# A defense of fitness-based dispersal, and what happens when it cannot occur

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# Motivation (from 2009 Fields Institute Talk)

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. Ecol. Evol. Syst.

# What should an animal be informed about?

Factors affecting birth and death rates -> fitness

- More versus less complete information about the above

QUESTIONS

- What happens to dynamics and what type of movement evolves when some components of fitness cannot be measured?
- Can single environmental parameter other than fitness inform movement decisions?
- Are costs and temporal variability important in answering the above questions?

# Recent questionable claims regarding the IdealFreeDistribution*

1. It is usually attained by real organisms in non-laboratory environments
2. Movement rules that produce it represent evolutionarily stable strategies, and will therefore replace other rules

*EITHER: a distribution of organisms/consumers across patches such that 'rewards' or 'fitness' are equalized across patches

OR: the distribution attained by organisms with no costs or constraints on movement and perfect information about patch qualities

# What is wrong with evidence and logic for observing the IFD?

1. Most studies have been done by proponents of the idea that it explains nature
    - Metapopulation studies that quantify fitness or population growth rates in different patches typically find differences
2. Study organisms that did not exhibit IFD were quickly discarded from lab experiments
    - e.g., goldfish, following N. Lester 1984 Behaviour
3. In theory, constraints on perception, movement speed, information gathering, etc. together with asynchronous temporal variation should prevent exact attainment of IFD or any other simple optimization criterion
    - Exact optimum never expected for other predictions in behavioural ecology
    - Exact optimization is not assumed by most models of the analogous process of 'switching' in predators, but adaptive (fitness-based) behaviour is.

IFD is defined by fitness equalization-

So what has led to the idea that movement rules based on the principle of increasing fitness do not evolve?

# Examples of criticism of fitness based movement

1. Flaxman Lou and Meyer 2011: "...conditional movement in our model is based upon local information individuals have about densities (e.g. Krivan 2008) which is more realistic than the assumption—made in a number of previous models—that organisms move based upon direct knowledge of fitness (Amarasekare 2010; Flaxman and Lou 2009).
2. Galanthay and Flaxman (2012): "...we show that when costs of sensory machinery are included , natural selection should favor movement strategies that completely ignore fitness information"

# Why arguments persist: The difficulty of understanding movement evolution with arbitrary strategies in a general metapopulation

- Limitations:
  - Fitness associated with movement traits is usually frequency dependent, and movement often has immediate costs with longer-term benefits
  - In most cases, environments vary (otherwise movement would not evolve), and movement changes this variation
    - E.g., movement can synchronize cycles, which then removes advantage of moving
- Consequence:
  - Simulation is often the only possible approach for biologically realistic cases
  - Therefore, few analyses of realistic scenarios have appeared

# Exceptions to fitness-based movement in models

1. Cases where several interacting species disperse simultaneously at discrete intervals (Sih, Luttbeg, Flaxman et al 2011)
   - No information available about conditions at the end of the dispersal event
2. Cases where the gradient in one variable is sharper than the fitness gradient and is perfectly correlated with it (Flaxman & Lou 2009)
   - Rare for realistic spatial heterogeneity
   - Requires assumption that 'other variable' can be measured with equal ease and cost (also likely to be rare)

# Exceptions to fitness-based movement/dispersal in models (continued)

3. 'Balanced dispersal' sensu McPeek and Holt outcompetes fitness-based dispersal
    - Not true for temporally varying relative habitat qualities
    - No dispersal favored over balanced when dispersal has constitutive costs
    - Recent article (Galanthay and Flaxman 2012) argues that unavoidable diffusive movement favors 'balanced' over fitness dependent, but 'balanced' is again bad with temporal variation

Rest of this part of the talk
provides details on above

# More on Galanthay and Flaxman's argument for balanced movement

- (similar to Cantrell et al 2008- advection must be infinite in gradient movement model to reach IFD)
- Presence of some diffusive movement prevents a <u>continuous</u> fitness-based movement model having equal rates in both directions when $w_1 = w_2$, from achieving IFD

True, but evolution of movement parameters reduces the deviation from IFD produced by random movement (which itself should be reduced by evolution)

In Abrams models with added random, patch-independent dispersal, m is decreased and $\lambda$ is increased by evolution in a temporally constant environment with no cost to movement or to parameters; both types of evolution make trajectory closer to IFD

