

Random perturbations of difference equations with Allee effect: switch of stability properties

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Abstract

For difference equations with the Allee effect, small initial values lead to extinction, while large enough values ensure survival. However, even a scarce (applied not every step) random perturbation with the zero mean can change stable behavior of such models: for all positive initial values, we can get essential extinction or unconditional survival. The bounds for stability changing random perturbations are established and illustrated by numerical simulations.

1 Introduction

The notion of the Allee effect goes back to the works of W. C. Allee [2] on cooperative behavior of animals. Later, this notion was used to describe the common effect of lower fitness and reproduction rates for small population densities due to possible difficulties in finding a mate, implement group defense etc. This leads to extinction if for some reason the population density falls below the critical value. Models which originally survive at low densities can suffer a similar type of behavior under a constant negative perturbation which can correspond to harvesting or migrations, which can lead to essential extinction [20]. The drastic drop of blue pike catches in mid 1950s [5], the reduction of Great Britain's grey partridge population in 1952 [1, 19] and the collapse of the Peruvian anchovy population in 1973 [12] can be examples of this dramatic decrease. For the recent overview of various aspects of the Allee effects see [13].

The dynamics of the simple one-species map

$$x_{n+1} = f(x_n), \tag{1.1}$$

where $f(x) > 0$ for $x > 0$, $f(0) = 0$, there exists some critical value x_{cr} such that $f(x) < x$ for $0 < x < x_{cr}$ (the Allee effect), there are several possibilities:

1. unconditional extinction, independently of the initial conditions;
2. unconditional survival, as far as the initial value $x > x_{cr}$;
3. extinction-survival scenario for $x > x_{cr}$.

As examples, we can use the following unimodal maps [3, 4]

$$x_{n+1} = x_n^\gamma \exp(r - cx_n), \quad 1 < \gamma \leq 2, \quad r > 0, \quad c > 0, \quad (1.2)$$

$$x_{n+1} = rx_n^\gamma \left(1 - \frac{x_n}{K}\right), \quad 1 < \gamma \leq 2, \quad r > 0, \quad K > 0, \quad (1.3)$$

$$x_{n+1} = rx_n^\gamma + rx_n \left(1 - \frac{x_n}{K}\right), \quad 1 < \gamma < 2, \quad 0 < r < 1, \quad K > 0, \quad (1.4)$$

and also the following two, generally, bimodal functions:

$$x_{n+1} = \frac{\rho x_n^2}{A + x_n^2}, \quad A > 1, \quad \rho > 1 \quad (1.5)$$

which was introduced in [14, 15], see also [7], and

$$x_{n+1} = x_n \left(A + \frac{Bx}{1 + x_n^\gamma} \right), \quad 0 < A < 1, \quad B > 0, \quad \gamma > 0, \quad (1.6)$$

which is a modification of the equation which was applied in [18] to model the growth of bob-white quail populations. For the detailed overview of all differential and difference equations experiencing Allee effect see [6].

We recall that $f(x) < x$ for $0 < x < x_{cr}$ and $f(x_{cr}) = x_{cr}$. In addition, everywhere below we will refer to the range of parameters where the critical value $x_{cr} > 0$ such that

$$f(x) > x, \quad x_{cr} < x < x_{cr} + \varepsilon \quad \text{for some } \varepsilon > 0$$

exists, to exclude the case of unconditional extinction when $f(x) < x$ for any $x > 0, x \neq x_{cr}$. We recall that this corresponds to the inequalities

$$e^r > \left(\frac{ec}{\gamma - 1} \right)^{\gamma-1}, \quad (1.7)$$

$$r > \frac{\gamma^\gamma}{(K(\gamma - 1))^{\gamma-1}} \quad (1.8)$$

and

$$\rho > 2\sqrt{A} \quad (1.9)$$

for (1.2), (1.3) and (1.5), respectively.

