Extinction and the Allee Effect in an Age Structured Population Model

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An age-structured, single-species model

The planar system

The evolution of certain types of biological populations from a period, or time interval, n to the next may be modeled by the discrete system

$$x_{n+1} = s_n x_n + s'_n y_n \tag{1}$$

$$y_{n+1} = x_n^{\lambda} e^{r_n - b x_{n+1} - c x_n} \tag{2}$$

where $\lambda, c > 0$, $b \geq 0$ with $s_n \in [0, 1)$, $s'_n \in (0, 1]$ and $r_n \in (-\infty, \infty)$ for all n.

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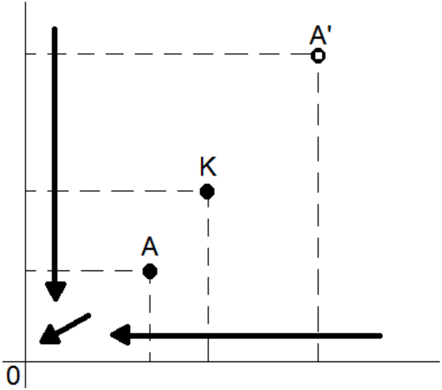
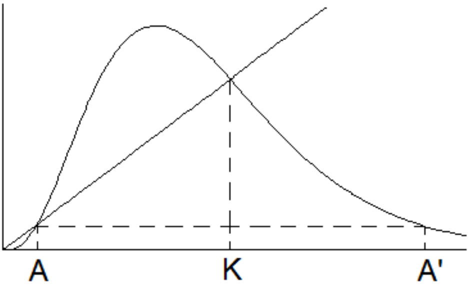
- s_n and s'_n denote the survival rates of adults and juveniles, respectively. The time dependence of the parameters r_n, s_n, s'_n reflect factors such as seasonal variations in the environment, migration, harvesting, predation, etc.
- The effects of inter-stage (adult-juvenile) interactions may be included with $b > 0$. In this case, Equation (2) indicates that the juvenile density in each period is adversely affected by adults present in the same period. Causes include competition with adults for scarce resources like food or in some cases, cannibalization of juveniles by adults.

The above system exhibits the "strong Allee effect". The underlying map of the system is characterized by three fixed points - the origin and two interior fixed points in $(0, \infty)^2$. The closer one of these to the origin is the "Allee equilibrium" A and the one that is farther from the origin is the "carrying capacity" K.



The Allee Effect in one dimension

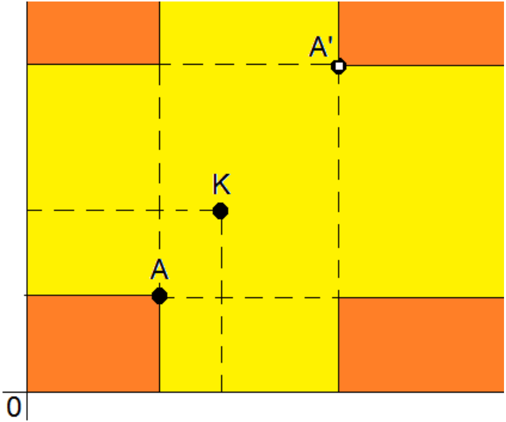
The one-dimensional case provides a simplified explanation. In the figure below when the population size or density is less than the Allee equilibrium A or greater than its pre-image A' the population decreases to 0. If the population size is between A and A' then it remains in this interval, which is invariant (because the maximum value of the function is less than A'). This interval is the “survival region” and its complement the “extinction region” or the basin of attraction of the origin.



One dimensional Ricker map

Extinction and survival regions

When generations do not interact (no inter-stage interactions or $b = 0$) the situation in two dimensions is still simple and can be explained using the one-dimensional Ricker map. The extinction region E (dark color in the figure below) is where the mix of adult and juvenile populations yields an orbit in the positive quadrant that converges to 0. The complement of E is the survival region (light color). Orbits in these regions do not converge to the origin.



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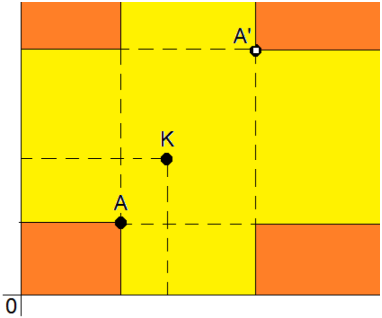

The main difference between the above planar region and the one-dimensional one is that for orbits in the light colored region *outside* the box with corners A and A' the orbit oscillates axis-to-axis, i.e. it converges to a limit set that is distributed on the two axes. In the simplest case, this limit set consists of the projections of K on the two axes so the orbit converges to a two-cycle.

