

Keep Moving

Topic 1. Fish Movement in the Everglades

Topic 2. Evolutionarily Stable Strategy for
Movement among Patches When There Are
Travel Losses



Donald L. DeAngelis, U. S. Geological Survey and University of Miami

Yuan Lou, Ohio State University

Gail Wolkowicz, McMaster University

Simeon Yurek, University of Miami

“Everything Disperses to Miami,” University of Miami, 13-15 December 2012

Both topics involve inspiration from and/or collaboration with Chris Cosner

Topic 1 can be traced in part to



Available online at www.sciencedirect.com



Theoretical Population Biology 67 (2005) 101–108

**Theoretical
Population
Biology**

www.elsevier.com/locate/ytobi

A dynamic model for the ideal-free distribution as a partial differential equation

Chris Cosner*

Department of Mathematics, University of Miami, Room 515, Ungar Computer Center, 1365 Memorial Drive, Coral Gables, FL 33124, USA

Cosner showed that partial differential equation models of dispersal in a spatial context could be formulated whose equilibria are solutions to a dynamic version of the ideal free distribution in continuous space.

This idea of active movement in response to habitat quality is incorporated in the work I will talk about modeling dynamics of the small fish functional group in the Everglades.

Topic 1: A basic question of Everglades research and restoration

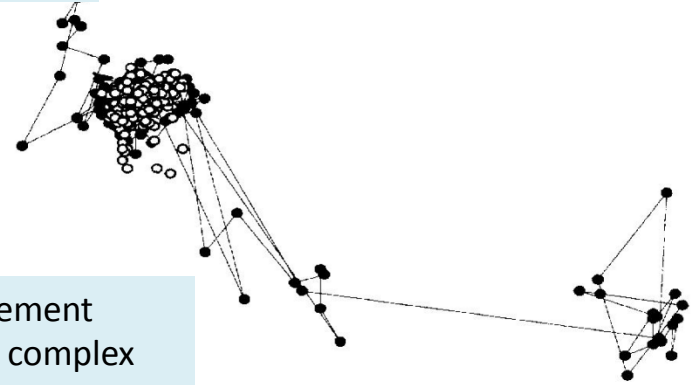
How do the landscape topography, seasonal hydrology (wet and dry seasons), the food base, and movement behavior of fish interact to create of available fish (through concentration and local stranding) to higher trophic levels, especially wading birds?

Study of fish dynamics in real ecosystem such as the Everglades can be difficult ...

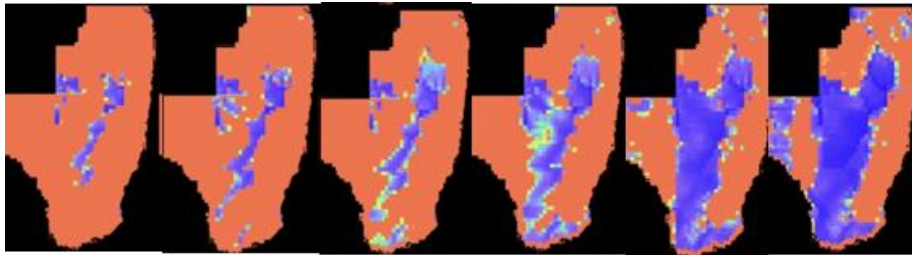


The physical environment is complex

Animal movement patterns are complex

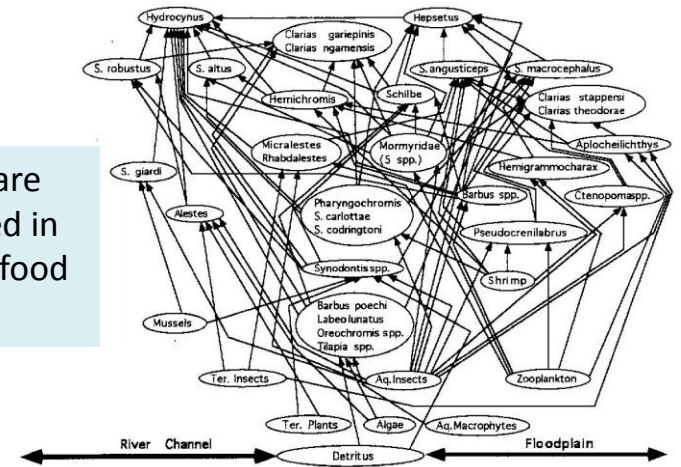


Aquatic habitat varies through time



Blue indicates flooded area over the wet season

Animals are enmeshed in complex food webs

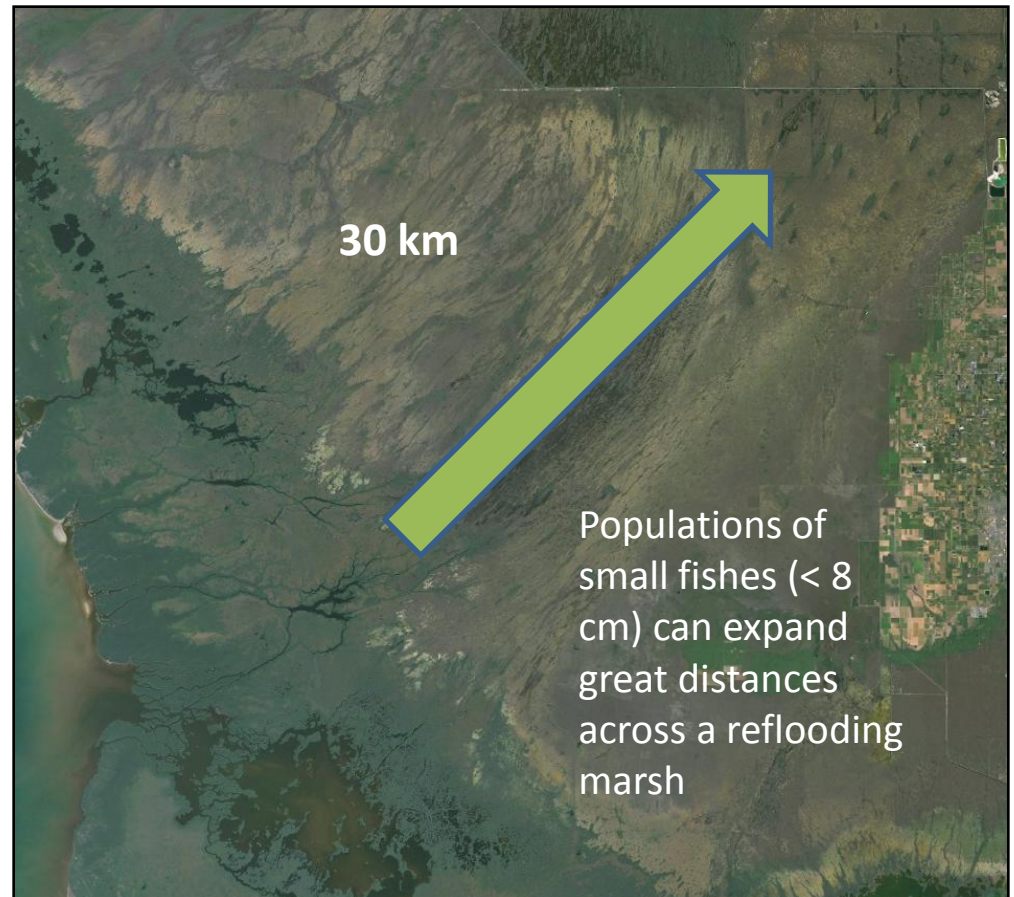


... However, well-focused questions can sometime be addressed with simple models and provide a basis for more detailed modeling.

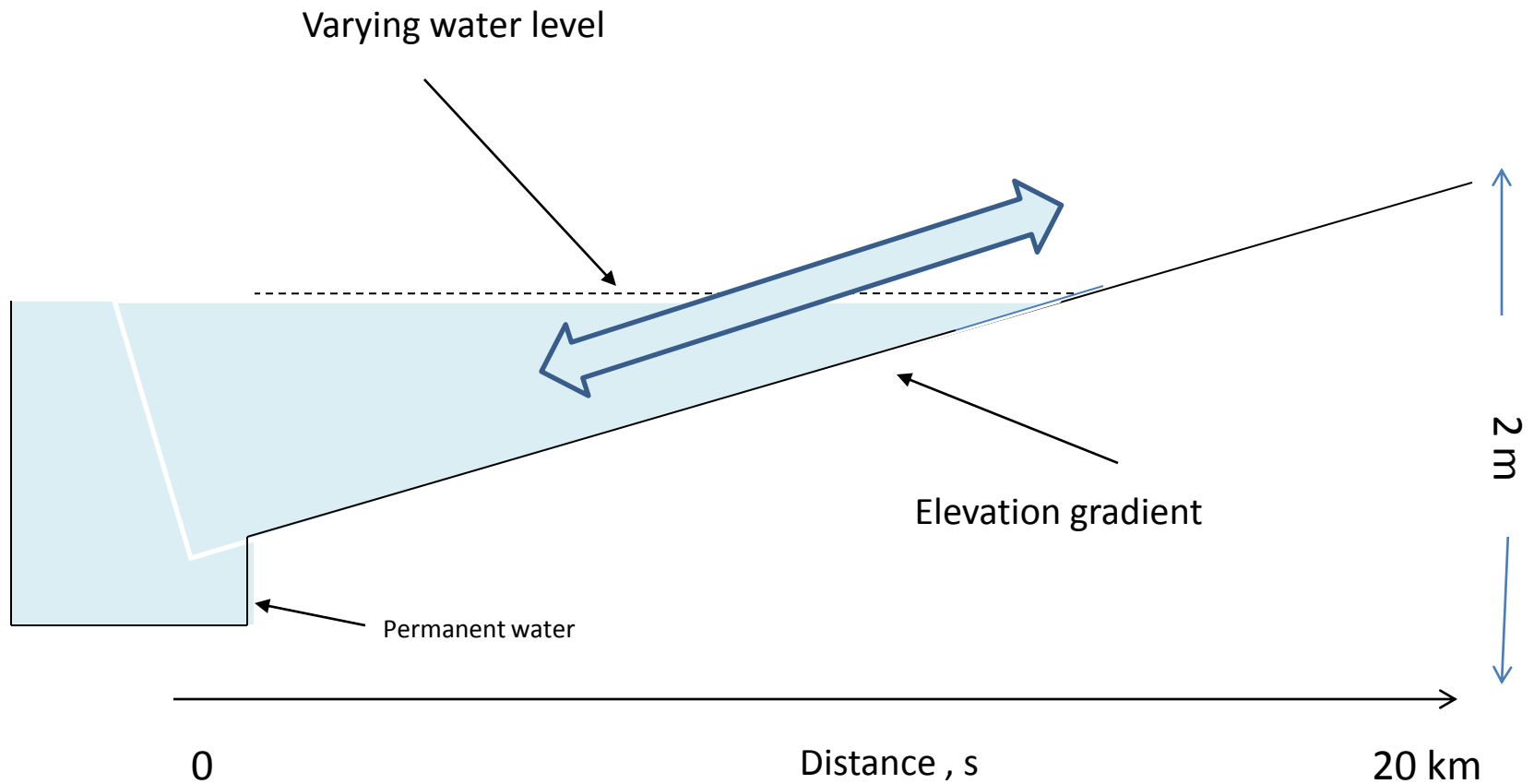
Fish movement in the Everglades

Question: Can diffusional movements of fish explain the ability of populations of small fishes to expand 10's of kilometers into newly flooded marsh, or is more directed movement necessary?

