# What is the functional form of ideal free movement, and why does it matter?

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- Translation: How do emigration from a patch and immigration into another patch depend on biotic and abiotic conditions?
- Question: why not assume infinitely fast movement to the currently best patch?

# This talk will:

1. Review published work that shows why functional form matters
2. Present some **unfinished** results on evolution of the functional form

# Framework of models

Two patches (sometimes 3)

Perfect information about present conditions in both patches

Assessing information and/or preparing to move takes time

Actual move is instantaneous

Physiological condition of individual equilibrates to new patch instantaneously

Simple Food web = 2-3 species food chain

# Basic Questions

1. Will adaptive movement permit a closer approach to an IFD for consumer species in food chains distributed across a small number of patches (than will random movement)?
2. Will adaptive movement produce greater stability of food chains distributed across a small number of patches (than will random movement)?
3. Will evolution lead to movement rules that influence the answers to questions 1 and 2?

Answers to 1 & 2 are usually assumed to be ‘yes’

More important questions: how does this affect scale transition for various community processes?

# Q1: Does adaptive movement equalize fitness?

What do we know about this question in 2-patch context with nonequivalent patches?

1. Perfectly adaptive movement (never move to worse patch; at least sometimes move to better patch) assures equal fitness across patches in a temporally stable system with one species and normal density dependence (Cressman and Krivan)
2. Random movement with such a species assures sources and (pseudo)sinks (NOT IFD) given heterogeneous patches

Cressman et al. (2004, 2006), Abrams (2007) suggest this simple picture is not so clear in 2+species systems

# Q2: Does adaptive movement produce more stable dynamics?

- Large body of work argues that this is true for adaptive movement by top predator
  - Krivan (1997), Post et al. (2000), McCann et al. (2005), McCann and Rooney (2009)
  - Predators go where there is more abundant prey, reducing areas of high prey density
- BUT, other models have argued that adaptive top predator movement can amplify cycles (various Abrams papers...)

# Abrams 2007 AmNat: Local Allee Effects often preclude IFDs and generate asynchronous fluctuations

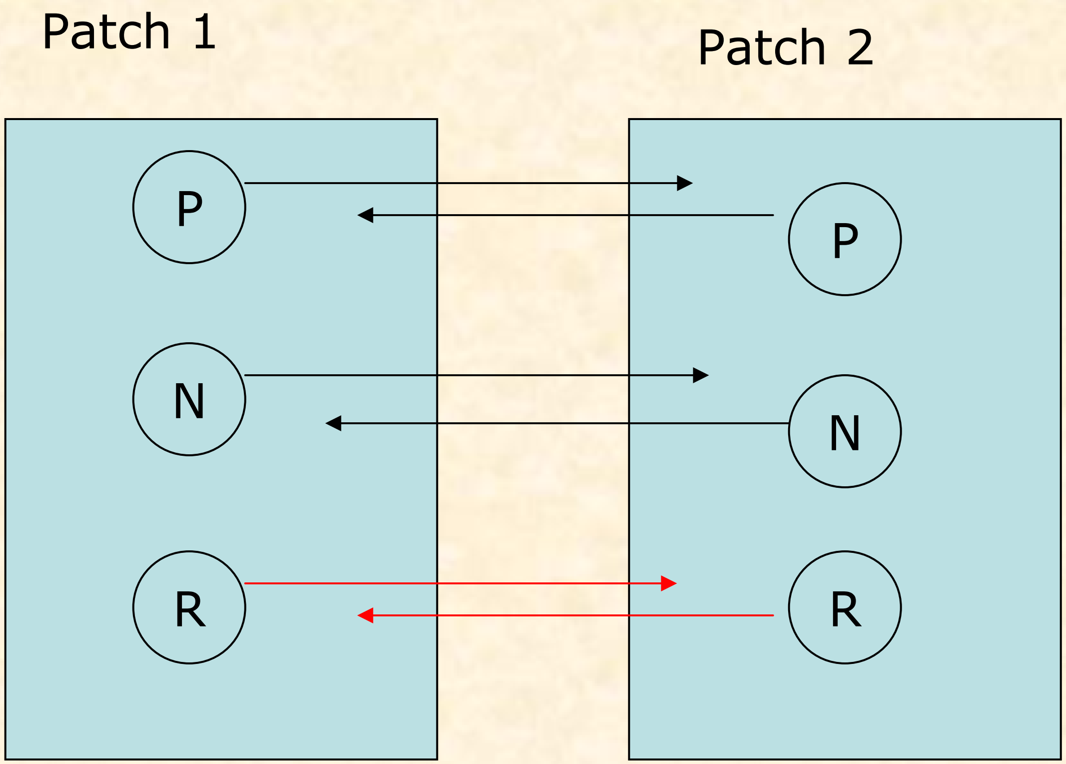
- Local Allee Effects implied by any advantages to aggregation
  - mate choice
  - social information
  - collective 'ecosystem engineering'
  - collective defense
- Local Allee Effects for prey implied by ‘type-2’ predator responses
  - satiation implies that risk from a given predator individual decreases when it has had more to eat

# A caveat

"Thus, although we find conclusive evidence for Allee effects due to a variety of mechanisms in natural populations of 59 animal species, we also find that existing data addressing the strength and commonness of Allee effects across species and populations is limited..."

-Kramer, Dennis, Liebhold,
Drake, 2009

# Predator-prey-resource model with two habitats and adaptive movement between habitats by one or both consumers



Metacommunity:
3 sp food chain;
2 patches

- Black arrows: fitness-related movements
- Red arrows: random movement

# Dynamics of prey species in patch 1 of a 2-patch system (Abrams 2007)

$$\frac{dN_1}{dt} = N_1\left(\frac{BC_1R_1}{1+C_1HR_1} - D_1 - \frac{S_1P_1}{1+S_1TN_1}\right) \pm movement$$

Consumption of resource: CR/(1 + CHR); converted to
new prey with efficiency B
'Handling time' - H for prey and T for predator
Per individual death rate within patch i is $D_i$;
Consumption by predators at total rate SPN/(1 + STN)

Per capita emigration from patch 1 for predator and prey have form: $C_1 \mathrm{Exp}[C_2(w_2 - w_1)]$, where $C_1$ is baseline movement; $C_2$ is sensitivity of movement to fitness

Prey parameters are $C_1 = m$; $C_2 = \lambda$; predator parameters are $m_2$ and $\gamma$

$$\frac{dR_1}{dt} = g_1(R_1) - N_1\frac{C_1R_1}{1 + C_1HR_1} - m_RR_1 + m_RR_2,$$

$$\frac{dR_2}{dt} = g_2(R_2) - N_2\frac{C_2R_2}{1 + C_2HR_2} + m_RR_1 - m_RR_2.$$

