How Biased Density Dependent Movement of a Species at the Boundary of a Habitat Patch May Mediate Its within Patch Dynamics

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Based on:

Cantrell and Cosner, Bulletin of Mathematical Biology **69** (2007), 2339-2360.

Cantrell and Cosner, Journal of Differential Equations **231** (2006), 768-804.

Cantrell, Cosner and Martinez, Proceedings of the Royal Society of Edinburgh **139A** (2009), 45-56.

Context (Edge Mediated Effects)

Fagan, Cantrell, and Cosner, American Naturalist **153** (1999), 165-182

Edges can change species interactions by altering species' movement patterns.

Altering species' movement near the boundary of a habitat patch can change the dynamics of the species at the scale of the patch as a whole.

Specific Motivation

Kuussaari et al, Oikos **82** (1998), 384-392.

Article reports on an empirical study of the Glanville fritillary butterfly in Finland. This species of butterfly cues upon conspecifics and it is observed that individuals are less likely to leave a bush if other butterflies are present. Kuussaari et al (1998) demonstrate that this behavior appears to induce an Allee effect within the patch.

Glanville Fritillary Butterfly

Model to test having bistable population dynamics at the patch level even though no such effect present in the local population dynamics within the patch

$$u_t = d\nabla^2 u + ru(1-u) \quad \text{in } \Omega \times (0, \infty),$$

$$\alpha(u)\frac{\partial u}{\partial n} + \big(1-\alpha(u)\big)u = 0 \quad \text{on } \partial\Omega \times (0, \infty)$$

Notation

Ω	represents a bounded habitat patch.
$\partial\Omega$	represents the boundary of Ω.
u	represents a population density on Ω.
r	represents the local population growth rate in Ω.
d	represents the diffusion rate of the population.
$1-\alpha$	describes the rate at which individuals leave the patch Ω if they encounter the boundary $\partial\Omega$. Specifically, if $1-\alpha=0$ then no individuals leave the patch but if $1-\alpha=1$ then all individuals that reach the boundary leave the patch. In general, we will allow α to depend on u but in some cases we will set α equal to a constant. (In the models α appears as a coefficient in the boundary conditions.)
$\lambda_1(\alpha^*)$	is the principal eigenvalue of the negative Laplace operator on Ω under the boundary conditions that would arise if $\alpha\equiv\alpha^*$ for some constant α^*. (This eigenvalue synthesizes the geometry of Ω with the boundary conditions determined by α^*. It measures the rate at which a population with no births or deaths and with diffusion rate $d=1$ would diffuse out of Ω under the boundary conditions defined by α. It is formally defined in Lemma 1 of Section 2.)

Allee Effect

Definition: per capita growth rate increases at low densities

Strong Allee effect: per capita growth rate is negative at low densities; can not invade an empty habitat

Weak Allee effect: per capita growth rate is positive at low densities; can invade an empty habitat, but size of such a habitat would be bigger than with logistic dynamics with the same maximal per capita growth rate

Causes

Less efficient feeding (Way and Banks, Ann. Appl. Biol. **59** (1967), 189-205)

Reduced effectiveness of anti-predator defenses (Kruuk, Behav. Suppl. 11 (1964), 1-29; Kenward, J. Animal Ecol. 47 (1978), 449-460)

Difficulty in finding mates (Stephens and Sutherland, TREE **14** (1999), 401-405; Boukal and Berec, J. Theor. Biol. 218 (2002), 375-394)

Nonspatial Model for an Allee Effect

$$\frac{du}{dt} = f(u)$$

$$f(u) = ru(u - a)(1 - u/K)$$

Remarks

In the previous slide, $r > 0$ and $0 < a < K$.

Allee effects depend upon scale. Kuussaari et al (1998) are observing Allee effects at the scale of a patch.

When passive diffusion is included as a dispersal mechanism, it can convert a weak Allee effect at the local level into a strong Allee effect on the population level for some patch sizes near the critical patch size for invasibility (Cantrell and Cosner, Wiley and Sons, 2003). See also Jiang and Shi, CRC Press, 2009, 33-61.

