# Evolution of Conditional Dispersal: Fast vs Slow Diffusers

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Joint work with Yuan Lou (MBI,Ohio State)

# Introduction

- Biological evolution is driven by selection and mutation.
- Ecological feedback loops (environmental conditions co-evolve) induces a wide spectrum of possible dynamics.

Basic Questions in the Evolution of Dispersal:

- How do species adopt their dispersal strategies?
- How will their dispersal behaviors evolve?
- Is there an "optimal" dispersal strategy associated with a given habitat condition?

# Unconditional and Conditional Dispersal

Unconditional Dispersal: Movement of organism that is independent of local environmental conditions.

- Diffusion
- Uniform stream flow

Conditional Dispersal: Movement that depends on local environmental conditions

- Movement biased toward favorable environments
- Cross-diffusion
- Fitness-dependent dispersal

# Unconditional Dispersal

The following situation is considered in [Hastings (1983)]. Suppose $u$ is the density of resident species obeying

$$u_t = \mu\Delta u + uF(x,u) \quad \text{and} \quad \left.\frac{\partial u}{\partial n}\right|_{\partial\Omega} = 0$$

where $F$ is decreasing in $u$. At equilibrium, $u$ defines the environment. Introducing a rare mutant $v$,

$$v_t = \nu\Delta v + vF(x,u+v) \quad \text{and} \quad \left.\frac{\partial v}{\partial n}\right|_{\partial\Omega} = 0.$$

**Theorem (Hastings (1983))**

*The mutant $v$ can invade when rare if and only if $\nu < \mu$.*

# Evolutionarily Stable (Unbeatable) Strategies

A strategy $\hat{\mu}$ is *Evolutionarily Stable* if, once the population adopting $\hat{\mu}$ is established, they cannot be invaded successfully by any small amount of mutant with slightly different strategies. [Maynard Smith and Price (1973)]

- In other words, Hastings has shown that there does not exist any ESS for the unconditional diffusion model.

# Unconditional Dispersal

- What happens after the rare mutant $v$ invades successfully?

The following more explicit model is considered by [Dockery et. al. (1998)].

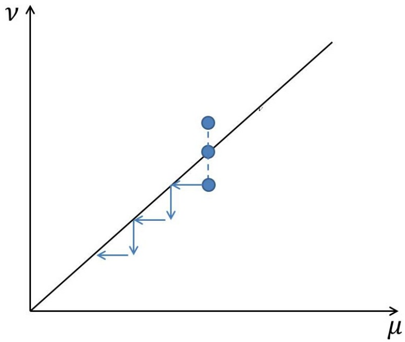
$$\begin{cases} u_t = \mu \Delta u + u(m - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \Delta v + v(m - u - v) & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) & \text{in } \Omega. \end{cases}$$

The slower diffusing mutant $v$ actually displaces the resident $u$.

**Theorem (Dockery et. al. (1998))**

*If $\nu < \mu$, then for any non-trivial initial condition, $v$ always drives $u$ to extinction.*

# Slower Diffuser Prevails




- Slower diffusion rate is "selected" by the environment.

# A Conditional Dispersal Model

The following model is considered in [Cantrell, Cosner, Lou (06',07')][Chen-Lou(08')][Chen-Hambrock-Lou(08')][Hambrock-Lou(09')]

$$\begin{cases} u_t = \mu\nabla\cdot(\nabla u - \eta u \nabla m) + u(m-u-v) & \text{in } \Omega\times(0,\infty), \\ v_t = \mu\nabla\cdot(\nabla v - \xi v \nabla m) + v(m-u-v) & \text{in } \Omega\times(0,\infty), \\ \frac{\partial u}{\partial n} - \eta u \frac{\partial m}{\partial n} = \frac{\partial v}{\partial n} - \xi u \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega\times(0,\infty), \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & \text{in } \Omega. \end{cases}$$

- $u, v$ are two phenotypes that disperse with a combination of diffusion and directed movement.
- $\eta, \xi$ denote rates of directed movement (1-d trait).
- $u, v$ confined to the habitat $\Omega$.
- What if the strategies of $u$ and $v$ are very similar? i.e. $\eta \sim \xi$.