# Evolution in spatially heterogeneous but temporally constant environments

- Hastings (1983), Holt (1985); condition-independent movement of any kind is selected against in spatially heterogeneous, temporally constant environments because fitness is equalized by population growth.
- McPeek and Holt (1992); (1-species-2-patch discrete model) movement can evolve if it involves patch-specific dispersal with rates inversely proportional to carrying capacities or average population sizes in the absence of movement ("BALANCED DISPERSAL")
  - BUT, balanced dispersal should lose to NO dispersal an any realistic setting in constant environments (lack of knowledge, cost of movement); it is not clear what should happen with temporal variation

# What IS 'fitness'?

- Expected future lifetime reproductive output with appropriate discounting for a growing or declining population
- Instantaneous per capita growth rate (pcgr) of a 'type' is a good measure with frequent reproduction; other measures needed with periodic reproduction (Abrams 1991 Ecology and others)
- Is some confusion: Galanthay and Flaxman's 2012 argument against fitness dependence in cases with survival cost of dispersal in o.d.e. models of population dynamics equates fitnes with pcgr

# Past use of fitness dependent dispersal; Schwinning & Rosenzweig 1990, Abrams, Armsworth, Rowell...

1. Main fitness components can be estimated - food intake rate and predator densities, 'other' mortality factors
2. No survival cost of dispersal; possible constitutive cost that is paid independent of use (E.G. cost of 'sensory machinery')

- CLAIM/CONJECTURE: In these cases, types which base dispersal on fitness will usually outcompete other types under temporal variation

Most cases examined are ordinary differential equation models of homogeneous populations; here fitness is instantaneous per capita growth rate

Will closely <u>approximate</u> IFDs in a variety of systems

- temporal lags always cause some deviations from IFD
- periodic large deviations if movement itself destabilizes dynamics (Abrams 2007)

# Some fitness-based movement functions I have used (can substitute quality, Q for fitness w)

Fitness-based movement with two unequal patches, some random movement and different types of adaptive movement rules:

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

1. $m_i N_{i1} \mathrm{Exp}[\lambda_i (w_{i2} - w_{i1})] \;+ a_i N_i$
2. $m_i N_{i1} \mathrm{Exp}[-\lambda_i w_{i1}] + a_i N_i$,
3. $m_i N_{i1} H(w_{i2} - w_{i1})\{\mathrm{Exp}[\lambda_i (w_{i2} - w_{i1})] - 1\} + a_i N_{i1}$, where H is the Heaviside theta function (unit step function)

- None of these can achieve IFD exactly when $a > 0$; only rule 3 does so when $a = 0$
- Balanced dispersal does so in a constant environment if $(M_{1i} + a_i) N_1 =$

  $(M_{2i} + a_i) N_2$

m is baseline movement (between patches of equal fitness);
λ is sensitivity to the fitness (W) difference between patches;
a is fixed, unavoidable random movement
Pure random movement is special case $\lambda = 0$

# Movement strategies that I have used as competing types in models also having a type with fitness-based movement (using previous slide's movement function templates)

1. Evolved patch-specific movement rates based on carrying capacities and fixed diffusive movement; rates produce balanced dispersal in a constant environment (Galanthay and Flaxman)
2. Movement towards a parameter that is correlated with fitness in temporally constant environments; e.g. (Flaxman & Lou 2009); movement between patches based on difference in the K of the moving species (i.e. $Q_i = K_i$)
3. Dependence on conspecific density or some other single variable that affects fitness (Amarasekare 2007, 2010); movement away from patches with higher conspecific abundance ($Q_i = -N_i$)

# What happens when a fitness-based movement type competes with a balanced or other conditional movement strategy?

- Is one excluded?
- If they coexist, which is more susceptible to extiction if conditions get worse?
- Do results depend on whether knowledge of conditions is local or global?
- Do results differ depending on the presence of constitutive or survival costs of movement?

