Overview of "adaptive movement and species interactions"

Space and movement are important for most questions in Ecology and Evolution

- Limited movement, localized interactions and spatial heterogeneity result in statics/dynamics of ecological and evolutionary processes that differ from those in well-mixed systems
  - Interactions between species when described for the global system differ from any comparable model of a homogeneous system
- Most interactions between species involve movement; how does the adaptive nature of such movement influence the functional form of the interaction?

Classical Movement

- Random
- Distances and directions independent of individual condition and environmental condition
- Current movements independent of past movements

BUT, the above properties conflict with the simple facts of movement in most organisms (even seeds)

A great deal is known about how random dispersal influences the outcome of species interactions. Very little, however, is known about how nonrandom dispersal strategies influence the outcome of species interactions. This is particularly true for communities characterized by both competitive and predator-prey interactions. And yet, such multitrophic interactions are the basic building blocks of all natural communities.

-Priyanga Amarasekare 2007 AmNat

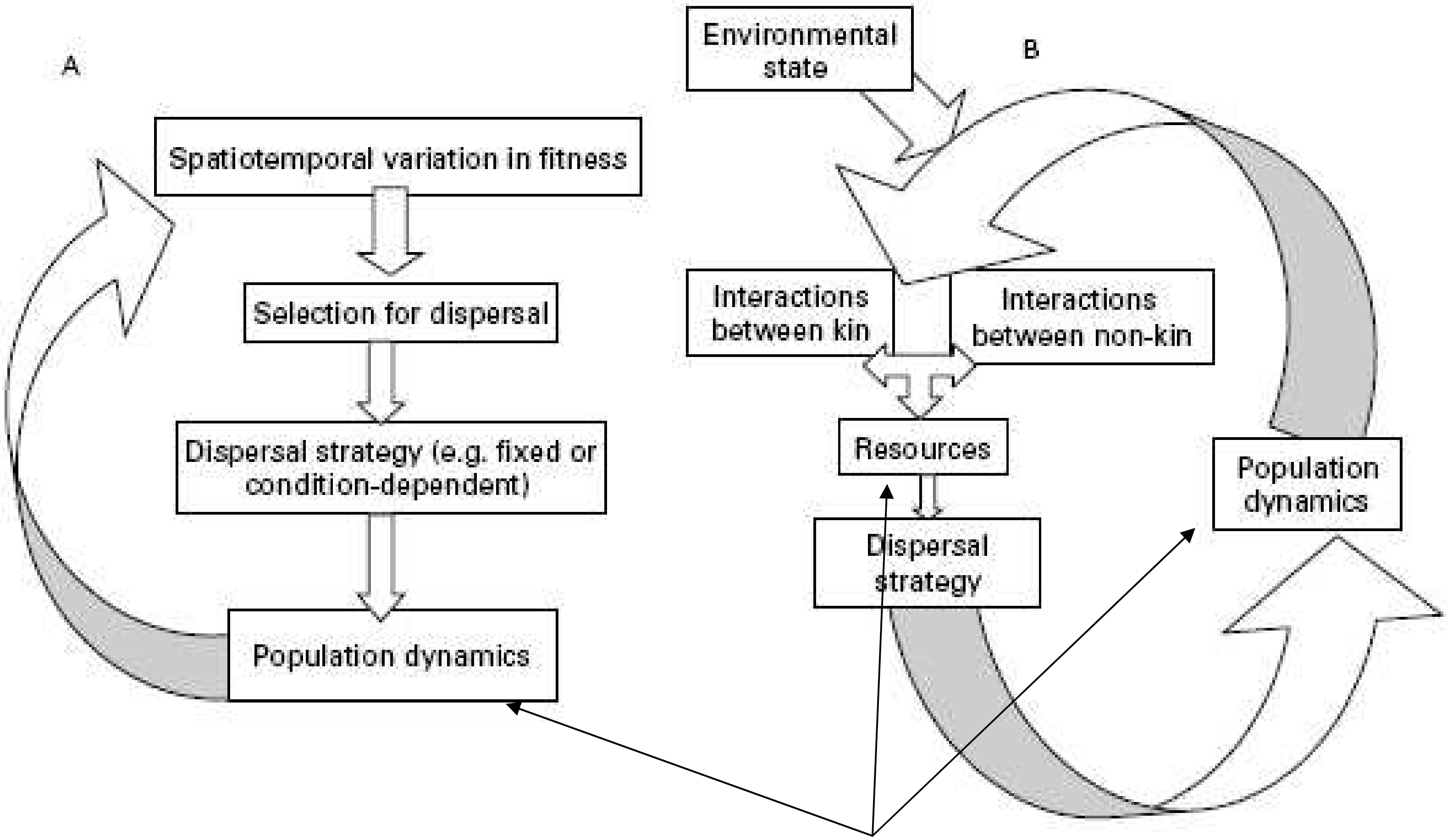
There are good theoretical reasons to believe that informed dispersal decisions would confer an evolutionary advantage over a blind process, unless patterns of variation in habitat quality are totally unpredictable or information acquisition is costly.