Key Term in the Model : $\alpha(u)$

- $\alpha(u) \in [0,1]$ when $u \in [0,1]$
- If $\alpha(u)=\alpha^*$ for all u in [0,1], α^* is increasing as the fraction of individuals that remain in the patch upon reaching the boundary increases
- If $\alpha^*=0$, all individuals that reach the boundary leave (Dirichlet)
- If $\alpha^* =1$, no individuals leave the patch (Neumann)
- $\alpha(u)$ assumed smooth and nondecreasing

The model when α(u)=α* for all u

$$u_t = d\nabla^2 u + ru(1-u) \quad \text{in } \Omega \times (0,\infty),$$

$$\alpha^* \frac{\partial u}{\partial n} + (1-\alpha^*)u = 0 \quad \text{on } \partial\Omega \times (0,\infty)$$

Predictions when α(u)=α* for all u

One considers the linear eigenvalue problem

$$
\begin{aligned}
&d\nabla^2\phi + r\phi = \sigma\phi && \text{in } \Omega, \\
&\alpha^*\nabla\phi\cdot\vec{\eta} + (1-\alpha^*)\phi = 0 && \text{on } \partial\Omega
\end{aligned}
$$

When the average rate of growth over the patch of the species in question at low densities (i.e., σ) is positive, positive solutions of the diffusive logistic problem tend over time to a unique globally attracting equilibrium $u(\alpha^*)$ which is positive in the patch. When this average rate of growth over the patch is nonpositive, all nonnegative solutions to the diffusive logistic problem tend to 0 over time. So the model has only two possible predictions : persistence via convergence to a globally attracting equilibrium or extinction.

$$\sigma = \sigma(\alpha^*, r, d) = r - d\lambda_{\alpha*}^1(\Omega)$$

$$\sigma(\alpha^*, r, d) > 0 \quad \Leftrightarrow \quad r/d > \lambda_{\alpha*}^1(\Omega)$$

The model when $\alpha(u)$ is density dependent and $\alpha(1) = 1$, so that $u = 0$ and $u = 1$ are both equilibria

Equilibria are given by solutions to

$$d\nabla^2 u + ru(1-u) = 0 \quad \text{in } \Omega,$$

$$\alpha(u)\frac{\partial u}{\partial n} + \big(1-\alpha(u)\big)u = 0 \quad \text{on } \partial\Omega$$

Linearized stability analysis

Linearization at 0 (Eqn. #1) with $\alpha^* = \alpha(0)$

$$
\begin{aligned}
&d\nabla^2\phi + r\phi = \sigma\phi && \text{in } \Omega, \\
&\alpha^*\nabla\phi\cdot\vec{\eta} + (1-\alpha^*)\phi = 0 && \text{on } \partial\Omega
\end{aligned}
$$

Linearization at 1: (Eqn #2)

$$d\nabla^2\psi - r\psi = \sigma\psi \quad \text{in } \Omega,$$

$$\frac{\partial\psi}{\partial n} - \alpha'(1)\psi = 0 \quad \text{on } \partial\Omega$$

u = 0 and u = 1 linearly stable

$$\alpha'(1)\sup_{\bar{\Omega}}\nabla^2 w + \alpha'(1)^2\sup_{\bar{\Omega}}|\nabla w|^2 < \frac{r}{d} < \lambda_1\big(\alpha(0)\big)$$

$$\partial w/\partial n = 1 \ on \ \partial\Omega$$

$$\rho = \psi / h \text{ where } h > 0$$

$$\begin{aligned} \nabla\psi &= h\nabla\rho + \rho\nabla h, \\ \nabla^2\psi &= h\nabla^2\rho + 2\nabla\rho\cdot\nabla h + \rho\nabla^2 h. \end{aligned} \tag{9}$$

From (6) and (9) we readily obtain

$$\begin{aligned} &d\nabla\cdot h^2\nabla\rho + \left(dh\nabla^2 h - rh^2\right)\rho = \sigma h^2\rho \quad \text{in } \Omega, \\ &\frac{\partial\rho}{\partial n} + \left[\frac{1}{h}\frac{\partial h}{\partial n} - \alpha'(1)\right]\rho = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{10}$$