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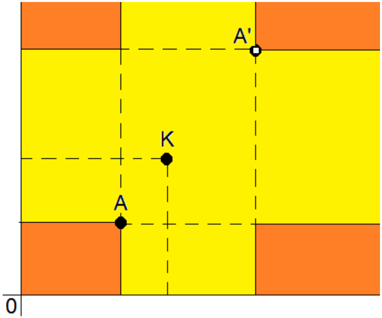

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On the other hand, as in the one-dimensional case the survival region (light color) is *connected*.

The extinction threshold

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- When $b > 0$ the positive quadrant can also be divided into an extinction region E that consists of all initial points where the solutions converge to 0 (basin of attraction of the origin) and the complement of this region i.e. survival region.

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- When $b = 0$ this threshold is simply the boundaries of the dark colored rectangular regions in the last figure.
- When $b > 0$ the positive quadrant can also be divided into an extinction region E that consists of all initial points where the solutions converge to 0 (basin of attraction of the origin) and the complement of this region i.e. survival region.
- But when $b > 0$ the extinction threshold is much more complicated. Also, the survival region may be disconnected when $b > 0$.

Extinction and survival with inter-stage interactions

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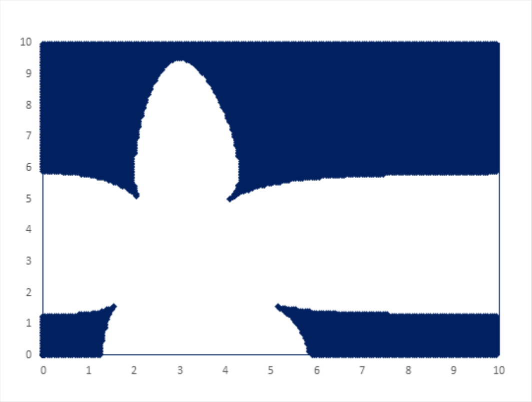
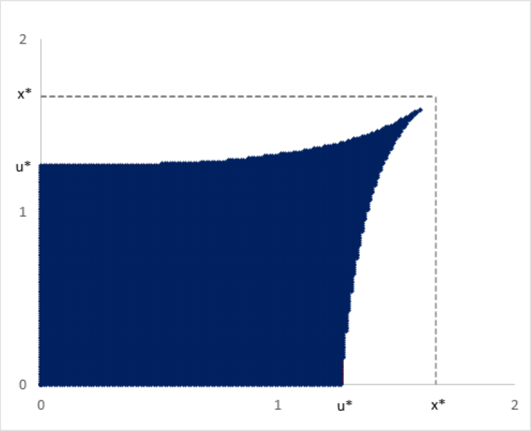
Here is a numerically generated diagram showing the extinction region (shaded) with

$$\lambda = 3, \quad a = 0.7936, \quad b = 0.0891, \quad s = 0 \quad s' = 1$$



Extinction and survival with inter-stage interactions

Here is the enlargement of the base component E_0 of the extinction region – note that the interior fixed point (x^*, x^*) in the above figure, which is the Allee equilibrium A, is not on the boundary (the extinction threshold)!



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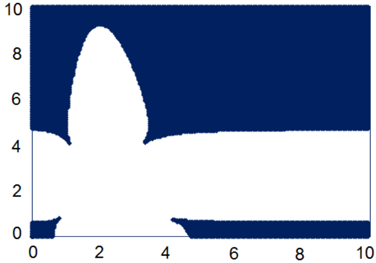
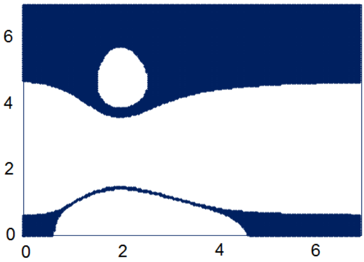
In fact, it is unbounded and has a nonempty interior as seen in the following numerically generated diagrams with two different values of b and