DeAngelis, D. L., J. C. Trexler, C. **Cosner**, A. Obaza, and F. Jopp. 2010. Fish population dynamics in a seasonally varying wetland. *Ecological Modelling* 221:1131-1137.



We assume a simple one-dimensional landscape along an elevation gradient over 20 km



Diffusion model of fish movement

A simple model with only diffusion by fish $F(s,t)$ and a stationary prey, $R(s,t)$, whose growth is triggered when the area is flooded (i.e., $\theta(s,t) = 1$ when area is flooded) and predation is a predator-dependent functional response, is

$$\frac{dR(s,t)}{dt} = r \left(\theta(s,t) - \frac{R(s,t)}{K} \right) R(s,t) - \frac{fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)}$$

Prey biomass

$$\frac{\partial F(s,t)}{\partial t} = \frac{\gamma R(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)} - mF(s,t) + D \frac{\partial^2 F(s,t)}{\partial s^2}$$

Fish biomass

Estimate of fish diffusion rate was needed, and was obtained from field studies



Minnow traps embedded in drift fences, underwater photography, and catch-per-unit effort estimates with throw traps were combined to estimate random velocities of fish. This was shown to vary seasonally and among species, ranging from 0.05 to $0.15 \text{ m}\cdot\text{sec}^{-1}$ for small poeciliids and killifishes to 0.1 to $1.5 \text{ m}\cdot\text{sec}^{-1}$ for *L. marginatus*.

These velocities were used to estimate diffusion rates.

Obaza, A., D. L. DeAngelis, and J. C. Trexler. 2011. Using data from an encounter sampler to model fish dispersal. *Journal of Fish Biology* 78:495-513.

An alternative hypothesis is active following of resource gradient by fish

But pure diffusion is only one hypothesis. We alternatively assume that the fish can follow that resource gradient, where again the resource growth is triggered when an area becomes flooded. The equations are

$$\frac{dR(s,t)}{dt} = r \left(\theta(s,t) - \frac{R(s,t)}{K} \right) R(s,t) - \frac{fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)}$$

Prey biomass

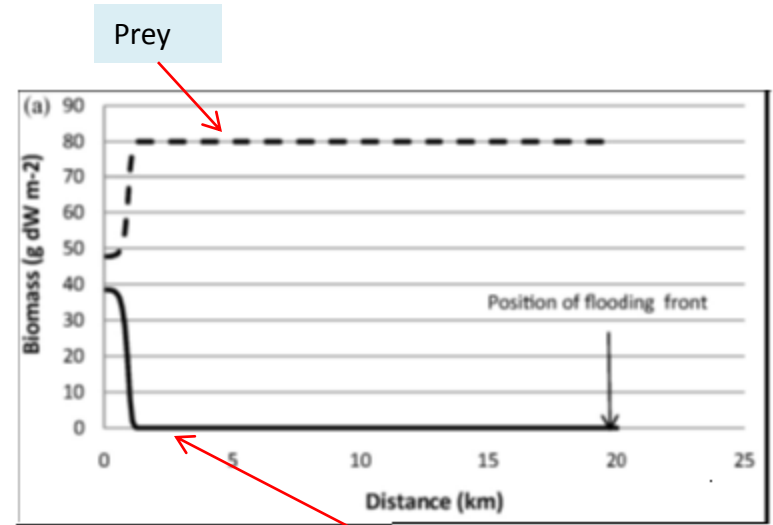
$$\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fR(s,t)F(s,t)}{1 + hfR(s,t) + wfF(s,t)} - mF(s,t) - \frac{\partial}{\partial s} \left[\epsilon \frac{\partial R(s,t)}{\partial s} F(s,t) \right]$$

Fish biomass

This can be called the 'dynamic IFD hypothesis'

These can be solved numerically over a 100 day flooding period with initial conditions.

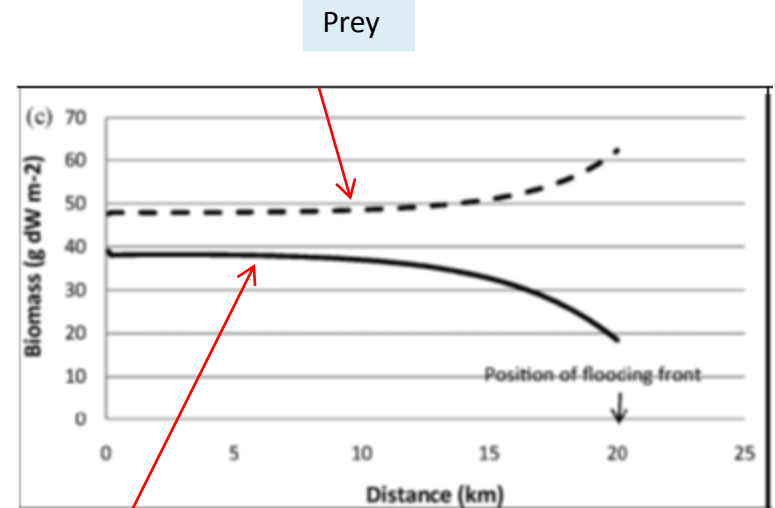
Top. Diffusion alone, with our best estimate of the diffusion coefficient.



Fish population does not advance to 1.5 km

Bottom. Advective following of resource (prey) gradient, given an estimate of the advection coefficient.

Although the advection coefficient is chosen arbitrarily, it is evident that fish following the prey gradient is more effective than diffusion at filling the seasonally flooded marsh.



Fish population advances with flooding front

Extending the lesson of fish active movement to complex situations through simulations

We are interested in real Everglades landscapes and want to address basic problem of fish stranding, as a function of topography, hydrology, and fish traits (growth rate, movement characteristics).

This led to some simulation modeling using ideas from the preceding implications on fish movement.

Spatially explicit mechanistic modeling of dynamic hydrology driving small fish biomass dispersal and stranding

S. Yurek^{a,e}, D. L. DeAngelis^{a,b}, J. C. Trexler^c, F. Jopp^a, and D. D. Donalson^d

^aDepartment of Biology, University of Miami

^bSoutheast Ecological Science Center, USGS, University of Miami





^cDepartment of Biological Sciences, Florida International University, Miami, FL

^dU.S. Army Corps of Engineers, Jacksonville, Florida

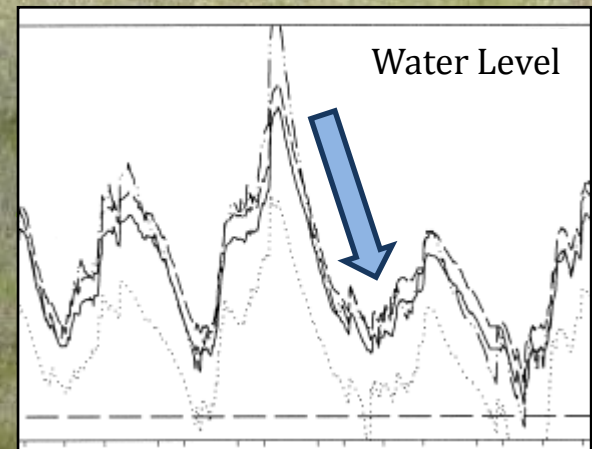


The community of small Everglades fishes is of interest here

TABLE 5.1
Fishes Collected by Throw-Trap Between July 1996 and April 1997
from Everglades Marsh Study Plots

	Species	Common Name	Total Collected	Maximum No. per m ²
	<i>Lepisosteus platyrhincus</i>	Florida gar	1	1
	<i>Esox niger</i>	Chain pickerel	5	1
	<i>Notropis maculatus</i>	Taillight shiner	1	4
	<i>Notropis petersoni</i>	Coastal shiner	60 ^b	9
	<i>Erimyzon sucetta</i>	Lake chubsucker	145 ^b	5
	<i>Ameiurus natalis</i>	Yellow bullhead	29	3
	<i>Noturus gyrinus</i>	Tadpole madtom	8	1
	<i>Clarias batrachus</i> (I) ^a	Walking catfish	4	3
	<i>Cyprinodon variegatus</i>	Sheepshead minnow	41 ^b	11
	<i>Fundulus chrysotus</i>	Golden topminnow	1,844 ^b	10
	<i>Fundulus confluentus</i>	Marsh killifish	87 ^b	4
	<i>Fundulus seminolis</i>	Seminole killifish	1	1
	<i>Jordanella floridae</i>	Flagfish	1,783 ^b	34
	<i>Lucania goodei</i>	Bluefin killifish	8,391 ^b	33
	<i>Lucania parva</i>	Rainwater killifish	1	1
	<i>Belonesox belizanus</i> (I) ^a	Pike killifish	3	1
	<i>Gambusia holbrooki</i>	Eastern mosquitofish	9,825 ^b	98
	<i>Heterandria formosa</i>	Least killifish	12,713 ^b	65
	<i>Poecilia latipinna</i>	Sailfin molly	1,699 ^b	48
	<i>Labidesthes sicculus</i>	Brook silverside	5	2
	<i>Elassoma evergladei</i>	Everglades pygmy sunfish	487 ^b	9
	<i>Enneacanthus gloriosus</i>	Bluespotted sunfish	238 ^b	6
	<i>Chaenobryttus gulosus</i>	Warmouth	18	3
	<i>Lepomis macrochirus</i>	Bluegill	6	1
	<i>Lepomis marginatus</i>	Dollar sunfish	14	1
	<i>Lepomis microlophus</i>	Redear sunfish	55 ^b	4
	<i>Lepomis punctatus</i>	Spotted sunfish	197 ^b	11
	<i>Lepomis</i> sp.	Unidentified sunfish	16	?

Their dynamics during the drying phase (December through May) is of particular interest, as the fish can become concentrated and stranded.



Chick et al., 2004

Drying phase:
Falling water levels

- Seasonal marshes disappear
- Habitat contracts
- **Concentration of prey items**
- **Organisms become stranded**

This will help predict food availability for higher trophic levels

As water levels go down during the dry season, some fish become trapped and concentrated in isolated depressions.



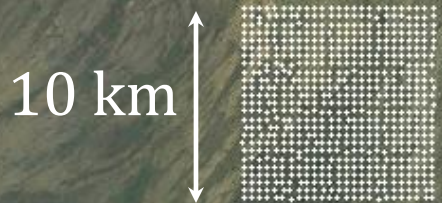
These concentrations of stranded fish provide food for wading bird breeding colonies.



Our goal is to predict the spatio-temporal pattern of fish stranding...