-Ophélie Ronce 2007 Ann Rev. E, E, S

D. Bowler and T. G. Benton 2005 view of Dispersal

Evolutionary loop

Ecological loop

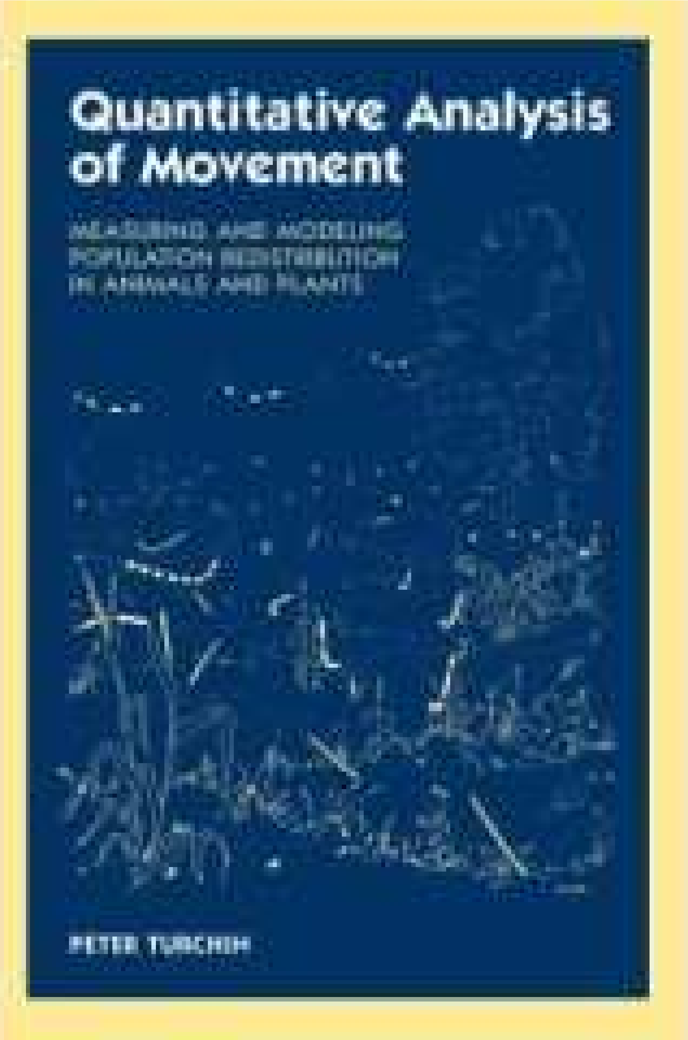


Community dynamics add complication here

Questions potentially affected by the nature of movement

- How common (and how extreme) are spatial differences in fitness (sources and sinks)?
- Under what circumstances are population fluctuations spatially synchronized?
- What are system-wide properties of the food web, such as relative abundances of trophic levels; top-down and bottom-up effects; variability?
- How do populations respond to global perturbations?
- What is species diversity? How is it distributed?

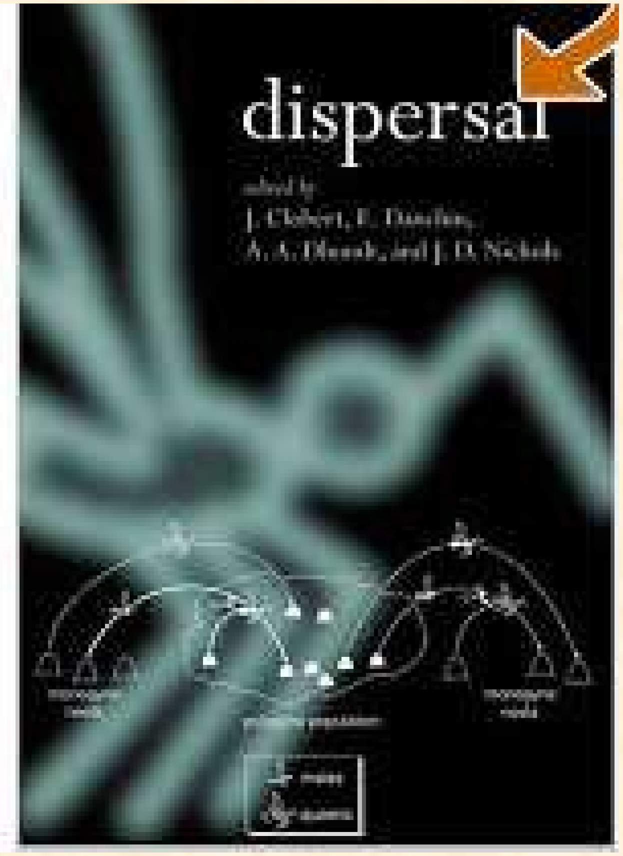
There is no shortage of literature on animal movement



Quantitative Analysis of Movement

MEASURING AND MODELING POPULATION REDISTRIBUTION IN ANIMALS AND PLANTS

PETER TURCHIN



dispersal

But most is not very useful regarding adaptive movement

Movement is studied under many (dis)guises

- *Foraging Theory* – short-term choice of habitat vs. *Dispersal Theory* – long-term choice of habitat
- *Switching predation* – is often, but need not be based on movement between habitats
- *Anti-predator behavior*
- *Habitat choice*

Movement has been studied using many mathematical frameworks

- Continuous space – p.d.e. or individual-based simulations
- Discrete patches – Spatially implicit patch models usually o.d.e.
  - 2, 3, or many patches
- Discrete patches – Spatially explicit patch models – almost always many patches but may be 1, 2, or 3 dimensional space
- Lattice models with individual locations

Movement is usually studied in the context of a single species

- Usually assumed to have density-dependent growth
- However, most ecological theory assumes that species interact with others
- Interacting movements are important when species interact
  - Sih (1980's) Behavioral response race
  - Schwinning and Rosenzweig 1990 (Oikos)
  - a number of more recent works

What makes movement adaptive?

- It increases fitness relative to no movement
- Does it maximize some measure of fitness, and, if so, over what time scale?
    - Are there short-term costs?
- What range of movement options are available?
- What information is available in choosing one of the options?

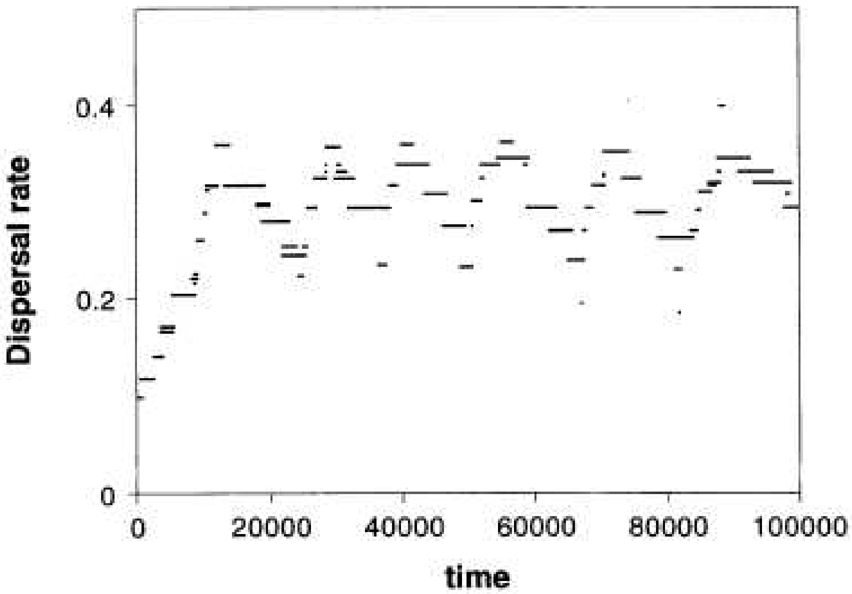
Adaptive aspects of random dispersal with one event per lifespan

- Assuming 'implicit space' & homogeneous environment
  - What is probability of dispersal vs. non-dispersal? (or set of probabilities)
  - What affects this probability; inbreeding; competition with kin; local adaptation; spatial and temporal heterogeneity; environmental bias in movement, cost of movement....
  - Should dispersal probability differ based on sex or age or size or condition or...?
- With explicit space (homogeneous environment); what is dispersal kernel?
  - Probability distribution of distances, directions...
- With explicit space and environmental heterogeneity;
  - What is dispersal bias given local gradient in fitness
  - What turning probabilities and angles characterize optimal search paths when other patches are rare