Outside the interval $[0, x_{cr} + \varepsilon]$, the function $f(x)$ can demonstrate various types of behavior: it may have one or more positive equilibria exceeding x_{cr} , in the case of the only positive equilibrium $K > x_{cr}$ it can decrease, increase or have a minimum point for $x > K$. Here the map of type (1.1) is considered under the following assumptions:

(A1) f is a continuous function on $[0, \infty)$ satisfying $f(x) > x$ for $x > 0, f(0) = 0$;

(A2) there exist two distinct positive equilibria $0 < x_{cr} < K$ such that $f(x) < x$ for $0 < x < x_{cr}$, $x > K$ and $f(x) > x$ for $x_{cr} < x < K$.

In this note, the issue how scarce random perturbations of a very simple type can influence extinction and survival will be investigated. There is a long history of study how constant perturbations

$$x_{n+1} = f(x_n) + \lambda \quad (1.10)$$

can change the behavior of the map, we mention here the papers of McCallum and Stone [17, 21] which demonstrated that otherwise chaotic perturbations exhibit stable 2-cyclic behavior under a constant perturbation, see also [8, 9, 10, 20].

We will assume everywhere the truncated perturbed version of (1.10)

$$x_{n+1} = \max\{f(x_n) + \lambda, 0\}, \quad (1.11)$$

see, for example, [16, 20] which certainly may be different from (1.10) for $\lambda < 0$ only.

Species whose dynamics is subject to the Allee effect become extinct at low densities but are believed to be on a safe side when the initial population size exceeds the critical value. In this note, we demonstrate that even high initial values do not guarantee population persistence if the critical value is large, and the distance between this value and the other positive equilibrium is small. This confirms that, generally, populations which experience Allee effect can be at risk even for high population levels at present. On the other hand, if the critical value is small compared to the other larger positive equilibrium, then for certain type of random perturbations, we have unconditional survival, independently of the positive initial value.

The paper is organized as follows. In Section 2 models are considered for which scarce random perturbations (applied at every k -th step, where k is large) can lead to essential extinction for any initial value. Section 3 deals with the case of the “weak Allee effect” when unconditional survival is achieved under scarce random perturbations. Finally, Section 4 involves discussion and presents some open problems.

2 Scarce random perturbations and extinction

In this and the next sections, we consider perturbed model (1.11), where the perturbation is a discrete random value λ applied not at each step but every k steps. To simplify the problem, we assume that λ takes the values of $\pm d$ only, each with probability 0.5. Let us note that different probabilities α and $1 - \alpha$ for d and $-d$ can be considered, this does not change the statements of the theorem, as far as $0 < \alpha < 1$ which means that any of the two values d and $-d$ occur in the sequence with probability one. Thus, persistence and extinction of the map

$$x_{n+1} = \begin{cases} \max\{f(x_n) + \lambda, 0\}, & n = kj - 1, j \in \mathbb{N}, \\ f(x_n), & n \neq kj - 1, j \in \mathbb{N} \end{cases} \quad (2.1)$$

is studied under the assumptions (A1), (A2) of the previous section for $\lambda = \pm d$.

We recall that a solution essentially becomes extinct if

$$\liminf_{n \rightarrow \infty} x_n = 0 \quad (2.2)$$

and persists if there exist $n_0 \in \mathbb{N}$ and $m > 0$ such that

$$x_n > m, \quad n \geq n_0, \quad (2.3)$$

which is guaranteed if

$$\liminf_{n \rightarrow \infty} x_n > 0. \quad (2.4)$$

Denote

$$M := \max_{t \in [x_{cr}, K]} f(t). \quad (2.5)$$

Theorem 2.1. *Suppose that the positive equilibria x_{cr} and K satisfy*

$$M < 2x_{cr} \quad (2.6)$$

and also for any $\varepsilon \in (0, 0.5x_{cr})$ we have

$$\mu_1 = \inf_{t \geq M + \varepsilon} [t - f(t)] > 0, \quad \mu_2 = \inf_{t \in [\varepsilon, x_{cr} - \varepsilon]} [t - f(t)] > 0. \quad (2.7)$$

Then, for any fixed d satisfying

$$\max_{t \in [x_{cr}, 2x_{cr}]} f(t) - x_{cr} < d < x_{cr}, \quad (2.8)$$

there exists N such that for any $k \geq N$ all solutions essentially extinct with probability one.