To define h, choose w to be a function so that $\partial w/\partial n = 1$ on $\partial\Omega$ then let $h = e^{\alpha'(1)w}$. (If the geometry of Ω is simple then it may be possible to explicitly construct w. It is always possible to construct w by solving the equation $\nabla^2 w - w = 0$ subject to the boundary condition $\partial w/\partial n = 1$ on $\partial\Omega$.) We then have $\partial h/\partial n = \alpha'(1)h$ on $\partial\Omega$ so the boundary condition in (10) becomes

$$\frac{\partial\rho}{\partial n} = 0. \tag{11}$$

Thus, the change of variables converts (6) into a classical eigenvalue problem. Multiplying (10) by ρ, integrating by parts via the divergence theorem and using (11) yields

$$\begin{aligned} \sigma\int_\Omega h^2\rho^2\,dx &= -\int_\Omega dh^2\,|\nabla\rho|^2\,dx + \int_\Omega \left(dh\,\nabla^2 h - rh^2\right)\rho^2\,dx \\ &\le d\int_\Omega \left[\left(\frac{\nabla^2 h}{h} - \frac{r}{d}\right)\right] h^2\rho^2\,dx. \end{aligned} \tag{12}$$

Since $\nabla^2 h = (\alpha'(1)\nabla^2 w + \alpha'(1)^2|\nabla w|^2)h$ it follows from (12) that $\sigma < 0$ provided

$$\alpha'(1)\nabla^2 w + \alpha'(1)^2|\nabla w|^2 < (r/d) \quad \text{on } \Omega. \tag{13}$$

Bifurcation approach when $\alpha(0) > 0$, $\alpha(1) = 1$ and $d\alpha/du(1) > 0$

Equlibria are the zeros of the map

$$F(\lambda, u) = \left(\nabla^2 u + \lambda u(1-u),\ \alpha(u)\nabla u \cdot \vec{\eta} + \big(1-\alpha(u)\big)u\right)$$

where $F : (-\infty,\infty) \times C^{2,\gamma}(cl\Omega) \rightarrow C^{\gamma}(cl\Omega) \times C^{1,\gamma}(\partial\Omega)$ and $\lambda = r/d \geq 0$.

The linearization about 0 is:

$$F_u(\lambda, 0)w = \left(\nabla^2 w + \lambda w,\ \alpha(0)\nabla w \cdot \vec{\eta} + \left(1 - \alpha(0)\right)w\right)$$

When $\lambda = \lambda_1(\alpha(0))$,the linearization is Fredholm of index zero with a one dimensional eigenspace spanned by the eigenfunction in Eqn. #1. Moreover, the compatablity condition in the Crandall-Rabinowitz local bifurcation theorem is met. So all nonzero equilibria near $(\lambda_1(\alpha(0)),0)$

have the form $(\lambda,u) = (\lambda(s),s\psi + s\rho(s))$ with $\lambda(s)$ and $\rho(s)$ smooth in a nbd of $s = 0$ with $\lambda(0) = \lambda_1(\alpha(0))$ and $\rho(0) =0$. Here $\lambda_1(\alpha(0))$ ranges between $\lambda_1(1) = 0$ and $\lambda_1(0) > 0$.

To consider $F(\lambda,u) = 0$ in a nbd of $u = 1$ we make a change of variables as before with $w = hu$, where $h > 0$ on the closure of Ω is chosen so that

$$\text{grad } h * \eta + K h = 0 \text{ on bd } \Omega$$

with $K > \max\{ 1, d\alpha/du(1)\}$. Then $w = h$ corresponds to $u = 1$. Let $w = \rho + h$. Then reformulate the problem in terms of the variable ρ. We get a map $G(\lambda, \rho)$ so that

$G(\lambda, \rho) = 0$ iff $F(\lambda,(\rho + h)/h) = 0$

whose linearization about 0 is Fredholm of index zero and

equivalent to Eqn #2

Linearization at 1: (Eqn #2)

$$d\nabla^2\psi - r\psi = \sigma\psi \quad \text{in } \Omega,$$

$$\frac{\partial\psi}{\partial n} - \alpha'(1)\psi = 0 \quad \text{on } \partial\Omega$$

Let λ_0 denote the principal eigenvalue of Eqn 2. There will be bifurcation from 1 at all the eigenvalues of Eqn #2. However, equilibria with values between 0 and 1 can only emanate from $\lambda_{0.}$

Lower estimate on λ_0

$$\lambda_0 > \alpha'(1)\,\frac{|\partial\Omega|}{|\Omega|} \quad \text{if } \alpha'(1) > 0$$