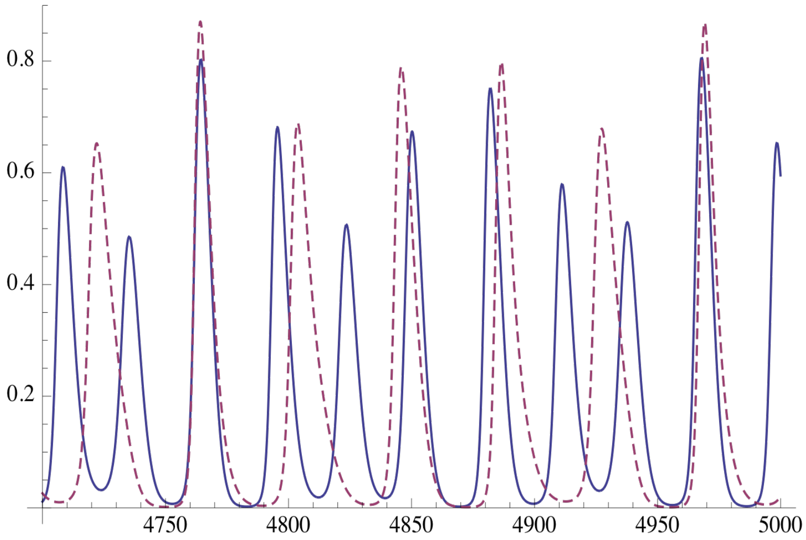
# Predator-prey model with two habitats, adaptive predator movement and varying prey growth, $r_i + s_i(t)$ in patch i

- Prey in each patch have logistic growth with sinusoidal variation in intrinsic growth rate, r and equilibrium population size; $dN/dt = (r + s(t) - kN)$ where $s(t)$ is sinusoidal function;
- Different periods (and/or different amplitudes) of variation in each patch
- Prey do not disperse
- Predators with linear functional responses disperse based on 'quality':
  - equilibrium N for current conditions, which is $[(r + s(t))/k]/C$
  - negative of current density ($-N$)
  - current fitness $(r + s(t) - kN)$
- In each case, net movement from patch 1 to patch 2 as a function of patch qualities, Q, is:

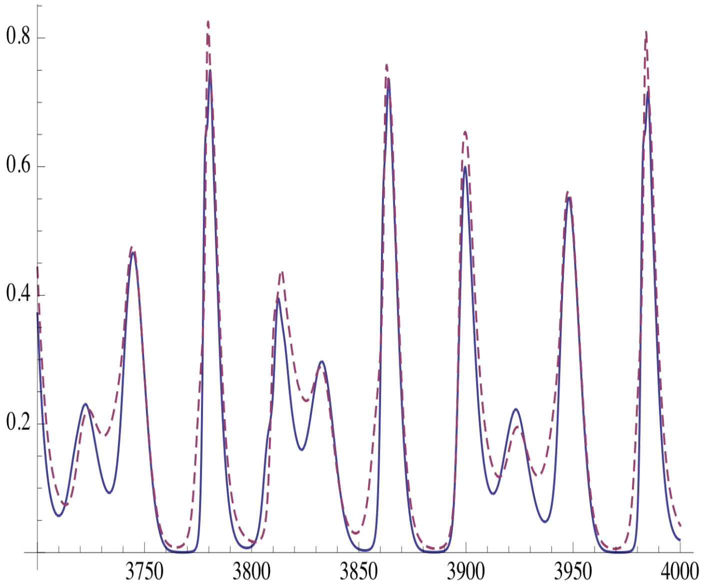
$$-mN_1 \mathrm{Exp}[-\lambda(Q_1 - Q_2)] + mN_2 \mathrm{Exp}[-\lambda(Q_2 - Q_1)] + a(N_2 - N_1)$$

# Competition between 'balanced' and fitness-based rules under asynchronous temporal variation (50% above and below mean) & spatial heterogeneity in mean r

Resource densities in patches 1 (solid) and 2 (dashed) with 'best' balanced dispersal