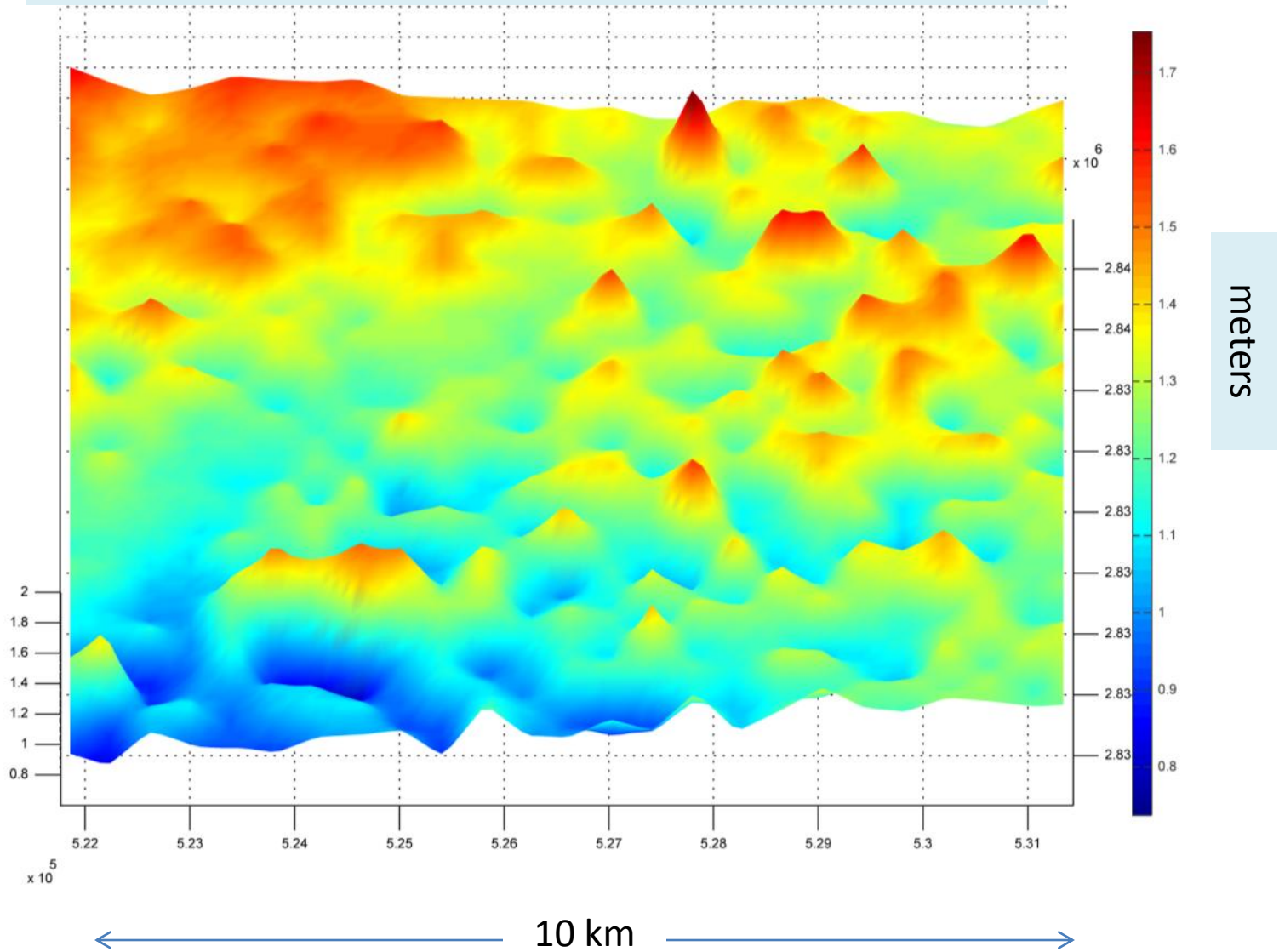
Greater Everglades, Florida, USA

For illustrative purposes here, we consider a part of the real landscape

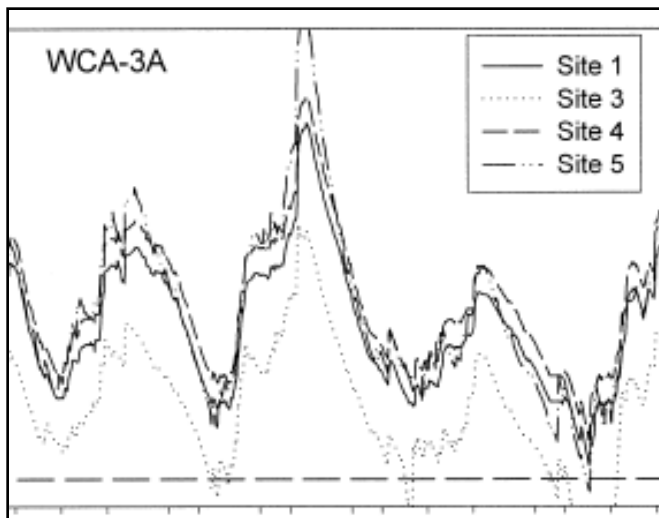
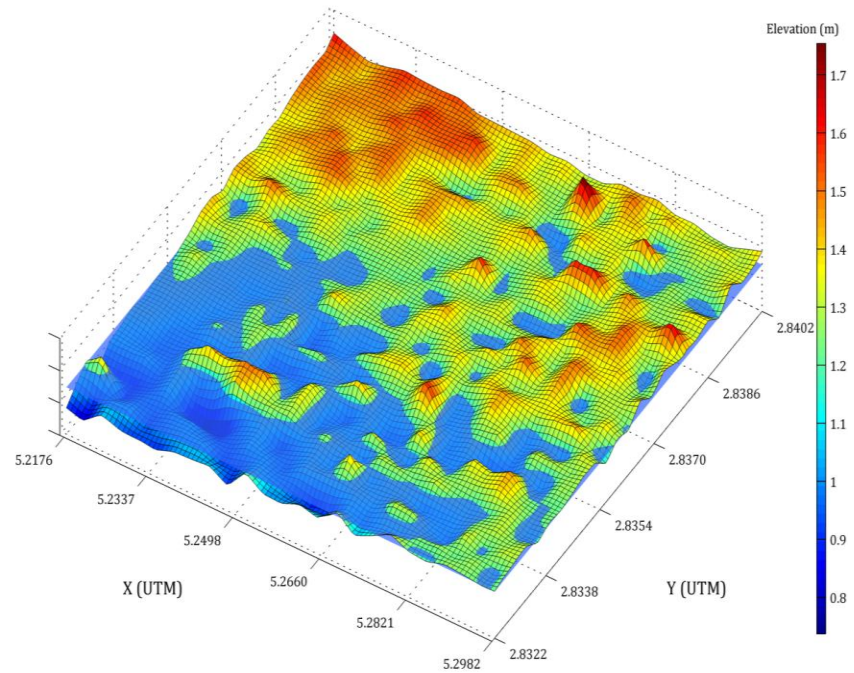


Gulf of Mexico

Shark River Slough USGS's HAED elevation interpolation mesh



Real Everglades landscapes, such as this 10 km x 10 km section, are modeled using 100 x 100 grid of 100 x 100 meter cells...



...using water level variation similar to real seasonal variation in water level

The different model fish species are given different traits

Fish 1:

- Early colonizer of newly flooded areas.
- Tends to become stranded in cells during drydown



Fish 3:

- Late colonizer of newly flooded areas
- Tends to escape cell during drydown.



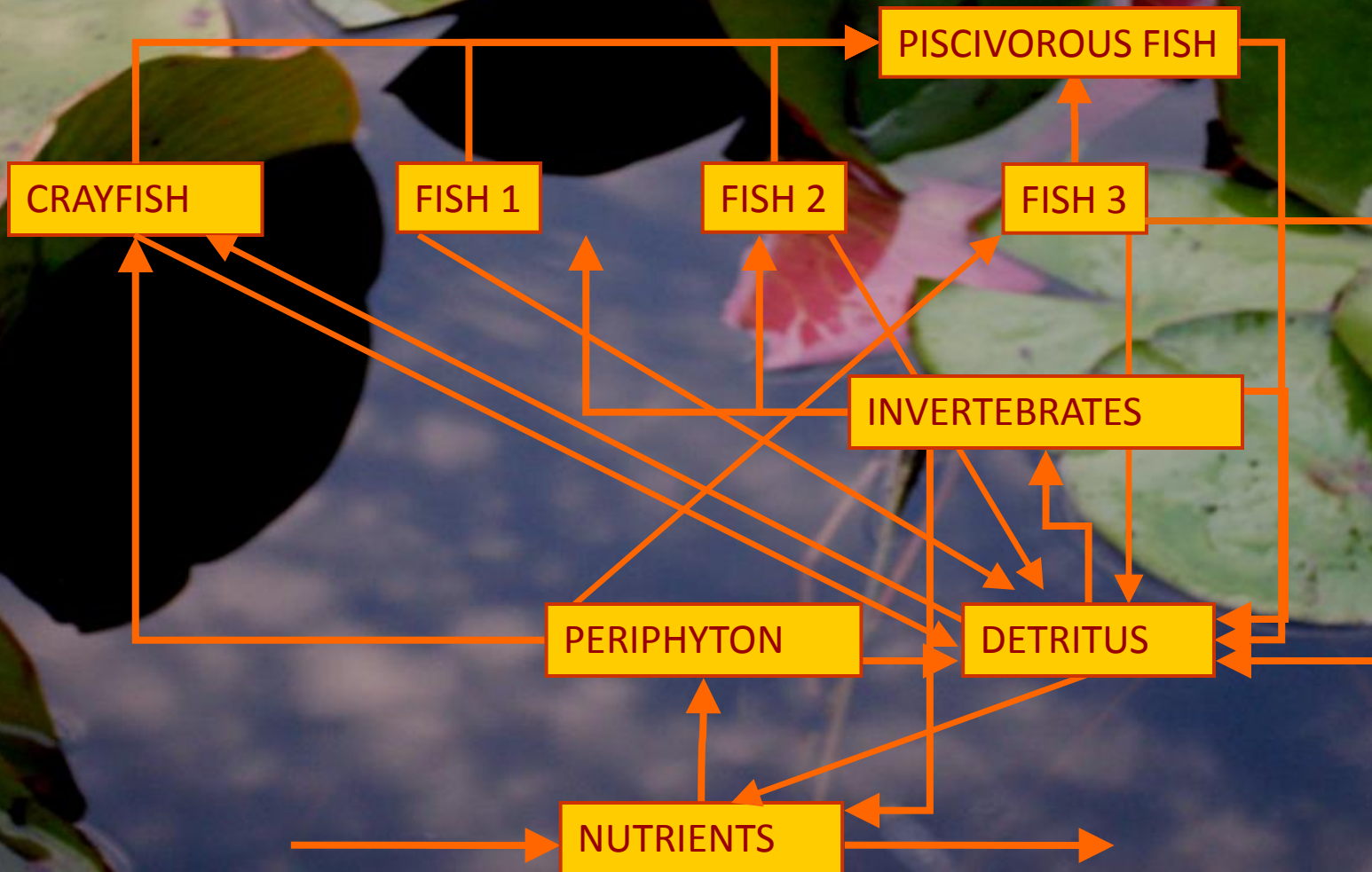
Fish 2:

- Intermediate personality

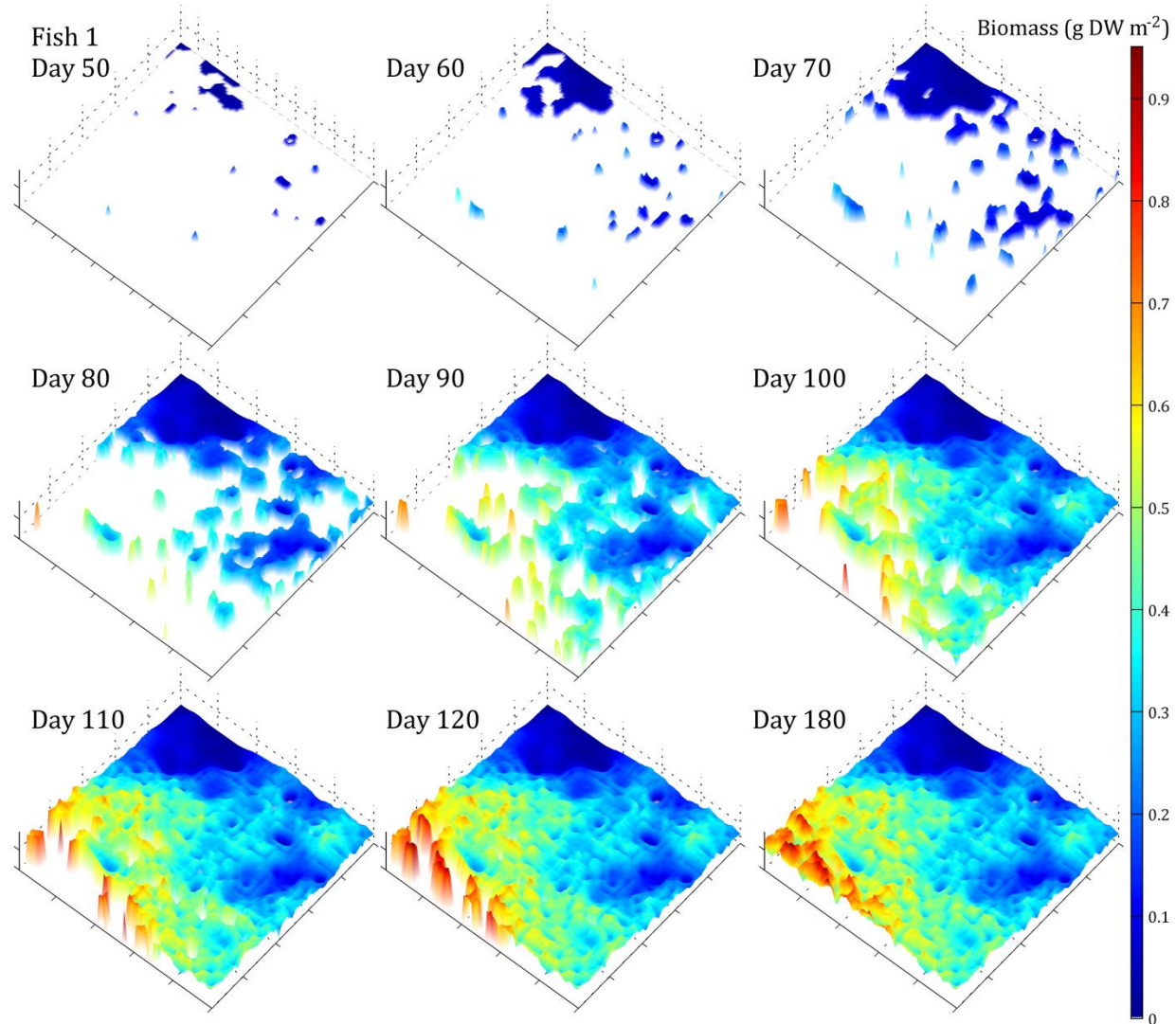


... and they are enmeshed in simplified but reasonable food webs by trophic interactions

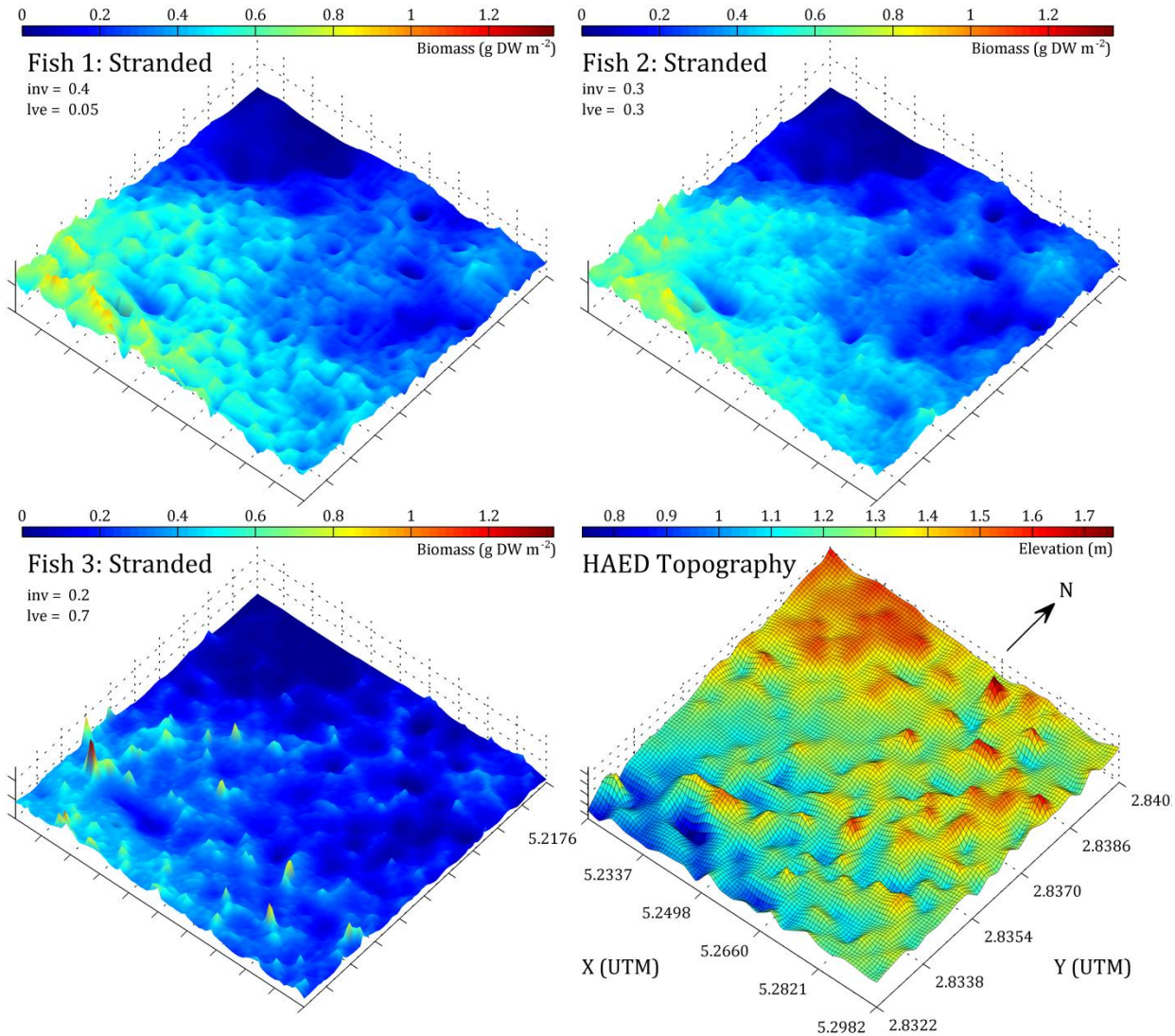
The results of some simulations are shown in the next few film clips created by Simeon Yurek.



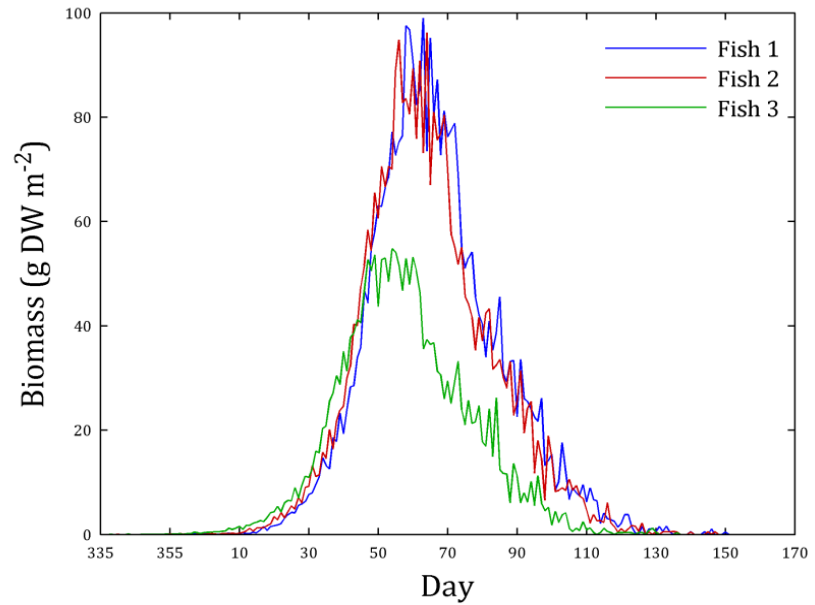
As water levels recede, stranding of fish starts to occur (on about day 50 of the calendar year) and continues throughout the period of drydown.



Cumulative strandings of Fish 1, 2, and 3 at end of drydown period



This shows the temporal pattern of fish stranding over the whole simulated area, showing availability of stranded fish over more than 100 days.



Conclusion. We can predict temporal pattern and locations of potential concentration of stranded fish (i.e. UTM coordinates) created by combinations of landscape topography, seasonal hydrology, and fish movement behavior.

We are proposing to study this more exhaustively on the Everglades landscape and attempt to confirm results empirically, perhaps by looking for phosphorus fingerprints of fish concentrations.

There is increasing theory concerning spatial movement

Topic 2: Evolutionarily Stable Strategy for Movement among Patches When There Are Travel Losses

This paper played a role in stimulating research on this topic described below.

Journal of Biological Dynamics
Vol. 1, No. 3, July 2007, 249–271



The ideal free distribution as an evolutionarily stable strategy

ROBERT STEPHEN CANTRELL*†, CHRIS COSNER†, DONALD L. DEANGELIS‡
and VICTOR PADRON§

†Department of Mathematics, University of Miami, USA

‡Department of Biology, University of Miami and U.S. Geological Survey, USA

§Institute of Mathematics and its Applications, Minneapolis, USA

Some findings of Cantrell et al. (2007), investigating evolutionary stability of dispersal strategies

Balanced dispersal, in which the equilibrium densities of organisms on each patch are the same whether there is dispersal or not, is shown to be an evolutionarily stable strategy in some settings.

Balanced dispersal leads to an IFD at equilibrium, as all individuals have the same fitness and there is no net movement of individuals between patches or states. Under general assumptions about the underlying population dynamics or species interactions, only such ideal free strategies can be evolutionarily stable.

Under somewhat more restrictive, but still general, assumptions, only such ideal free strategies are evolutionarily stable.