$$\lambda = 2, \quad a = 1.1, \quad s = 0 \quad s' = 1$$

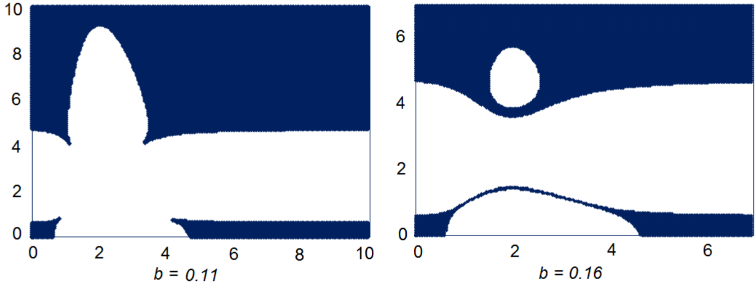


b = 0.11



b = 0.16

Survival regions without interior system fixed points



We see that with $b > 0$ the survival region may be disconnected. Finding the trace of the boundary curve, or the extinction threshold is an open problem in this case.

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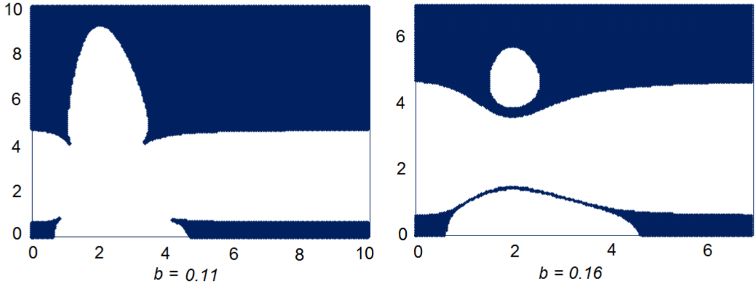

We see that with $b > 0$ the survival region may be disconnected. Finding the trace of the boundary curve, or the extinction threshold is an open problem in this case.

We see later that E is unbounded by showing that it contains certain rectangular regions in the positive quadrant.

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- In terms of populations of adults and juveniles, starting from initial adult and juvenile population densities x_0 and y_0 respectively, a solution $\{x_n\}$ of the scalar equation (4) yields the adult population density. The juvenile population density y_n is found via (3). The initial values for (4) are x_0 and $x_1 = s_0 x_0 + s'_0 y_0$.

Extinction

The following result is stated for the second-order equation.

Theorem

Assume that $\lambda > 1$, $s \doteq \sup_{n\geq 0}\{s_n\} < 1$ *and* $A \doteq \sup_{n\geq 0}\{a_n\} < \infty$.
(a) If

$$\rho = \exp\left(-\frac{A - \ln(1-s)}{\lambda - 1}\right).$$

and $\{x_n\}$ *is a solution of (4) with* $x_1, x_0 < \rho$ *then* $\lim_{n\to\infty} x_n = 0$.

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Remark

For the original planar system this theorem implies that if $\lambda > 1$ *then* E *is nonempty and further, for some parameter values* $E = [0, \infty)^2$.

The fixed points

In the autonomous case

$$x_{n+1} = sx_n + x_{n-1}^{\lambda} e^{a - bx_n - x_{n-1}} \tag{6}$$

where all parameters are constants we consider the existence of fixed points.

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(c) If (7) does not hold, i.e.

$$a < \ln(1-s) + (\lambda - 1)[1 + \ln(b+1) - \ln(\lambda - 1)] \tag{9}$$

then (6) has no positive fixed points.

The fixed points and their stability

Note that if $x^*, \bar{x}$ are fixed points of (6) then the fixed points of the system (1)-(2) are obtained using (3) as

$$\left(x^*, \frac{1-s}{s'} x^*\right), \quad \left(\bar{x}, \frac{1-s}{s'} \bar{x}\right).$$

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Remark

The first of the above fixed points is always unstable, while the second may be unstable or asymptotically stable.

A convergence criterion

Lemma

Assume that $\lambda > 1$ *and let* a_n, b_n *be sequences of real numbers such that* $a = \sup_{n \geq 1} a_n < \infty$ *and* $b_n \geq 0$ *for all* n. *Further, assume that the mapping* $f(u) = u^{\lambda} e^{a-u}$ *has an Allee fixed point* u^*. *If* $x_k \in (0, u^*)$ *for some* $k \geq 0$ *then the terms* $x_k, x_{k+2}, x_{k+4}, \ldots$ *of the corresponding solution of the equation*

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decrease monotonically to 0. Thus, if k *is even (or odd) then the even-indexed (respectively, odd-indexed) terms of the solution eventually decrease monotonically to zero.*

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Remark

By the above result if $x_k, x_{k+1} \in (0, u^*)$ *for some* $k \geq 0$ *then the solution* $\{x_n\}$*converges to 0 (usually* ***not*** *monotonically).*

The unbounded extinction region

Now consider the special case of equation (6) with $s = 0$, i.e.