# Conditional Dispersal

**Theorem (Hambrock-Lou(09'))**

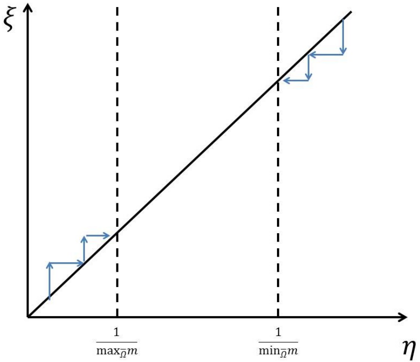
*Let* $\Omega = (0,1)$ *and* $m, m_x > 0$ *in* $[0,1]$.

(i) *If* $0 \leq \eta \leq \frac{1}{\max_{\bar{\Omega}} m}$, *the for* $\xi \searrow \eta$, $(0, \tilde{v})$ *is globally asymptotically stable.*

(ii) *If* $\eta \geq \frac{1}{\min_{\bar{\Omega}} m}$, *then for* $\xi \nearrow \eta$, $(0, \tilde{v})$ *is globally asymptotically stable.*

- $(0, \tilde{v})$ is the equilibrium state when $u$ is extinct.

# Conditional Dispersal




- "Selection Gradient" reverses.
- Intermediate advection rate is favored.
- No ESS outside of $[\frac{1}{\max_{\bar{\Omega}} m}, \frac{1}{\min_{\bar{\Omega}} m}]$.

# The Invasion Exponent $\lambda = \lambda(\eta, \xi)$

Let $(\tilde{u}, 0)$ be a semi-trivial steady state, where $\tilde{u} = \tilde{u}(\eta)$ is the unique positive solution of

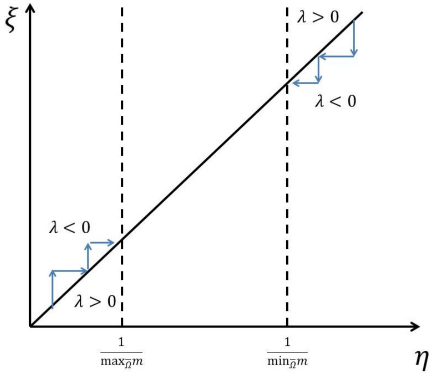
$$\mu \nabla \cdot (\nabla \tilde{u} - \eta \tilde{u} \nabla m) + \tilde{u}(m - \tilde{u}) = 0 \quad \text{and no-flux b.c.}$$

Let $\lambda = \lambda(\eta, \xi)$ be the principal eigenvalue that determines the local stability of $(\tilde{u}, 0)$, which satisfies

$$\mu \nabla \cdot (\nabla \varphi - \xi \varphi \nabla m) + (m - \tilde{u})\varphi + \lambda \varphi = 0 \quad \text{and no-flux b.c.}$$

- i.e. $\lambda$ is the Invasion Exponent: $\lambda < 0 \Rightarrow v$ can invade while $\lambda > 0 \Rightarrow v$ fails to invade and goes extinct.
- Note: $\xi = \eta \quad \Rightarrow \quad \lambda = 0 \quad$ with $\quad \varphi = \tilde{u}$.
- $\frac{\partial}{\partial \xi}\lambda = \lambda_\xi$ is the Selection Gradient.

# Conditional Dispersal

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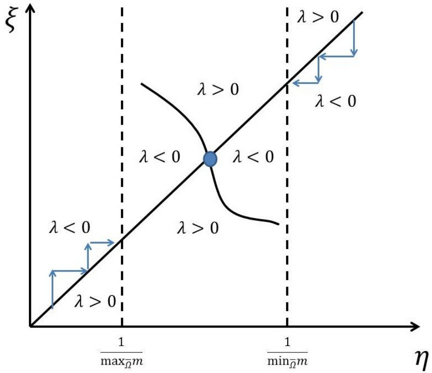


- "Selection Gradient" reverses.
- Intermediate advection rate is favored.
- Is there an ESS strategy in the interval $[\frac{1}{\max_{\bar{\Omega}} m}, \frac{1}{\min_{\bar{\Omega}} m}]$?