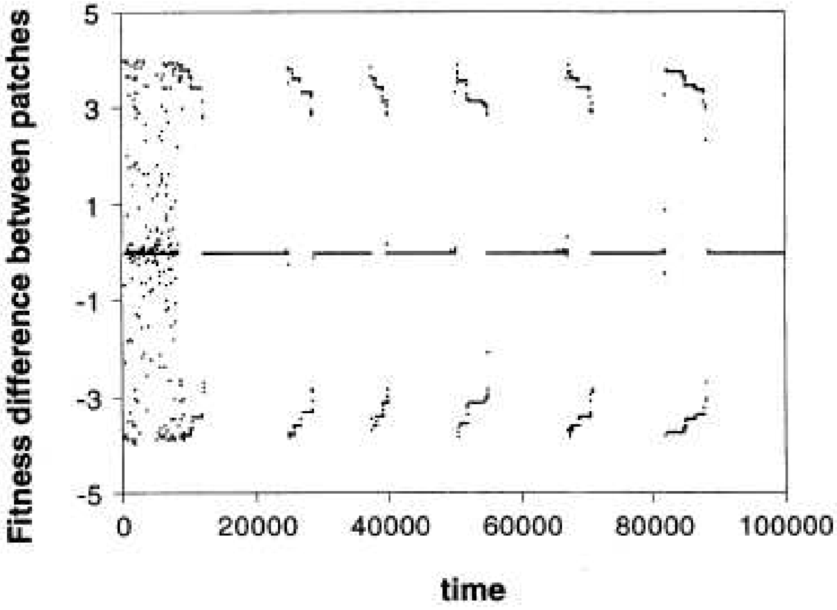
Even with purely intraspecific interaction, implicit space, & equivalent patches, evolution of dispersal is complicated

- Complex dynamics in patchy systems with local density dependence (Hastings, Jansen, etc.)
- Adaptive change in dispersal probability alters the dynamics that determine the adaptive landscape
  - Holt and McPeek 1996; Doebeli and Ruxton 1997
  - frequency dependence, chaos, alternative attractors, polymorphisms....

2b



2c



Results for evolution of dispersal in a 2-patch meta-population having strong within patch density dependence

-Doebeli & Ruxton 1997

When patches have synchronized cycles, dispersal is selected against because of costs

Low dispersal eventually desychronizes patches, selecting for higher dispersal, which eventually synchronizes them

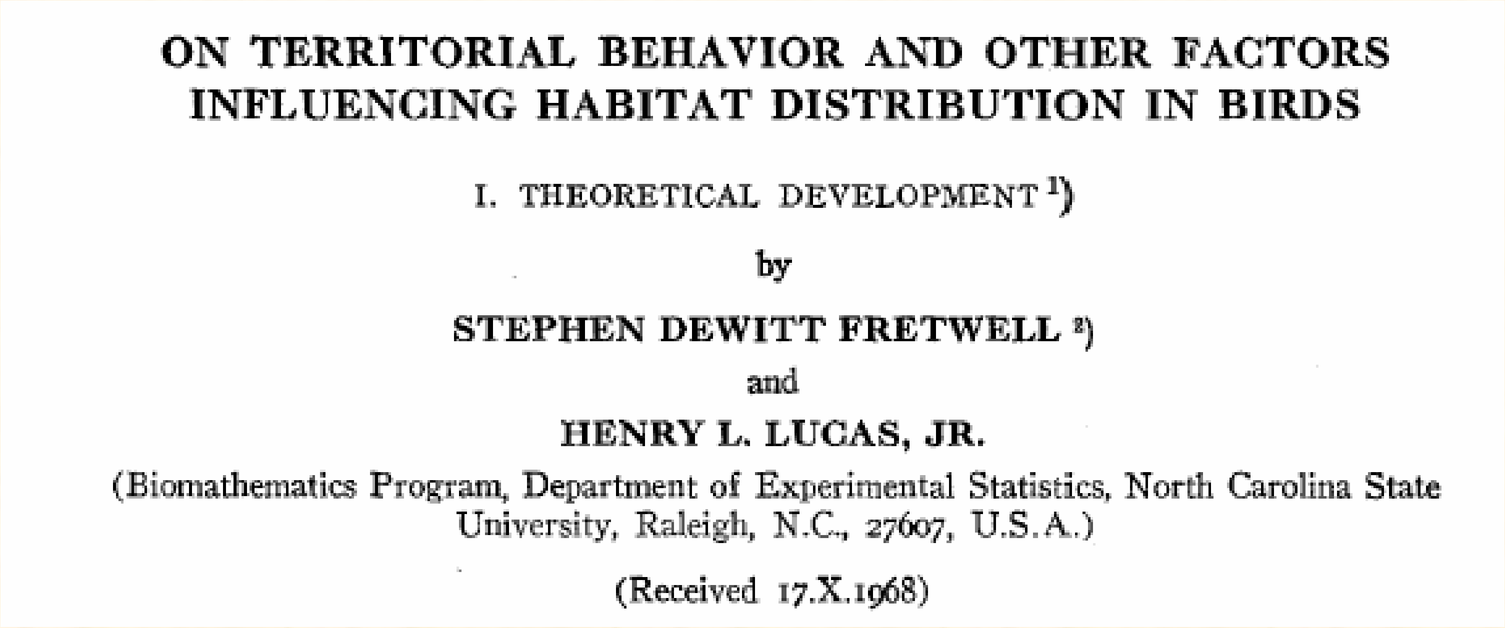
Adaptive aspects of movement that occurs frequently within a lifespan

- Patch selection to obtain resources or avoid predation
- Movement on a gradient of some fitness determining variable/parameter
- More work has been addressed the proposed end point of such movement (often an ideal free distribution) rather than getting to that endpoint

Ideal free distributions

NOT the pop band from Lexington, KY

The origin of Ideal Free Distribution (IFD)



ON TERRITORIAL BEHAVIOR AND OTHER FACTORS INFLUENCING HABITAT DISTRIBUTION IN BIRDS

I. THEORETICAL DEVELOPMENT [1])

by

STEPHEN DEWITT FRETWELL [2])

and

HENRY L. LUCAS, JR.