Upper estimate on λ_0

$$\lambda_0 \leqslant \lambda^1_{\alpha^*}(\bar{\Omega}) + \sup 2|\nabla k|^2/k^2$$

$$\alpha^* = \frac{1}{1+\alpha'(1)}$$

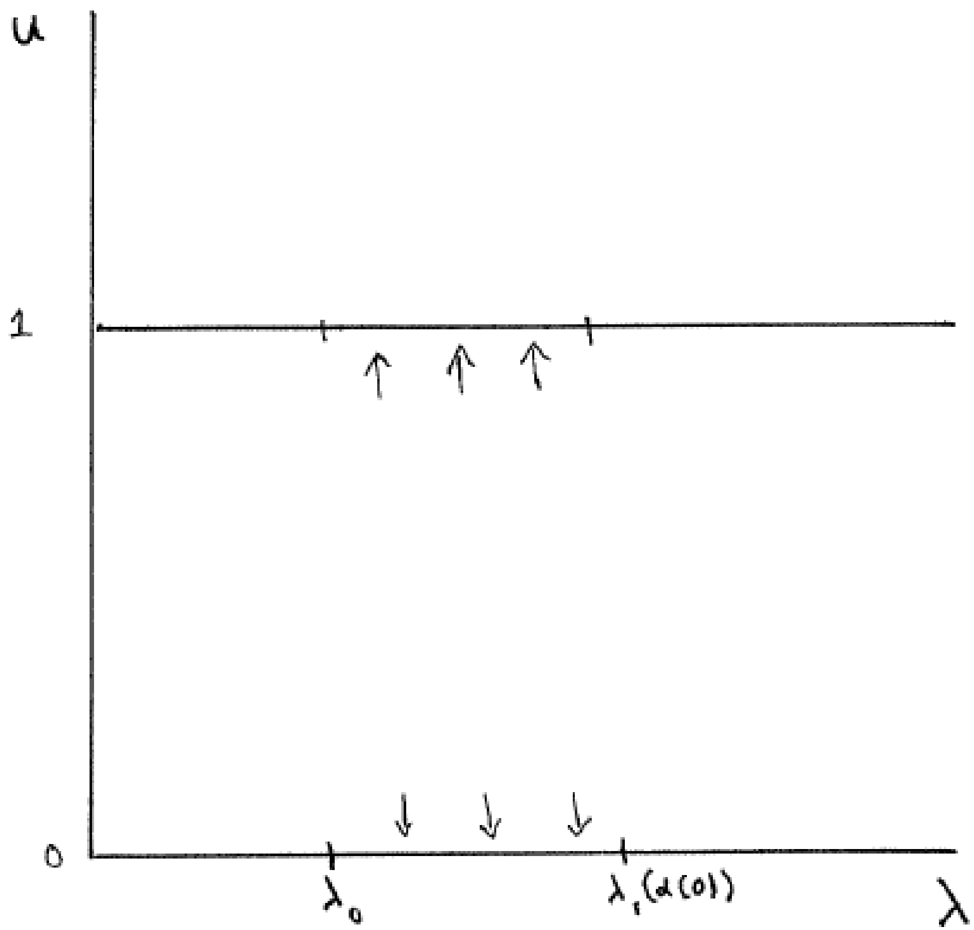
$$\begin{aligned} -\nabla^2 k &= \lambda k && \text{in } \Omega, \\ \nabla k \cdot \vec{\eta} + \alpha'(1)k &= 0 && \text{on } \partial\Omega. \end{aligned}$$

So λ_0 converges to 0 as $d\alpha/du(1)$ converges to 0 and converges to ∞ as $d\alpha/du(1)$ converges to ∞.

The equilibrium $u = 0$ is stable when $\lambda < \lambda_1(\alpha(0))$ and unstable when $\lambda > \lambda_1(\alpha(0))$.

The equilibrium $u = 1$ is stable when $\lambda > \lambda_0$ and unstable when $\lambda < \lambda_0$.

$\lambda_0 < \lambda_1(\alpha(0))$



u = 0 and u = 1 linearly stable (Allee effect)

$$\alpha'(1)\sup_{\bar{\Omega}}\nabla^2 w + \alpha'(1)^2\sup_{\bar{\Omega}}|\nabla w|^2 < \frac{r}{d} < \lambda_1\big(\alpha(0)\big)$$

