# Problems related to the coexistence and diversification of competing species

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# Outline

- A short introduction to ecology
- A short introduction to competition for resources
- Will evolution (coevolution) increase or decrease the probability of coexistence of competitors?
- Some recent work on competition and coevolution among specialists and generalists

# Ecology 101

- The study of the distribution, abundance, diversity and characteristics of species
- Central problems
  - How do the population sizes and characteristics of species respond to environmental changes
  - How can we account for temporal or spatial differences in the number of species and their characteristics
- These problems are inherently mathematical

# Will harvesting seals increase hake populations in the Benguela?

S. African Fur Seals

Hake

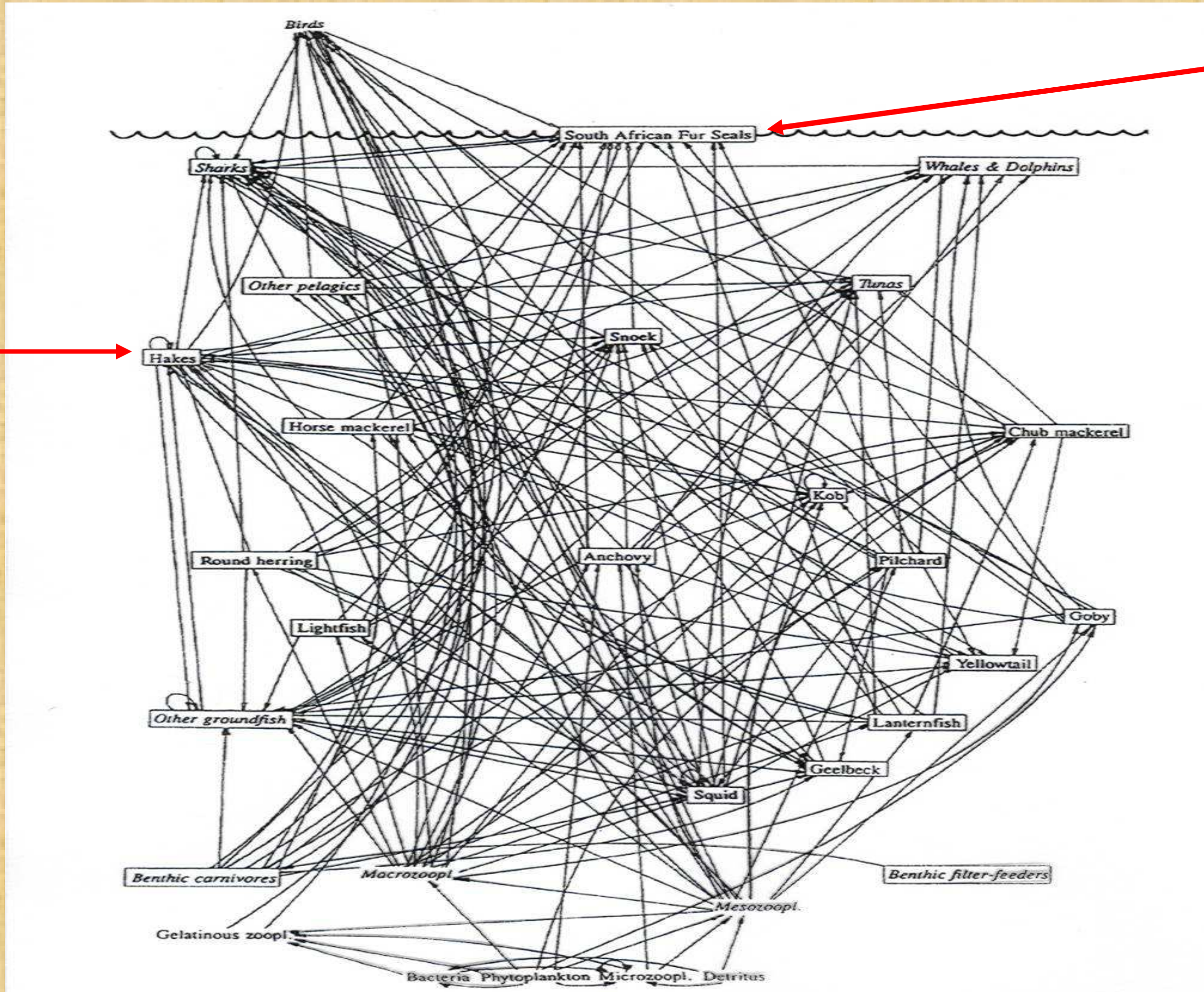



*Figure 35.6.* A food web for the Benguela ecosystem (modified from the web used by Field et al. (1991)).

# Competition for resources

- Resources: Substances that are consumed, whose consumption increases the per-individual population growth rate of the consumer, and whose abundance is decreased by consumption
- Competition for resources occurs when consumption reduces resource abundance enough that consumer intake is reduced
  - Occurs within and between species; intraspecific and interspecific
  - Determines whether different consumer species are able to coexist
  - Is a major determinant of the number and relative abundance of species

# The competitive exclusion principle

- Originated with Vito Volterra (1926)

Dynamics of two consumers, $N_i$ and one resource, R:

$dN_1/dt = N_1 f_1(R)$, $dN_2/dt = N_2 f_2(R)$, where

$f_i$ is a nondecreasing function of resource abundance, R; f = 0 has a unique root for each consumer, $R_i^*$ ($f_i(R_i^*) = 0$, $f_i(0) < 0$)

$dR/dt = g(R) - N_1 c_1(R) - N_2 c_2(R)$

where g(R) is resource growth;

$c_i$ is per individual consumption of resource by consumer i, and is a nondecreasing function

1. A equilibrium point has only a single consumer characterized by the smaller R* ($R_1^* = R_2^*$ is considered impossible by most ecologists)
2. Competitive exclusion limits the number of consumer species to be less than or equal to the number of resources (at a stable point)

## *What allows more species?*

- Nonequilibrium conditions (Armstrong & McGehee, 1970's)
- Lots of resources (MacArthur & Levins 1960's)

Both of the above conditons are the rule-not the exception

But, the possibility of coexistence does not imply that coexistence is likely

- How much of a difference in resource use is needed for coexistence on 2+ resources?
- What other conditions are needed for variability to allow coexistence?

# Coexistence on two resources- Robert MacArthur, Richard Levins

$$\frac{dR_1}{dt} = R_1 g_1(R_1) - C_{11} R_1 N_1 - C_{21} R_1 N_2$$

$$\frac{dR_2}{dt} = R_2 g_2(R_2) - C_{12} R_2 N_1 - C_{22} R_2 N_2$$

$$\frac{dN_1}{dt} = N_1 f_1\left(C_{11} R_1 + C_{12} R_2\right) \; with \;\; f(d_1) = 0$$

$$\frac{dN_2}{dt} = N_2 f_2\left(C_{21} R_1 + C_{22} R_2\right) \; with \;\; f(d_2) = 0$$

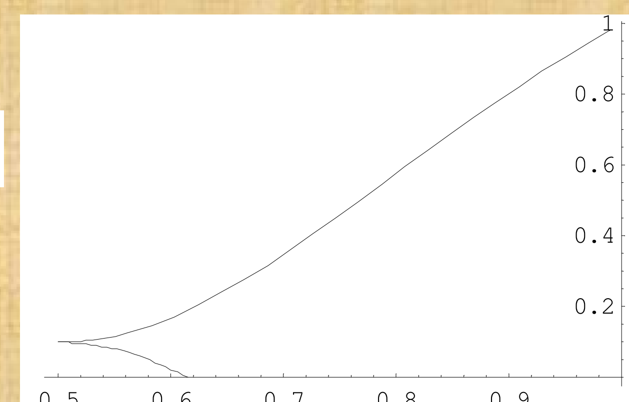
Coexistence at a stable equilibrium is possible for some finite range of $d_1$ - $d_2$, iff

