Allee effect, extinction is now allowed and thus (0,0) becomes stable. This can be clearly appreciated in the trajectories B and D of Fig. 4 . Mean- while, in all the cases, the stability of (1,0) and (0,1) is only defined by the values of αij . This is apparent when we calculate the Ja- cobian evaluated at those equilibria (see the Appendix). A second difference emerges around the fourth equilibrium. While a suffi- cient condition for it to exist when considering Eqs. (11) and (12) is that αij < 1 , when considering Eq. (13) we also need that the equi- librium values are both larger than the corresponding thresholds, t1 and t2 . The former, being not a limitation for Eq. (12), leads to an unrealistic oscillatory solution around the equilibrium values, as shown in the trajectory A of Fig. 4 (bottom). It is in fact the disappearance of some equilibria for cer- tain parameter values what establishes the difference between Eqs. (12) and (13). The cubic terms introduce new nullclines, responsible for the new five equilibria, which behave differently in Eqs. (12) and (13). If the dynamics of a population drives its number below the survival threshold, the corresponding population should get extinct. At this moment there should be a saddle-node bifurcation that eliminates all the equilibria with the exception of those where the extinction of the corresponding solution is predicted. However, Eq. (12) erroneously predicts a transcritical bifurcation in which the threshold value turns into a stable equilibrium. This fact induces non-realistic behaviors. These include the above- mentioned oscillations and the stabilization of some of the equilibria in which the values t1 and t2 are involved. If we observe Fig. 4 we can note the differences between trajectories starting from initial conditions A, B, and C that in the case of the Nagumo model end in a non-realistic equilibrium or behavior (limit cycle). As expected, these stable equilibria are not present when a proper formulation, Eq. (13), is considered. The additional nullclines trace new limits for the basin of attraction of the old (and new) equilibria, resulting in a temporal behavior dependent on the initial conditions. The last was only the case for αij > 1 when considering Eq. (11). It is also important to note that, within the range of validity of Eq. (12), the dynamic behavior predicted by both equations is exactly the same. This is the case when the coexistence solution is stable. We show in Fig. 5 exemplary trajectories starting at differ- ent conditions. In all the cases the trajectories are overlapped. In particular, initial condition A ends in the coexistence equilibrium.

4. CONCLUSION

The consideration of the Allee effect when studying population dynamics is more than a subtle detail. In many circumstances, like the ones described in the present article, the Allee effect can be responsible for the extinction of a population, otherwise supposed to survive no matter how low its population falls. A mathematical description of the Allee effect, especially when dealing with in- teracting populations and changing environments, should be done with care. The main reason is that, while the threshold for survival depends mostly on the population under study, the carrying capacity of the environment can suffer from variations that can lead 5 to a degrading and non-sustainable situation. Examples of such scenarios can be found in Refs. [14, 16] . Once a population num- ber is driven by environmental factors below its critical thresh- old, the collapse is unavoidable. While the Allee effect can be captured by various mathematical formulations, Nagumo's equation is one of the most widely used. This equation is valid as long as the carrying capacity remains above the survival threshold, but in its usual formulation, it fails when this is not fulfilled. In particular, the carrying capacity might be affected by the interaction of the species constituting the ecosystem. In this work, we have pre- sented two examples of interacting populations: a predator-prey system and a competitive situation. In both cases, we have consid- ered the Allee effect and constructed the respective equations to mathematically describe the dynamic behavior of the populations subject to this effect. Our equations correct the issues that the traditional formulation presents, as described above. We have shown that Nagumo-kind models, with a third-degree polynomial, which are usual in single population modeling, give meaningless results for interacting populations under certain plausible conditions. We also showed a correct way to model the strong Allee effect, in the sense that the ecologically sensible dynamics can be studied with- out confusion. The study of the correct equations allowed us to understand the true consequences of including the Allee effect, reflected in the stabilization of the extinction of the species and in the strong dependence of the steady-state on the initial conditions. The latter occurs due to the appearance of new basins of attraction with respect to the models lacking the Allee effect. Regardless of the cases analyzed in this work, where the in- teraction between species is responsible for an effective time- dependent carrying capacity, the formulation presented here is of great relevance when the system under study presents a stochastic behavior [14] or even seasonal dynamics that affects the characteristics of the environment. While in this work we studied systems of only two interacting species it could be easily expanded to cases with multiple species, with different interacting relationships among them, that induce more complex behaviors even without the Allee effect [17] . Considering its inclusion in those systems is certainly worth studying, and will be the subject of future works.