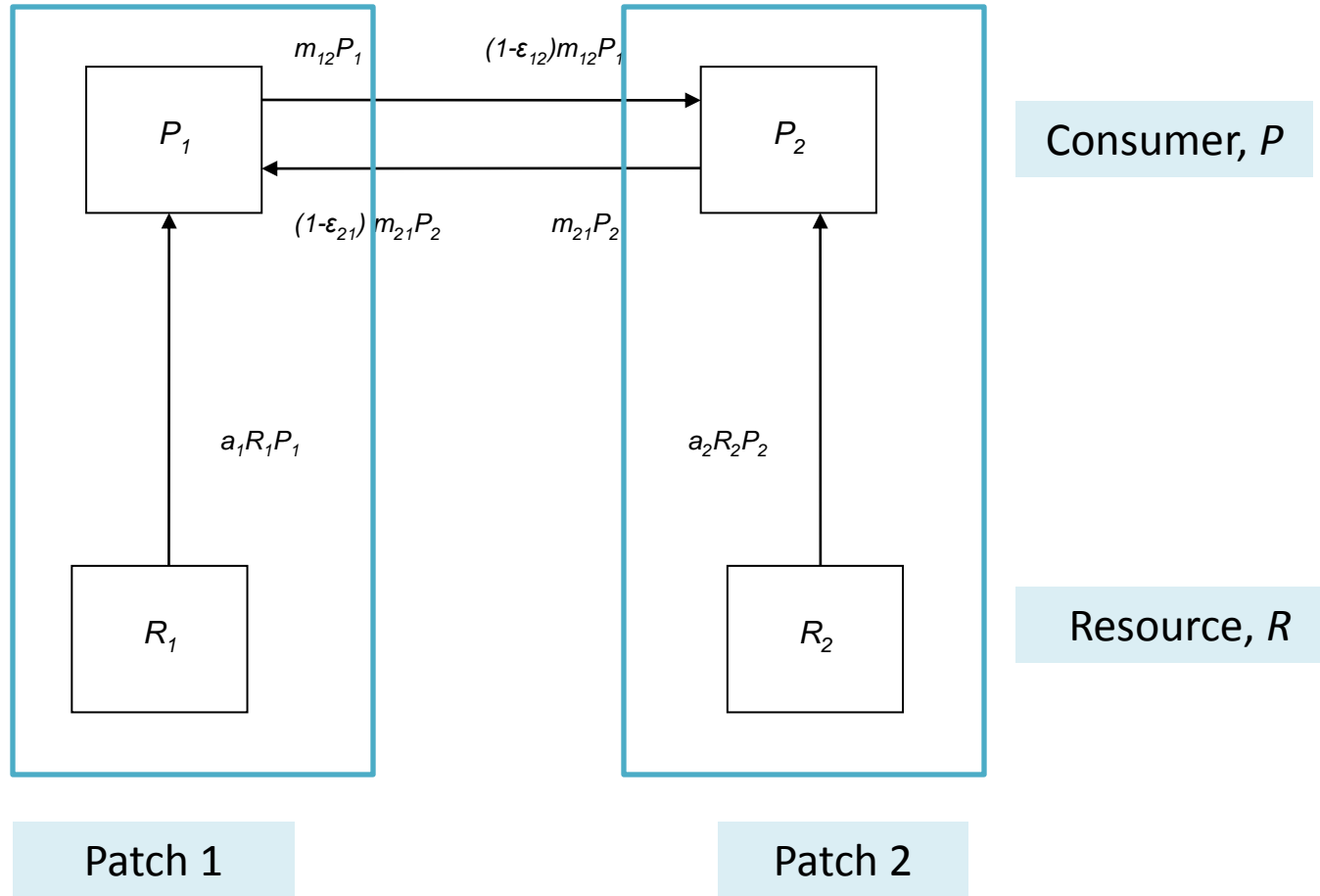
Purpose of work*: Extend ESS to systems in which there is loss during movement

A usual assumption of the Ideal Free Distribution (IFD) is that there are no losses in moving between habitat patches. However, because many populations exhibit more or less continuous population movement between patches, and travelling loss is a frequent factor, it is important to determine the effects of losses on expected population movement patterns and spatial distributions .

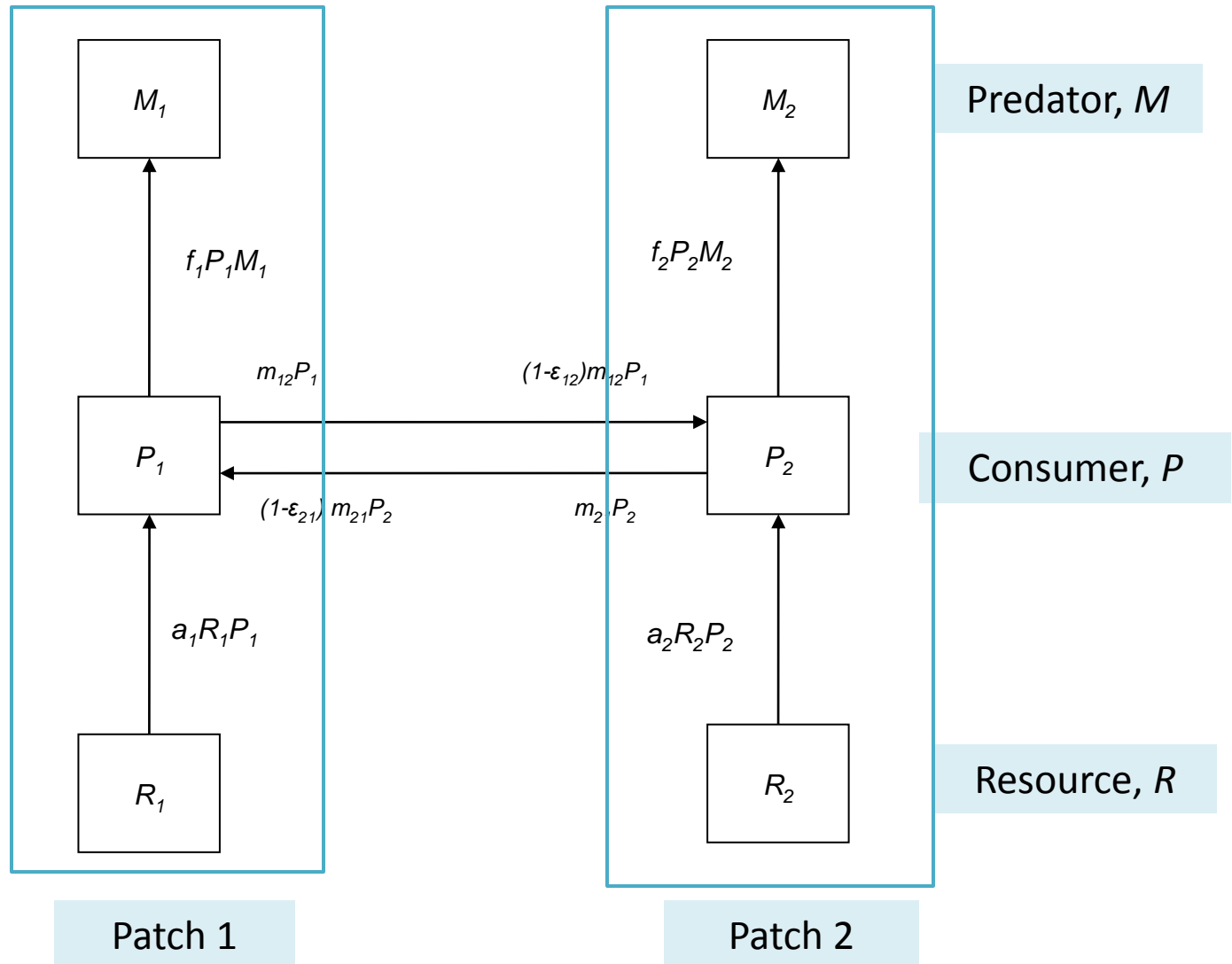
*Result of a NIMBioS workshop: *Population and Community Ecology Consequences of Intraspecific Niche Variation* (Bolnick et al. PIs)

DeAngelis, D. L., Gail S. K. Wolkowicz, Yuan Lou, Yuexin Jiang, Mark Novak, Richard Svanback, Marcio Araujo, YoungSeung Jo, and Erin Cleary. 2011. The effect of travel loss on evolutionary stable distributions of populations in space. *The American Naturalist* 178:15-29.

We considered bitrophic chains in which the consumer can move freely and continuously between two distinct patches with prey that are isolated in each patch, and has perfect knowledge of the patches...



... and we also considered tritrophic chains in which only the consumer can move freely between patches.



The equations for the two systems are as follows...

$$\frac{dR_1}{dt} = r_1 R_1 \left(1 - \frac{R_1}{K_1} \right) - a_1 R_1 P_1$$

Bitrophic

$$\frac{dR_2}{dt} = r_2 R_2 \left(1 - \frac{R_2}{K_2} \right) - a_2 R_2 P_2$$

$$\frac{dP_1}{dt} = b_1 a_1 R_1 P_1 - d_1 P_1 - m_{12} P_1 + m_{21} (1 - \epsilon_{21}) P_2$$

$$\frac{dP_2}{dt} = b_2 a_2 R_2 P_2 - d_2 P_2 + m_{12} (1 - \epsilon_{12}) P_1 - m_{21} P_2$$

$$\frac{dR_1}{dt} = r_1 R_1 \left(1 - \frac{R_1}{K_1} \right) - a_1 R_1 P_1$$

$$\frac{dR_2}{dt} = r_2 R_2 \left(1 - \frac{R_2}{K_2} \right) - a_2 R_2 P_2$$

$$\frac{dP_1}{dt} = b_1 a_1 R_1 P_1 - d_1 P_1 - f_1 P_1 M_1 - m_{12} P_1 + m_{21} (1 - \epsilon_{21}) P_2$$

$$\frac{dP_2}{dt} = b_2 a_2 R_2 P_2 - d_2 P_2 - f_2 P_2 M_2 + m_{12} (1 - \epsilon_{12}) P_1 - m_{21} P_2$$

$$\frac{dM_1}{dt} = c f_1 P_1 M_1 - d_{m1} M_1$$

$$\frac{dM_2}{dt} = c f_2 P_2 M_2 - d_{m2} M_2$$

Tritrophic

Tritrophic case

What we then did is assume there is an invading competing consumer, P_1' and P_2' .

Note that the migration rates from patch 1 to patch 2 are the same, m_{12} , while the migration rates from patch 2 to patch 1, m_{21} and m_{21}' , differ in general.

Otherwise the two competing consumers are identical

$$\frac{dP_1}{dt} = ba_1R_1P_1 - dP_1 - f_1P_1M_1 - m_{12}P_1 + m_{21}(1 - \varepsilon_{12})P_2$$

$$\frac{dP_2}{dt} = ba_2R_2P_2 - dP_2 - f_2P_2M_2 + m_{12}(1 - \varepsilon_{21})P_1 - m_{21}P_2$$

$$\frac{dP_1'}{dt} = ba_1R_1P_1' - dP_1' - f_1P_1'M_1 - m_{12}P_1' + m_{21}'(1 - \varepsilon_{12})P_2'$$

$$\frac{dP_2'}{dt} = ba_2R_2P_2' - dP_2' - f_2P_2'M_2 + m_{12}(1 - \varepsilon_{21})P_1' - m_{21}'P_2'$$

$$\frac{dR_1}{dt} = rR_1\left(1 - \frac{R_1}{K}\right) - a_1R_1P_1 - a_1R_1P_1'$$

$$\frac{dR_2}{dt} = rR_2\left(1 - \frac{R_2}{K}\right) - a_2R_2P_2 - a_2R_2P_2'$$

$$\frac{dM_1}{dt} = cf_1P_1M_1 + cf_1P_1'M_1 - d_{m1}M_1$$

$$\frac{dM_2}{dt} = cf_2P_2M_2 + cf_2P_2'M_2 - d_{m2}M_2$$

Bitrophic case is analogous

We solved for the variables at equilibrium.