$C_{11}/(C_{11} + C_{12}) \neq C_{21}/(C_{21} + C_{22})$

Define $C_{i1}/(C_{i1}+C_{i2}) = p_i$

**RESOURCE PARTITIONING; can allow wide 'coexistence bandwidth'**

$d_{1max}$, $d_{1min}$




p

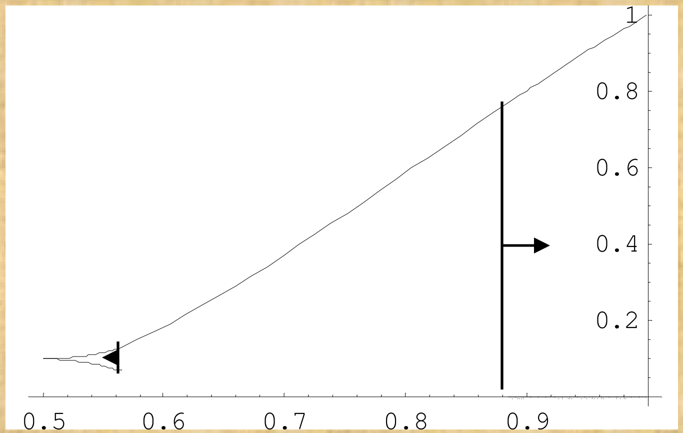
If competitors have 'mirror image' p values ($p_1 = 1 - p_2$), then the range of relative mortalities allowing coexistence increases at an accelerating rate with p in an example with $d_2 = 0.1$, standard logistic resources

# Is resource partitioning and similar efficiencies (R*) sufficient for coexistence? No

$$\frac{dR_1}{dt} = R_1(1-R_1) - C_{11}R_1N_1$$

$$\frac{dR_2}{dt} = \rho R_2(1-R_2) - C_{12}R_2N_1$$

$$\frac{dN_1}{dt} = N_1\left(b_1(C_{11}R_1 + C_{12}R_2) - d_1\right)$$




$d_{max}$

$d_{min}$

p

If $C_{11} > C_{12}$, and $d_i$ sufficiently small, $R_i = 0$ at equilibrium with one consumer.

Therefore coexistence with a second consumer at a stable point is impossible.

E. g., if $d_{resident} = 0.1$

1. Two almost identical generalists can coexist
2. Two different partial specialists cannot coexist
3. Different near-complete specialists can coexist for wide range of d

# Coexistence on one resource due to difference in the shapes of the intake rate functions and variation in resource abundance

$$\frac{dR_1}{dt} = rR\left(1-\frac{R}{K}\right)-\frac{C_1RN_1}{1+C_1h_1R}-\frac{C_2RN_2}{1+C_2h_2R}$$

$$\frac{dN_1}{dt} = N_1\left(\frac{b_1C_1R}{1+C_1h_1R}-d_1\right)$$

$$\frac{dN_2}{dt} = N_2\left(\frac{b_2C_2R}{1+C_2h_2R}-d_2\right)$$

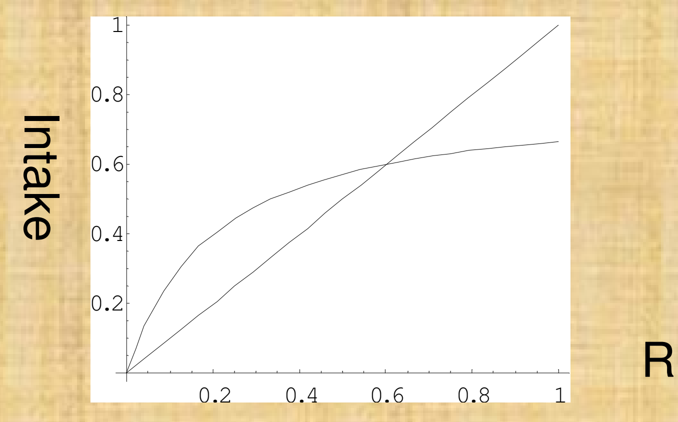
h denotes handling time per resource item consumed (when additional intake is not possible); $h_2 >> h_1$

b denotes conversion efficiency of resources into new consumers

d is a per capita death rate (or equivalently the scaled intake rate needed for ZPG)

RESULTS OF NUMERICAL ANALYSIS
Coexistence of 2 species can occur with varying resource densities

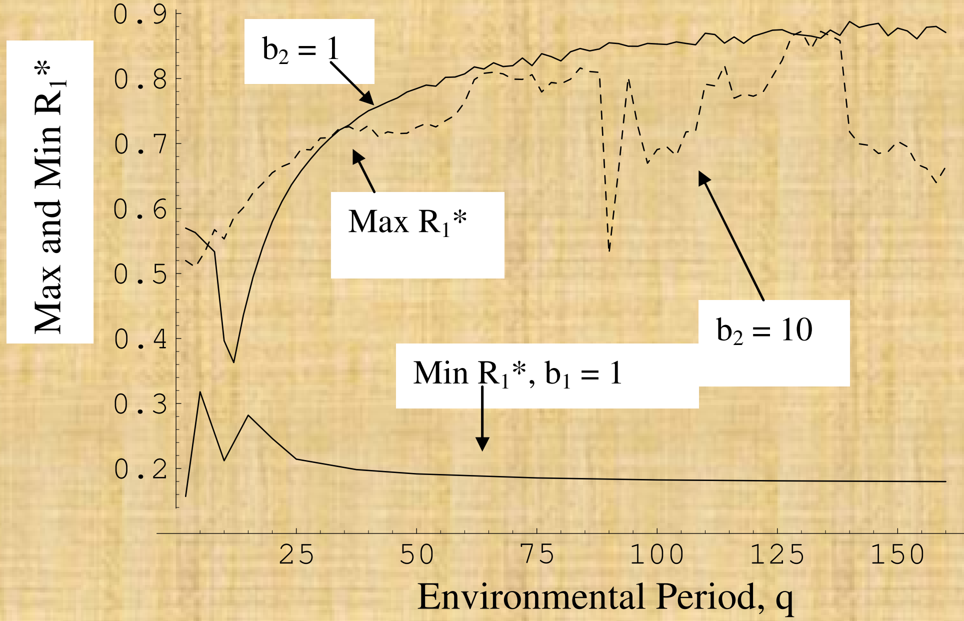
Coexistence of 3+ species requires very delicate balancing of parameters



# How does coexistence occur?

- Consumer 2, with a more strongly saturating response has a lower R*
- But, consumer 2 when alone approaches a limit cycle where $\langle R_{(2)} \rangle > R_1^*, R_2^*$; thus consumer 1 increases when invading a system with consumer 2
- Consumer 1 when alone approaches a stable point $R_1^* > R_2^*$; thus, consumer 1 increases when rare
- In this simple model, mutual invasion implies coexistence (attractor bounded away from axes of phase space exists)

# "Coexistence bandwidth" due to endogenous and exogenous cycles with a difference in consumer functional response shape




$$\frac{dN_1'}{dt'} = b_1 N_1'(R' - d_1)$$

$$\frac{dN_2'}{dt'} = b_2 N_2'\left(\frac{R'}{1+hR'} - d_2\right)$$

$$\frac{dR'}{dt'} = R'\left(1 + \gamma Sin\left[\frac{2\pi t'}{q}\right] - R'\right) - \frac{R' N_1'}{1+hR'} - R' N_2'$$

Parameters in scaled model:
$h = 10$; $d_2 = 0.06$; $b_1 = 1$ or $10$

Coexistence occurs for R* values of consumer 1 that span most of the range of potential R* (0,1).

Coexistence depends on demographic speed of linear consumer

See Abrams 2004 Ecology 85:372-382.

# How much does each mechanism (resource partitioning vs. temporal variation) contribute to coexistence in natural communities?