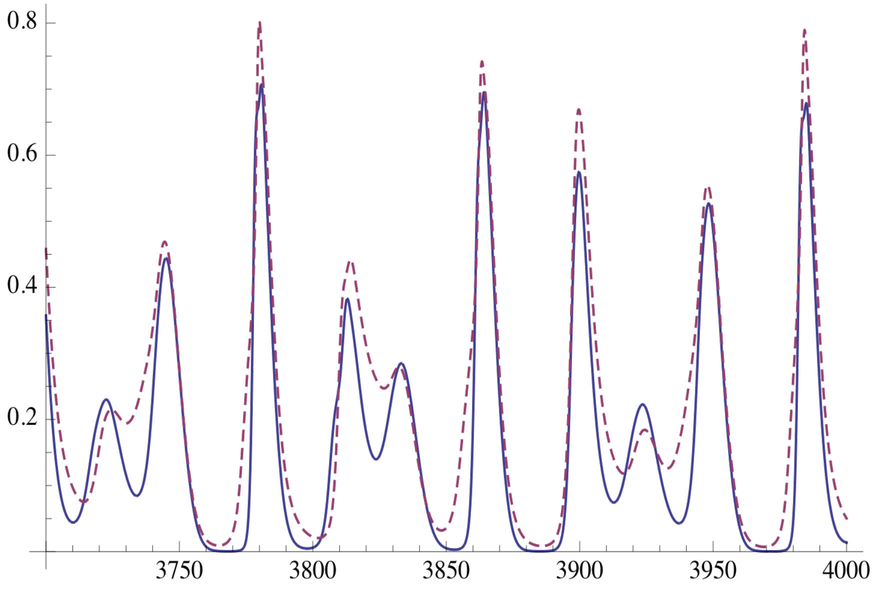


Resource densities under an accurate adaptive movement rule

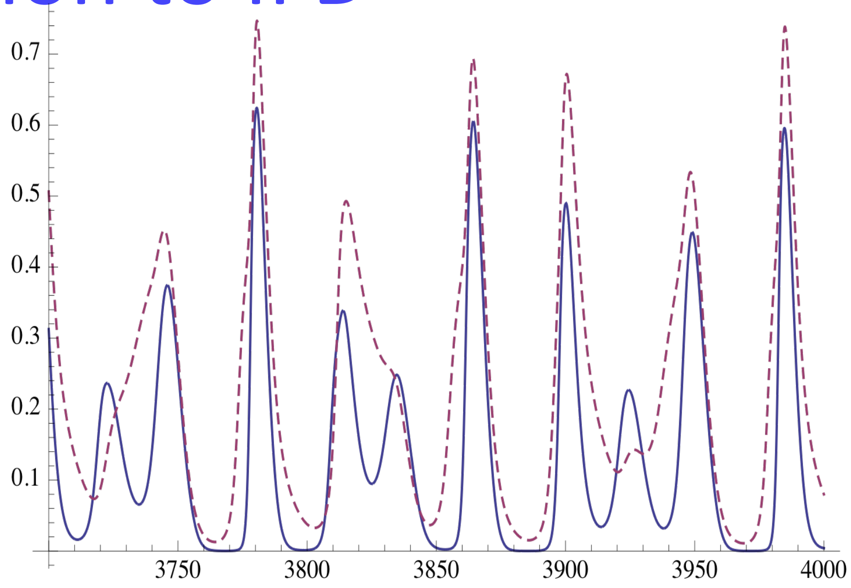


Result of competition is exclusion of balanced by fitness based rule

# Results for increasing frequency of diffusive movement by adaptive mover on approximation to IFD



Zero Random Movement -> Close approximation to IFD (R1 = R2)