$$\partial w/\partial n = 1 \; on \; \partial\Omega$$

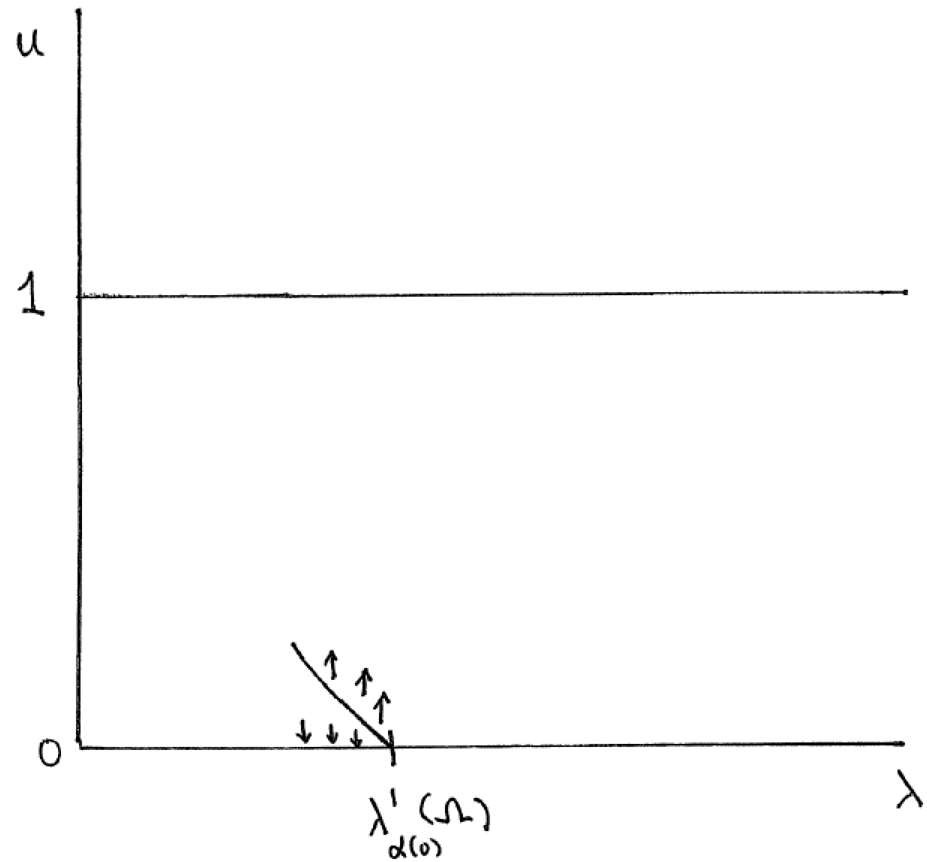
Direction of bifurcation from u = 0

$$\lambda'(0) = \frac{\lambda^1_{\alpha(0)}(\Omega)\int_\Omega \phi^3\,dx - \frac{\frac{d\alpha}{du}(0)}{(\alpha(0))^2}\int_{\partial\Omega}\phi^3\,dS}{\int_\Omega \phi^2\,dx}$$

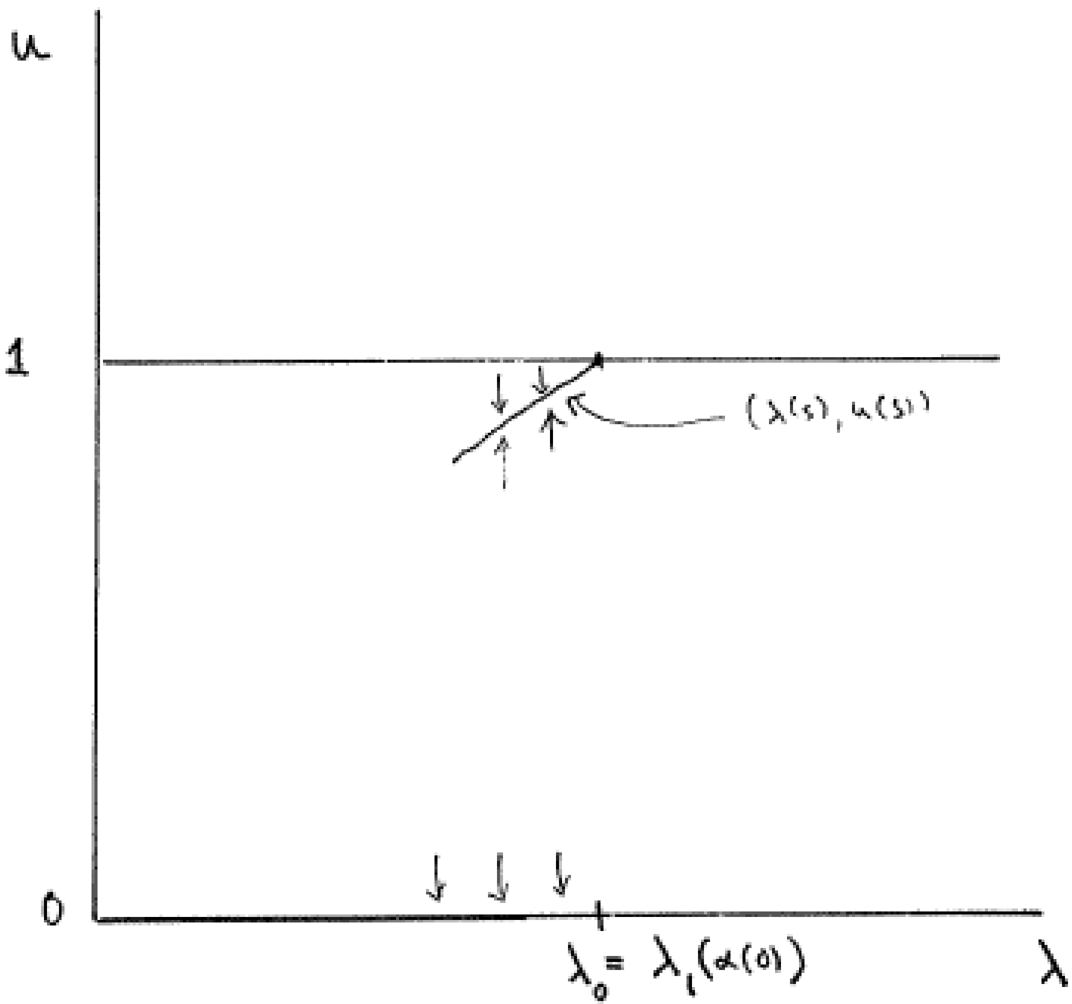
Allee effect via subcritical bifurcation