- Why is it important to know?
- Why is this hard to answer?
  - Effective partitioning is hard to measure
  - Quantifying temporal variation requires long-term records of environment variables and their effects on population growth
  - Theory on the potential mechanisms by which variation affects coexistence is still at an early stage of development

# Does evolution affect coexistence and/or species diversity?

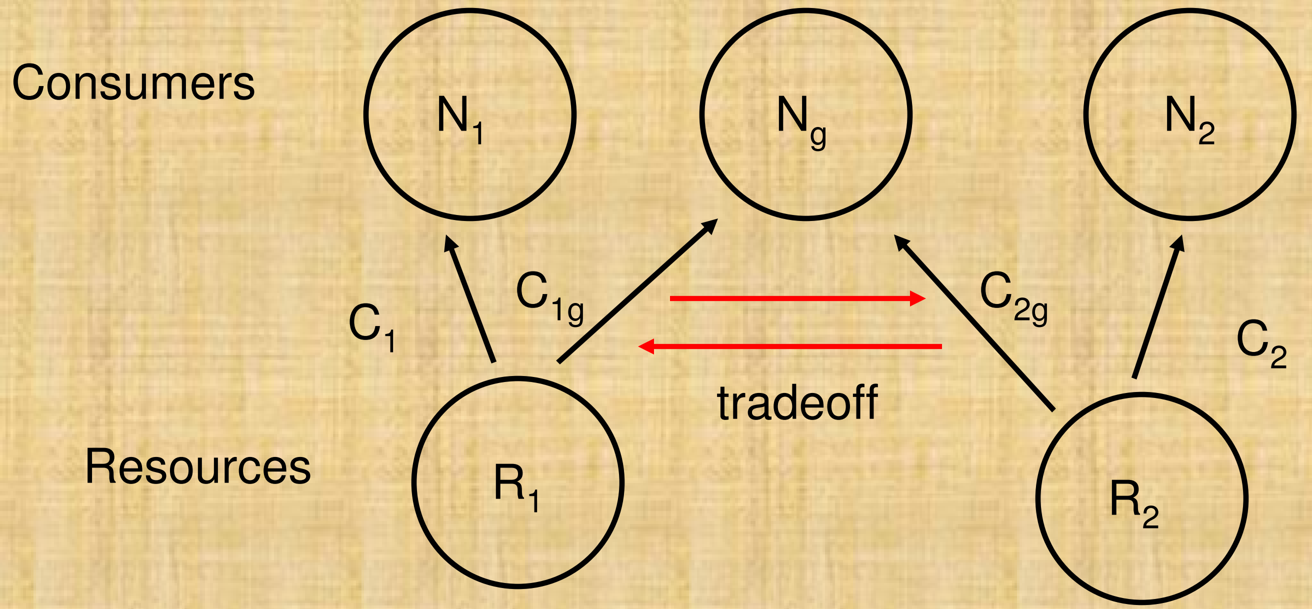
- Species must coexist to evolve (coevolve)
- Evolution may increase or decrease the coexistence bandwidth for a given pair of species
- Evolution within species usually makes stable communities less invasible by other species, by decreasing resource densities
- If evolution results in speciation into more specialized descendent species it increases diversity

# New Work: Coexistence and coevolution of specialists and generalists with little difference in response shape

- Most plants are fed upon by specialist and generalist herbivores
- Most herbivorous insects are attacked by both specialist and generalist parasitoids
- Many organisms are attacked by an array of specialists with different degrees of specialization

How do they coexist and coevolve?

# The foodweb




Consumer population dynamics are determined by resource consumption

If the generalist has capture rates, $C_{1g}$ and $C_{2g}$ based on a specified tradeoff; the position on this tradeoff curve may be fixed or flexible (behaviour)

PREREQUISITES FOR COEXISTENCE GIVEN SIMILAR FUNCTIONAL AND NUMERICAL RESPONSE SHAPES FOR ALL CONSUMER SPECIES

- Nonlinearity of consumer dynamics-saturating resource intake function
- Asynchronous resource fluctuations -due to differences in the two specialist-resource subsystems
- Generalist disadvantage under constant conditions

# Why are these prerequisites for coexistence?

- The generalist must have an advantage when it is rare, and that advantage must disappear when it gets common
  - Advantage is less variability in food intake, which occurs when fluctuations in abundance of the two resources differ
  - Variation in resource intake is bad because of the nonlinear functional response
  - Advantage disappears as generalist grows because an abundant generalist synchronizes fluctuations in different resources and (possibly) reduces their amplitude

# Specialist-generalist competition endogenous cycles-inflexible choice-1 habitat

$$\frac{dR_1}{dt} = I_1 + r_1 R_1 \left(1 - \frac{(R_1 + \alpha R_2)}{K_1}\right) - \frac{C_1 N_1 R_1}{1 + hC_1 R_1} - \frac{p^n C_1 N_g R_1}{1 + h\left(p^n C_1 R_1 + (1-p)^n C_2 R_2\right)}$$

$$\frac{dR_2}{dt} = I_2 + r_2 R_2 \left(1 - \frac{(R_2 + \alpha R_1)}{K_2}\right) - \frac{C_2 N_2 R_2}{1 + hC_2 R_2} - \frac{(1-p)^n C_2 N_g R_2}{1 + h\left(p^n C_1 R_1 + (1-p)^n C_2 R_2\right)}$$

Logistic resource growth with competition and immigration

$$\frac{dN_1}{dt} = N_1 \left(\frac{b_1 C_1 R_1}{1 + hC_1 R_1} - d_1\right)$$

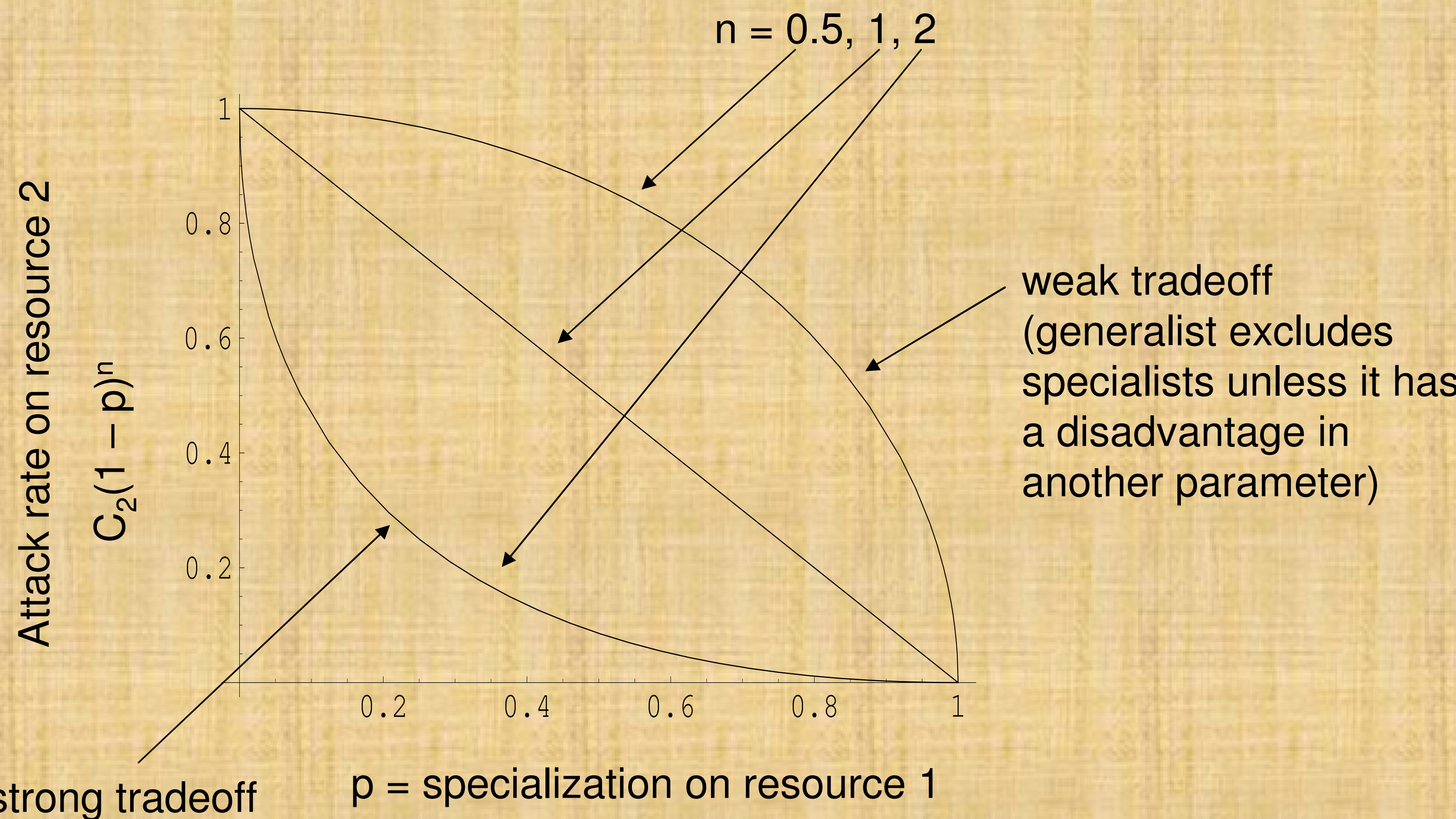
$$\frac{dN_2}{dt} = N_2 \left(\frac{b_2 C_2 R_2}{1 + hC_2 R_2} - d_2\right)$$