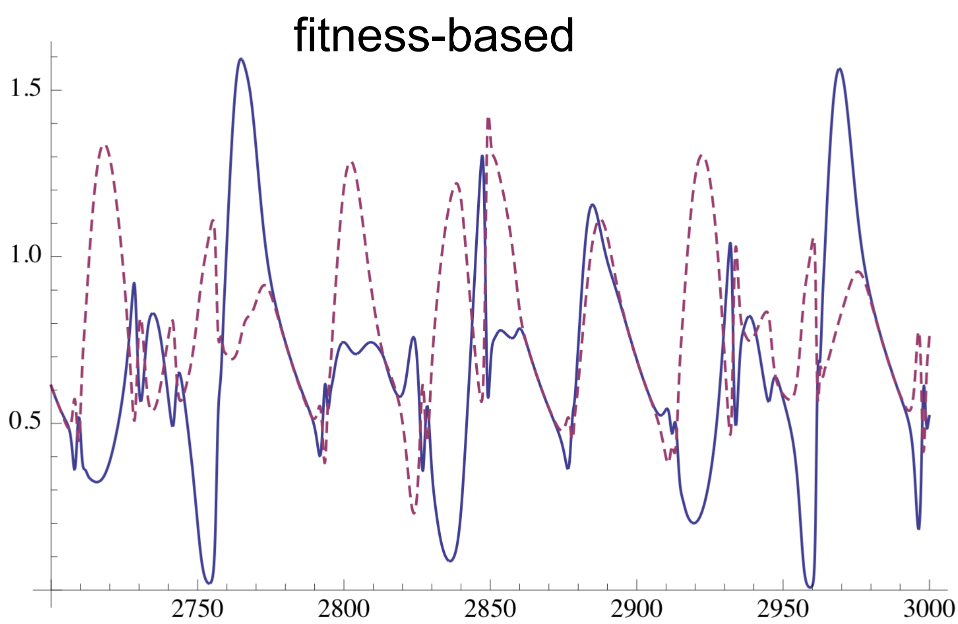


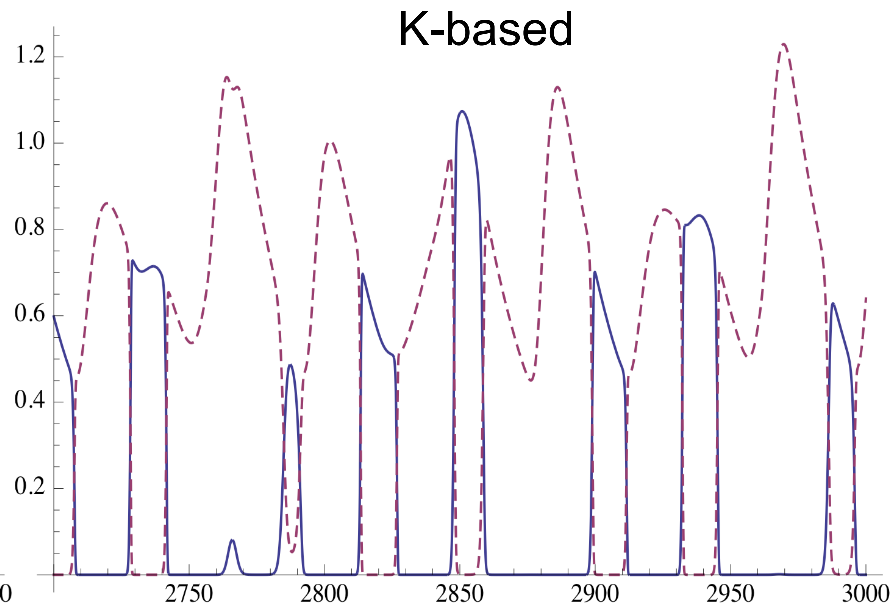
Random movement of 0.6;
This and all random movement up to and above 2.0 exclude optimal balanced movement

# Preliminary Results for fitness-based vs. K- or N-based, under asynchronous variation

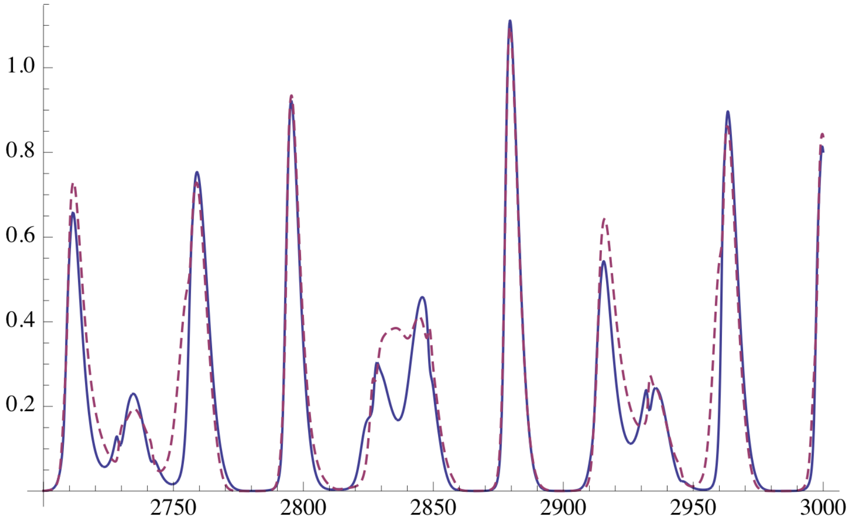
1. Fitness-based mover often excludes other types (always excludes type with movement based on consumer density)
2. Frequent coexistence between K-based and fitness-based types:
    1. If variation is low and heterogeneity is large; K-based occupies better patch while fitness-based moves between the two
    2. If variation is high, K-based mover gets to high K patch more rapidly because K changes more rapidly than does fitness