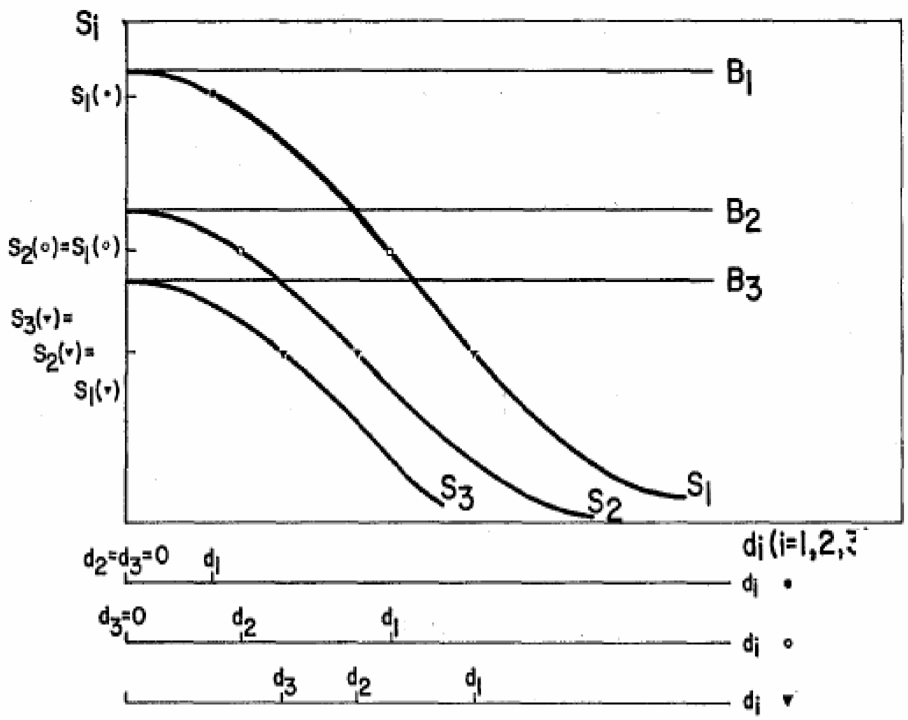
(Biomathematics Program, Department of Experimental Statistics, North Carolina State University, Raleigh, N.C., 27607, U.S.A.)

(Received 17.X.1968)

From Acta Biotheoretica 1970   19:16-36

A distribution in which equivalent individuals have equal fitness in all occupied patches, and have a greater fitness than they would have in a currently unoccupied patch

OR The distribution achieved when individuals have perfect information and no constraints on movement



Fretwell and Lucas analysis of ordinary density dependence: 3 habitats:

FITNESS VS. LOCAL POPULATION SIZE

Fretwell and Lucas analysis of density dependence under “Allee’s Principle”: “…species following Allee’s principle may exhibit erratic changes in distribution with small changes in population.”

FRETWELL’S FORGOTTEN FIGURE

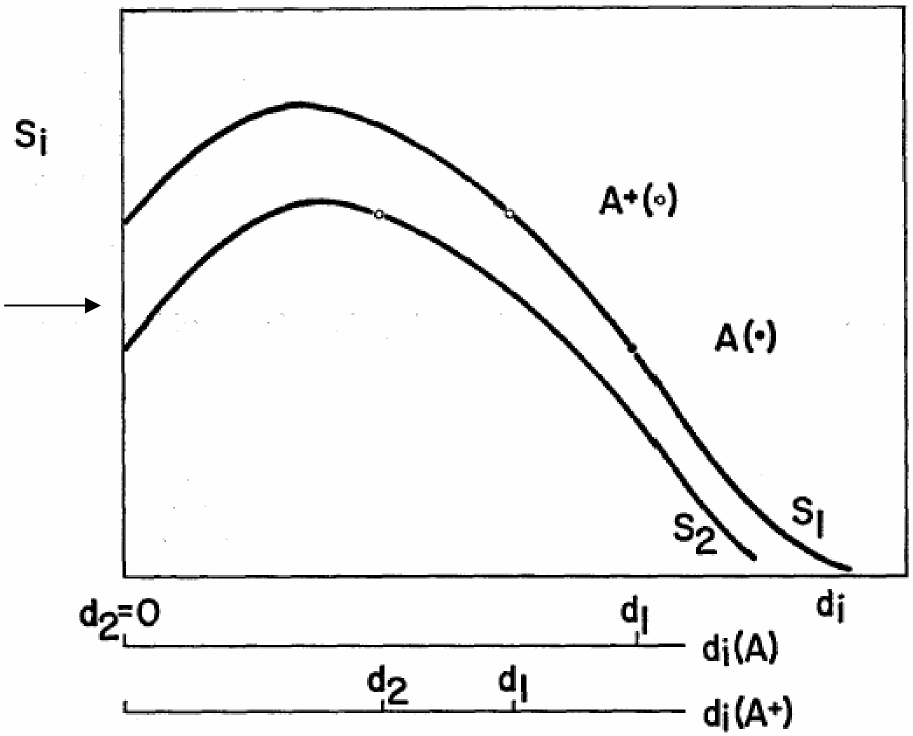


Figure 3. Suitability versus density under ALLEE's principle. At population size A the density in habitat 1 is d_1 (A). At population size A+ the density in 1 is d_1 (A+) while the density in 2 has increased to d_2 (A+). See text for explanation.

It should have been clear that the 'movement rule' may determine whether an IDF is achieved

- Deciding on movement rule is almost always necessary in two contexts
  - Rapid temporal fluctuations in relative quality of environments
  - Interacting species that are also changing adaptively
- Has been growing interest in both of these topics

Temporal variation as a cause of deviations from IFD

- Example: mayfly larvae eating diatoms off rocks in streams (Peckarsky et al.)
  - Algae can grow to carrying capacity in one week
  - Local productivity changes with seasonal changes in illumination and flow
  - Mayflies move repeatedly during larval period, in response to both food and predators


TROUTNUT
www.utahonthefly.com

Rate of movement of individuals of consumer species (with population N) from patch i to patch j in a 2-patch system with resource densities (R_i) from Abrams (2000, Ecology)

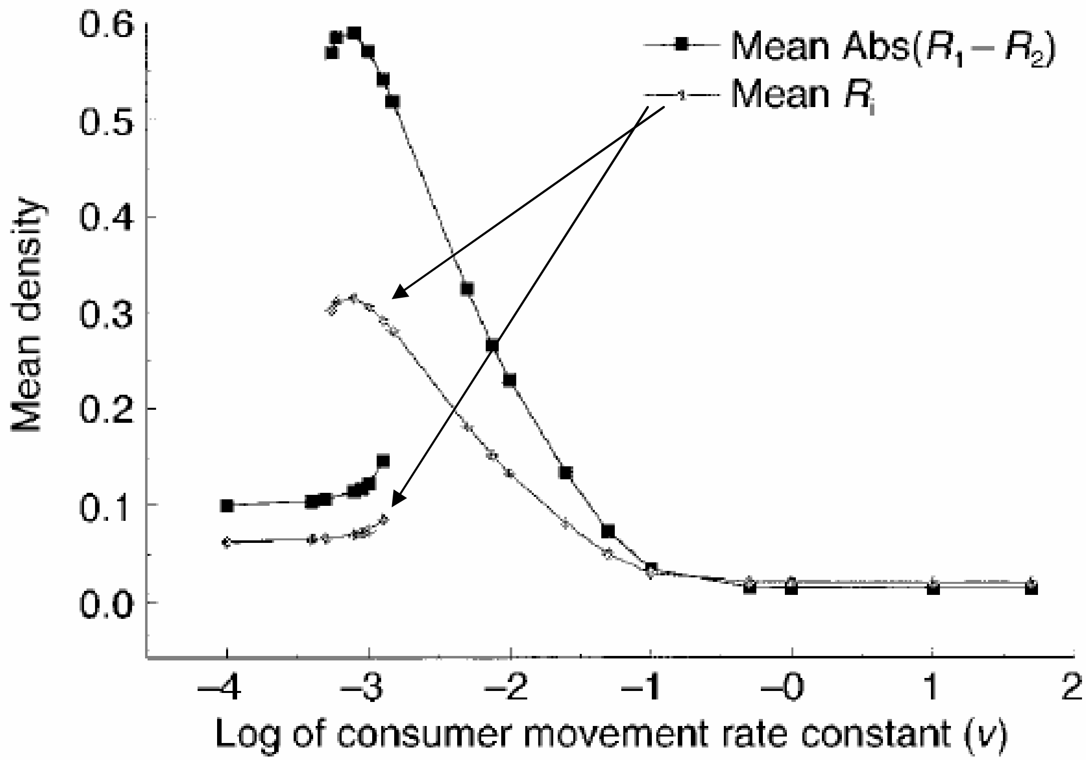
$$Np_iv\exp\left[s\left(-\frac{b_iC_iR_i}{1+C_ih_iR_i}+\frac{b_jC_jR_j}{1+C_jh_jR_j}\right)\right]$$