# Evolutionarily Stable (Unbeatable) Strategies

**Definition**

We call $\hat{\eta}$ an Evolutionarily Singular Strategy if $\frac{\partial}{\partial \xi}\lambda(\hat{\eta},\hat{\eta}) = 0$.

**Definition**

$\hat{\eta}$ is a *local ESS* if there exists $\delta > 0$ such that $\lambda(\hat{\eta},\xi) > 0$ for all $\xi \in (\hat{\eta}-\delta, \hat{\eta}+\delta) \setminus \{\hat{\eta}\}$.

- Since $\lambda(\eta,\eta) = 0$, $\lambda(\hat{\eta},\cdot)$ attains a <u>local minimum</u> at $\xi = \hat{\eta}$.

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(i) *$\hat{\eta}$ is an Evolutionarily Singular Strategy if it is an ESS.*

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**Corollary**

(i) *$\hat{\eta}$ is an Evolutionarily Singular Strategy if it is an ESS.*

(ii) *If $\frac{\partial}{\partial \xi}\lambda(\hat{\eta},\hat{\eta}) = 0$ and $\frac{\partial^2}{\partial \xi^2}\lambda(\hat{\eta},\hat{\eta}) > 0$, then $\hat{\eta}$ is a local ESS.*

# Main Results

Recall: Evolutionarily Singular Strategies are candidates for ESS.

**Theorem (Lam-Lou)**

*Suppose* $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq 3 + 2\sqrt{2}$. *Given any* $\Lambda > 0$, $\mu$ *small, there is exactly one evolutionarily singular strategy, denoted as* $\hat{\eta}$, *in* $[0, \Lambda]$. *Moreover,* $\hat{\eta} \to \eta_0$ *as* $\mu \to 0$, *where* $\eta_0$ *is the unique positive root of*

$$g_0(\eta) = \int_\Omega m \nabla m \cdot \nabla(e^{-\eta m} m) = \int_\Omega e^{-\eta m} m(1 - \eta m)|\nabla m|^2.$$

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**Corollary**

*Let* $\Omega = (0, 1)$ *and* $m_x > 0$ *in* $[0, 1]$*. Then for* $\mu$ *small, there exists a unique evolutionarily singular strategy in* $[0, \infty)$*.*

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- Is $\hat{\eta}$ an ESS?

# Main Results

**Theorem (Lam-Lou)**

*Supppose that $\Omega$ is convex with diameter $d$, and*

$$d\|\nabla \ln m\|_\infty \leq \alpha_0 \approx 0.814.$$

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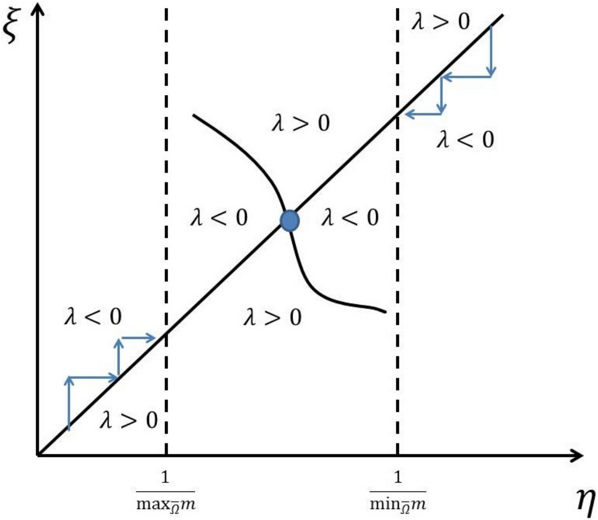
*Then for $\mu > 0$ sufficiently small, $\hat{\eta}$ is a local ESS.*

- $\alpha_0$ is the unique root of $t \mapsto 4t + e^{-t} + 2\ln t - 2 - 2\ln \pi$.
- $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq \exp d\|\nabla \ln m\|_\infty \leq e^{\alpha_0} \approx 2.257 < 3 + 2\sqrt{2}$.