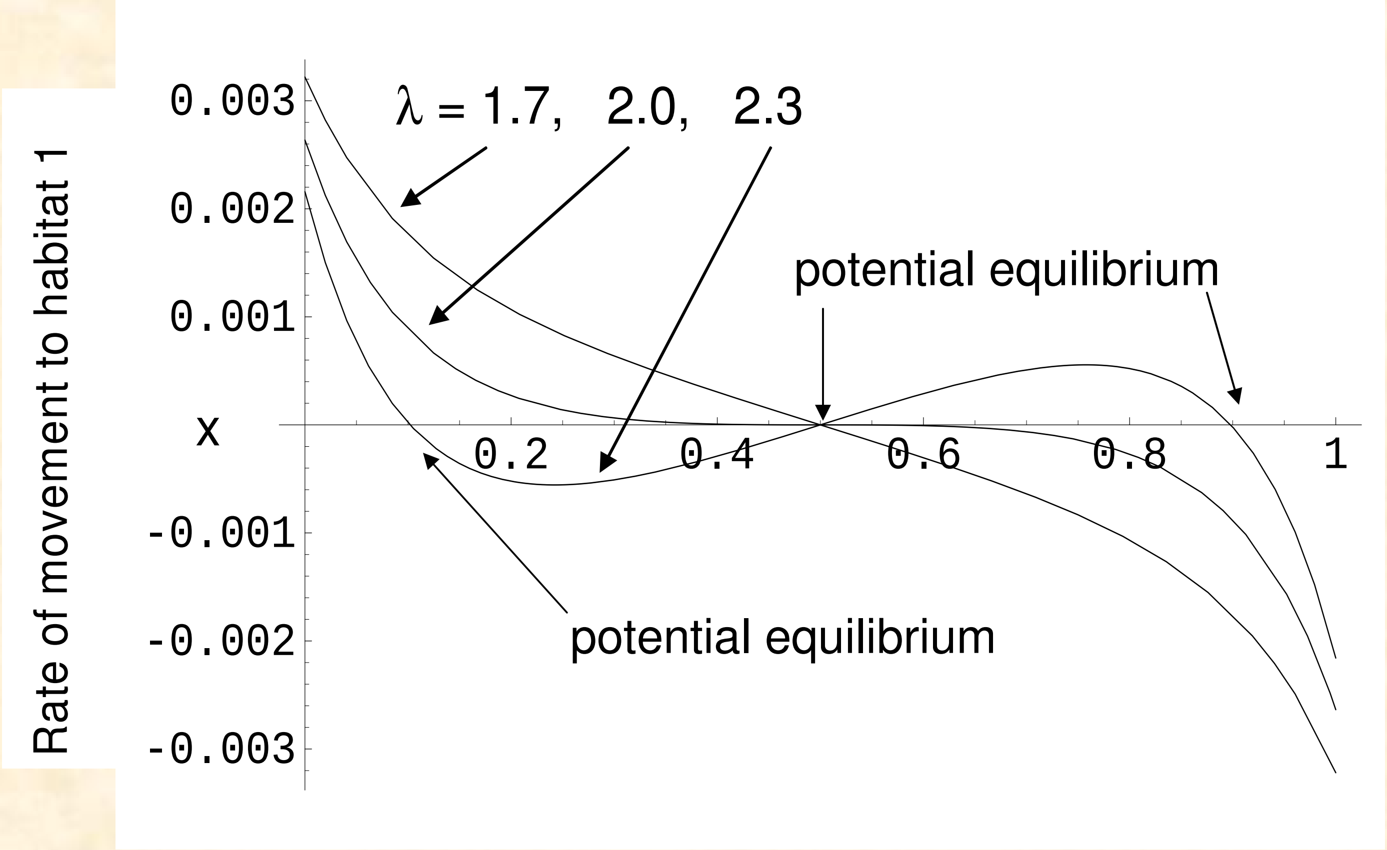
$$\begin{aligned}\frac{dN_1}{dt} = {} & N_1\left(\frac{BC_1R_1}{1 + C_1HR_1} - D_1 - \frac{S_1P_1}{1 + S_1TN_1}\right) \\ & - m_NN_1\exp\left[\lambda(W_2 - W_1)\right] + m_NN_2\exp\left[\lambda(W_1 - W_2)\right],\end{aligned}$$

$$\begin{aligned}\frac{dN_2}{dt} = {} & N_2\left(\frac{BC_2R_2}{1 + C_2HR_2} - D_2 - \frac{S_2P_2}{1 + S_2TN_2}\right) \\ & + m_NN_1\exp\left[\lambda(W_2 - W_1)\right] - m_NN_2\exp\left[\lambda(W_1 - W_2)\right].\end{aligned}$$

$$\begin{aligned}\frac{dP_1}{dt} = {} & P_1\left(\frac{ES_1N_1}{1 + S_1TN_1} - d_1\right) - m_PP_1\exp\left[\gamma(W_2 - W_1)\right] \\ & + m_PP_2\exp\left[\gamma(W_1 - W_2)\right],\end{aligned}$$

$$\begin{aligned}\frac{dP_2}{dt} = {} & P_2\left(\frac{ES_2N_2}{1 + S_2TN_2} - d_2\right) + m_PP_1\exp\left[\gamma(W_2 - W_1)\right] \\ & - m_PP_2\exp\left[\gamma(W_1 - W_2)\right].\end{aligned}$$

SYSTEM WITH 2 EQUIVALENT PATCHES & COMPLETE KNOWLEDGE OF OTHER PATCH; CONSTANT R, N, P: Movement only by prey. When fitness sensitivity, λ, becomes large enough for some aggregation, degree of aggregation increases rapidly with further increases in λ



x = fraction in patch 1

1. x = 1/2 means that within-patch fitnesses are equal

2. x ≅ 1 or x ≅ 0 fitnesses unequal

# Dynamics of full system: See Abrams 2007 AmNat for more

- High enough sensitivity of prey movement to fitness produces cycles by two mechanisms:
  1. Prey aggregate in one patch – predators move in – prey aggregate in the other patch – predators move there, etc.  ("predator chase" cycles)
  2. Prey aggregate in one patch- predators don’t move (much), BUT either resources get depleted or the local predator population grows – prey eventually move – resource recovers in original patch – prey move back, etc. ("resource depletion" cycles)

# I. Cycles are likely when:

(1) total predator density is large enough

(2) predator handling time and prey population density are intermediate

(3) the prey's movement is sufficiently sensitive to fitness differences; ('no errors' model almost guarantees cycles)

(4) the parameters of the system do not make one habitat much more favorable than the second for either predator or prey

(5) the predator isn't too much better/faster at habitat selection than is the prey