$$\frac{d\alpha}{du}(0) > \left(\alpha(0)\right)^2 \lambda^1_{\alpha(0)}(\Omega)\,\frac{\int_\Omega \phi^3\,dx}{\int_{\partial\Omega} \phi^3\,ds}$$

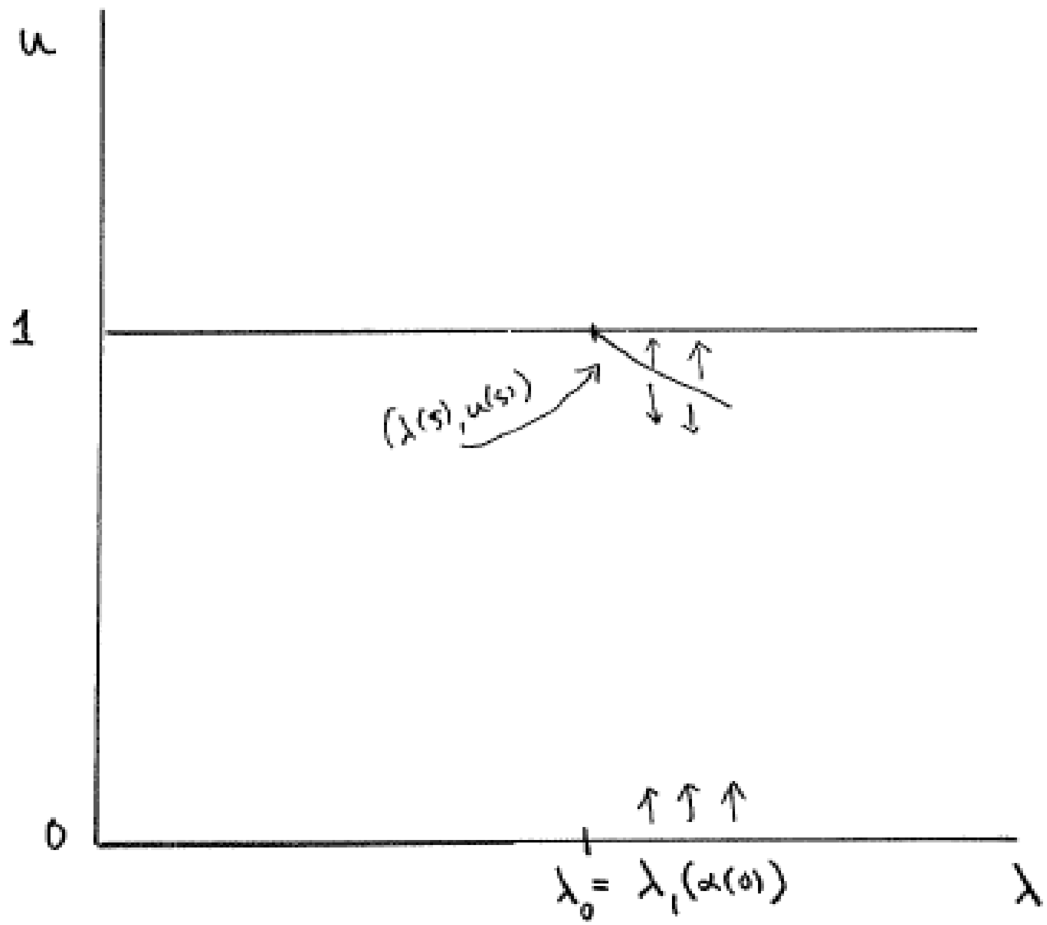
Allee effect via subcritical bifurcation