antiphase temporal variation in logistic resource growth

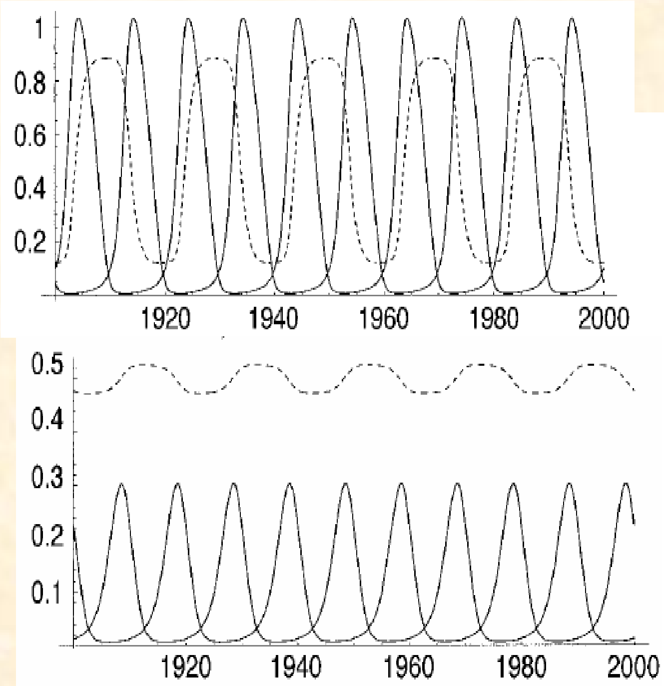
p_i is proportion of consumer individuals in patch i

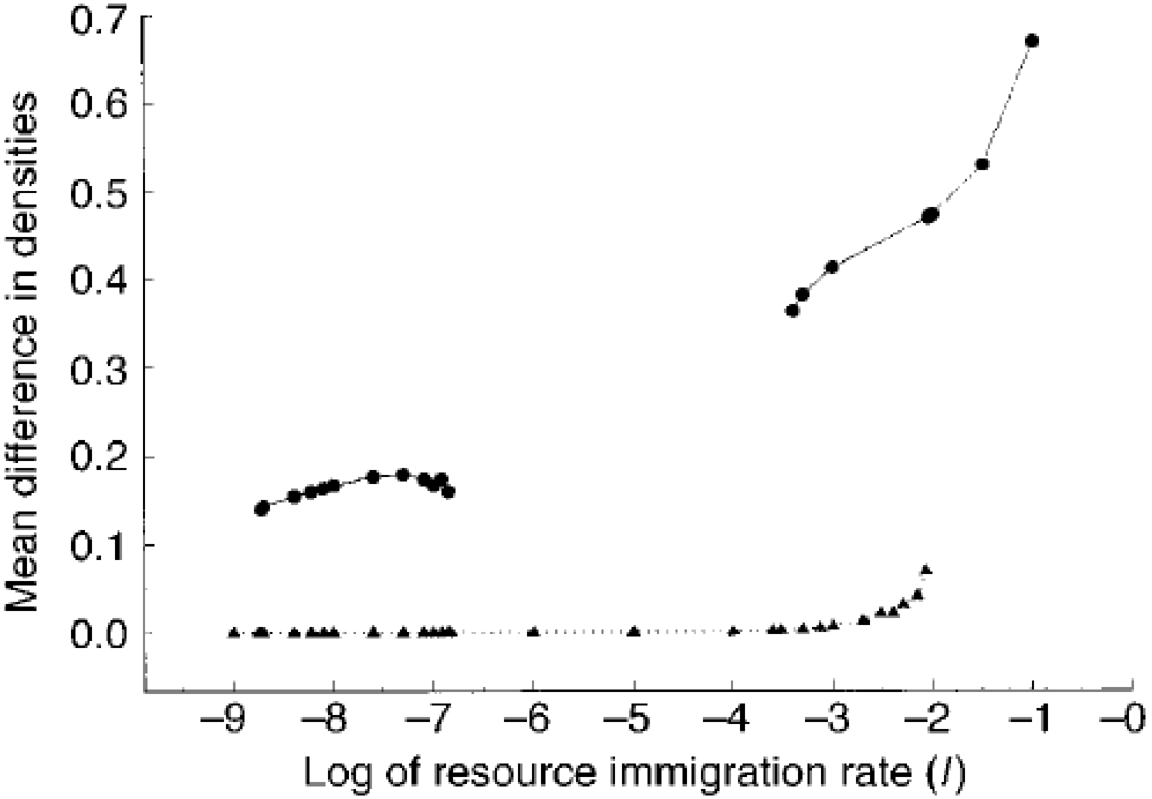
s, v are movement rate parameters

b_i, C_i, and h_i are conversion efficiency, attack rate, handling time



Alternative attractors exist for many movement rates (and are affected by external immigration of resources)