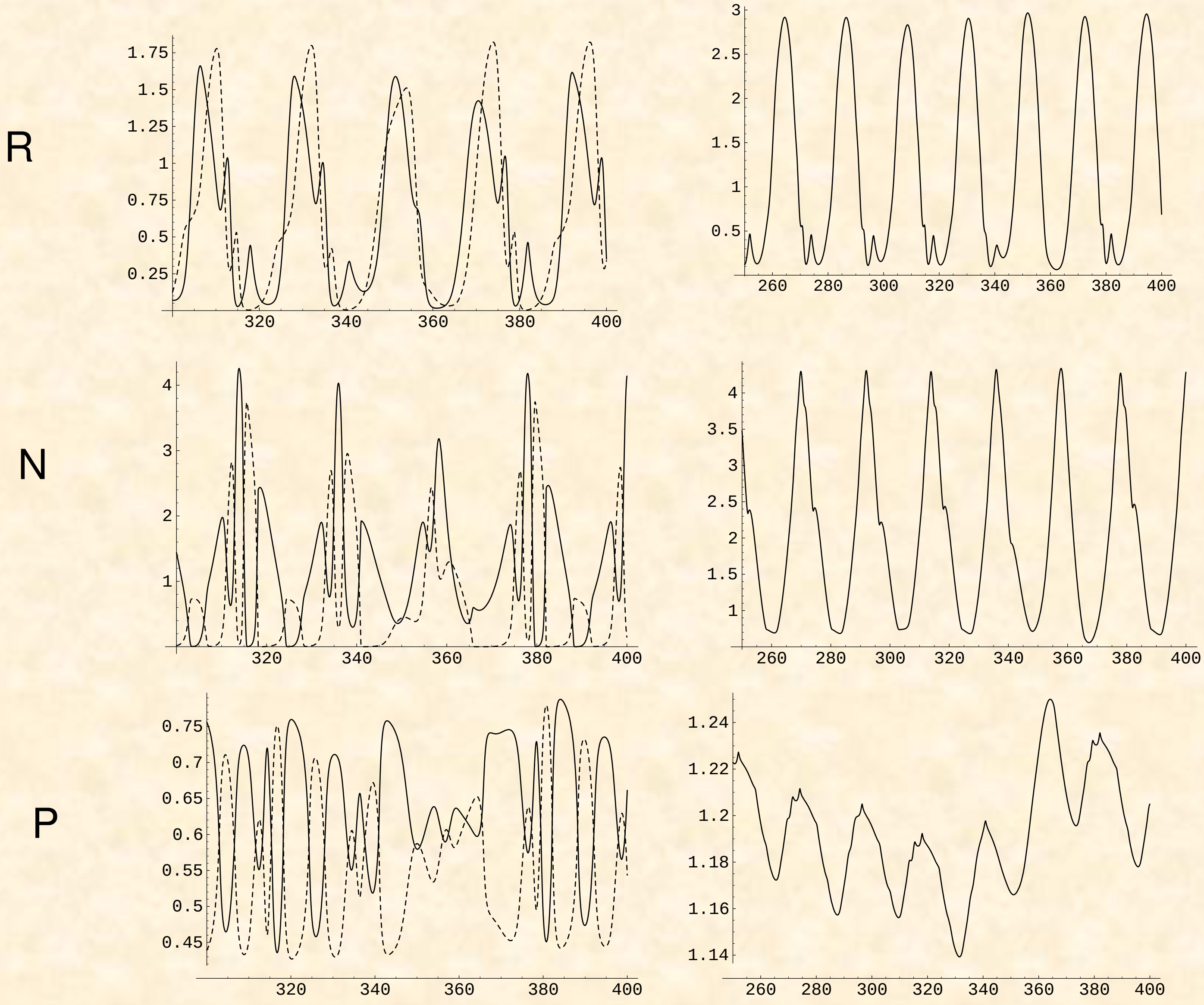
(6) prey do not make 'group decisions'

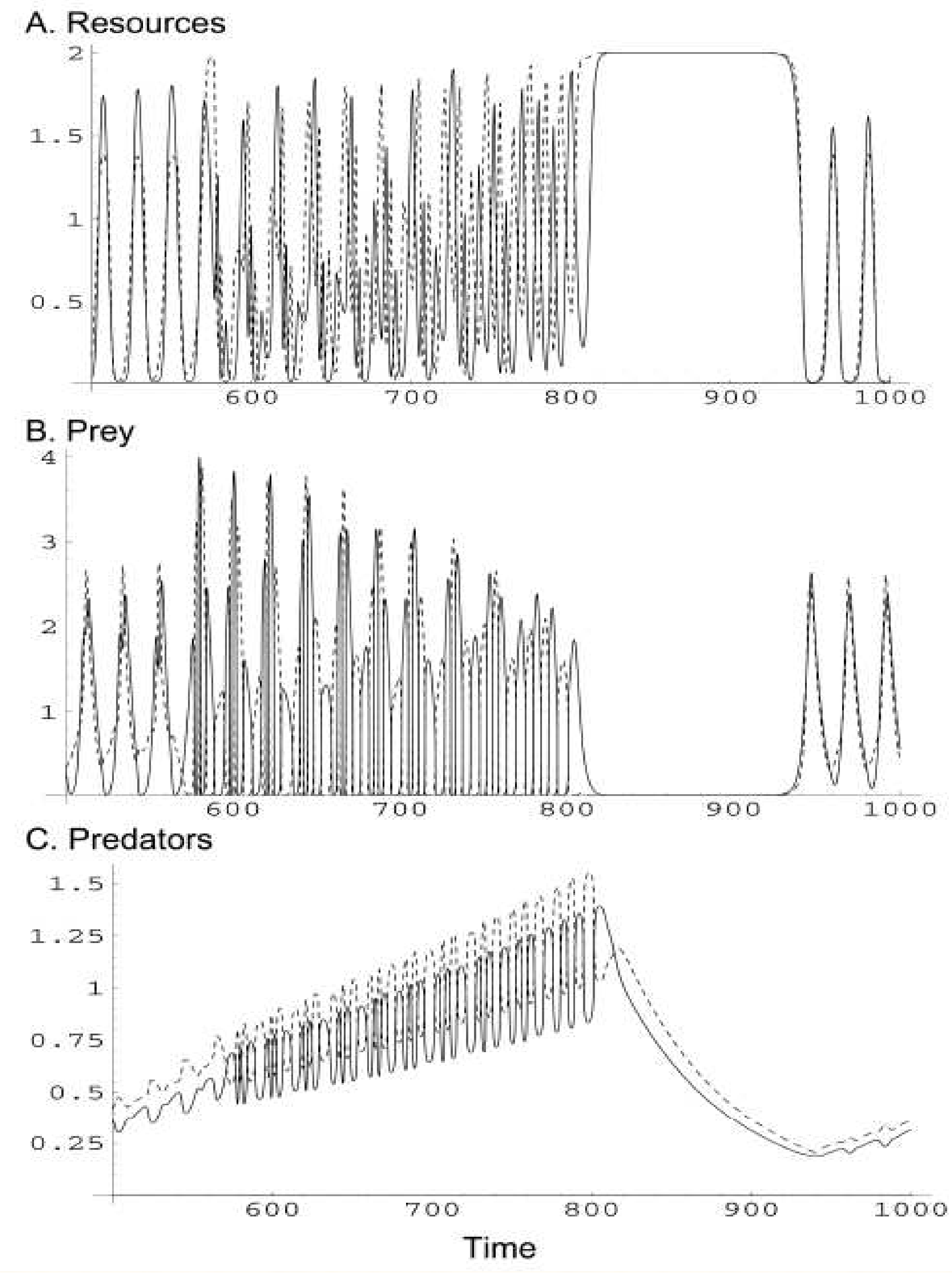
# Example of full 3-level, 2 patch system with prey and predator moving: unstable R-N subsystem: $r_1 = 1.25$; $r_2 = 0.75$

Patch dynamics-left

Total densities over longer time - right

Lower variance in densities than for non-adaptive model



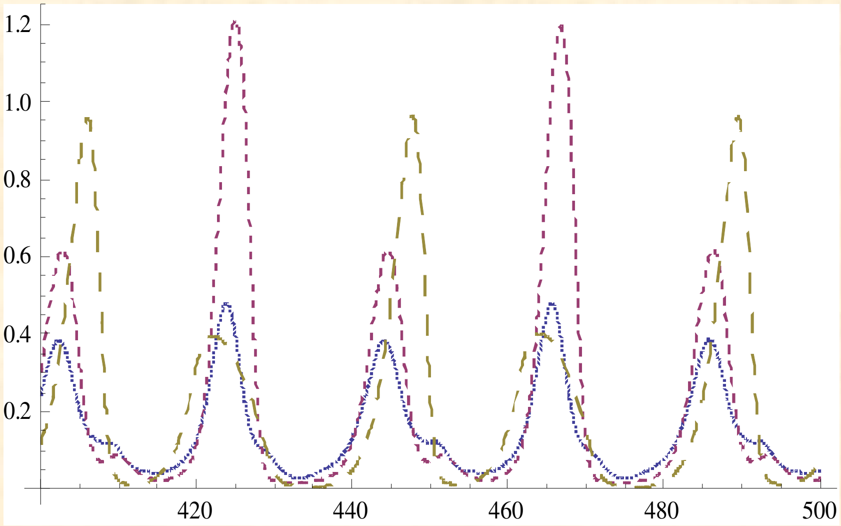


An example of very complex dynamics that occur with adaptive movement of predator and prey