Appendix A. Linear stability analysis

Here we analyze the stability of the equilibria corresponding to the predator-prey and competition systems, by studying the eigenvalues of the corresponding Jacobian matrices evaluated at each equilibrium.

This case presents multiple behaviors. Depending on the com- bination of parameter values the equilibrium can be a stable node, a stable spiral, a saddle node or an unstable spiral enclosed by a limit cycle.

Both eigenvalues are real and negative, so (0,0) is a stable node. The last case is when the carrying capacity of one of the species is above its threshold (for example u_1) and the other below it. In this case $(1 - \alpha_{12} u_2) > t_1$ and $(1 - \alpha_{21} u_1) \leq t_2$. There are three equilibria: (1,0), (0,0) and (t_1 ,0), though (0,0) is just a limiting case because in that case, as $u_1 = 0$ then $t_2 = 1$. The Jacobian matrix evaluated at each equilibrium follows.

REFERENCES

[1] Allee WC . Animal aggregations. A study in general sociology. Chicago: Univer- sity of Chicago Press; 1931.

[2] Stephens PA , Sutherland WJ , Freckleton RP . What Is the Allee Effect? Oikos 1999;87: 185–90 .

[3] Stephens PA , Sutherland WJ . Consequences of the Allee Effect for Behaviour, Ecology and Conservation. Trends Ecol Evol 1999; 14:401–5.

[4] Lidicker WZ . The Allee Effect: Its History and Future Importance. Open Ecol J 2010; 3:71–82 .

[5] Courchamp F , Berec J , Gascoigne J . Allee effects in ecology and conservation. New York: Oxford University Press; 2008.

[6] Courchamp F , Clutton-Brock T , Grenfell B . Inverse density dependence and the Allee effect. Trends Ecol. Evol. 1999; 14:405–10.

[7] Dennis B . Allee effects: population growth, critical densitv. and the chance of extinction. Nat Res Model 1989; 3:481–538.

[8] Gascoigne JC , Lipcius RN . Allee effects driven by predation. J App Ecol 2004;41:801–10.

[9] Nagumo J , Arimoto S , Yoshizawa S . An Active Pulse Transmission Line Simulat- ing Nerve Axon. Proc IRE 1962;50:2061–70.

[10] Wang J , Shi J , Wei J . Predator–prey system with strong Allee effect in prey. Math Biol 2011; 62:291–331.

[11] Sun GQ. Mathematical modeling of population dynamics with Allee effect. Nonlinear Dyn 2016; 85:1–12.

[12] Clerc M , EscaffD , Kenkre VM . Patterns and localized structures in population dynamics. Phys Rev E 2005; 72:056217.

[13] Abramson G, Giuggioli L, Parmenter RR, Kenkre VM. Quasi-one-dimensional waves in rodent populations in heterogeneous habitats: A consequence of ele- vational gradients on spatio-temporal dynamics. J Theor Biol 2013; 319:96–101.

[14] Liebhold A, Bascompte J. The Allee effect, stochastic dynamics and the eradica- tion of alien species. Ecol Lett 2003; 6:133–40.

[15] Murray JD . Mathematical biology. I. An introduction (Interdisciplinary Applied Mathematics, vol. 17). 4th ed. Berlin: Springer-Verlag; 2002.

[16] Wang G , Liang XG , Wang FZ . The competitive dynamics of populations subject to an Allee effect. Ecol Mod 1999;124: 183–92.

[17] Kuperman MN , Laguna MF, Abramson G, Monjeau JA, Lanata JL . Metapopula- tion oscillations from satiation of predators. Physica A 2019; 527:121288.