# Conditional Dispersal



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- Hunch: the other two are local ESS.

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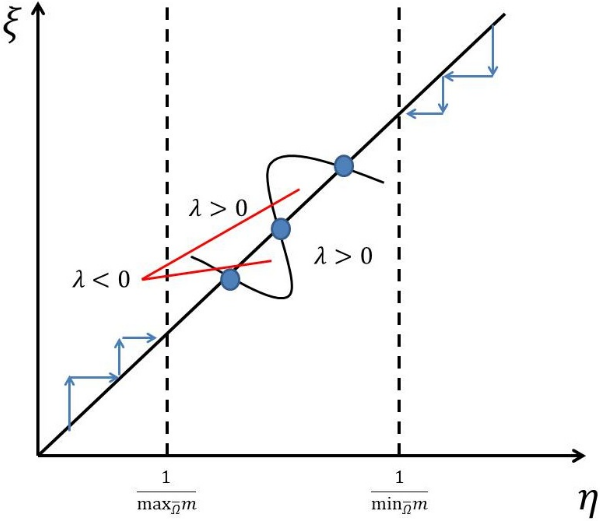

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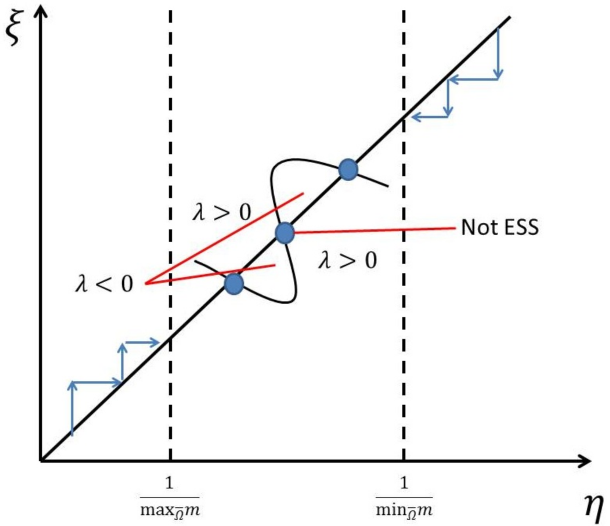

# Plan

We shall sketch the proof of Theorems 1 and 2, and comment on the proof of Theorem 3.

# Formula for $\lambda_\xi = \frac{\partial \lambda}{\partial \xi}$

By arguments involving integration by parts, one can derive the following formula for the selection gradient.

$$\frac{\lambda_\xi}{\mu}(\eta, \eta) \int_\Omega e^{-\eta m} \tilde{u}^2 = -\int_\Omega \tilde{u} \nabla m \cdot \nabla (e^{-\eta m} \tilde{u}).$$

It remains to study its roots as $\mu \to 0$.

# Convergence of $\tilde{u} \to m$ as $\mu \to 0$

$$\begin{cases} \mu\nabla\cdot(\nabla\tilde{u} - \eta\tilde{u}\nabla m) + \tilde{u}(m - \tilde{u}) = 0 & \text{in } \Omega, \\ \frac{\partial\tilde{u}}{\partial n} - \eta\tilde{u}\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

**Theorem**

*$\tilde{u} \to m$ in $L^\infty(\Omega)$ as $\mu \to 0$.*

- Proof: e.g. Method of upper/lower solution.

## Convergence of $\tilde{u} \to m$ as $\mu \to 0$

In addition to the fact that $\tilde{u} \to m$ uniformly in $\bar{\Omega}$, we have

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$$\mu \int_\Omega |\nabla(m - \tilde{u})|^2 + \int_\Omega \tilde{u}(m - \tilde{u})^2$$
$$= \mu \int_{\partial\Omega} \frac{\partial m}{\partial n}(m - \tilde{u}) - \mu \int_\Omega \Delta m(m - \tilde{u})$$

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$$\begin{aligned} &\mu \int_\Omega |\nabla(m - \tilde{u})|^2 + \int_\Omega \tilde{u}(m - \tilde{u})^2 \\ &= \mu \int_{\partial\Omega} \frac{\partial m}{\partial n}(m - \tilde{u}) - \mu \int_\Omega \Delta m(m - \tilde{u}) \\ &= C\mu\|\tilde{u} - m\|_\infty = o(\mu) \end{aligned}$$