# Example; coexistence of fitness-based and K-based movers


fitness-based


K-based

Resource densities in two patches (equality implies IFD)



But, K-based mover only exists for a narrow range of relative death rates (or sensory costs); fitness dependent type exists over a many-fold wider range of deaths/costs

# 2009 Fields talk; competition between types with perfect and imperfect fitness-based movement ('perfect' = never go to poorer patch)

Assumptions: asynchrony is due to consumer-resource cycles with between-patch differences in resource growth (r and k); No unavoidable random movement, a.

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

Need for more work on types that can only assess local conditions; this is particularly important with 3 or more patches

# A final argument against fitness dependence

Movement based on the value of one fitness-related population density or environmental variable (Amarasekare 2010; Flaxman et al. 2011)

- Assumes organisms can estimate one parameter better than several –little evidence for this (100s of studies show that food AND predator abundance influence foraging behaviour (which is often patch choice))

BUT, sometimes information on some components of fitness is absent...

# Part 2: What happens, and what evolves when a variable affecting fitness cannot be detected?

- Will concentrate on predator density
  - Is possible due to predator traits that prevent detection (esp. likely for human predators)
  - Review effects on dynamics of movement based solely on other fitness components (mainly resources)
  - Relevant to applied problems in fisheries

# Outline of the rest of the talk

1. Review of dynamics in 2-patch-2-trophic-level models with fitness-based movement of top level
2. Responses to harvesting top trophic level in models with one protected patch (harvesting = presence of undetectable generalist predator in one patch)
3. Responses to harvesting in models with different types of movement or harvesting
4. Evolution of movement under this scenario

# Model with homogeneous patches; $r_1 = r_2 = r$; $k_1 = k_2 = k$, $C_1 = C_2$

$$\frac{dR_i}{dt} = R_i(r - kR_i) - \frac{CR_iN_i}{1+ChR_i}$$

Prey (resource) dynamics

$$\frac{dN_i}{dt} = N_i\left(\frac{bCR_i}{1+ChR_i} - d\right) - mN_i \exp[-\lambda(W_i - W_j)]$$
$$+ mN_j \exp[-\lambda(W_j - W_i)]$$

Predator (consumer) dynamics

$$i,\ j = 1,2, \text{ where } W_i = \frac{bCR_i}{1+ChR_i} - d$$

1. Predator-prey cycles can occur within each patch; these require a high enough r/k; or, a low enough d (low-d cycles require hr/k >1)
2. Accurate movement means low m (baseline rate) and high λ (fitness sensitivity)
3. In general, conditions (parameters) differ between patches

# Detailed results for dynamics in unharvested case presented in:

- Abrams, P.A. and L. Ruokolainen. 2011. How does adaptive consumer movement affect population dynamics in consumer-resource metacommunities with homogeneous patches? Journal of Theoretical Biology. 277:99-110.
- Ruokolainen, L., P. A. Abrams, K. S. McCann, and B. J. Shuter. 2011. Spatial coupling of heterogeneous consumer-resource systems: the effect of adaptive consumer movement on synchrony and stability. J. Theoretical Biology. 291:76-87.