Proof. First, let us note that d satisfying (2.8) exists since $\max_{t \in [x_{cr}, 2x_{cr}]} f(t) < 2x_{cr}$ due to (2.6) and the inequality $f(x) < x$ for $x \in (K, 2x_{cr}]$. Further, let us fix d satisfying (2.8) and $\varepsilon \in (0, 0.5x_{cr})$ such that

$$M + \varepsilon < 2x_{cr}, \quad 2\varepsilon < x_{cr} + d - M, \quad 2\varepsilon < x_{cr} - d, \quad (2.9)$$

where the right hand side of the second inequality is positive by the left inequality in (2.8). The second inequality also implies

$$2\varepsilon < d < x_{cr}, \quad (2.10)$$

since $x_{cr} < K \leq M$.

Next, let us set μ_1, μ_2 as in (2.7) and fix the number of steps

$$k > \max \left\{ \frac{d}{\mu_1}, \frac{x_{cr} - 2\varepsilon}{\mu_2} \right\} + 1. \quad (2.11)$$

The scheme of the proof is the following:

1. We prove that for any $x_0 > M + \varepsilon$, there exists N_1 such that $x_{kj-1} < M + \varepsilon$ for any $j > N_1$.
2. We demonstrate that for any $x_0 \in (0, x_{cr} - \varepsilon)$, the subsequence $x_{kj-1} \rightarrow 0$ as $j \rightarrow \infty$.

3. We justify that for any $x_0 < M + \varepsilon$ we have $j \in \mathbb{N}$ such that $x_{kj} \in (0, x_{cr} - \varepsilon)$ with probability one.

This would mean that any sequence will eventually be attracted to the interval $[0, x_{cr})$. In the absence of a positive perturbation d , it will obviously either tend to zero or be identically equal to zero, however, even with a positive perturbation, whenever $d < x_{nk} < x_{cr}$, we will demonstrate that $0 < x_{(n+1)k} < x_n$.

1) Since for $x_0 \geq M + \varepsilon$ we have $x - f(x) \geq \mu_1$ by (2.7) and K satisfies (2.11), after $k - 1$ steps either

$$x_{k-1} = f^{k-1}(x_0) \leq x_0 - (k-1)\mu_1 \leq x_0 - \frac{d}{\mu_1}\mu_1 < x_0 - d$$

or some x_j , $0 < j \leq k - 1$ satisfies $x_j < M + \varepsilon$. Let us note that $f(x) < M + \varepsilon$ for any $x \leq M + \varepsilon$ by definition of $M \geq K$ and the fact that $f(x) < x$ for $x > K$, so once $x_j < M + \varepsilon$, $0 < j \leq k - 1$, we also have $x_{k-1} < M + \varepsilon$.

2) If $x_0 \in (0, x_{cr} - \varepsilon)$, then $x_0 > x_1 > \dots > x_{k-1}$; by (2.7) and the third inequality in (2.9) we have

$$f^{k-1}(x_0) < x_0 - \mu_2(k-1) \leq x_0 - \mu_2 \frac{x_{cr} - 2\varepsilon}{\mu_2} < x_0 - x_{cr} + 2\varepsilon < x_0 - d$$

as far as $x_1 \geq \varepsilon, \dots, x_{k-1} \geq \varepsilon$. This implies for $\lambda = d$

$$f^k(x_0) < \max\{x_0, \varepsilon + d\},$$

and thus the sequence x_{jk} is either decreasing or becomes less than ε . We can assume that for j large enough $x_{jk} < 2\varepsilon$, so

$$2\varepsilon > x_{jk} > x_{jk+1} > \dots$$

Next, there is an infinite number of $\lambda = -d$ (with probability 1) in the sequence at steps kj_s , which by (2.10) will lead to $x_{kj_s} = 0$, thus $\liminf_{n \rightarrow \infty} x_n = 0$.