$\lambda_0 = \lambda_1(\alpha(0))$ (a)



$\lambda_0 = \lambda_1(\alpha(0))$ (b)



Global Bifurcation Results

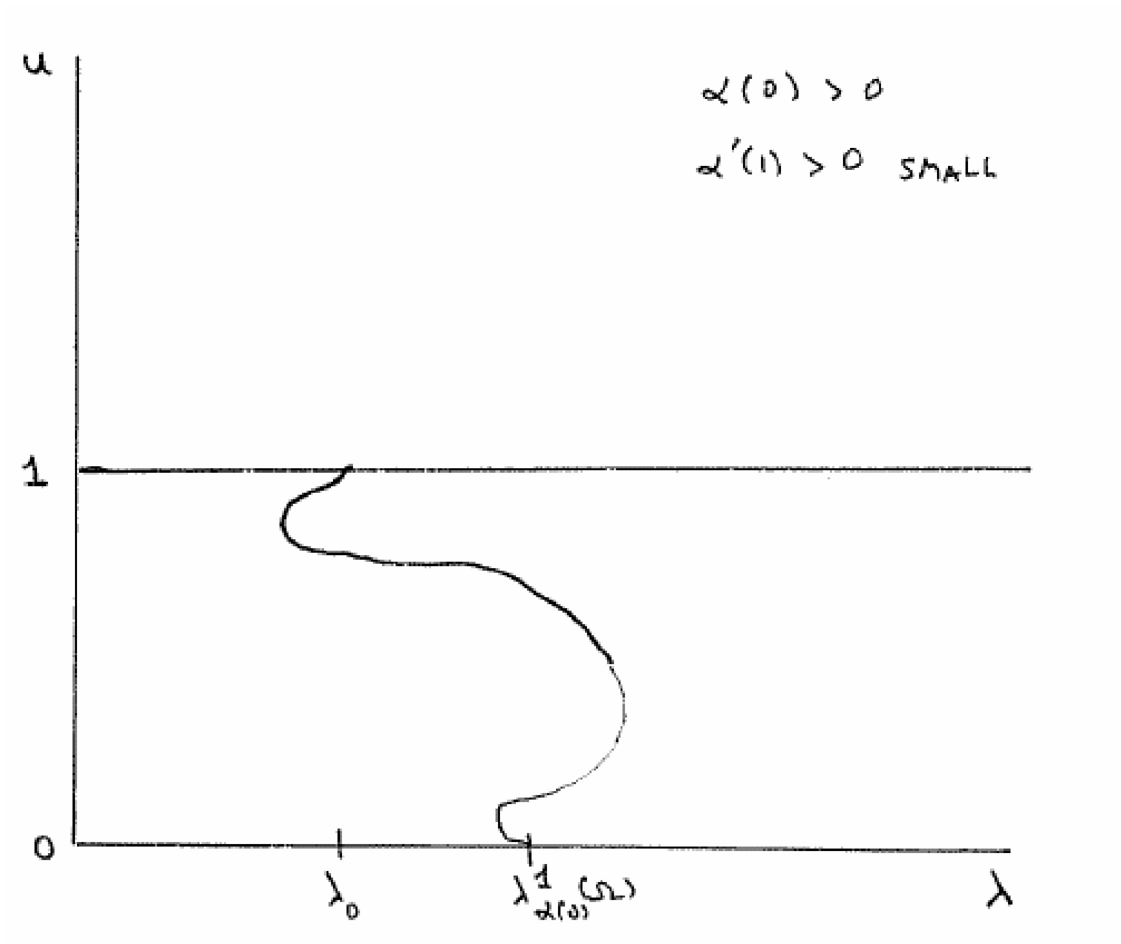
Important Question That Now Arises: Can we link equilibrium solutions that emanate from $u \equiv 0$ to equilibrium solutions that emanate from $u \equiv 1$?