Movement rules themselves can cause deviation from IFD

Cressman Krivan Garay 2004; Abrams, Cressman Krivan 2007

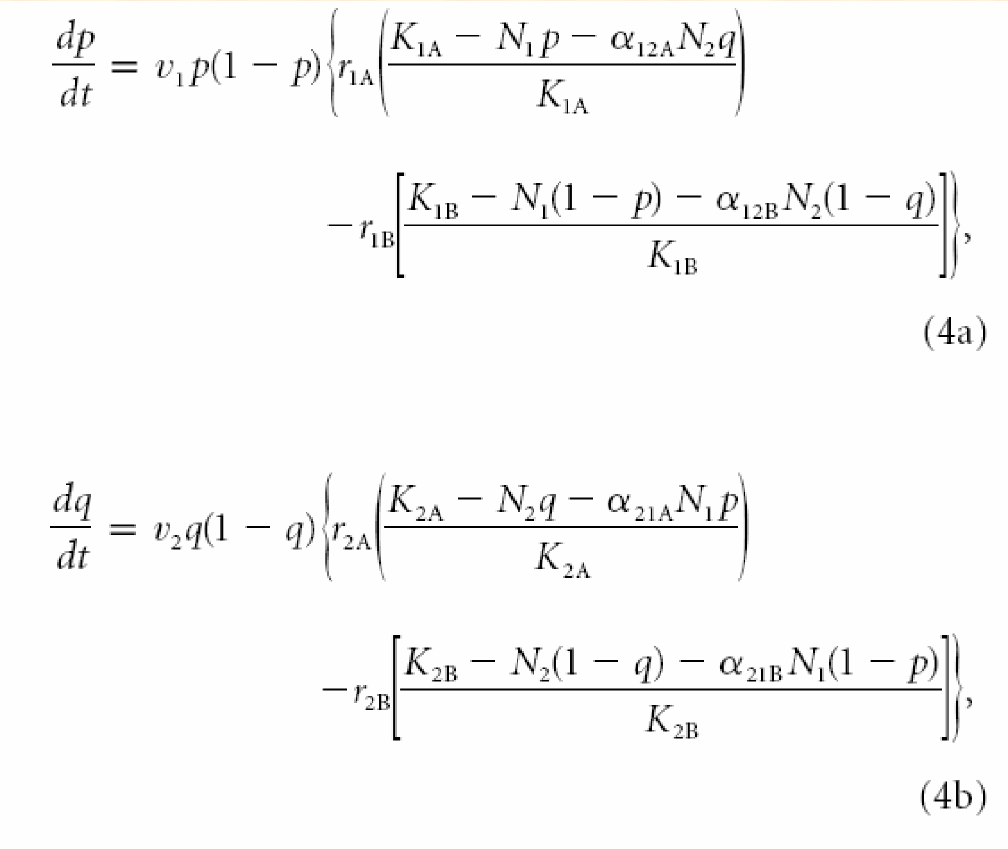
Replicator dynamics for habitat distribution: 2 species in 2 habitats

L-V competition in each habitat

p is proportion of species 1 in habitat A;

q is proportion of species 2 in habitat A;

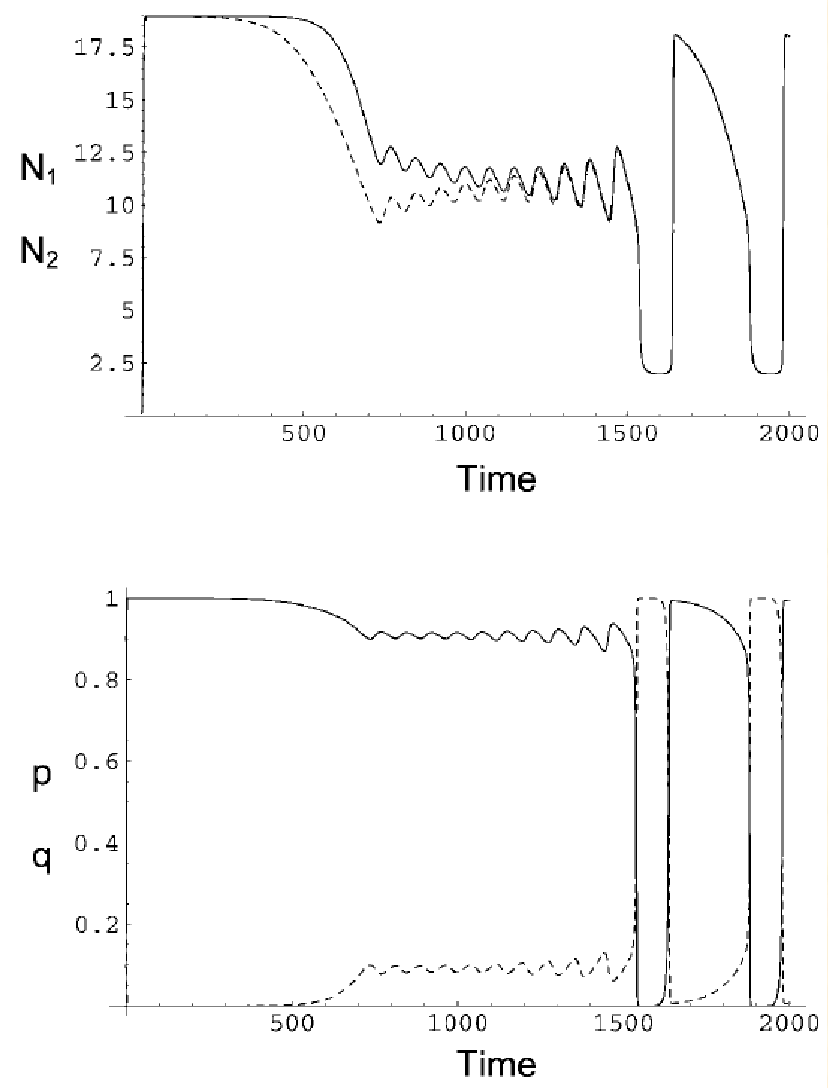
(1-p) and (1-q) in habitat B



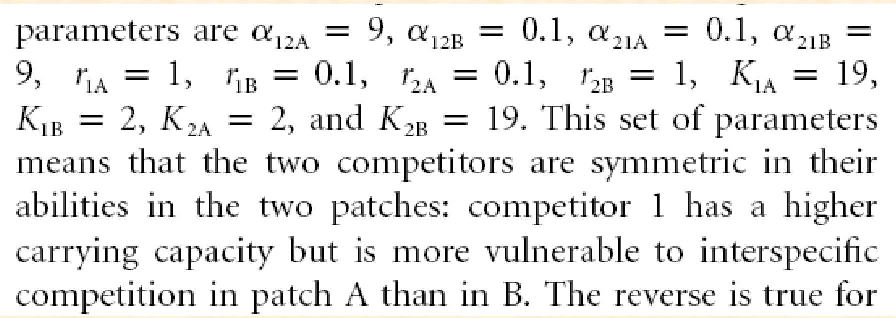
$$\frac{dp}{dt} = v_1 p(1-p)\left\{ r_{1A}\left(\frac{K_{1A} - N_1 p - \alpha_{12A} N_2 q}{K_{1A}}\right) - r_{1B}\left[\frac{K_{1B} - N_1(1-p) - \alpha_{12B} N_2(1-q)}{K_{1B}}\right]\right\}, \tag{4a}$$

$$\frac{dq}{dt} = v_2 q(1-q)\left\{ r_{2A}\left(\frac{K_{2A} - N_2 q - \alpha_{21A} N_1 p}{K_{2A}}\right) - r_{2B}\left[\frac{K_{2B} - N_2(1-q) - \alpha_{21B} N_1(1-p)}{K_{2B}}\right]\right\}, \tag{4b}$$