3) Since eventually all x_{kj-1} do not exceed $M + \varepsilon$, $M + \varepsilon - d < x_{cr} - \varepsilon$ by the second inequality in (2.9) and there is $\lambda = -d$ with probability 1, even for the values of x_{kj-1} exceeding the critical one which satisfy

$$x_{cr} < x_{kj-1} \leq M + \varepsilon$$

we have a switch of the stability domain, when $x_{kj} < x_{cr} - \varepsilon$. Thus, $\liminf_{n \rightarrow \infty} x_n = 0$ by Part 2, and all solutions essentially extinct with probability 1, which completes the proof.

Remark 2.1. Let us note that for all the functions presented in the previous section condition (2.7) is satisfied. The first equality in (2.7) is satisfied for any f such that $\liminf_{t \rightarrow \infty} (x - f(x)) > 0$, in particular, for $\lim_{t \rightarrow \infty} (x - f(x)) = \infty$ which is valid for all examples. The second equality is satisfied for any continuous function f , since everywhere positive function $x - f(x)$ should attain its minimum on $[\varepsilon, x_{cr} - \varepsilon]$.

Remark 2.2. In fact, from the proof of Theorem 2.1 we obtain more than essential extinction: there are infinitely many $x_{kj} = 0$, and eventually all x_n are below the critical value.

Example 2.2. Consider equation (2.1) with

$$f(x) = \frac{2.2x^2}{1.1 + x^2}, \quad (2.12)$$

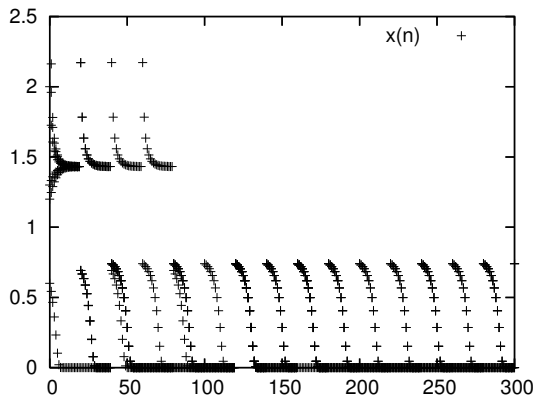


Figure 1: The results of several numerical runs of equation (2.1) with f as in (2.12) and a random perturbation $\lambda = \pm 0.74$ applied at every 20-th step.

which has 2 equilibria

$$x_{cr} \approx 0.768, \quad K \approx 1.432.$$

Here also $K = M$ since $f(x)$ is increasing for $x > 0$, so $1.432 \approx M < 2x_{cr} \approx 1.536$. Thus, for any d satisfying

$$f(2x_{cr}) - x_{cr} < 0.733 \leq d < x_{cr} \approx 0.768$$

we have essential extinction. In the numerical runs, we assume $\lambda = \pm 0.74$, $k = 20$. We observe that eventually all the values are close to zero unless a positive perturbation of $\lambda = 0.74$ occurs; after the perturbation, the solution decreases and approaches zero; after a negative perturbation, we have the zero solution at 20 successive steps at least. Figure 1 presents results of several numerical simulations.

3 Scarce random perturbations and survival

In this section, we also consider perturbed model (2.1), where λ takes the values of $\pm d$ only, each with probability 0.5. Persistence and extinction of the map (2.1) is studied under the assumptions (A1), (A2). Below, we consider the case when a scarce random perturbation can lead to unconditional survival with probability one.