Saturating intake functions (functional responses)

$$\frac{dN_g}{dt} = N_g \left(\frac{b_g p^n C_1 R_1 + b_g (1-p)^n C_2 R_2}{1 + h\left(p^n C_1 R_1 + (1-p)^n C_2 R_2\right)} - d_g\right)$$

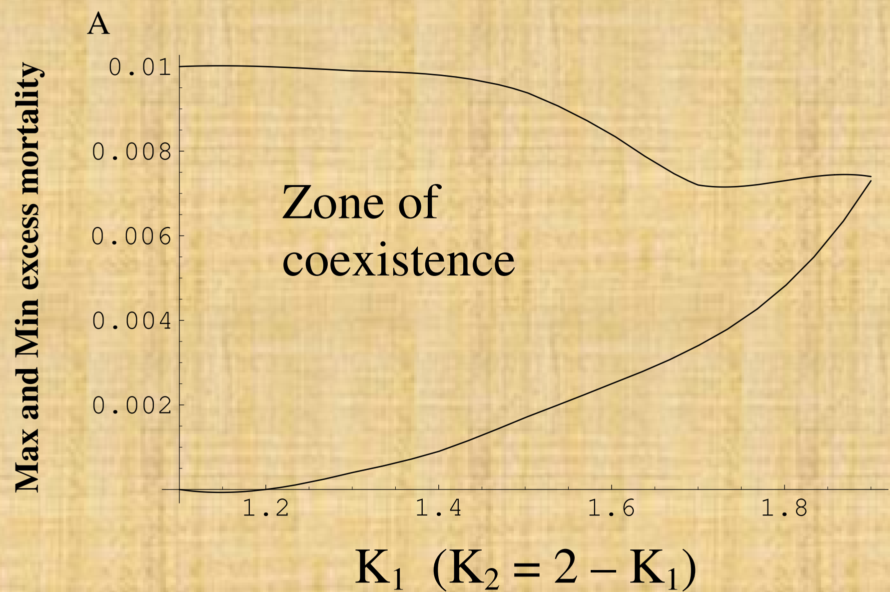
The generalist has a tradeoff with a shape determined by n. Value of resource choice trait, p, is fixed (for this part of the presentation)

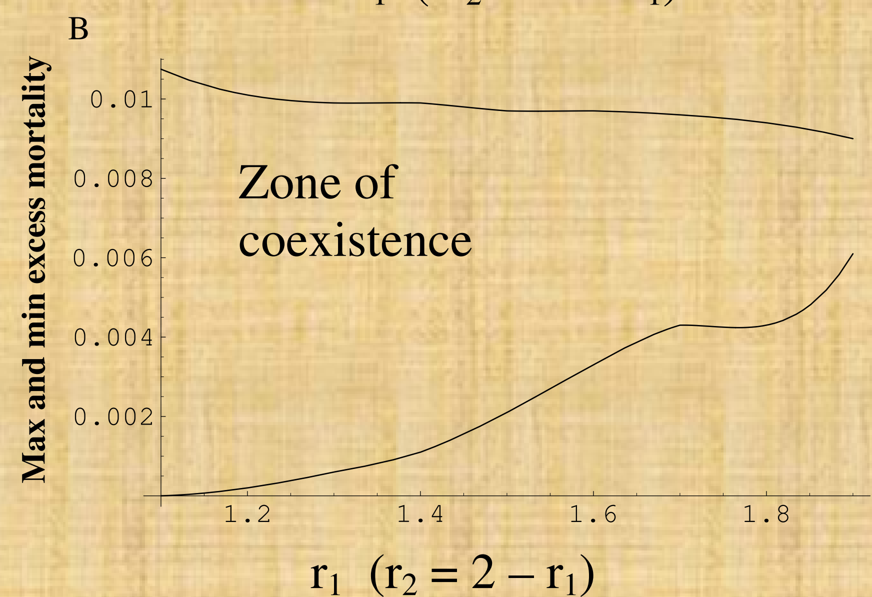
Tradeoffs exist due to: association of resource with habitat, or different morphological requirements for different resources (beak size in birds)




Fitness when $R_1 = R_2$ has intermediate minimum when $n > 1$ & intermediate maximum when $n < 1$

Quantifying coexistence; how much can the generalist mortality differ from that of the specialists, and still allow coexistence? {Resources differ in K or r}



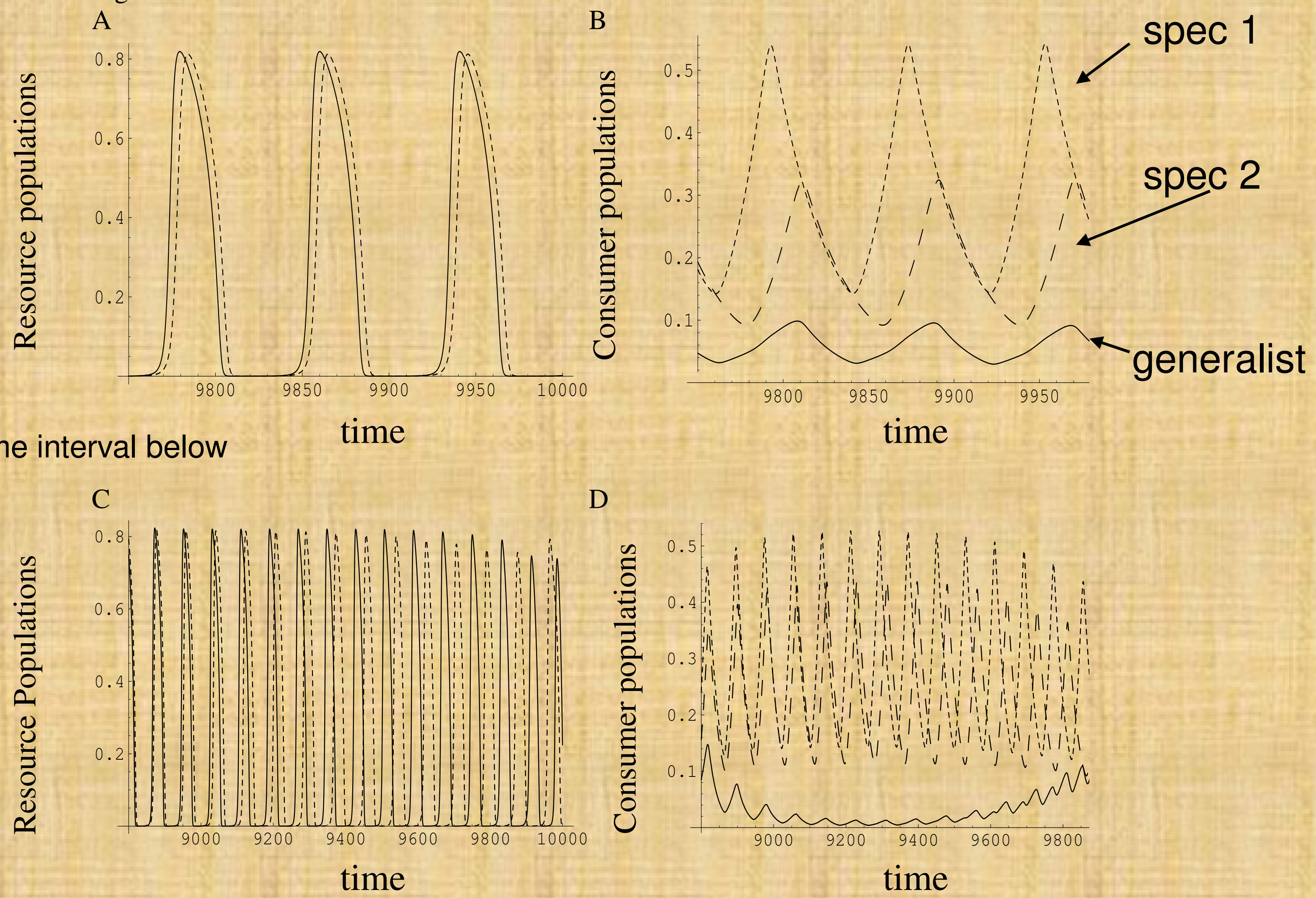




Note:

1. Assumes a linear (n=1) tradeoff with p constant (p = 0.5)
2. Maximum excess mortality in the absence of competition is 0.05333
3. Range of excess generalist mortality is 33% as large as specialist mortality, d = 0.03

Population dynamics when excess generalist mortality is low (top panels) or high (bottom panels); 1.5x difference in r-values for resources 1 (solid) and 2 (dashed)

Fig 2




longer time interval below

# Numerical results depend strongly on:

1. Large value of ChK (≥ approx. 4), or equivalent nonlinearity in response (ChK = ratio of 'handling' time to search time when $R_i$ = $K_i$)
2. Specialists ignore 'other' resource
3. Cycles due to endogenous cycles (exogenous can allow coexistence for a narrow range of parameters)
4. No behavioural choice (choice favours coexistence)
5. No competition between resources (competition favors coexistence)

# Numerical results relatively insensitive to:

1. Nature of resource growth (given cycles)
2. Differences between the maximum capture rates of the 2 resources, $C_1$, $C_2$
3. Tradeoff exponent, n, or specialization, p

Generalist coexists by consuming negative covariance in resource abundances

# Consequences of adding adaptive choice of resource in the generalist

The choice trait p has behavioral dynamics, modeled by independent fitness gradient dynamics of each of several behavioral 'types', i - (Abrams and Matsuda 2004. Population Ecology 46:13-25).

$$\frac{dp_i}{dt} = v\left(\frac{dW_i}{dp_i}\right) + \frac{\varepsilon}{p_i^{\,2}} - \frac{\varepsilon}{(1-p_i)^2}$$

dW/dp is rate of increase in fitness with a unit change in p

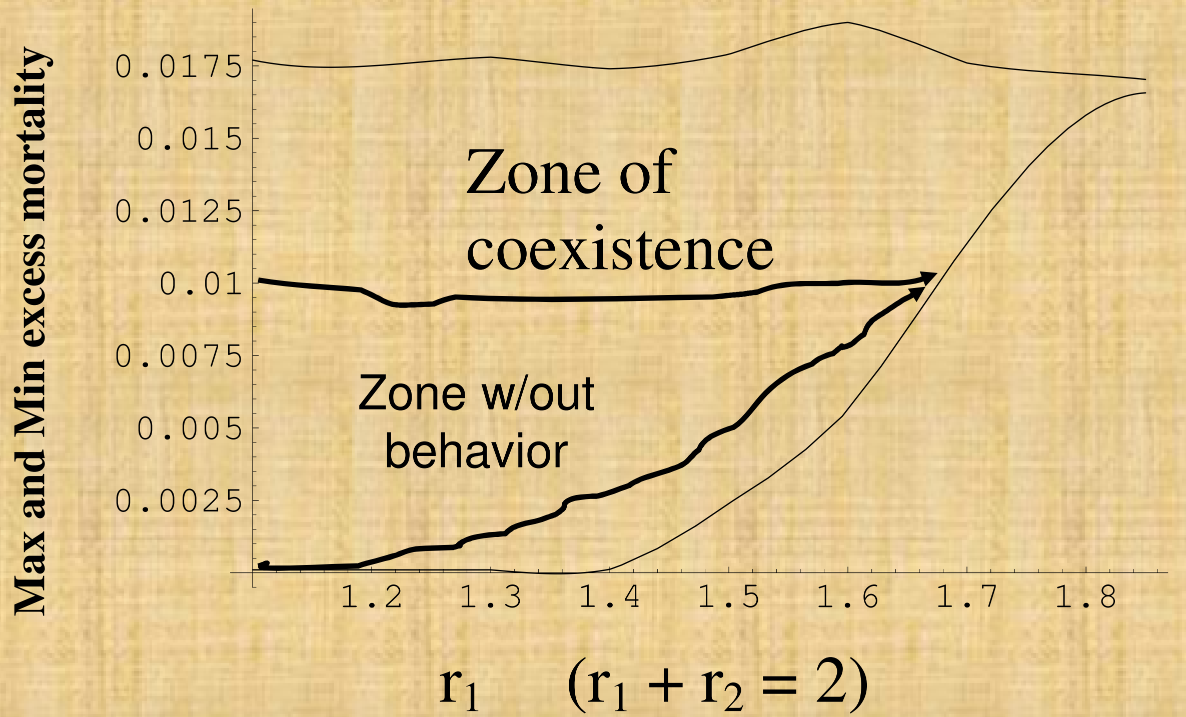
v is a constant of proportionality

ε is a very small number (e.g. $10^{-6}$)

ε terms represent biased behavioral change at extreme values

In most cases, different types converge to a single cycling strategy

"Coexistence bandwidth" with endogenous cycles and switching




n = 1

p shifts adaptively

GREATER COEXISTENCE BANDWIDTH BECAUSE

1. Cycle amplitude is damped by abundant switching generalists
2. Stronger resource synchronization due to more rapid response
3. Generalist can sustain a higher excess mortality because switching allows it to obtain more resources

# Other consequences of adaptive behavioural choice

1. Exogenous cycles often produce an even wider coexistence bandwidth than endogenous cycles (and more easily allow coexistence of 2 or more generalist types)
2. Coexistence becomes less sensitive to other variables (such as handling time)
3. Coexistence becomes less senstive to other aspects of the model (such as whether resources can be encountered in same habitat)

Will evolution of generalist lineages lead to (or eliminate) three or more coexisting types?

(Models with inflexible behavior)

# Evolution of the choice trait, p; endogenous cycles; summary

$$\frac{dp_i}{dt} = v\left(\frac{dW_i}{dp_i}\right) + \frac{\varepsilon}{p_i^{\,2}} - \frac{\varepsilon}{(1-p_i)^2}$$

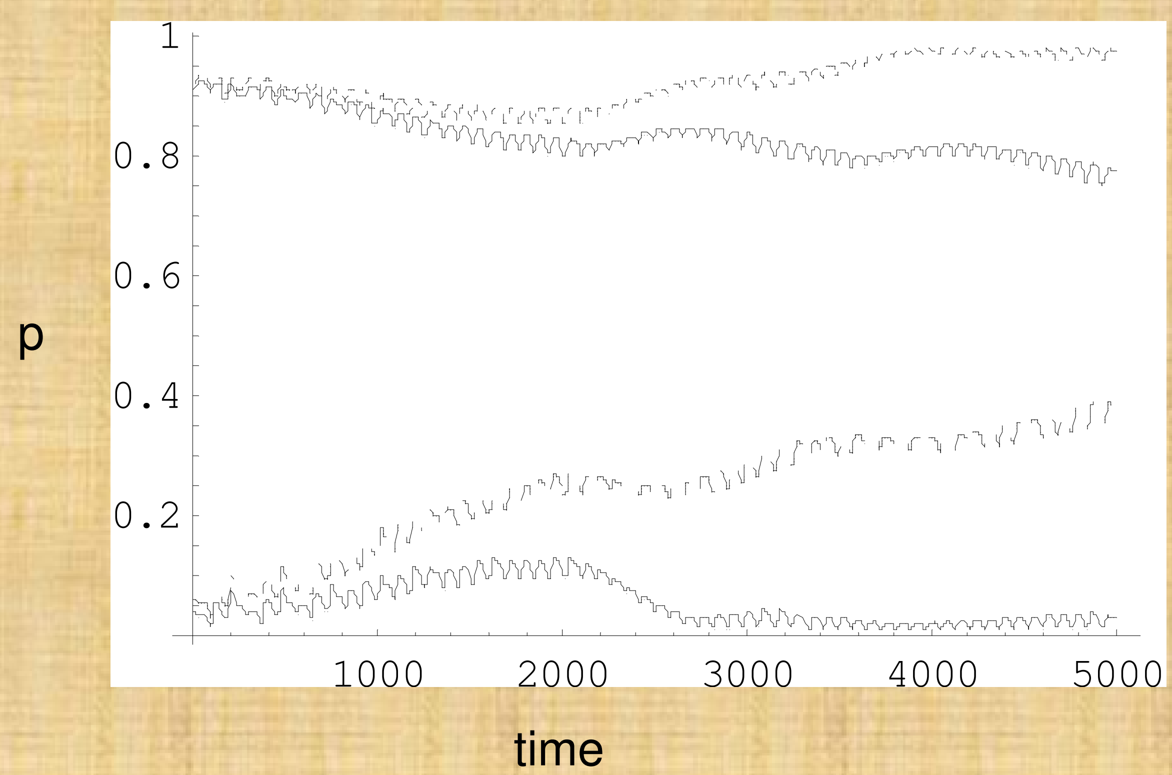
v << 1; ε reflects biased mutation near extreme p; several reproductively isolated types, i