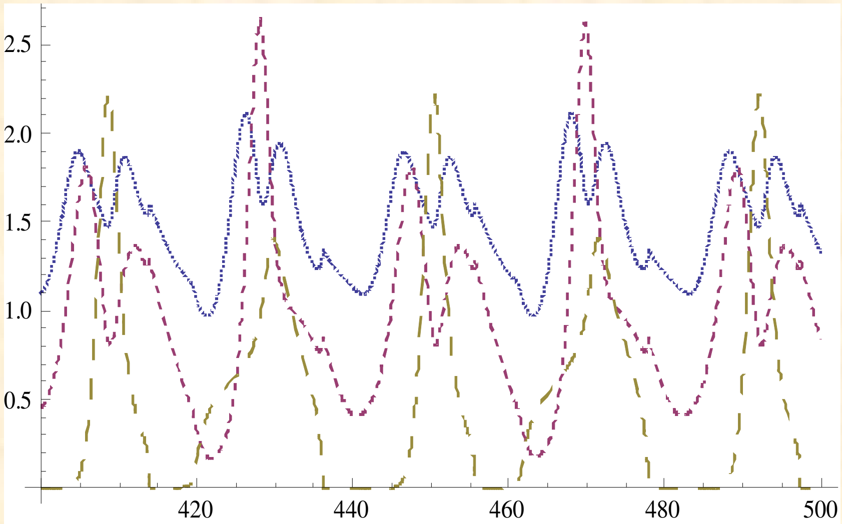
(appendix: Abrams 2007 AmNat)

# Is this an artifact of 2-patches? 3-patch system; emigration based only on current patch quality; $r_1 = 1.5$; $r_2 = 1$; $r_3 = 0.5$

Resources



Consumers



Patch 1 solid line; Patch 2 short dashed line; Patch 3 long dashed line.

System has fixed predator densities; Immigration is random

Is stable with random emigration at rate $m = 0.2$; $N_1 = 1.47$, $N_2 = 0.99$, $N_3 = 0.67$

# Eco-evo consequences of cycles driven by patch choice with conspecific attraction

1. (Often) stabilization of system-wide dynamics in spite of local instability; (Sometimes) destabilization or increased amplitude of cycles
2. System does not approach IFD
3. Effects of system-wide fertilization are very different with adaptive habitat choice by prey
    1. Can reduce predator abundance
    2. Can stabilize food chain
4. Response of predator to system-wide harvesting is very different with adaptive habitat choice by prey (some results later in this talk)
5. Exploitation of resources by consumer varies in time, changing selection on exploitation and life history characters at all levels (plausible speculation)

i.e., nonspatial theory is often not good enough

# BUT, is the movement function actually adaptive (or as adaptive as it could be)?

- "Smarter" strategies seem more reasonable
  - Move more readily if local fitness is declining and less readily if local fitness is increasing--But, these are only beneficial when $w_1 \approx w_2$, and the resulting advantage is small in these cases
  - Never move to a poorer patch—this is considered in later slides
- Strategies based on species other than predator or prey perform poorly (resource tracking always loses in competition to fitness tracking)
- Costly movement is the norm – would this change the results?

# Preliminary (undigested) results on three related issues

What sort of movement rule is favored by evolution?

How do the movement parameters of one movement rule evolve, and how is this altered by a survival cost to movement?

How does adaptive habitat choice change the response to harvesting of the top predator in a food chain? (two particular scaling up questions)

# Two movement functions

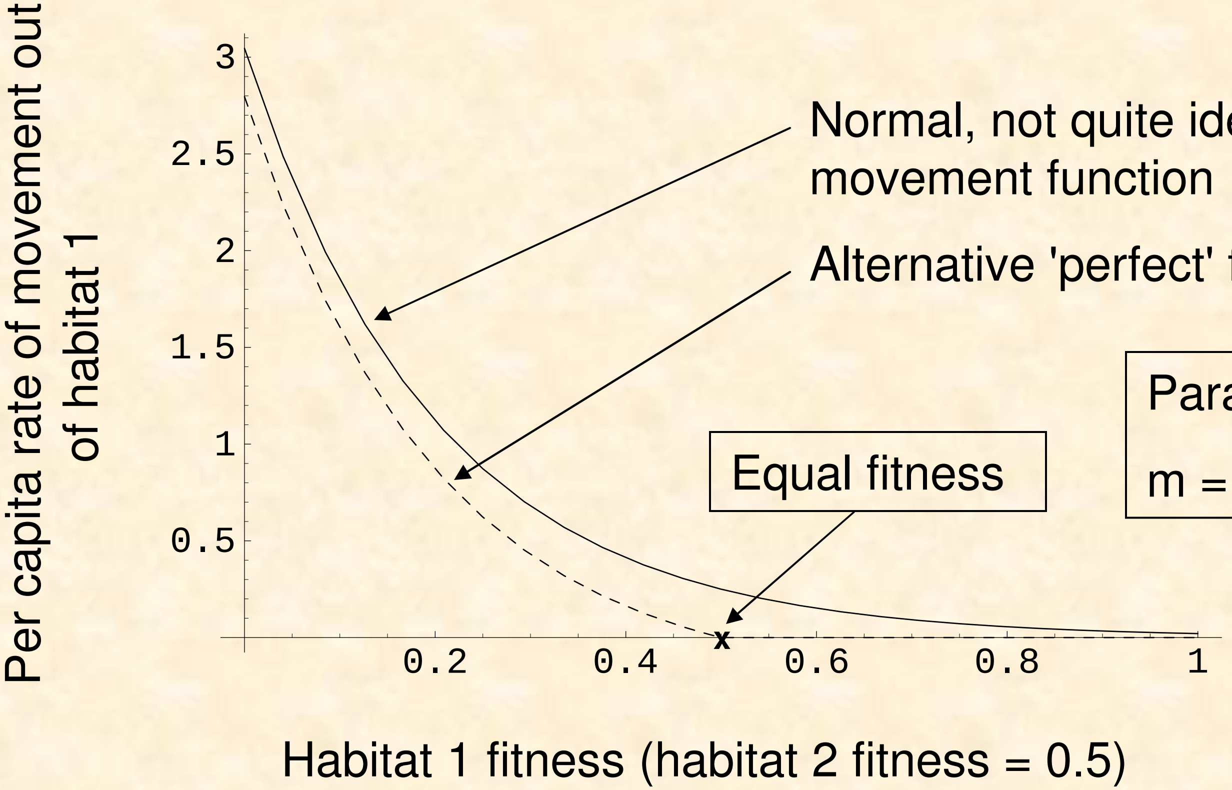
Number of species i leaving habitat 1 per unit time is:

1. $m_i N_{i1} \mathrm{Exp}[\lambda(w_{i2} - w_{i1})]$, or
2. $m_i N_{i1} H(w_{i2} - w_{i1})\{\mathrm{Exp}[\lambda(w_{i2} - w_{i1})] - 1\}$, where H is the Heaviside theta function (unit step function)

In first case, $\lambda = 0$ implies movement is insensitive to fitness; m is rate of movement with no fitness difference and also scales how movement rate increases with prospective fitness gain

In the second case $\lambda = 0$ implies no movement; m scales the movement rate to prospective fitness gain; movement approaches zero as $w_1$ approaches $w_2$

# Comparison of perfect and imperfect



Normal, not quite ideal, exponential movement function

Alternative 'perfect' function

Equal fitness

Parameters:

$m = 0.25$; $\lambda = 5$

# What happens when these compete?: numerical results for a few C-R systems from dual invasion analysis & simulations

Results when asynchrony is due to consumer-resource cycles with between-patch differences in resource growth (r and k)

1. With equal m and equal $\lambda$, the two strategies coexist; imperfect mover is more abundant.
2. Higher $\lambda$ is favored in the imperfect lineage; causes relative abundance of the lineage to increase
3. Lower $\lambda$ favored in the perfect lineage: Relative abundance of perfect mover INCREASES (!) as its $\lambda$ (or m or both) decrease—it dominates the more productive patch but is almost absent from the second patch

# Results when asynchrony is due to anti-phase environmental forcing in two otherwise equivalent patches

1. Perfect lineage is excluded with equivalent parameters that include a moderate or large $\lambda$
2. Many-fold advantage in $\lambda$ or m for the perfect lineage required to get coexistence; large enough advantage will produce exclusion of the imperfect type
3. Coexistence of non-mover and mover appears to be very difficult or impossible
4. Coexistence of types with similar parameters is easier when environmental phase difference is relatively small

# Same type of analysis for competition between two (or 3) ‘perfect’ lineages

- larger λ and larger m are favored over slightly smaller values
- If a type with a larger λ has a smaller m, coexistence usually does not occur, and fitness is more sensitive to λ than to m
- A type with m or λ very close to zero can coexist stably with a high m-, λ-type by persisting in the high r/K patch (often at similar densities to the mover). In such a dimorphic state
  - the density of nonmover declines very rapidly as m or λ increases above 0
  - Relative density of fast mover declines (!) as its λ increases, even though larger λ is favored (replaces smaller λ)

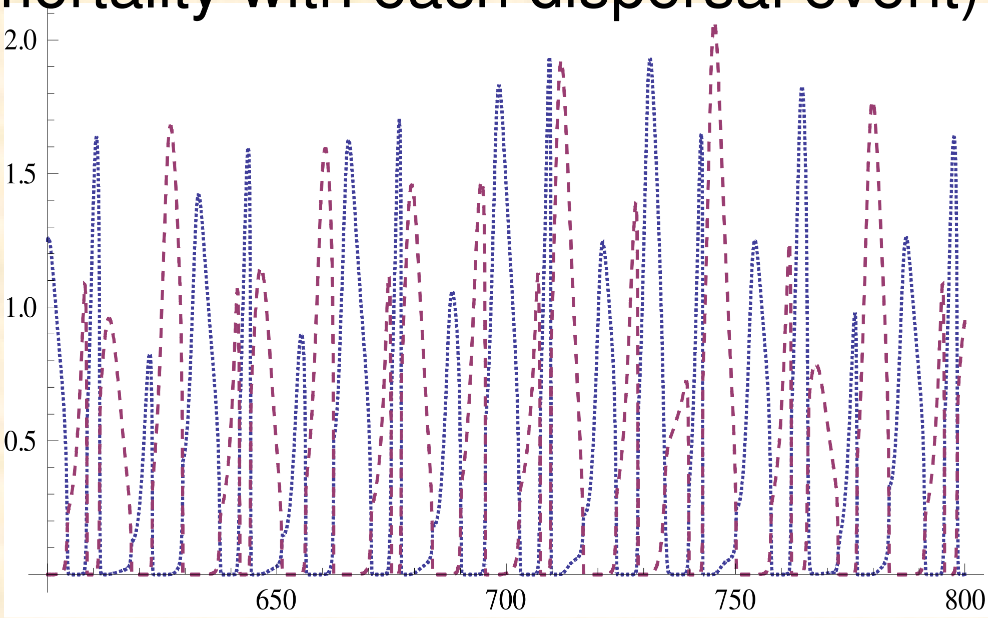
# Results of simulations with imperfect (exponential) function: competition between movement strategies, no cost of movement

- Case 1: types differ in baseline movement, m or sensitivity, λ → Higher fitness sensitivity λ always favoured
  - Several outcomes of selection on m:
  1. low λ, each patch stable in isolation: m = 0 favoured
  2. low λ, more productive patch unstable in isolation:
     - Low movement produces instability; this selects for larger m
     - BUT, large enough m stabilizes system, leading to selection for smaller m; usually get a polymorphism with some m above and some below stability threshold
  3. large λ; resource depletion cycles in each patch when isolated
     - Selection for ever larger m (becomes weaker as m grows)
  4. Other outcomes probably occur

# Case 2: Same as case 1, but with survival cost of movement

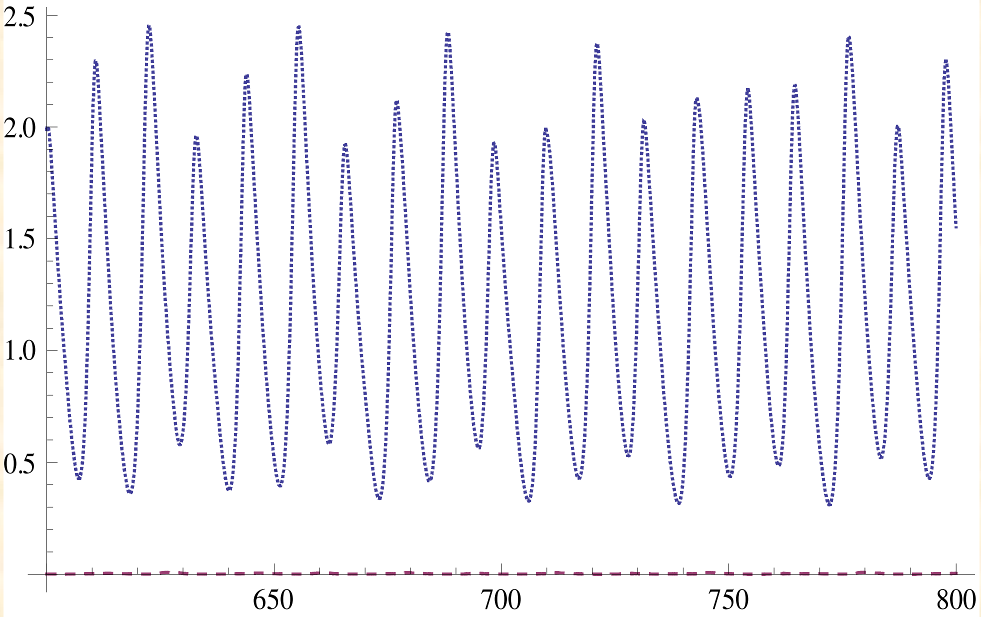
- Selection still favours largest possible $\lambda$;
- Selection usually favours intermediate m when movement costs are moderate
- Selection can produce many possible outcomes when costs are high
  1. Dimorphism of m = 0 and a positive m, when within-patch dynamics are cyclic
  2. Dimorphism as in #1 or zero movement, depending on initial conditions.
     - Movers can be excluded if non-movers are initially abundant, because there are no cycles and equal fitnesses in both patches; movers pay cost with no benefit
     - Nonmovers excluded if movers generate large local cycles
     - Non-mover often restricted to better patch {one-way priority effect can occur where abundant non-mover can exclude mover, but not vice versa}