Theorem 3.1. *Suppose that f and the positive equilibria x_{cr} and K satisfy*

$$K > 3x_{cr}, \quad m := \min_{t \in [K, M+2x_{cr}]} f(x) > 2x_{cr}, \quad (3.1)$$

where M was defined in (2.5), and also for any $\varepsilon \in (0, 0.5x_{cr})$ we have

$$\mu_1 = \inf_{t \geq M+\varepsilon} [t - f(t)] > 0, \quad \mu_2 = \inf_{t \in [x_{cr}+\varepsilon, K-\varepsilon]} [t - f(t)] > 0. \quad (3.2)$$

Then, for any fixed d satisfying

$$x_{cr} < d < \min\{m - x_{cr}, 2x_{cr}\} \quad (3.3)$$

there exists N such that for any $k \geq N$ all solutions persist with probability one.

Proof. The proof will follow the scheme of Theorem 2.1. First, we fix d satisfying (3.3) and $\varepsilon \in (0, x_{cr})$ such that

$$\varepsilon < d - x_{cr}, \quad 2\varepsilon < m - x_{cr} - d, \quad (3.4)$$

where the right-hand sides of the inequalities are positive by (3.3).

Next, we set μ_1, μ_2 as in (3.2), fix the perturbation step

$$k > \max \left\{ \frac{d}{\mu_1}, \frac{m - x_{cr} - \varepsilon}{\mu_2} \right\} + 1 \quad (3.5)$$

and justify the statement of the theorem using the following steps:

1. We prove that for any $x_0 > M + \varepsilon$, there exists N_1 such that $x_{kj-1} < M + \varepsilon$ for any $j > N_1$.
2. We demonstrate that for any $x_0 \in (x_{cr} + \varepsilon, M + \varepsilon)$, the subsequence $x_{kj-1} \in (m - \varepsilon, M + \varepsilon)$, which implies by (3.4) that for $\lambda = -d$

$$x_{kj} = f(x_{kj-1}) - d > m - \varepsilon - d > x_{cr} + \varepsilon.$$

3. The claim that for any $x_0 \in (0, x_{cr})$ we have $j \in \mathbb{N}$ such that $x_{kj} > x_{cr} + \varepsilon$ with probability one is obvious from the first inequality in (3.4), since any positive $\lambda = d$ will bring x_{nj} to the level of $d > x_{cr} + \varepsilon$.

1) The proof of the first step repeats Part 1 of the proof of Theorem 2.1.

2) Further, let $x_0 \in (x_{cr} + \varepsilon, M + \varepsilon)$. After $k - 1$ steps, there are two possibilities. First, we may have $x_0, x_1, \dots, x_{k-1} \in (x_{cr} + \varepsilon, K)$; then, by (3.2), (3.4) and (3.5) we have

$$x_{k-1} > x_0 + \mu_2 \frac{m - x_{cr} - \varepsilon}{\mu_2} > x_{cr} + \varepsilon + m - x_{cr} - \varepsilon = m > x_{cr} + \varepsilon + d,$$

so for $\lambda = -d$ we still have $x_k > x_{cr} + \varepsilon$. Second, there may be values $x_j > K$; however, by the definition of m in (3.1) any further $x_{j+n}, n \geq 1$, satisfies $x_{j+n} \geq m$ which also exceeds $x_{cr} + \varepsilon$ by the second inequality in (3.4). Thus $m \leq x_{k-1} \leq M$,

$$x_k \geq m - d > x_{cr} + \varepsilon \quad \text{and} \quad x_k \leq M + d < M + 2x_{cr},$$

where the second inequality implies $x_{k+1} = f(x_k) \geq m$ by (3.1). The definitions of K and μ_1 also yield that $x_{2k-1} < M + \varepsilon$.

3) Part 3 is obvious, since $x_0 \in (0, x_{cr})$ means that $x_{kj} > x_{cr} + \varepsilon$ for some j , where λ at step j equals d , with probability one.

Thus, we have justified that eventually any solution is in the interval $(x_{cr} + \varepsilon, M + 2x_{cr})$, and hence proved that the solution is persistent, with the lower bound of x_{cr} .