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\end{aligned}$$

Actually one can prove, locally uniformly in $\eta$, that

$$\int_\Omega |\nabla\tilde{u} - \nabla m|\phi^2 \le C\|\tilde{u} - m\|_\infty \|\phi\|^2_{H^1}.$$

# Proof of Theorem 1

Hence

$$\frac{\lambda_\xi}{\mu} = -\frac{\int_\Omega \tilde{u}\nabla m \cdot \nabla(e^{-\eta m}\tilde{u})}{\int_\Omega e^{-\eta m}\tilde{u}^2}$$

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Hence it remains to study the **roots** of limiting function

$$g_0(\eta) = \int_\Omega m\nabla m \cdot \nabla(e^{-\eta m}m).$$

# Proof of Theorem 1: Limiting Problem

**Theorem**

*If* $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq 3 + 2\sqrt{2}$, *then*

$$g_0(\eta) = \int_\Omega m \nabla m \cdot \nabla(e^{-\eta m} m) = \int_\Omega e^{-\eta m} m(1 - \eta m)|\nabla m|^2$$

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- $g_0'(\eta) = \int_\Omega e^{-\eta m} m^2(\eta m - 2)|\nabla m|^2$
- $g_0'(\eta) < 0$ in $\eta \leq \frac{2}{\max_{\bar\Omega} m}$ (Done if $L := \frac{\max m}{\min m} \leq 2$).

# Proof of Theorem 1: Limiting Problem

More generally, $\eta^p g_0(\eta)$ is strictly decreasing if

$$\eta \in \left[ \frac{p+2-\sqrt{p^2+4}}{2\min_{\bar{\Omega}} m}, \frac{p+2+\sqrt{p^2+4}}{2\max_{\bar{\Omega}} m} \right].$$

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Let $x_0 = 2$, $x_i = 1 + (1 - \frac{x_{i-1}}{L})^{-1}$ and $p_i = \frac{x_{i-1}(2L - x_{i-1})}{L(L - x_{i-1})}$, then $x_{i-1} < x_i$ and $\eta^p g_0(\eta)$ is strictly decreasing in $\left[ \frac{x_{i-1}}{\max_{\bar{\Omega}} m}, \frac{x_i}{\max_{\bar{\Omega}} m} \right]$.

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- If $L < 3 + 2\sqrt{2}$, then $x_{i_0} \geq L$ for some $i_0$.
- If $L = 3 + 2\sqrt{2}$, then use infinitely many $i$'s.

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$$m'(x) = \begin{cases} L_1 & x \in [0, \epsilon/L_1], \\ L_2 & x \in [1 - \epsilon/L_2, 1], \\ L_3 := \frac{(b-\epsilon)-(a+\epsilon)}{1 - \frac{\epsilon}{L_1} - \frac{\epsilon}{L_2}} & \text{otherwise.} \end{cases}$$

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**Corollary**

*If* $\lambda_\xi(\hat{\eta}) = 0$ *and* $\lambda_{\xi\xi}(\hat{\eta}) > 0$*, then* $\hat{\eta}$ *is a local ESS.*

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- Step 4: Optimal Estimate by Payne and Weinberger for convex domains

**Theorem (Payne-Weinberger(60'))**

*Suppose $\Omega$ is convex with diameter $d$, then*

$$\mu_2^N \geq \frac{\pi^2}{d^2}.$$

# Summary and Future Work

Related Work:

"Ideal Free Distribution" implies ESS. [Cantrell, Cosner, Lou (2010)][Averill et. al.(2012)]

Summary:

For the first time, existence and uniqueness/multiplicity result for ESS which is not ideal free is obtained in the context of spatial models, which is the natural setting for the discussion of evolution of dispersal.

Future Work:

Can one derive a model for the polymorphic situation?
$u = u(x, t; \eta)$ and under some scaling,

$$u \to \sum \rho_i(t)\delta_i(x - \bar{x}(t)).$$

Thank you!