# Part 2: Application to a spatially restricted harvest (e.g., marine protected area)

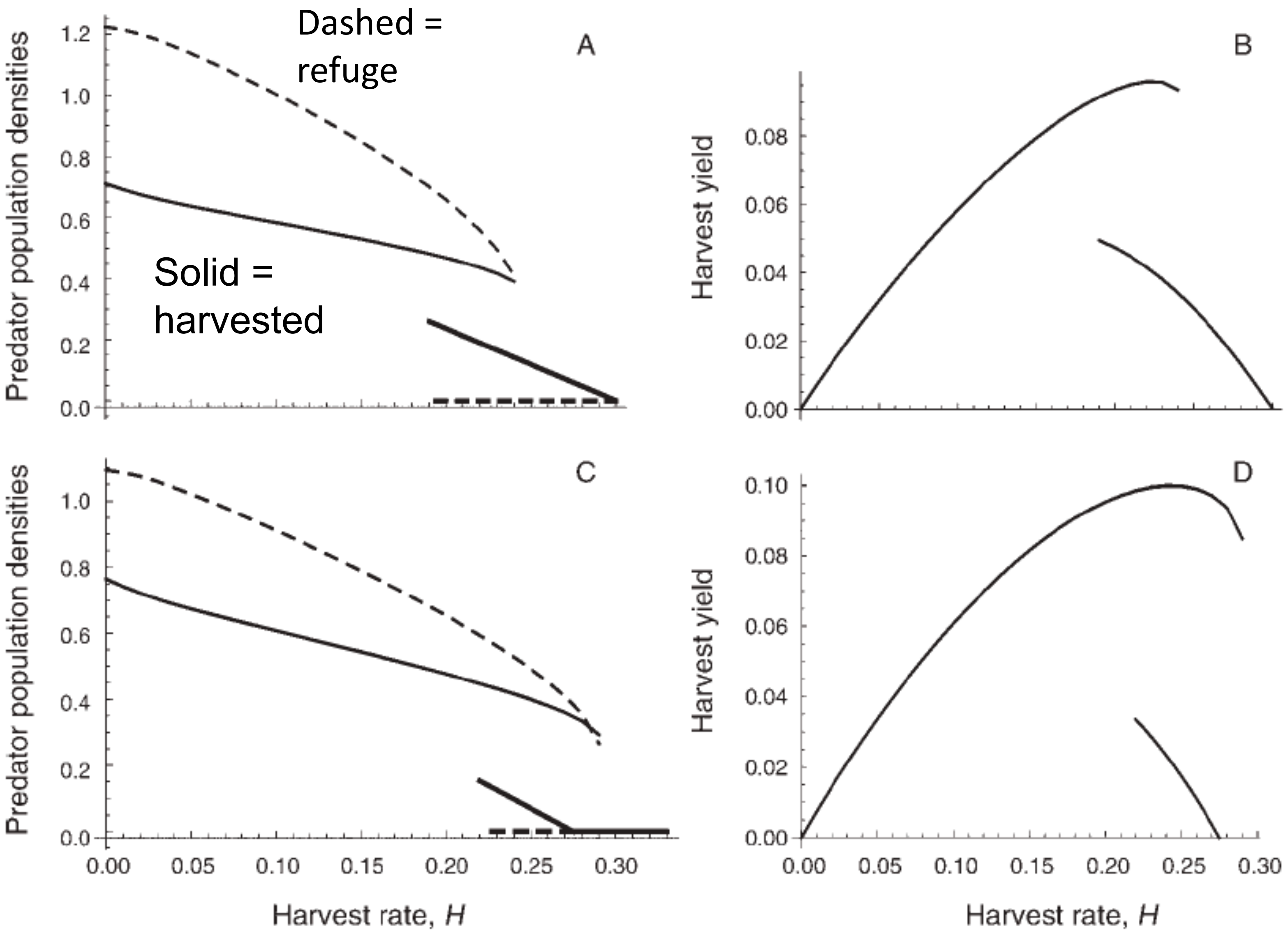
- Basic scenario;
  - (i) Harvesting restricted to one patch (patches may differ);
  - (ii) Risk from harvesting is (usually) not detectable;
  - (iii) Same model as before except fitness 'W' is <u>perceived</u> fitness with invisible risk from harvesting or novel predator (food and background mortality are factors perceived)
- For details see: Abrams, P. A., L. Ruokolainen, B. J. Shuter and K. S. McCann. 2012. Harvesting creates ecological traps: Consequences of invisible mortality risks in predator-prey metacommunities. Ecology 93:281-293.