Whether bifurcating from $u \equiv 0$ or from $u \equiv 1$, we use $w = uh$ to recast the problem.

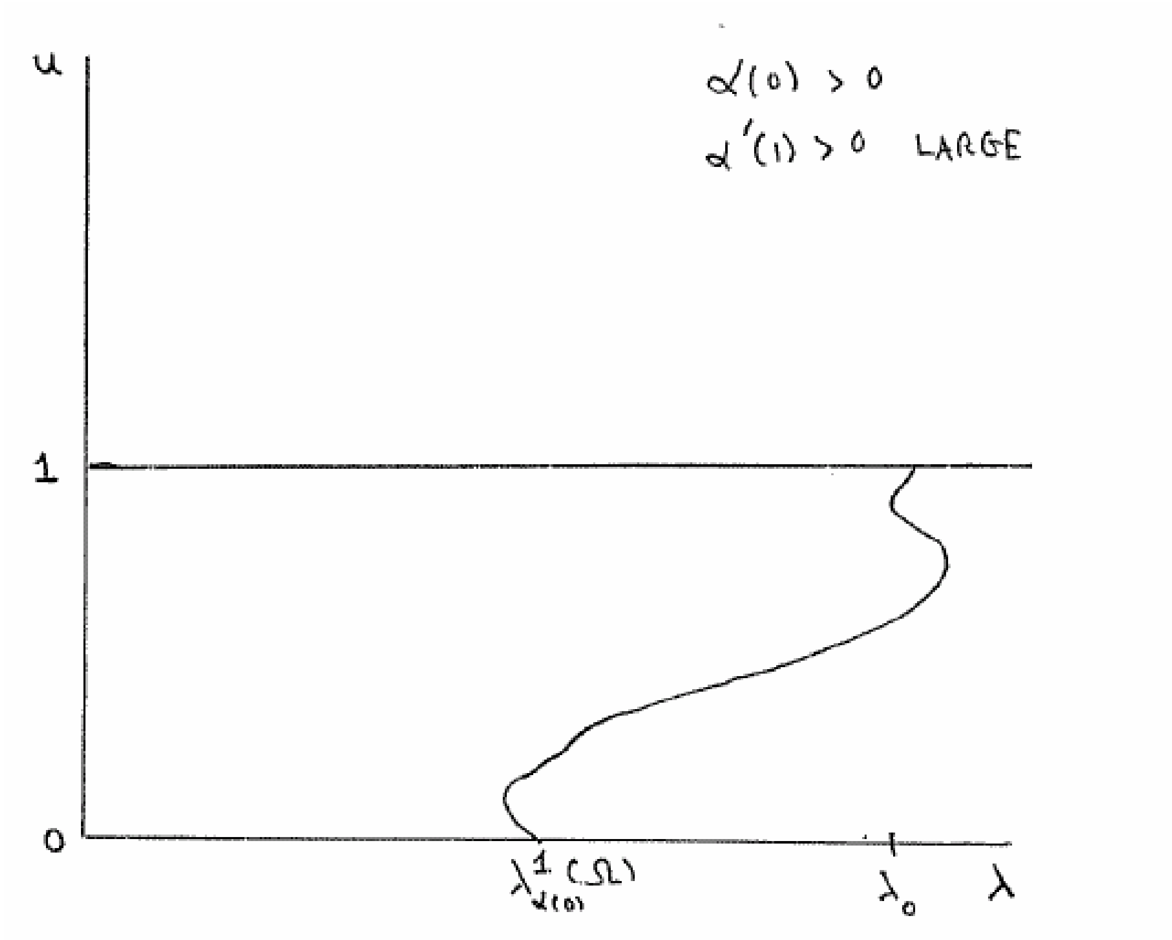
Functional analytic constructions needed to apply a global bifurcation theory (Rabinowitz, Alexander-Antman, etc) are involved.

The construction involves density dependence in the boundary conditions and needs the *a priori* estimates from Ladyzhenskaya and Ural'tseva.

BIFURCATION DIAGRAM # 1



BIFURCATION DIAGRAM # 2



BIFURCATION DIAGRAM # 3