# Example of mover – nonmover polymorphism (60% mortality with each dispersal event); 'imperfect' movers



'Movers' in patch 1 (blue-dotted line; high r patch) and 2 (red dashed line; low r patch)

λ = 10; m =0.175



'Nonmovers'; almost all in patch 1

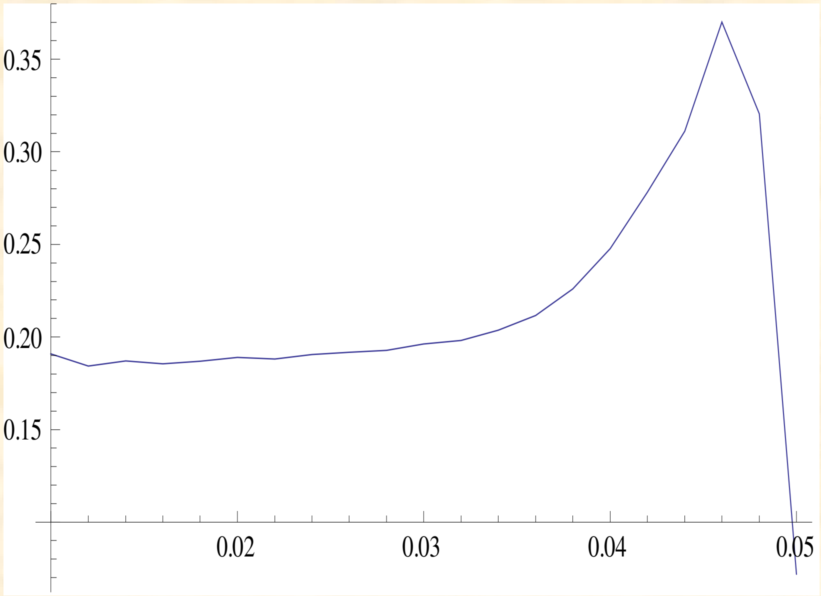
λ = 10; m =0.000001

More analysis needed!

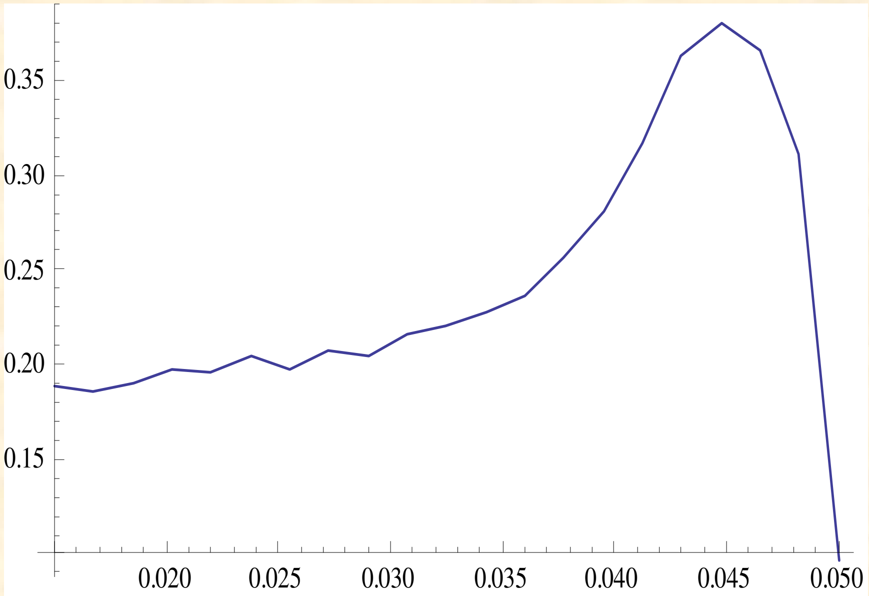
# Response of mean total predator density to increased per capita mortality in various 3-level systems with adaptive movement

System has identical patches; 'perfect' movement function

Case 1: No movement of higher trophic levels; low random movement of resource



Case 2: Adaptive predator movement; no prey movement; low random resource movement