1. If tradeoff is weak, only one type evolves
   - Generalist under stabilizing selection
   - Generalist is superior to specialists
2. If tradeoff is moderately strong (1 < n < 1.8*), trimorphism with 2 specialists and a generalist is common, given 3 or more lineages
3. If tradeoff is very strong (n > 1.8*), only dimorphism with two specialists when 2 or more lineages

*depends on magnitude of ChK

# Evolution of trimorphism depends on number of lineages, but seldom on initial trait values of lineages

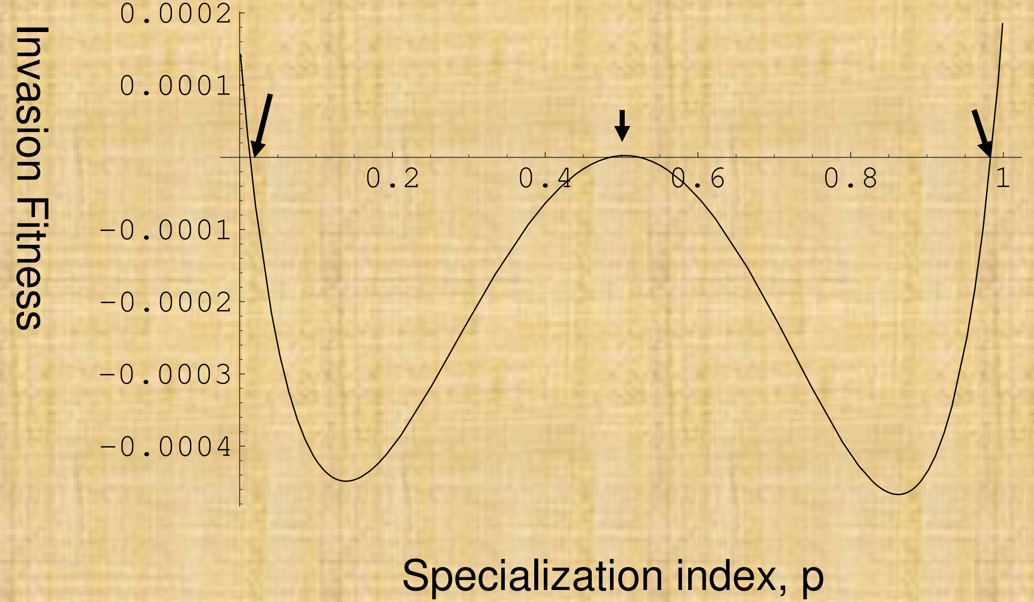
One generalist gives rise to 2 specialists; One or both specialists can always be invaded by a generalist, given the conditions




Example where the two specialist lineages each give rise to a new lineage, and the resulting new lineages eventually converge

# More than 3 lineages cannot both evolve and coexist (for systems studied so far)

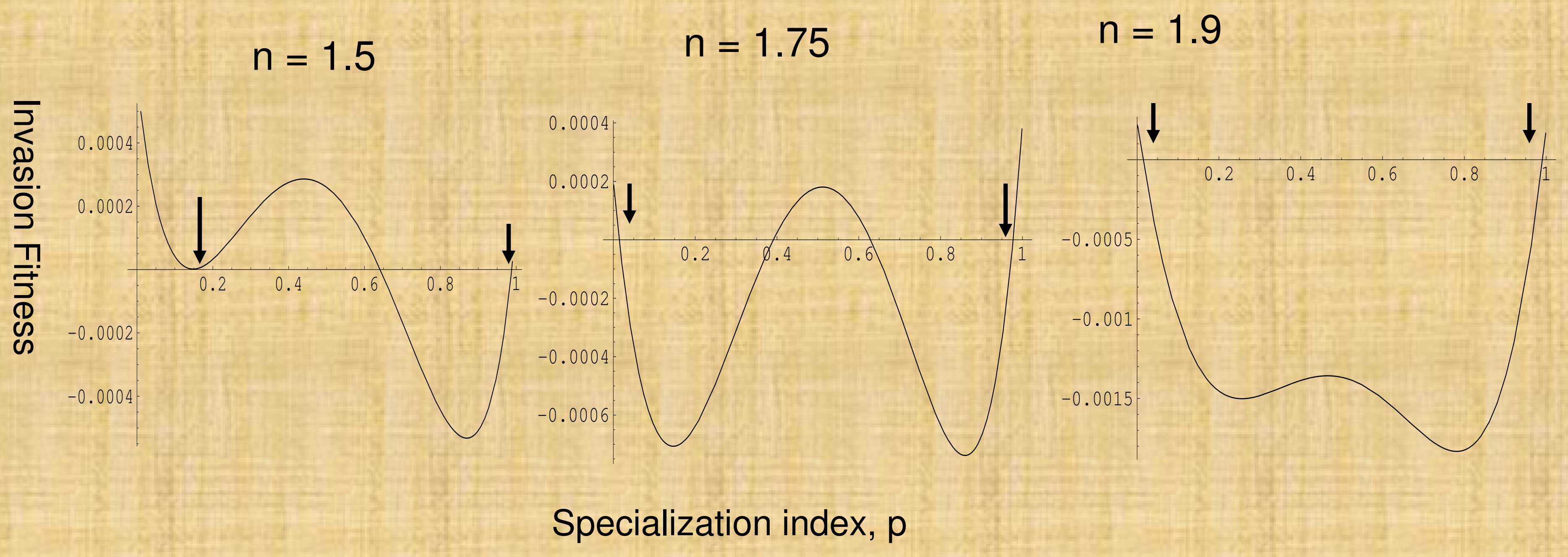
Fitness of a rare invading type with trait p, 3 resident types given by arrows