# There is a risk of abrupt extinction at a threshold level of harvest when:

- the protected patch has *inherently* poorer growth conditions than does the harvested patch
- adaptive movement is sufficiently fast and accurate

Extinction due to positive feedback; higher harvest makes harvested patch more attractive, while reducing the productivity of the refuge

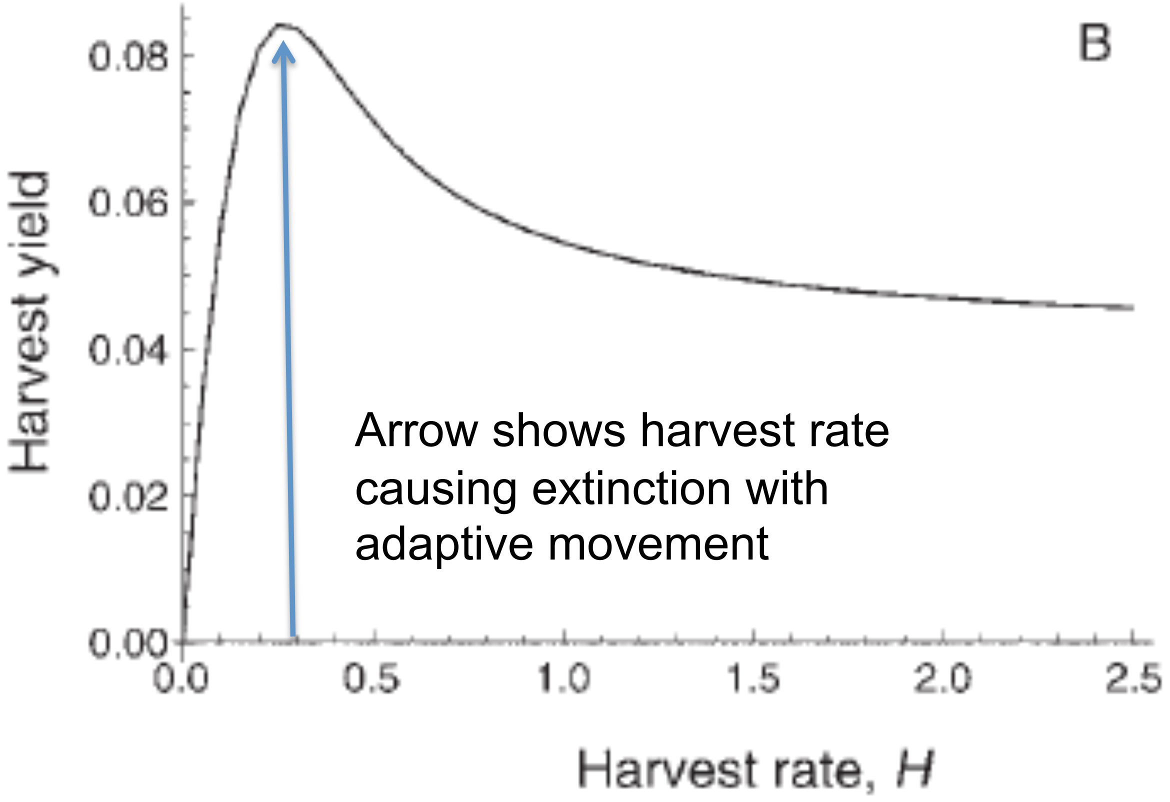
Here exploited predator has a higher prey capture ability in the exploited patch
Panels C&D have lower between-patch heterogeneity(Predator capture rates of prey, C, are 1.2 and 0.8) than patches A&B (C's are 1.3 and 0.7) (NOTE: no cycles in this example)



Dashed = refuge

Solid = harvested

# Yield curves for same system as A&B from previous slide, but with random movement



Arrow shows harvest rate causing extinction with adaptive movement

# Results of competition between random movement and misguided adaptive movement (assuming latter can persist alone)

1. Random movement strategy may exclude or coexist with the misguided adaptive strategy.
    1. Exclusion implies that selection reduces ability to detect and respond to the environment
    2. Exclusion also argues against evolution of fitness-based strategies based on one variable in at least this case
2. Exclusion of random strategy does not occur because predator-free patch always has too few of the misguided adaptive types

# General conclusions for the art of deducing movement rules likely to describe natural populations

1. Most mobile organisms are likely to at least have some individuals with fitness-based movement, but polymorphisms are likely in variable environments
2. Assessing the biological plausibility of movement rules should be done in the context of asynchronous temporal variation within patches
3. Assessment based on one fitness component can be a very bad strategy
4. Everything is possible and evolution can favor ignoring incomplete fitness-related information