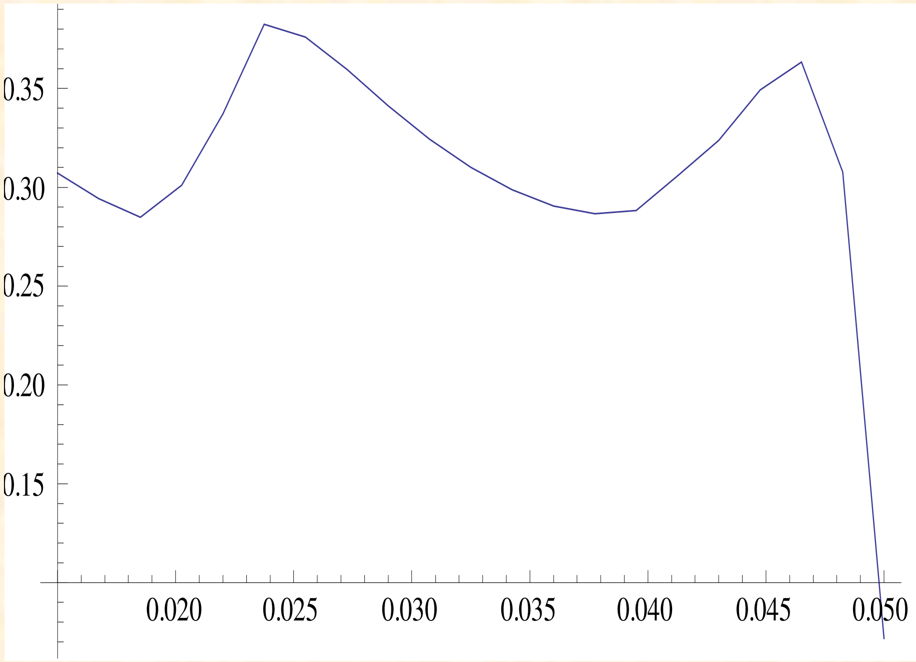


P

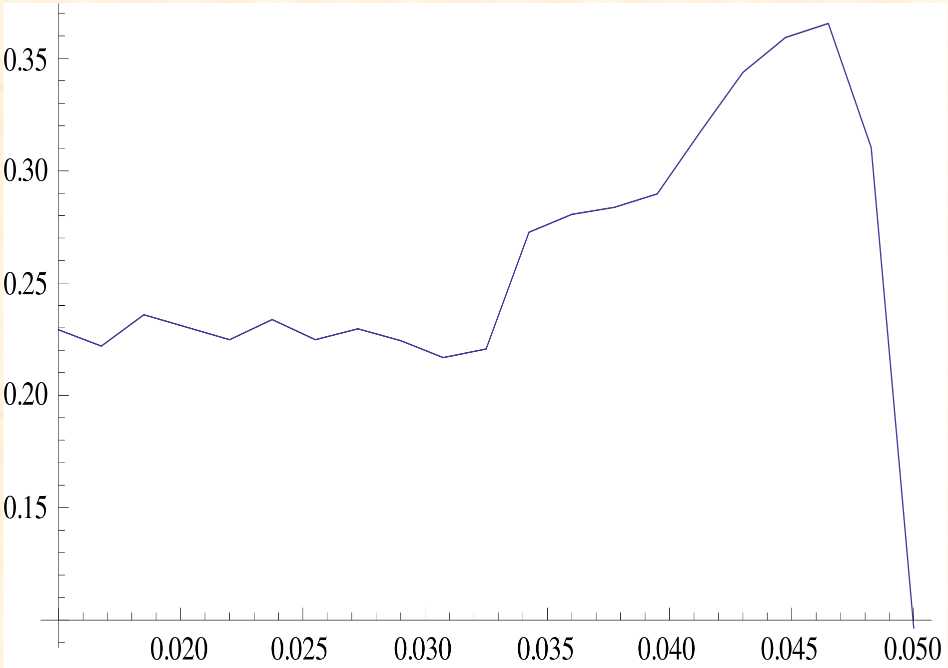
Per Capita Mortality, d

# More graphs of predator population vs. per capita mortality in the 2-patch system

Case 3: Adaptive prey movement; no predator movement; low random resource movement



Case 4: Adaptive movement of predator and prey; low random resource movement

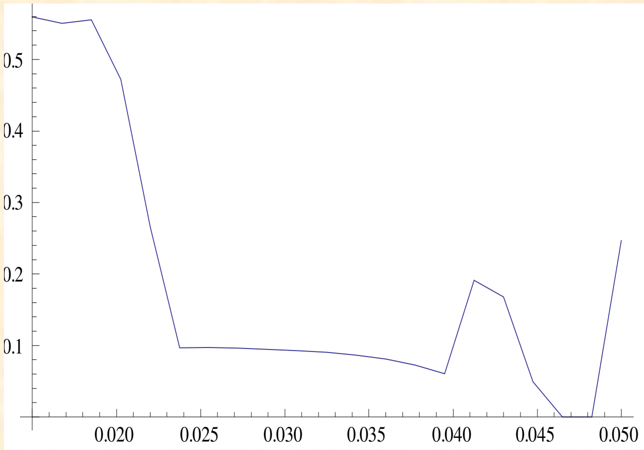


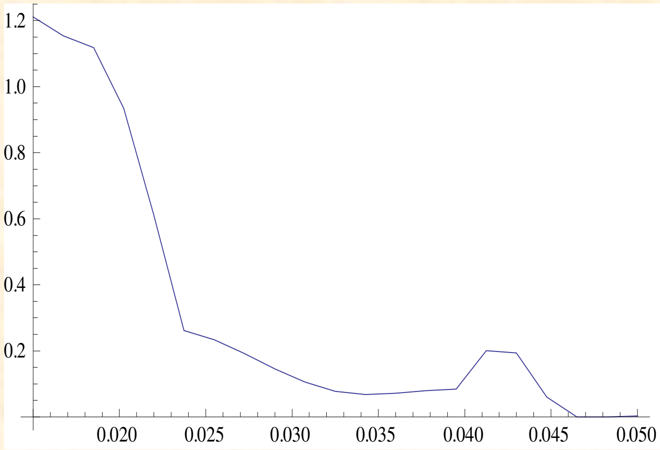
# Does adaptive predator movement stabilize the system?