Equilibrium solution for tritrophic case

$$\widehat{P}_2^\bullet = \frac{(1 - \epsilon_{12})m_{12}d_{m1}c_2f_2 - d_{m2}c_1f_1m_{21}}{c_1c_2f_1f_2(\widehat{m}_{21} - m_{21})},$$

$$P_2^\bullet = \frac{(1 - \epsilon_{12})m_{12}d_{m1}c_2f_2 - d_{m2}c_1f_1\widehat{m}_{21}}{c_1c_2f_1f_2(m_{21} - \widehat{m}_{21})},$$

$$\widehat{P}_1^\bullet = \frac{\widehat{m}_{21}\widehat{P}_2^\bullet}{(1 - \epsilon_{12})m_{12}},$$

$$P_1^\bullet = \frac{m_{21}P_2^\bullet}{(1 - \epsilon_{12})m_{12}},$$

$$R_1^\bullet = K_1 - \frac{a_1K_1}{r_1} \left(\widehat{P}_1^\bullet + P_1^\bullet \right) = K_1 \left(1 - \frac{a_1d_{m1}}{r_1c_1f_1} \right),$$

$$R_2^\bullet = K_2 - \frac{a_2K_2}{r_2} \left(\widehat{P}_2^\bullet + P_2^\bullet \right) = K_2 \left(1 - \frac{a_2d_{m2}}{r_2c_2f_2} \right),$$

$$M_1^\bullet = \frac{1}{f_1P_1^\bullet} [b_1a_1R_1^\bullet P_1^\bullet - d_1P_1^\bullet - m_{12}P_1^\bullet + (1 - \epsilon_{21})m_{21}P_2^\bullet]$$

$$M_2^\bullet = \frac{1}{f_2P_2^\bullet} [b_2a_2R_2^\bullet P_2^\bullet - d_2P_2^\bullet - m_{21}P_2^\bullet + (1 - \epsilon_{12})m_{12}P_1^\bullet]$$

Equilibrium solution for bitrophic case

$$R_2^\bullet = \frac{d_2}{b_2 a_2},$$

$$R_1^\bullet = \frac{1}{b_1 a_1} (d_1 + m_{12} - m_{12}(1 - \epsilon_{12})(1 - \epsilon_{21})),$$

$$\hat{P}_2^\bullet = \frac{1}{(\hat{m}_{21} - m_{21})} \left[\frac{(1 - \epsilon_{12})m_{12}r_1}{a_1} \left(1 - \frac{R_1^\bullet}{K_1}\right) - \frac{m_{21}r_2}{a_2} \left(1 - \frac{R_2^\bullet}{K_2}\right) \right],$$

$$P_2^\bullet = \frac{1}{(m_{21} - \hat{m}_{21})} \left[\frac{(1 - \epsilon_{12})m_{12}r_1}{a_1} \left(1 - \frac{R_1^\bullet}{K_1}\right) - \frac{\hat{m}_{21}r_2}{a_2} \left(1 - \frac{R_2^\bullet}{K_2}\right) \right],$$

$$\hat{P}_1^\bullet = \frac{\hat{m}_{21}\hat{P}_2^\bullet}{(1 - \epsilon_{12})m_{12}},$$

$$P_1^\bullet = \frac{m_{21}P_2^\bullet}{(1 - \epsilon_{12})m_{12}}.$$

What is interesting is that there is a value of m_{21} that the resident can choose such that it cannot be successfully invaded by any possible competitor (or any invader can replace any other strategy. Call it $m_{21,opt}$.

$$m_{21,opt} = (1 - \epsilon_{12})m_{12} \frac{d_{m1}c_2f_2}{d_{m2}c_1f_1}$$

Tritrophic case

$$m_{21,opt} = (1 - \epsilon_{12})m_{12} \frac{a_2r_1K_2(K_1 - R_1^*)}{a_1r_2K_1(K_2 - R_2^*)}$$

Bitrophic case

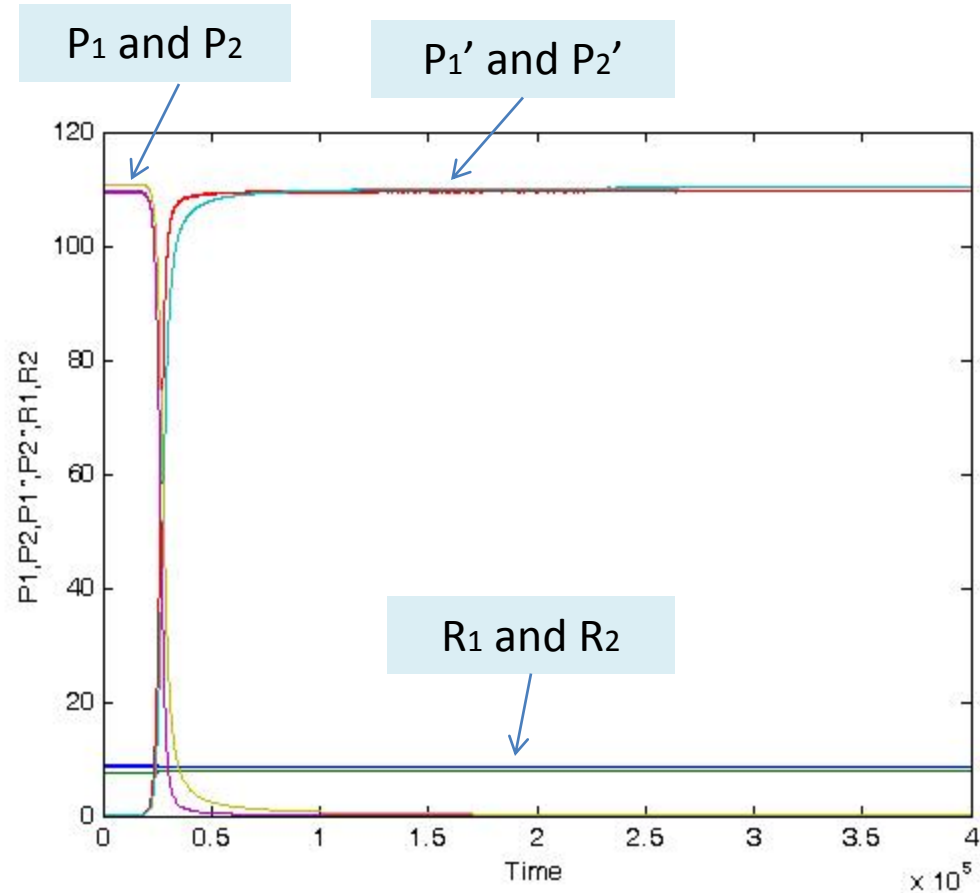
This was shown to be an ESS. We can demonstrate numerically that a resident with any $m_{21} \neq m_{21,opt}$, can be successfully invaded by an invader that has $m_{21}' = m_{21,opt}$ (or that satisfies other conditions, see later). Suppose the two patches are entirely identical (all parameters are the same for the prey and consumers, in the bitrophic case). Suppose also that the resident has $m_{12} = 0.01m_{21,opt}$.

Then let an invader with m_{12} and with $m_{21}' = m_{21,opt}$ appear.

Bitrophic model simulations confirm that an invader with m_{12}' at the optimal value of $m_{21,opt}$, starting from very small initial values, can exclude any alternative resident strategy.

Parameters

$b_1 = b_2 = 0.5;$
 $K_1 = K_2 = 100.;$
 $r_1 = r_2 = 3.0;$
 $a_1 = a_2 = 0.025;$
 $d_1 = d_2 = 0.1;$
 $m_{12} = m_{12,opt}$
 $m_{12}' = 0.01 * m_{12,opt}$
 $\epsilon_{12} = 0.5$
 $\epsilon_{21} = 0.99$

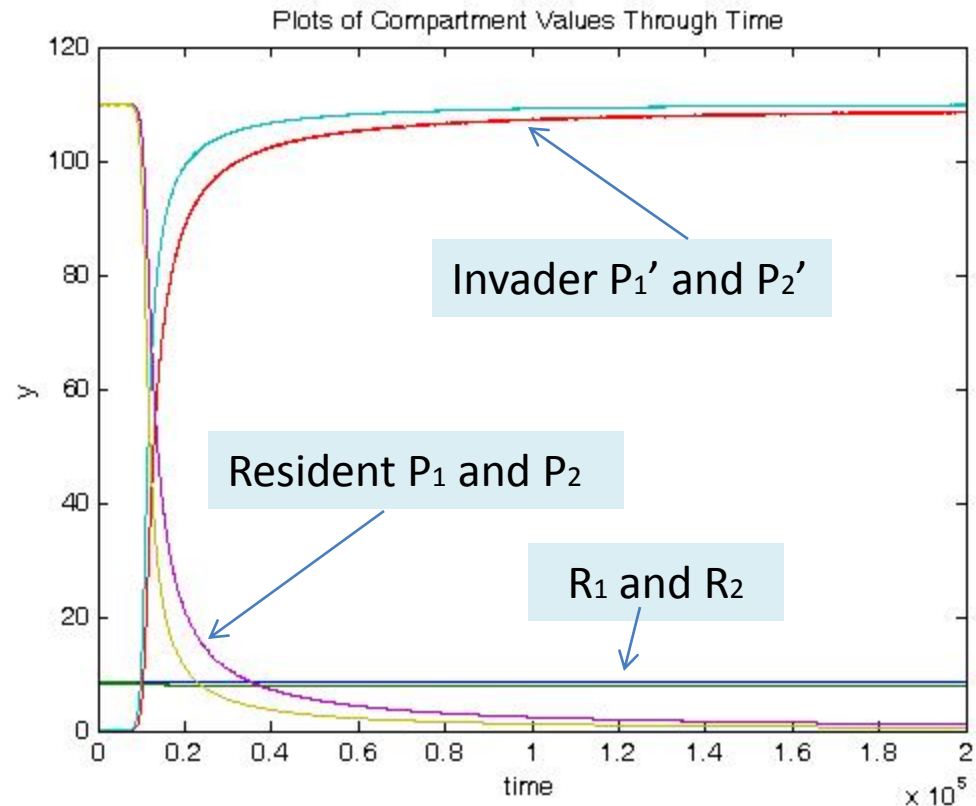


Note that although the loss rate, ϵ_{21} , for returning to patch 1 is huge, $\epsilon_{21} = 0.99$, the strategy using the optimal return rate easily excludes the strategy using low return rate.

Selection for spatial asymmetry: bitrophic case

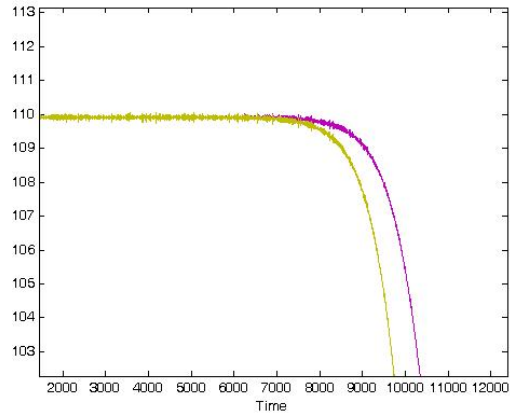
There are some interesting properties of this result. One is the following. Suppose the two patches are entirely identical (all parameters are the same for the prey, predator, and consumers).