*Invasion fitness is negative except at inaccessible extreme values*

*Trimorphism occurs for most mortality rates within the range that yield cycles*

# Invasion fitness at a two-specialist evolutionary equilibrium-3 cases

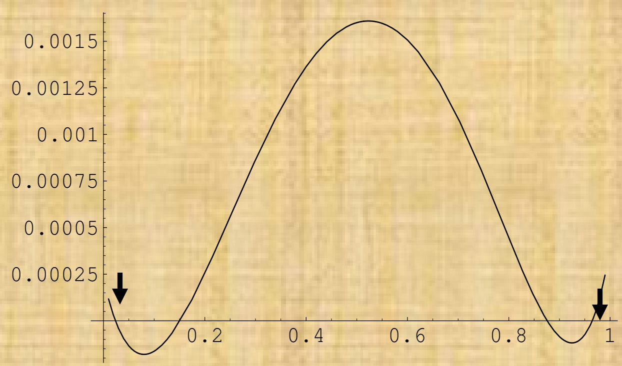



n = 1.75 can become trimorphic only if a new lineage with 0.4 < p < 0.6 invades

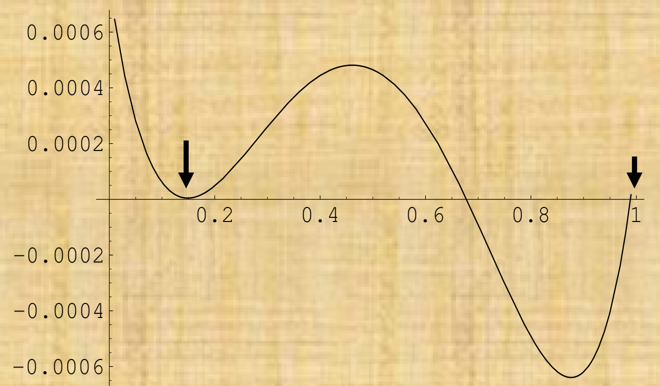
n = 1.9 case must remain dimorphic

# Some dynamic complexities

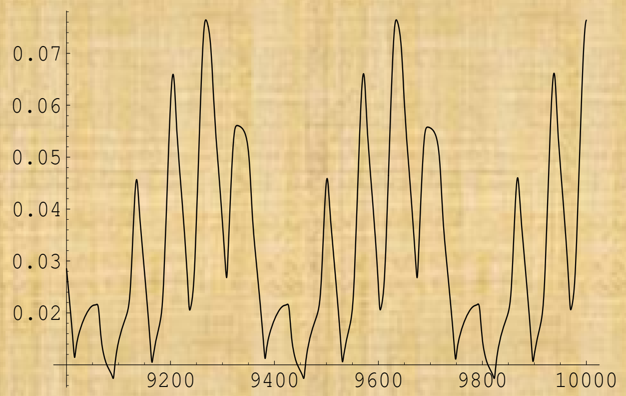
Attractor #1 for $n$ = 1.6
invasion fitness



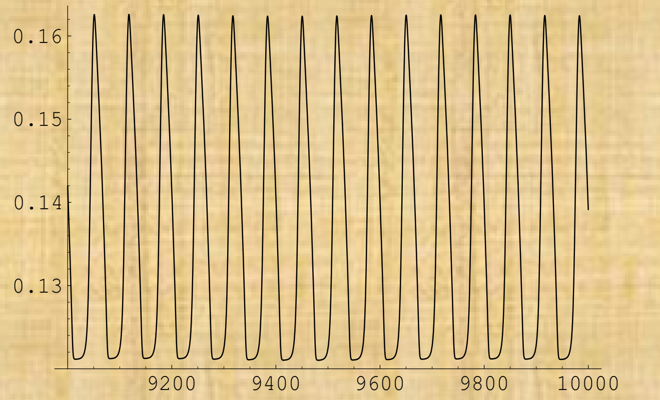

*Attractor* #2 for $n$ = 1.6
invasion fitness




$p_2$ vs. time #1 for $n$ = 1.6




$p_2$ vs. time #2 for $n$ = 1.6



# Conditions for diversification leading to a generalist + 2 specialists in the absence of behavioural switching

- Source of asynchronous cyclic dynamics needed
- Large ChK and endogenous cycles
- Moderately strong tradeoff $1 < n < 2$ (generalist must be able to coexist with same mortality as specialists)
- Death rates intermediate in range with cycles
- (Exogenous forcing can cause diversification for narrow range of parameters)

NOTE: If lineages differ in their underlying fitness functions, coexistence is easy to achieve, and evolution will expand the range of parameters allowing coexistence

Will evolution of generalist lineages lead to (or eliminate) three or more coexisting types?

(Models with *flexible* behavior)

A model of many consumer lineages sharing 2 resources, and adaptively changing via behavioral choice (determined by z) and morphology (determined by x)

$$\frac{dR_1}{dt} = f_1(R_1,t) - \sum_{i=1}^{i\max} \frac{F_1(z_i)C_1(x_i)N_iR_1}{1+h\left(F_1(z_i)C_1(x_i)R_1 + F_2(z_i)C_2(x_i)R_2\right)}$$

$$\frac{dR_2}{dt} = f_2(R_2,t) - \sum_{i=1}^{i\max} \frac{F_2(z_i)C_2(x_i)N_iR_2}{1+h\left(F_1(z_i)C_1(x_i)R_1 + F_2(z_i)C_2(x_i)R_2\right)}$$

$$\frac{dN_i}{dt} = N_i\left(b\frac{F_1(z_i)C_1(x_i)R_1 + F_2(z_i)C_2(x_i)R_2}{1+h\left(F_1(z_i)C_1(x_i)R_1 + F_2(z_i)C_2(x_i)R_2\right)} - d\right) = N_iW_i$$

$$\frac{dx_i}{dt} = v_x\left(\frac{dW_i}{dx_i}\right) + \frac{\varepsilon_x}{x_i^{\,2}} - \frac{\varepsilon_x}{(1-x_i)^2}$$

$$\frac{dz_i}{dt} = v_z\left(\frac{dW_i}{dz_i}\right) + \frac{\varepsilon_z}{z_i^{\,2}} - \frac{\varepsilon_z}{(1-z_i)^2}$$

$F_1$ and $F_2$ denote fractional changes in attack rates caused by the behavioural trait z.

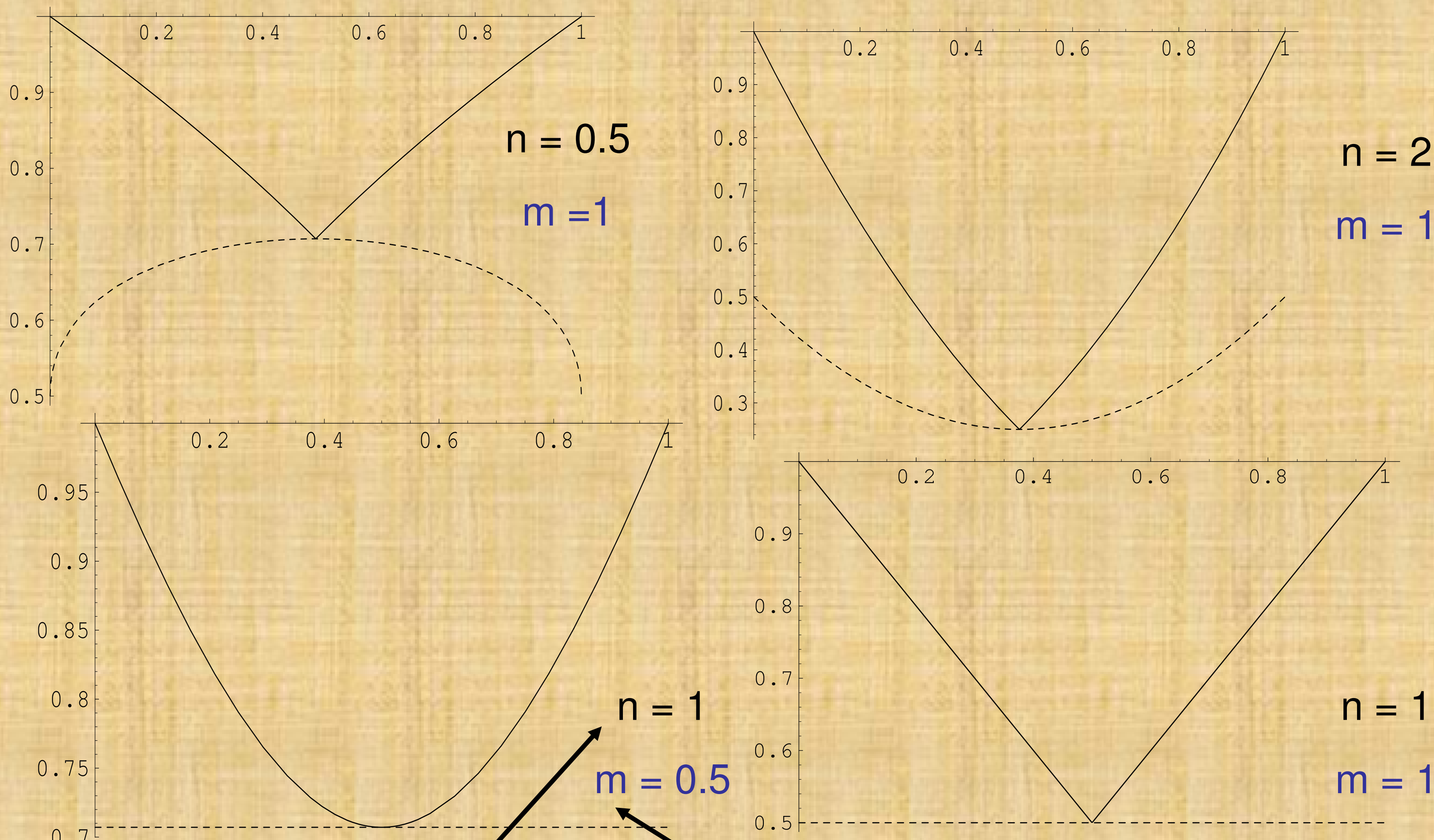
x is a morphological trait that determines relative specialization on resources 1 and 2;