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For this equation we can easily show that the extinction set E has unbounded components as follows:

Corollary

Assume that $\lambda > 1$ *and*

$$a > (\lambda - 1)[1 - \ln(\lambda - 1)] \tag{12}$$

Let u_* *be the pre-image of* u^*, *i.e.* $f(u_*) = u^*$ *where* $f(u) = u^{\lambda} e^{a-u}$. *If*

$$(x_0, x_1) \in R_{0,1} \cup R_{1,0} \cup R_{1,1}$$

where the rectangles $R_{0,1}, R_{1,0}, R_{1,1}$ *are defined as*

$$R_{0,1} = [0, u^*) \times [u_*, \infty), \quad R_{1,0} = [u_*, \infty) \times [0, u^*), \quad R_{1,1} = [u_*, \infty) \times [u_*, \infty)$$

then corresponding orbits of (11) converge to zero, i.e. the above set is contained in the extinction region E.

Some details for the extinction and survival sets

Theorem

Assume that $\lambda > 1$.
(a) If

$$(\lambda - 1)[1 - \ln(\lambda - 1)] < a < (\lambda - 1)[1 - \ln(\lambda - 1) + \ln(b + 1)] \tag{13}$$

then (11) has no positive fixed points but it has positive solutions that do not converge to 0.

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(b) Assume that

$$b \leq \frac{\lambda - 1}{\lambda} e^{1/(\lambda - 1)} - 1 \tag{14}$$

holds and further,

$$(\lambda - 1)[1 - \ln(\lambda - 1) + \ln(b + 1)] \leq a \leq \lambda - (\lambda - 1) \ln \lambda. \tag{15}$$

If x^* *is the smaller of the positive fixed points of (11) then there are initial values* $x_1, x_0 \in (0, x^*)$ *for which the corresponding positive solutions of (11) do not converge to 0.*

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If x^* *is the smaller of the positive fixed points of (11) then there are initial values* $x_1, x_0 \in (0, x^*)$ *for which the corresponding positive solutions of (11) do not converge to 0.*
(c) If (14) and (15) hold, then the solutions of (11) from initial values $(x_0, x_1) \in ([x^*, \lambda] \times [0, x^*]) \cup ([0, x^*] \times [x^*, \lambda])$ *do not converge to the origin.*

Further details for the extinction and survival sets

An immediate consequence of the preceding theorem is that the base component E_0 of the extinction set is properly contained in the rectangular set having the origin and the fixed point $(x^*, x^*/s')$ as its corner points.

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By (c) of the Theorem, the boundaries of E_0 that are not on the coordinate axes are not in E_0 .

Since E_0 is a connected set with points within the square $[0, x^*) \times [0, x^*/s')$ the following is clear:

Further details for the extinction and survival sets

An immediate consequence of the preceding theorem is that the base component E_0 of the extinction set is properly contained in the rectangular set having the origin and the fixed point $(x^*, x^*/s')$ as its corner points.

By (c) of the Theorem, the boundaries of E_0 that are not on the coordinate axes are not in E_0 .

Since E_0 is a connected set with points within the square $[0, x^*) \times [0, x^*/s')$ the following is clear:

Corollary

Under the hypotheses of Theorem 8(b) $E_0 \subset [0, x^*) \times [0, x^*/s')$ *where the inclusion is proper.*

References

Ackleh, A.S. and Jang, S.R.-J., A discrete two-stage population model: continuous versus seasonal reproduction, *J. Difference Eq. Appl.* **13**, 261-274, 2007

Cushing, J.M., A juvenile-adult model with periodic vital rates, *J. Math Biology,* **53**, pp.520-539, 2006

Franke, J.E., Hoag, J.T. and Ladas, G., Global attractivity and convergence to a two-cycle in a difference equation, *J. Difference Eq. Appl.* **5**, 203-209, 1999

Liz, E. and Pilarczyk, P., Global dynamics in a stage-sturctured discrete-time population model with harvesting, *J. Theor. Biol.* **297**, 148-165, 2012

Zipkin, E.F., Kraft, C.E., Cooch, E.G., and Sullivan, P.J., When can efforts to control nuisance and invasive species backfire? *Ecol. Appl.* **19**, 1585-1595, 2009