Suppose also that the resident has $m_{12} = m_{21}$. Let an invader with $m_{21}' = m_{21,opt}$ appear with low numbers (0.000001).

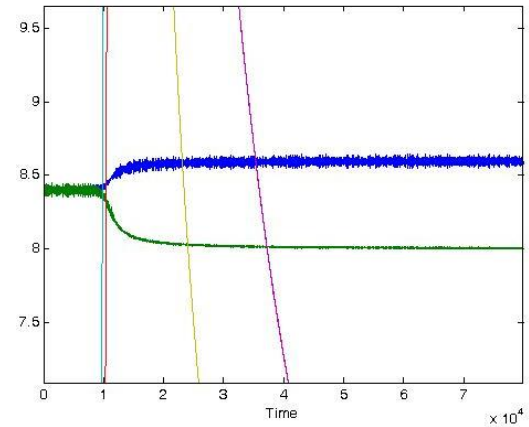


Closer views of result, showing the emergence of asymmetry

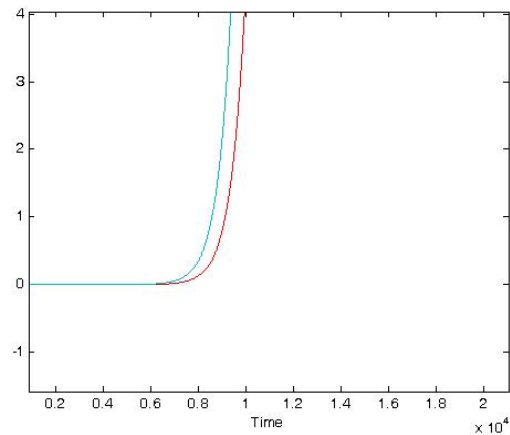
P_1 and P_2 have identical values, then start to decline



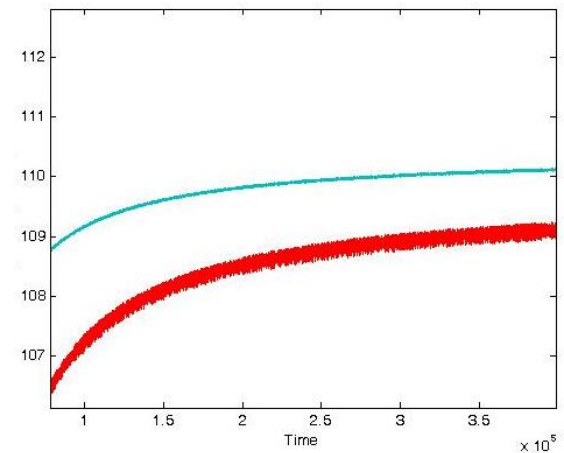
R_1 and R_2 separate



P_1' and P_2' increase from very low values



P_1' and P_2' approach different long-term values.



Result

This implies that the evolutionarily stable strategy for the distribution between identical patches is spatially asymmetric.

Natural selection creates asymmetry in an initially homogeneous system when there is loss in traveling.

The Effect of Travel Loss on Evolutionarily Stable Distributions of Populations in Space

Donald L. DeAngelis,^{1,*} Gail S. K. Wolkowicz,² Yuan Lou,³ Yuexin Jiang,⁴ Mark Novak,⁵ Richard Svanbäck,⁶ Márcio S. Araújo,^{7,†} YoungSeung Jo,⁸ and Erin A. Cleary²

1. U.S. Geological Survey, Department of Biology, University of Miami, Coral Gables, Florida 33124; 2. Department of Mathematics, McMaster University, Hamilton, Ontario L8S 4K1, Canada; 3. Department of Mathematics, Ohio State University, Columbus, Ohio 43210; 4. Section of Integrative Biology, University of Texas, Austin, Texas 78712; 5. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060; 6. Department of Ecology and Genetics/Limnology, Uppsala University, SE-752 36 Uppsala, Sweden; 7. Marine Sciences Program, Florida International University, North Miami, Florida 33181; 8. Department of Biology, University of Miami, Coral Gables, Florida 33124

Submitted July 30, 2010; Accepted March 9, 2011; Electronically published June 2, 2011

Online enhancements: appendixes.

SIAM J. APPL. MATH.
Vol. 71, No. 5, pp. 1801–1820

© 2011 Society for Industrial and Applied Mathematics

GLOBAL DYNAMICS OF A TRITROPHIC MODEL FOR TWO PATCHES WITH COST OF DISPERSAL*

YUAN LOU[†] AND CHANG-HONG WU[‡]

Abstract. To understand how cost of dispersal affects population dynamics, we study a three-trophic level food chain model, proposed by DeAngelis et al. [D. DeAngelis, G. S. K. Wolkowicz, Y. Lou, Y. X. Jiang, M. Novak, R. Svanback, M. Araujo, Y. S. Jo, and E. A. Cleary, *Am. Nat.*, 178 (2011), pp. 15–29], in two patches. The system consists of one resource species, two consumers, and a top predator. The top predator feeds on two consumers and both consumers feed on the resource. Only consumers move between the patches, possibly with a fraction of loss in population during the movement. The two competing consumers are identical in every aspect except their dispersal rates between two patches. If two consumers have the same dispersal rate from patch 1 to patch 2, we completely determine the global dynamics of the model and show that there exists an “optimal” dispersal rate from patch 2 to patch 1 for the consumer such that, in terms of the theory of adaptive dynamics, it is a globally evolutionarily stable strategy and also a convergent stable strategy. If there is a minimum dispersal speed from patch 1 to patch 2, we are able to completely determine the evolutionarily stable strategy for dispersal between two patches. Our results offer insights into the evolution of dispersal in multitrophic level food chains, e.g., how the evolution of fast or slow dispersal for the consumer species depends upon the variation of the predation risk in the habitat. Our result suggests that even if most individuals die during the movement, a positive dispersal rate can still evolve.

Mathematical details can be found in the appendices of DeAngelis et al. (2011) and in Lou and Wu (2011).

The latter includes proof of the ESS for the tritrophic case using a Lyapunov function approach.

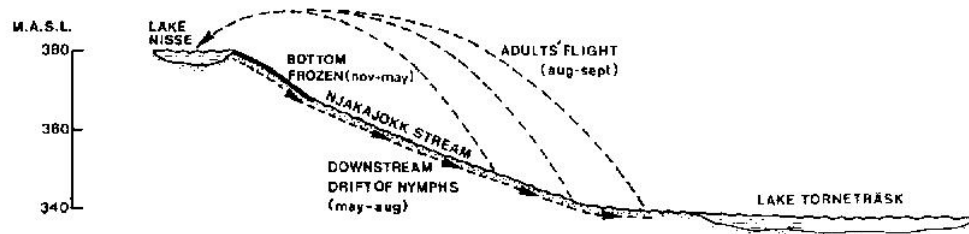
Implications in nature: Stream drift

The Colonization Cycle of Freshwater Insects

K. Müller

University of Umeå, Department of Ecological Zoology, S-90187 UMEÅ, Sweden

The passive downstream drift caused by one-directional flow of water is a common pattern and Müller (1954, 1982) hypothesized that insects compensate for downstream drift by a tendency for the adult forms to fly upstream to oviposit.



Implications in nature: Stream drift

Empirical studies have not conclusively supported the hypothesis that upstream movement of adults compensates for the loss, but have shown that substantial degree of compensation often occurs (Hershey et al. 1993 for mayflies)

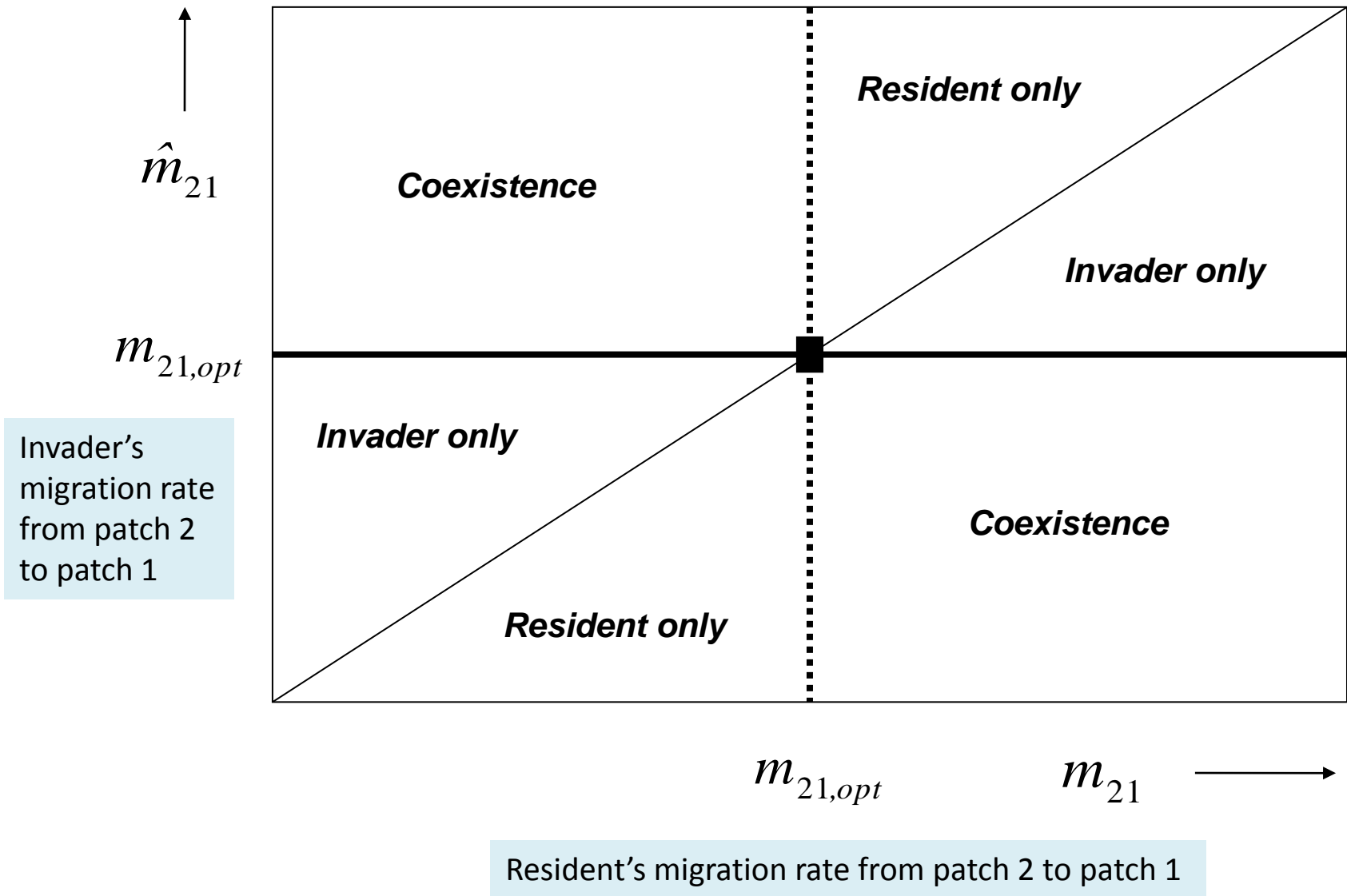
Anholt (1995) proposed that such upstream movement may not be necessary, as density dependence occurs in the aquatic stages of many insects, and drift of individuals from a habitat patch may be compensated for by an increase in the survival rate of those remaining on the patch.