$v_z >> v_x$

Assume $F_1 = z^m$; $F_2 = (1 - z)^m$; $C_1 = x^n$; $C_2 = (1 - x)^n$

case of very rapid behavioural choice

# Fitness vs. morphological trait x when $R_1 = R_2$
# Dashed line-random choice; solid-adaptive choice



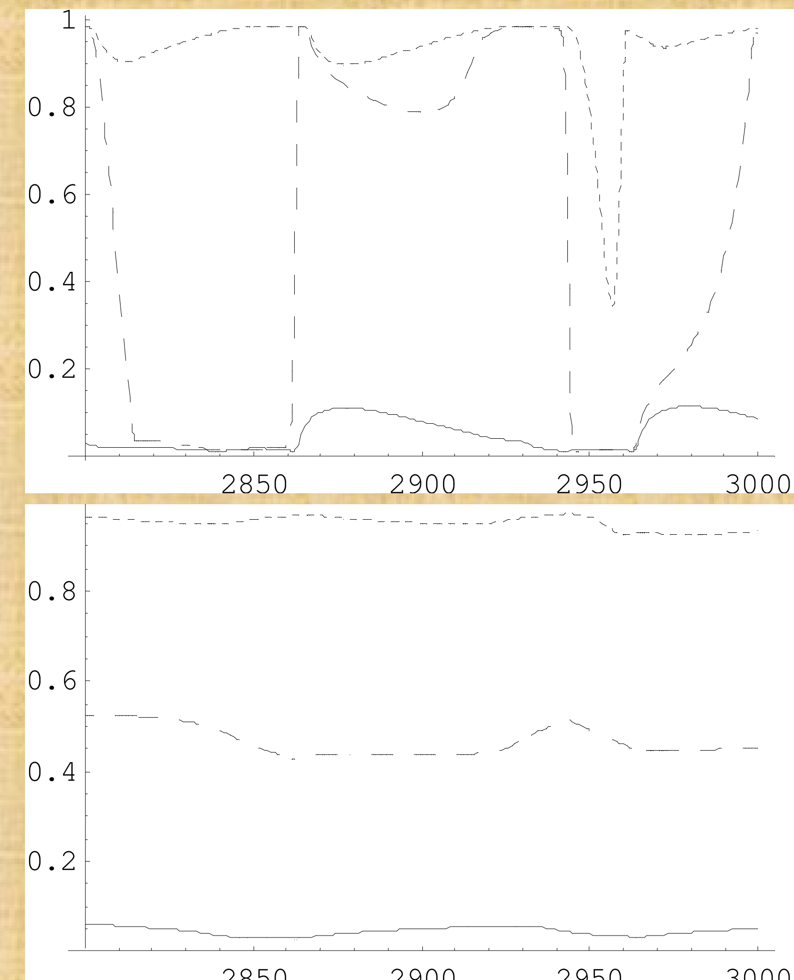

morphological tradeoff exponent

behavioural tradeoff exponent

- Adaptive choice changes the morphological trait-fitness relationship so that it always has a minimum for $p = 0.5$ when $n > 1 - m$
- Therefore, evolution of two lineages produces two specialists
- Behaviour improves chances for additional (3+ lineage) diversification.
  - Under **endogenous** cycles trimorphism occurs for wider range of n ($\sim 0.5 < n < \sim 2.5$)
  - Under **exogenous** cycles many consumer morpho-types can arise and persist

# An example of trimorphism under endogenous cycling

Final dynamics of traits in a system with $n = 3/2$; $v_x = 0.05$; $v_z = 20$; $r_1 = 1.5r_2$

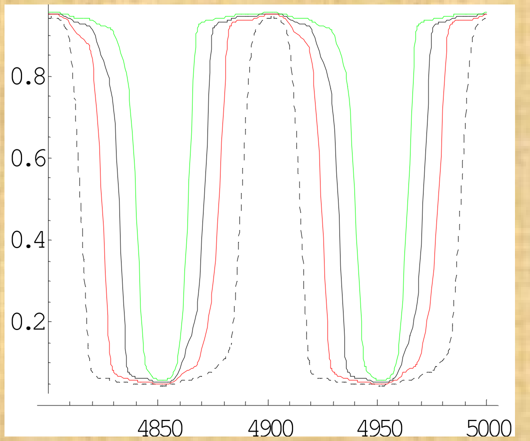



Behavioral traits at trimorphic cycle (solid line is the species specialized on resource 2; short dashed line-resource 1 specialist; long dashed line-generalist)

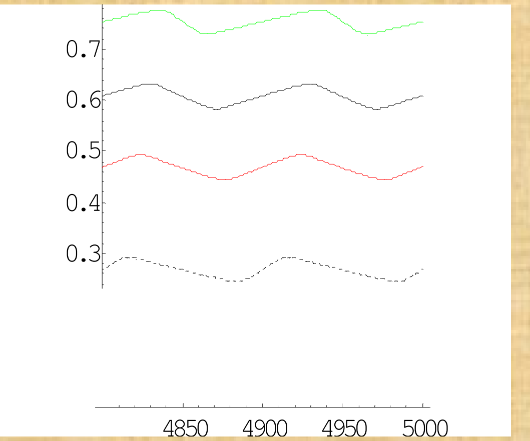
Corresponding morphological traits on a 0-1 scale

# An example of multimorphism (4 types) under exogenous cycling

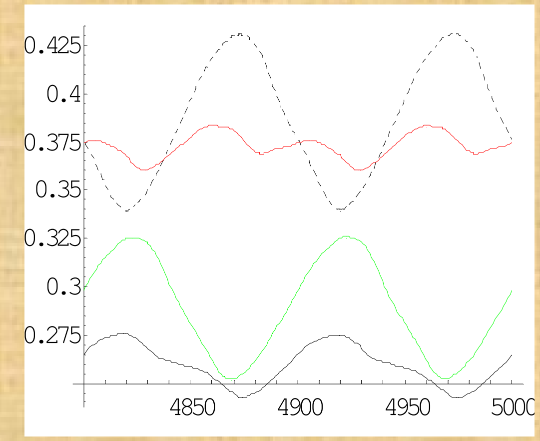
Behavioural traits



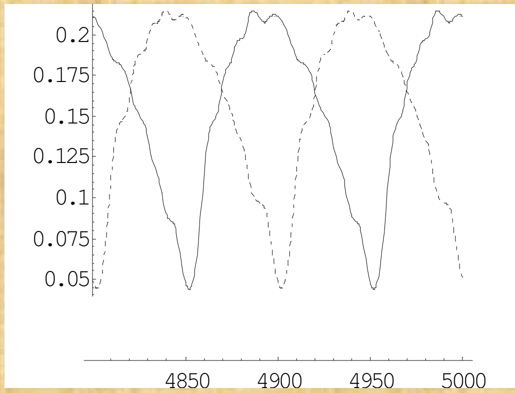

Morphological traits




Consumers




Resources




Model has abiotic resources; equal input rates

n = 1/2;  m = 1;

out-of-phase sinusoidal variation in input with period of 100; range .05-1.95xmean

# Summary of new work

1. Variable resource densities in systems with 2+ resources can allow coexistence by a different mechanism than in single resource systems

2. Evolution can often produce the maximum diversity that is permitted by coexistence

3. Behaviour plays a key role in allowing both coexistence and evolutionary diversification.

# Why are these results important?

- They add significantly to the < 5 theoretical analyses of the coevolution of competing species in variable environments
- They argue for studying the variation of generalist abundance with resource cycle synchronization (apparently never done)
- They provide another argument for including behaviour in ecological models (something that is almost never done)
- They may eventually help develop conservation plans for endangered species in variable environments