Symmetrical 2-species-2-patch example from Abrams, Cressman, Krivan 2007



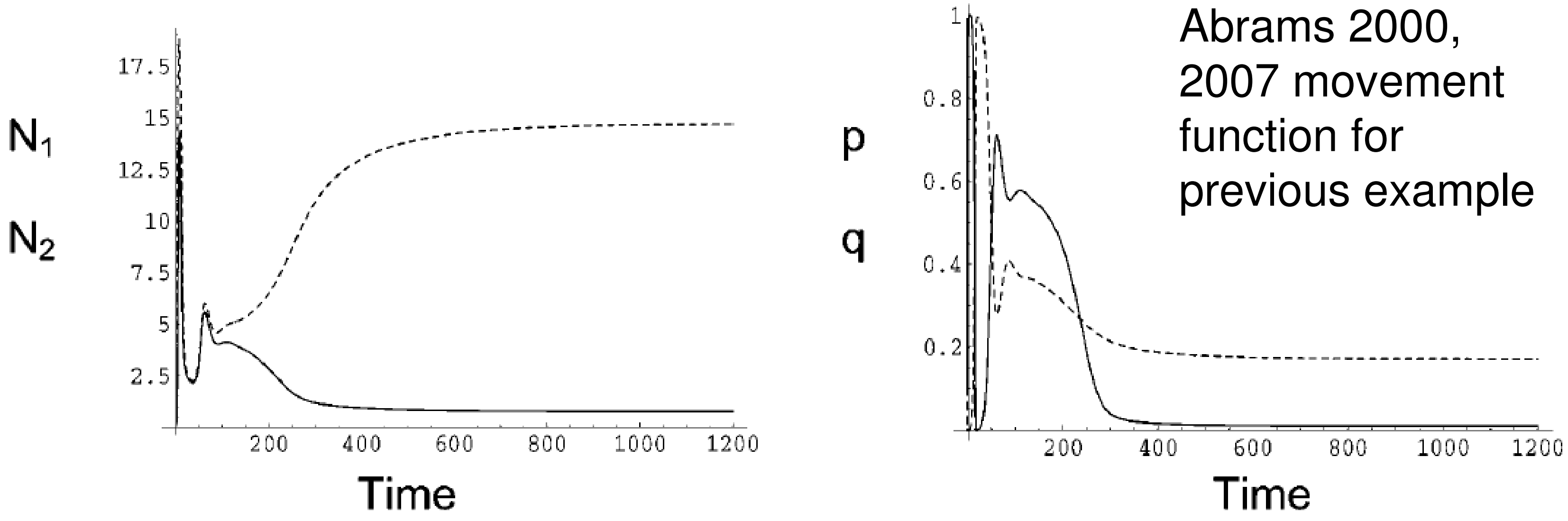
replicator dynamics with mutation: many other possibilities for different parameters



parameters are $\alpha_{12A} = 9$, $\alpha_{12B} = 0.1$, $\alpha_{21A} = 0.1$, $\alpha_{21B} = 9$, $r_{1A} = 1$, $r_{1B} = 0.1$, $r_{2A} = 0.1$, $r_{2B} = 1$, $K_{1A} = 19$, $K_{1B} = 2$, $K_{2A} = 2$, and $K_{2B} = 19$. This set of parameters means that the two competitors are symmetric in their abilities in the two patches: competitor 1 has a higher carrying capacity but is more vulnerable to interspecific competition in patch A than in B. The reverse is true for

A.

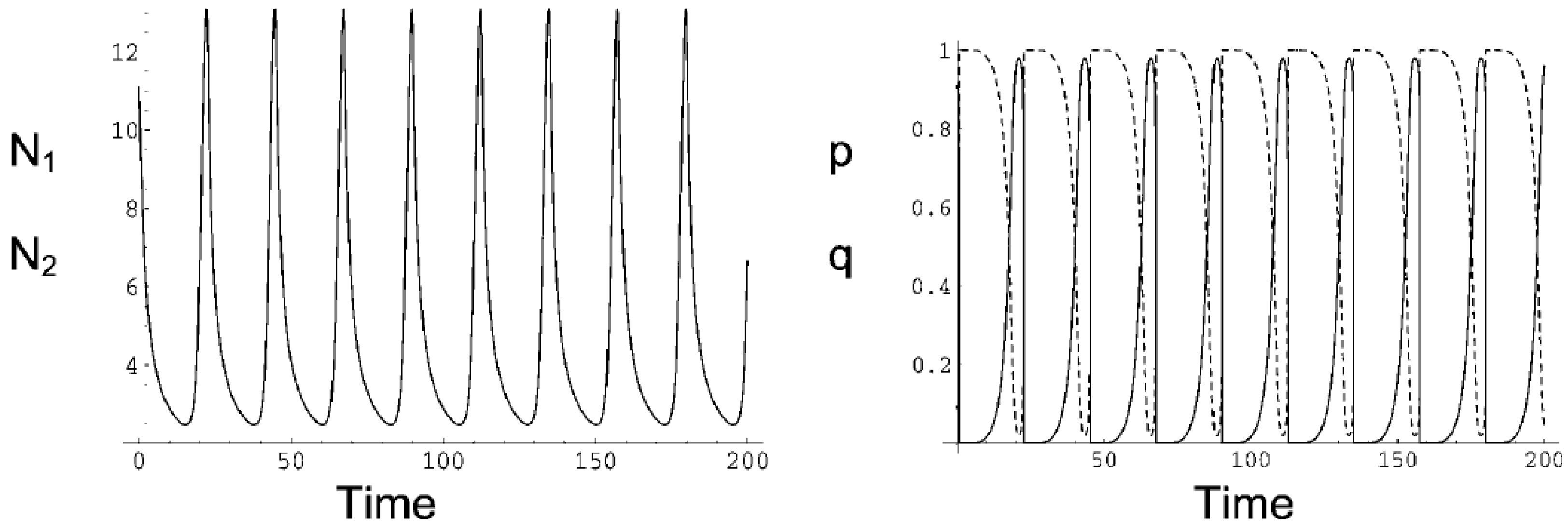
m = 0.01, λ = 8



Abrams 2000, 2007 movement function for previous example

B.

m = 0.1 λ = 5



How to model adaptive movement

- To what extent should we consider simple rules of thumb for adaptive movement?
  - e.g. Abdllaoui et al 2007; predator movement inversely proportional to prey density; prey movement proportional to predator density
  - Are cases of dependence on the density of a single species cases in which other densities cannot be estimated?
- How do abiotic conditions modify effects of density?
- How frequently do different movement rules make different predictions? IF ANSWER IS 'OFTEN', THEN
  - What circumstances lead to the existence of different categories of movement rules
  - Are rate and direction more important than functional form?