Remark 3.1. Let us note that for all the functions presented in the previous section condition (3.2) is satisfied. The first equality in (2.7) is satisfied for any f such that $\liminf_{t \rightarrow \infty} (x - f(x)) > 0$, in particular, for $\lim_{t \rightarrow \infty} (x - f(x)) = \infty$ which is valid for all examples. The second equality is satisfied for any continuous function f , since everywhere positive function $x - f(x)$ should attain its minimum on $[x_{cr} + \varepsilon, K - \varepsilon]$.

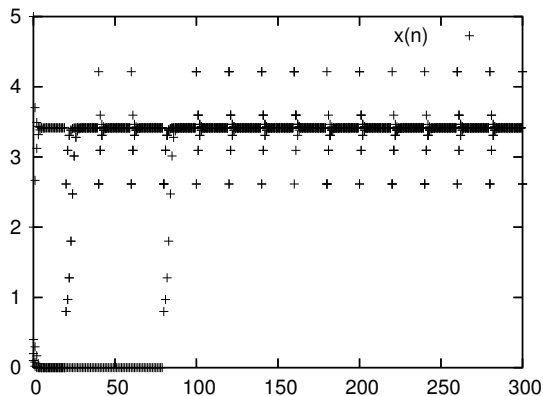


Figure 2: The results of several numerical runs of equation (2.1) with f as in (3.6) and a random perturbation $\lambda = \pm 0.8$ applied at every 20-th step.

Remark 3.2. In the proof of Theorem 3.1, in addition to survival, it was justified that the lower bound of any positive solution eventually exceeds the critical value:

$$\liminf_{n \rightarrow \infty} x_n > x_{cr}.$$

Example 3.2. Consider equation (2.1) with

$$f(x) = \frac{4x^2}{2 + x^2}, \quad (3.6)$$

which has 2 equilibria

$$x_{cr} \approx 0.586, \quad K \approx 3.414.$$

Here $K > 3x_{cr}$, $m = K > 2x_{cr}$, and for any d satisfying

$$x_{cr} \approx 0.586 < 0.6 \leq d \leq 1.1 < \min\{2x_{cr}, K - x_{cr}\}$$

we have unconditional survival. In the numerical runs, we take $d = 0.8$, $k = 20$. Figure 2 presents results of several numerical simulations. We observe that it took up to 4 perturbations to get to the stability domain, but once in the stability domain, solutions tend to K , with some outbreaks close to $K \pm d$.

4 Summary and Discussion

The present paper demonstrates that for various equations with solution persistence which is subject to a large enough initial value (the Allee effect), an introduction of a scarce random perturbation can significantly change stability properties of the system. Let us outline the results presented in the illustrating examples for the function $f(x) = rx^2/(A + x^2)$ which is strictly increasing for $x > 0$. If the distance between the critical value x_{cr} and the positive equilibrium K is small compared to this critical value, then a random switching perturbation which is between $K - x_{cr}$ and x_{cr} leads to essential extinction. If the distance between the critical value x_{cr} and the positive

equilibrium K is large compared to K then a random switching perturbation exceeding x_{cr} but smaller than $K - x_{cr}$ will lead to survival even for small initial values with probability one.

It is easy to imagine the situation when a negative constant λ leads to essential extinction [16, 20]. Since $f(x) > 0$, a positive λ will lead to persistence with the lower bound not less than λ . However, the interplay of the Allee effect and a random perturbation with the zero mean value can lead to either essential extinction or unconditional survival. To the best of our knowledge, this type of results for discrete systems with the Allee effect has never been reported before.

Finally, let us formulate some open problems, topics for research and discussion.