Kopp et al. (2001), nevertheless, showed through invasion analysis simulation, that even in such cases, upstream movement should be favored, because an insect genotype in which losses to drift from upstream to downstream patches are exactly compensated for by upstream movement will exclude any genotype for which this is not true.

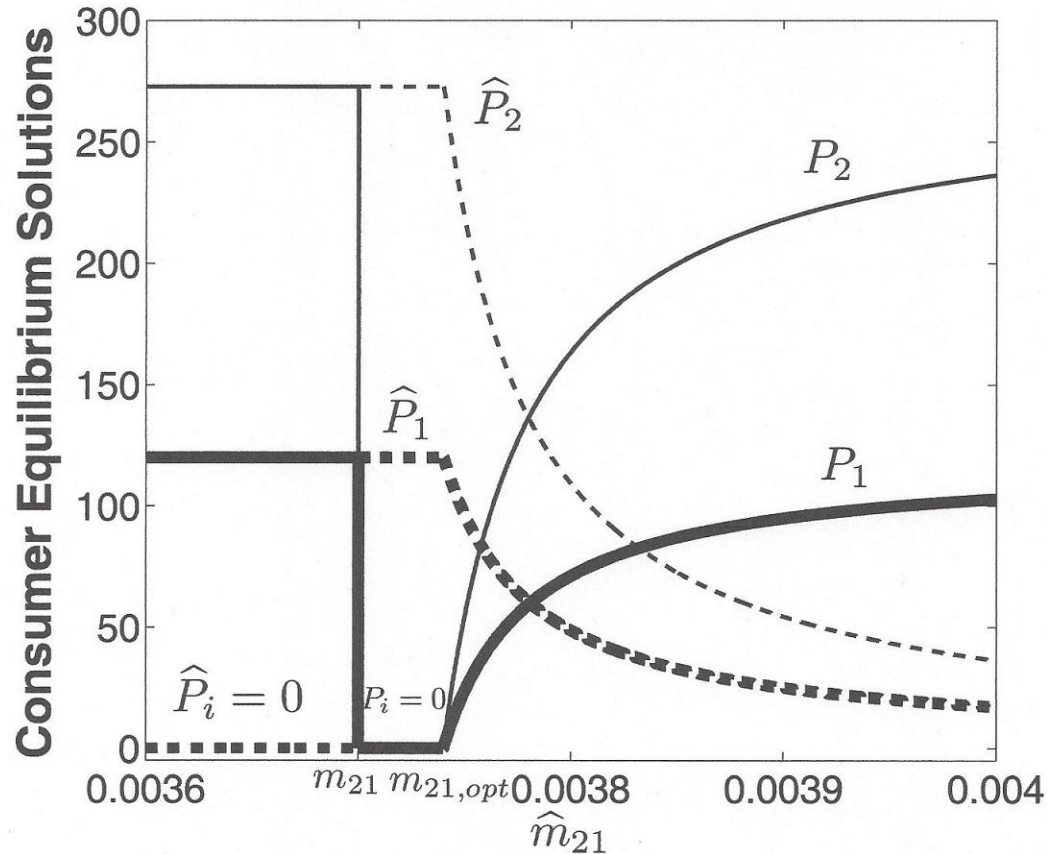
Our results are more general than those of Kopp et al. (2001) and imply that if there are losses in either direction or both, the optimal level of compensation through upstream migration should be less than exact matching.

Further properties of ESS

When neither resident nor invader has the optimal migration rate the results are more complex.



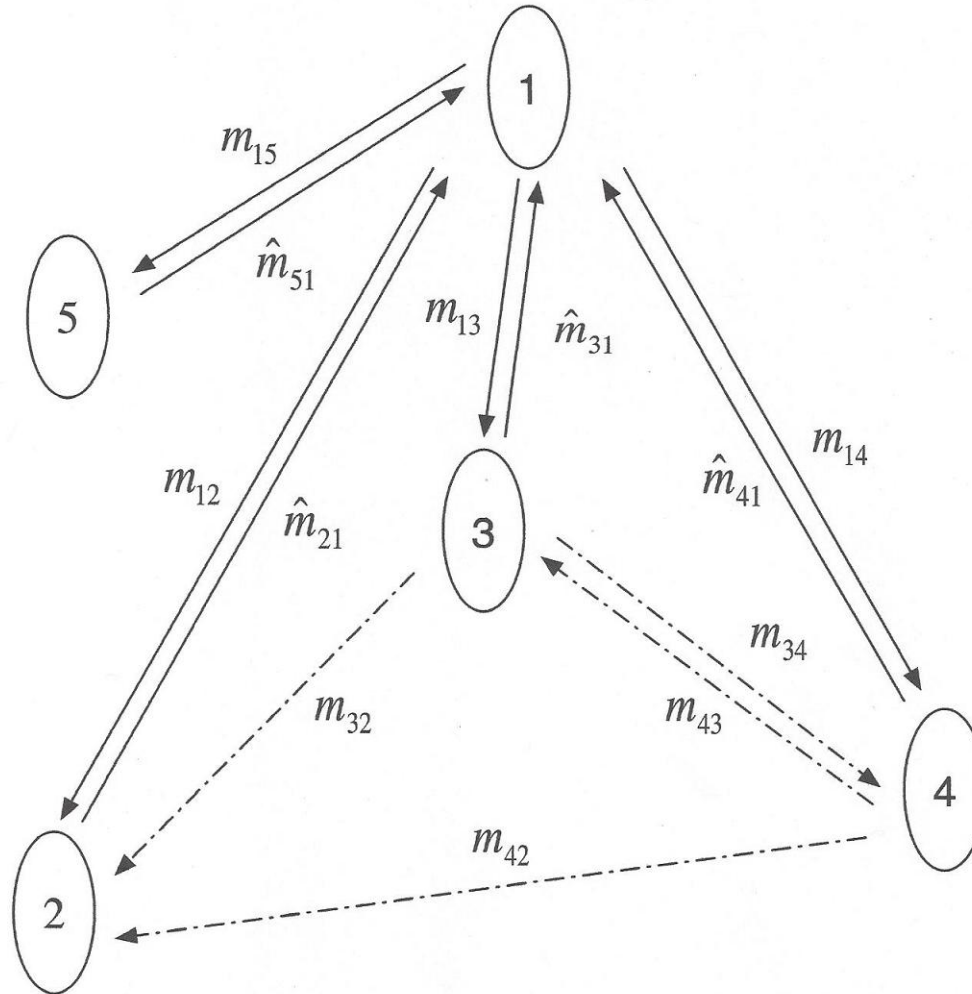
Note that if neither of the consumers has a travel rate exactly at m , then the sizes of the resident and invader populations is complex.



If both m_{12} and m_{12}' are on the same side of $m_{21,opt}$, then only the population with closest rate to $m_{21,opt}$ exists.

If m_{12} and m_{12}' are on opposite sides of $m_{21,opt}$, then there is coexistence.

The results can be extended to a limited extend to N-patch systems



For a set of patches $i = 1, N$, the relevant equations for the tritrophic case can be written as

$$\frac{d\hat{P}_i}{dt} = \hat{P}_i [b_i a_i R_i - d_i - f_i M_i] - \left(\sum_{j=1}^N \hat{m}_{ij} \right) \hat{P}_i + \left(\sum_{j=1}^N (1 - \epsilon_{ji}) \hat{m}_{ji} \hat{P}_j \right),$$

$$\frac{dP_i}{dt} = P_i [b_i a_i R_i - d_i - f_i M_i] - \left(\sum_{j=1}^N m_{ij} \right) P_i + \left(\sum_{j=1}^N (1 - \epsilon_{ji}) m_{ji} P_j \right),$$

$$\frac{dR_i}{dt} = R_i \left[r_i \left(1 - \frac{R_i}{K_i} \right) - a_i P_i - a_i \hat{P}_i \right],$$

$$\frac{dM_i}{dt} = M_i (c_i f_i P_i + c_i f_i \hat{P}_i - d_{mi}).$$

It seems very difficult to get solutions for the resident and invader, but a unique solution with the invader absent can be obtained.

$$P_i^* = \frac{d_{mi}}{c_i f_i},$$

$$R_i^* = K_i \left(1 - \frac{a_i}{r_i} P_i^* \right),$$

$$M_i^* = \frac{1}{f_i} \left[b_i a_i R_i^* - d_i - \sum_{j=1}^N m_{ij} + \left(\sum_{j=1}^N (1 - \epsilon_{ji}) m_{ji} \frac{P_j^*}{P_i^*} \right) \right]$$

An optimal movement rate can be obtained, but only under the assumption that all rates, when obtained, are positive.

$$m_{i1,opt} = (1 - \epsilon_{1i}) m_{1i} \frac{P_1^*}{P_i^*} + \frac{1}{P_i^*} \sum_{j=2}^N \left((1 - \epsilon_{ji}) m_{ji} P_j^* - \frac{(1 - \epsilon_{ij})(1 - \epsilon_{j1})}{(1 - \epsilon_{i1})} m_{ij} P_i^* \right)$$

From the above it seems there are a lot of open questions.

It should be again noted that we have made several assumptions

- It is assumed there is movement from at least one patch, which occurs from an 'upstream' patch.
- Populations are self-sustaining on every patch
- The different species or genotypes are identical in all respects except in their return rates to the first patch.

The above is only a small part of theory involving traveling with loss. Much work relaxes the assumption of perfect knowledge.



Oikos 119: 1469–1483, 2010

doi: 10.1111/j.1600-0706.2010.18196.x

© 2010 The Authors. Journal compilation © 2010 Oikos

Subject Editor: Justin Travis. Accepted 7 January 2010

Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: departures from the ideal free distribution

Shuichi Matsumura, Robert Arlinghaus and Ulf Dieckmann

S. Matsumura (matsumur@gifu-u.ac.jp) and U. Dieckmann, Evolution and Ecology Program, Int. Inst. for Applied Systems Analysis, Schlossplatz 1, AT-2361 Laxenburg, Austria. Present address for SM: Faculty of Applied Biological Sciences, Gifu Univ., Yanagido 1-1, Gifu City, JP-501-1193 Gifu, Japan. – R. Arlinghaus, Dept of Biology and Ecology of Fishes, Leibniz-Inst. of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, DE-12587 Berlin, Germany and: Inland Fisheries Management Laboratory, Dept for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-Univ. of Berlin, Philippstrasse 13, Haus 7, DE-10115 Berlin, Germany.

VOL. 179, NO. 4 THE AMERICAN NATURALIST APRIL 2012

Generalized Movement Strategies for Constrained Consumers: Ignoring Fitness Can Be Adaptive

Theodore E. Galanthay^{1,*} and Samuel M. Flaxman²

1. Department of Applied Mathematics, University of Colorado, Boulder, Colorado 80309; 2. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309

Submitted April 19, 2011; Accepted December 22, 2011; Electronically published March 6, 2012

Online enhancements: appendixes, zip file. Dryad data: <http://datadryad.org/handle/10255/dryad.hd301f6n>.

Conclusion



Keep Moving