Predator CV vs. mortality

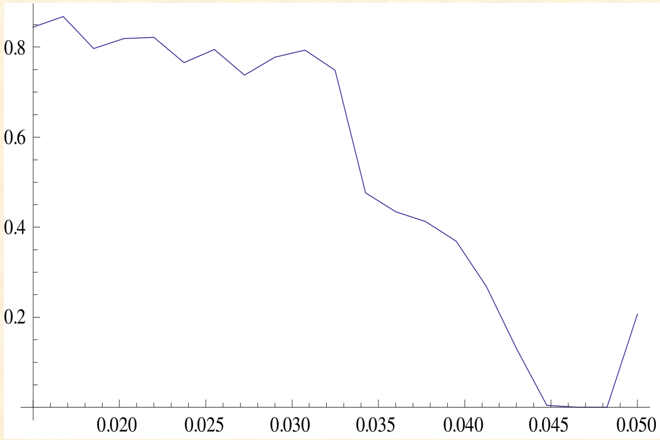
Prey CV vs. mortality

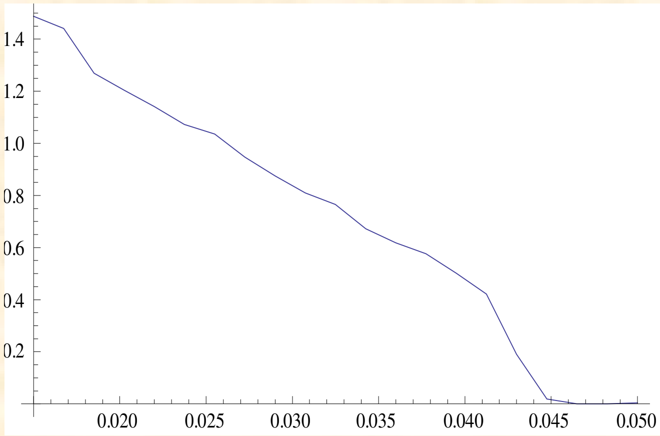
only
prey
adaptive





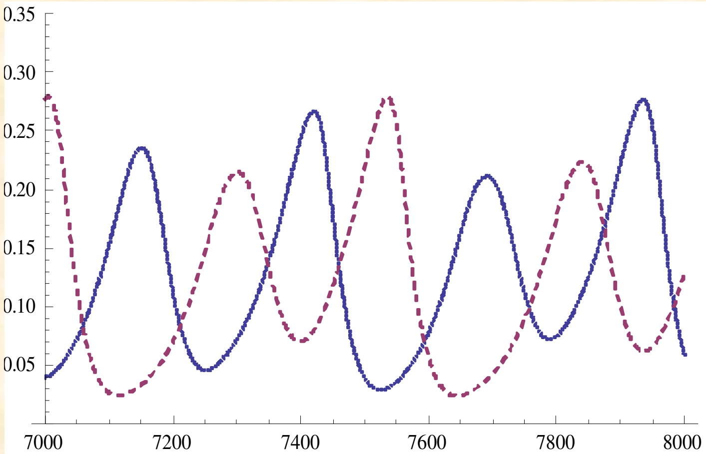
both
consumers
adaptive



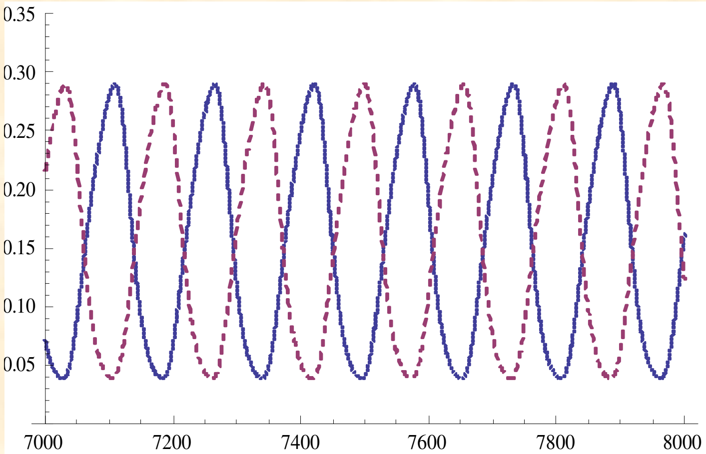


# Predator dynamics of the 4 cases for one parameter set (patch 2 dashed)

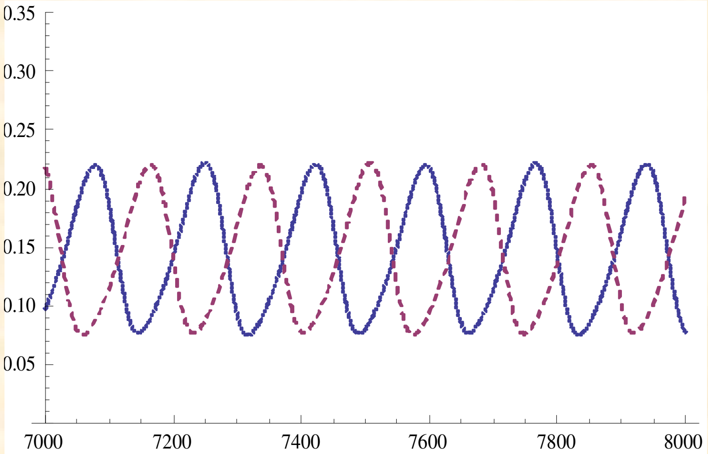
## random R only



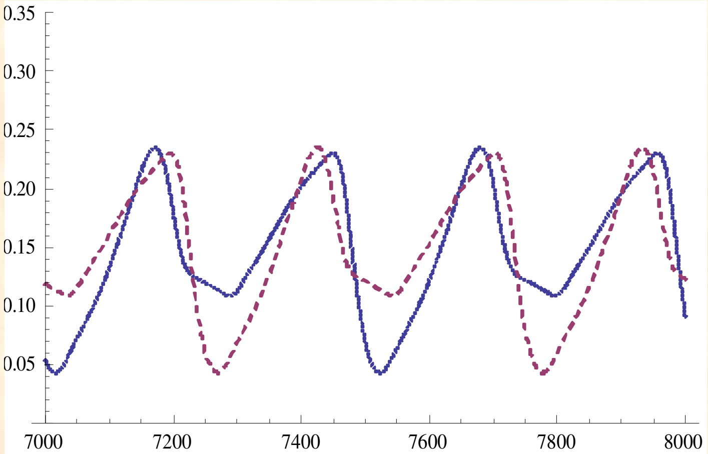
## plus adaptive predator



## plus adaptive prey



## plus adaptive predator & prey



# Summary: In spite of complicated and incomplete results...

- Dynamics and system level attributes can be changed greatly by adaptive movement between patches
- Complex dynamics and polymorphism of movement traits likely to be common
- Coexistence of spatially restricted slow-movers and widely distributed rapid-movers is likely to be common

# Returning to Original Questions

1. Will adaptive movement permit a closer approach to an IFD for consumer species in food chains distributed across a small number of patches (than will random movement)? often not in systems with fluctuations
2. Will adaptive movement produce greater stability of food chains distributed across a small number of patches (than will random movement)? often not in systems with fluctuations
3. Will evolution lead to movement rules that influence the answers to questions 1 and 2?

Answer to 3: yes, but exactly how is unclear

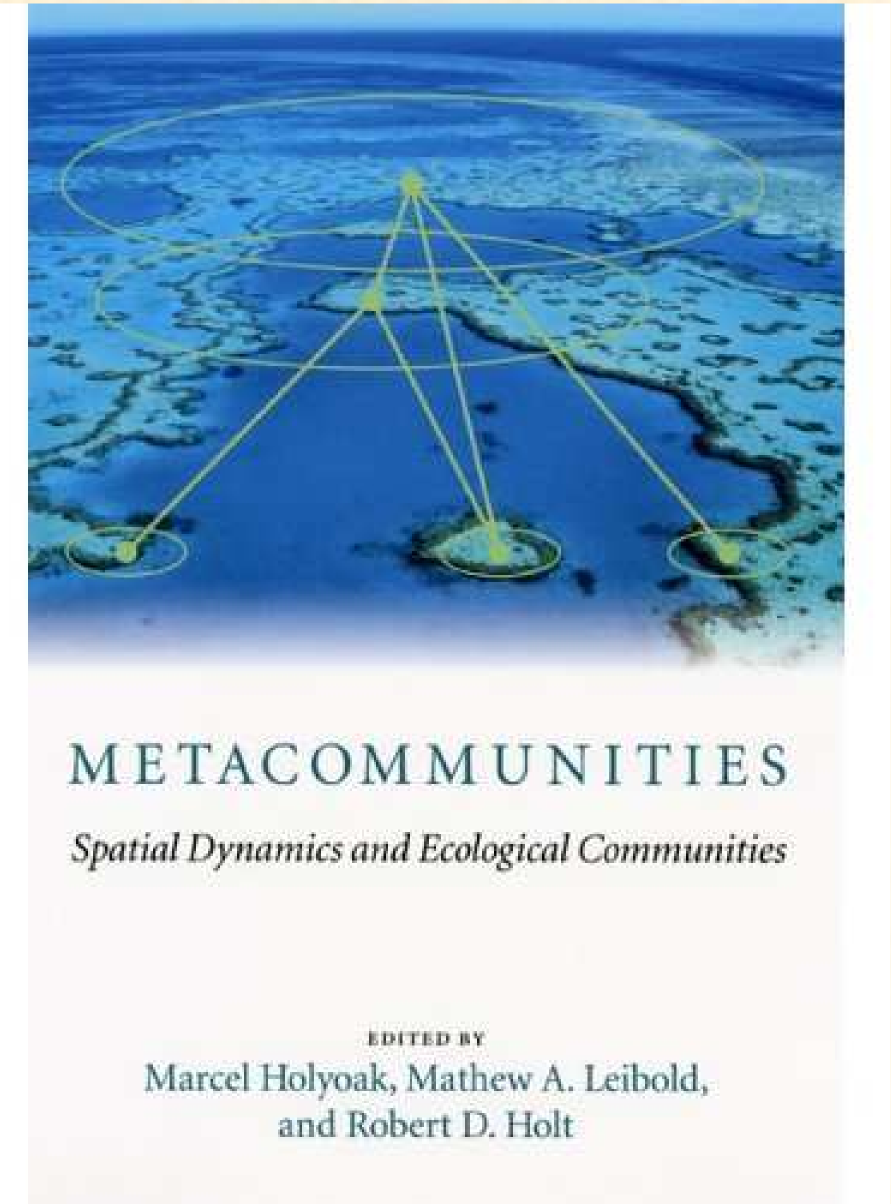
# Some Remaining Theoretical Questions:

1. What strategies prevail, given larger array of patches and movement-types when movement is costly?
2. How does adaptive predator movement affect evolution of adaptive movement strategies in prey?
3. What is the impact of uncertain knowledge of conditions?
4. What are effects of linkages or tradeoffs in parameters?

# Some Remaining Empirical Questions:

1. What are the dynamics of habitat choice behaviours?
2. Does adaptive movement with local Allee Effects explain any (many) observed non-ideal distributions?
3. How does adaptive movement change the dynamics of meta-communities?

Any consideration of (mutual) adaptive movements of interacting species would be an advance



METACOMMUNITIES

*Spatial Dynamics and Ecological Communities*

EDITED BY

Marcel Holyoak, Mathew A. Leibold,
and Robert D. Holt

2005, University of Chicago Press