1. For equation (1.5) with a monotone function f in the right-hand side, global bistability of positive solutions can be easily established, see, for example, [11]. However, the global bistability of some other models subject to the Allee effect, under the condition that $f'(K) > -1$, is still an open problem.
2. In the present paper, the size and frequency of perturbations were matched to a specific model. For given perturbations, explore originally bistable models with the Allee effect which become stable. In addition, consider the dynamics of (2.1) in the range of parameters where neither essential extinction nor survival can be guaranteed. Describe the areas where survival properties differ from the non-perturbed model.
3. In (2.1), a very simple type of perturbations was introduced. Consider (2.1) with a random perturbation of a more general form. Can it change bistability of the original equation?

References

- [1] N. J. Aebischer and J. A. Ewald, *Managing the UK Grey Partridge *Perdix perdix* recovery: population change, reproduction, habitat and shooting*, *IBIS* **146** (2004), 181–191.
- [2] W. C. Allee, *Animal Aggregations, a Study in General Sociology*, University of Chicago Press, Chicago, 1931.
- [3] M. A. Asmussen, *Density-dependent selection II. The Allee effect*, *Am. Nat.* **114** (1979), 796–809.
- [4] L. Avilés, *Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality*, *Evol. Ecol. Res.* **1** (1999), 459–477.
- [5] A. H. Beeton, *Changes in the environment and biota of the great lakes, Eutrophication: Causes, Consequences, Corrections* (Washington, D.C.), National Academy of Sciences, 1969, 150–187.
- [6] D. S. Boukal and L. Berec, *Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters*, *J. Theor. Biol.* **218** (2002), 375–394.
- [7] F. Brauer and C. Castillo-Chavez, *Mathematical Models in Population Biology and Epidemiology*, Texts in Applied Mathematics **40**, Springer–Verlag, 2001.
- [8] E. Braverman, *On a discrete model of population dynamics with impulsive harvesting or recruitment*, *Nonlin. Anal.* **63** (2005), e751–e759.

- [9] E. Braverman and J. Haroutunian, *Chaotic and stable perturbed maps: 2-cycles and spatial models*, *Chaos* **20** (2010), 11 pp.
- [10] E. Braverman and D. Kinzebulatov, *On linear perturbations of the Ricker model*, *Math. Biosci.* **202** (2006), 323–339.
- [11] E. Braverman and E. Liz, *Global stabilization of periodic orbits using a proportional feedback control with pulses*, *Nonlinear Dynamics*, to appear; DOI 10.1007/s11071-011-0160-x.
- [12] C. W. Clark, *Mathematical Bioeconomics. The Optimal Management of Renewable Resources*, second edition, *Pure and Applied Mathematics (New York)*, John Wiley & Sons, New York, 1990.
- [13] H. T. M. Eskola and K. Parvinen, *The Allee effect in mechanistic models based on inter-individual interaction processes*, *Bull. Math. Biol.* **72** (2010), 184–207.
- [14] F. C. Hoppensteadt, *Mathematical Methods of Population Biology*, Cambridge University Press, Cambridge, MA, 1982.
- [15] J. Jacobs, *Cooperation, optimal density and low density thresholds: yet another modification of the logistic model*, *Oecologia* **64** (1984), 389–395.
- [16] E. Liz, *Complex dynamics of survival and extinction in simple population models with harvesting*, *Theor. Ecol.* **3** (2010), 209–221.
- [17] H. I. McCallum, *Effects of immigration on chaotic population dynamics*, *J. Theoret. Biol.* **154** (1992), 277–284.
- [18] J. G. Milton and J. Bélair, *Chaos, noise, and extinction in models of population growth*, *Theor. Popul. Biol.* **37** (1990), 273–290.
- [19] G. R. Potts and N. J. Aebischer, *Population dynamics of the grey Partridge *Perdix-perdix* 1793-1993: monitoring, modelling and management*, *IBIS* **137** (1995), S29–S37.
- [20] A. J. Schreiber, *Chaos and population disappearances in simple ecological models*, *J. Math. Biol.* **42** (2001), 239–260.
- [21] L. Stone, *Period-doubling reversals and chaos in simple ecological models*, *Nature* **365** (1993), 617–620.