Time constraints on movement can be important: Abrams/Kawecki 2-patch parasitoid host model (1999)

1. Type 2 IFD- parasitoid attacks most abundant host/patch; then attacks both at a rate that maintains equality of reward. Patches with more hosts produce more eggs per parasitoid
2. Type 1 IFD- parasitoid has a brief window of time for moving between patches/hosts and a subsequent limited time for attacking; Movement during time window assesses local abundances of both parasitoids and hosts; IFD means equal number of offspring per parasitoid in each patch

Results

Mean Difference between Host Densities in two equivalent patches for Inflexible and Ideal Free Parasitoids

Attack rate *A (= 2)* and prey growth rate, *r,* determine dynamics in a homogeneous system)

r	Inflexible	Ideal Free 1	Ideal Free 2
1.1	0	0.370	0
1.5	0	0.560	0
1.75	0	0.665	0.559
2.0	0	0.750	0.748
2.25	0	0.805	0.804
2.5	0	0.845	0.837
2.75	0	0.755	0.705
3.0	0.730	0.665	0.547
3.1	0.734	0.685	0.600
3.2	0.740	0.735	X
3.3	0.748	0.840	X
3.4	0.755	0.970	X

X = Predator always goes extinct (population density $<10^{-16}$).

How does movement (particularly adaptive) alter the evolution of interactions?

- Choosing (behaviorally) to be in a particular habitat changes the shape of the fitness tradeoff for morphological generalist/specialist traits (Egas et al 2004; Abrams 2006)
  - generalists get less benefit from behavioral habitat selection than do specialists
  - Thus adaptive habitat choice usually increases disruptive selection

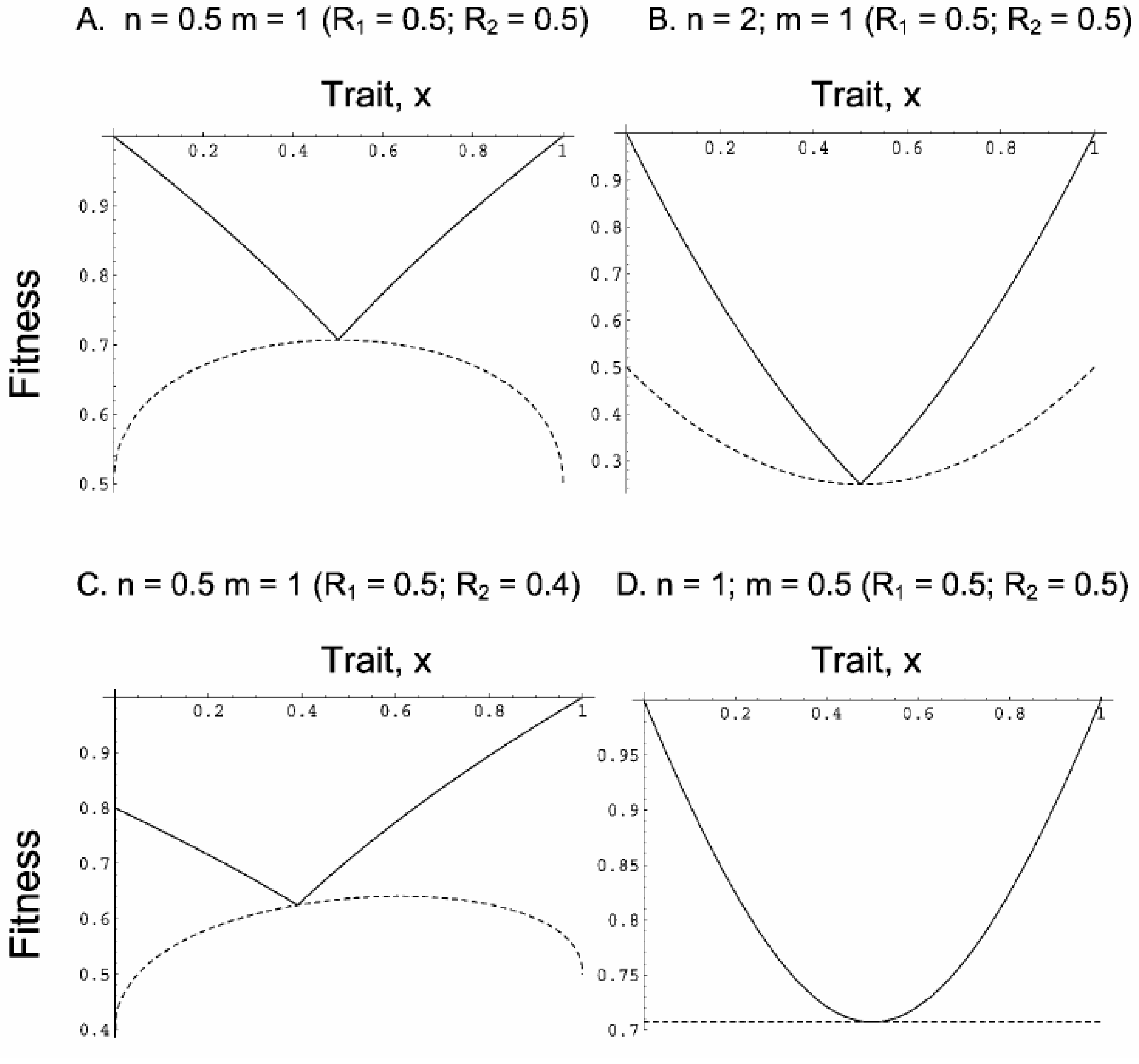
MOVEMENT CHANGES FITNESS LANDSCAPE

Fitness vs. trait in environment with 2 equally abundant resources in 2 different habitats;

Dashed line is in the absence of adaptive habitat choice

n is exponent of morphological tradeoff;

m is exponent of behavioral tradeoff



A. n = 0.5 m = 1 ($R_1 = 0.5$; $R_2 = 0.5$)

B. n = 2; m = 1 ($R_1 = 0.5$; $R_2 = 0.5$)

C. n = 0.5 m = 1 ($R_1 = 0.5$; $R_2 = 0.4$)

D. n = 1; m = 0.5 ($R_1 = 0.5$; $R_2 = 0.5$)

There exists a huge range of unstudied questions

- How does adaptive movement affect likelihood of coexistence of strong competitors (a la 1974 S. Levin)?
- How does adaptive movement affect mortality vs. yield in a two patch environment (a la 1985 R.D. Holt)?
- How does adaptive evolution of movement alter range expansion of invasive species ? (Travis 2009, J. Theor Biol.)
- What is impact of adaptive movement on ecological properties of particular systems (Klausmeier, McCann, Luttscher, ...)?