Fitness based prey dispersal and prey persistence in intraguild predation systems

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Follow Up To:

Avoidance behavior in intraguild predation communiities : A cross-diffusion model

D. Ryan and R.S. Cantrell, *Discrete and Continuous Dynamical Systems A* **35** (2015), 1641-1663.

Intraguild Predation(IGP) : A predator and prey also compete for a shared resource

a. Occurs widely in nature (**Arim** and **Marquet**, Ecology Letters 2004)

b. Significant early modeling of IGP (**Holt** and **Polis**, American Naturalist 1997): 3 species ODE models. Found strong IGP was particularly prone to species exclusions even though IGP wide spread in nature. Offered various suggestions for research into mitigating mechanisms, one of which was environmental heterogeneity.

c. Empirical studies (**Durant**,Behavioral Ecology 2000; **Lucas** et al,Environmental Entomology 2000; **Palomares** and **Ferreras**, Journal Applied Ecology 1996; **Sergio** et al, Journal Animal Ecology 2003; **Thomson** and **Gese**, Ecology 2007) suggest mechanism of a nonrandom dispersal strategy in which IG prey concentrate in areas of marginal habitat quality to avoid predation risk of high quality areas where IG predator tends to congregate.

d. **Amarasekare** was the first to model IGP in heterogeneous environments via a three patch three species system of ODE's (9 total equations). She incorporated random movement strategies (**Amarasekare**, Journal of Theoretical Biology 2006) and then nonrandom strategies (density dependent, habitat dependent, fitness dependent) (**Amarasekare**, American Naturalist 2007).

ORIGINAL MODEL

$$\frac{\partial u}{\partial t} = d_1 \Delta u + f(x,u,v,w)u$$

(1) $$\frac{\partial v}{\partial t} = \Delta[M(u,w)v] + g(u,v,w)v$$

$$\frac{\partial w}{\partial t} = d_3 \Delta w + h(u,v,w)w$$

IN $\Omega \times (0,\infty)$

WITH

(2) $$\frac{\partial u}{\partial \vec{\eta}} = \frac{\partial v}{\partial \vec{\eta}} = \frac{\partial w}{\partial \vec{\eta}} = 0$$

ON $\partial\Omega \times (0,\infty)$

Ω : BOUNDED DOMAIN IN $\mathbb{R}^2$ WITH SMOOTH BOUNDARY

$u(x,t)$: DENSITY OF RESOURCE SPECIES
$v(x,t)$: DENSITY OF IG PREY
$w(x,t)$: DENSITY OF IG PREDATOR

MODIFIED MODEL

$$\frac{\partial u}{\partial t} = d_1 \Delta u + \tilde{f}(x,u,v,w)u$$

$$(1)^{\sim} \qquad \frac{\partial v}{\partial t} = \Delta[\tilde{M}(u,v,w)v] + \tilde{g}(u,v,w)v$$

$$\frac{\partial w}{\partial t} = d_3 \Delta w + \tilde{h}(u,v,w)w$$

IN $\Omega \times (0,\infty)$

WITH

$$(2) \qquad \frac{\partial u}{\partial \vec{\eta}} = \frac{\partial v}{\partial \vec{\eta}} = \frac{\partial w}{\partial \vec{\eta}} = 0$$

ON $\partial\Omega \times (0,\infty)$

Ω : BOUNDED DOMAIN IN $\mathbb{R}^N$ WITH SMOOTH BOUNDARY

ORIGINAL PER CAPITA GROWTH RATES (FITNESS FUNCTIONS)

$$(3) \quad f(x,u,v,w) = r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u} - \frac{a_2 w}{1 + h_2 a_2 u + h_3 a_3 v}$$

$$(4) \quad g(u,v,w) = \frac{e_1 a_1 u}{1 + h_1 a_1 u} - \frac{a_3 w}{1 + h_2 a_2 u + h_3 a_3 v} - \mu_1 - \omega_2 v$$

$$(5) \quad h(u,v,w) = \frac{e_2 a_2 u + e_3 a_3 v}{1 + h_2 a_2 u + h_3 a_3 v} - \mu_2 - \omega_3 w$$

MODIFIED PER CAPITA GROWTH RATES (FITNESS FUNCTIONS)

$$(3)^{\sim} \quad \tilde{f}(x,u,v,w) = r(x) - \omega_1 u - \frac{a_1 v}{1 + h_1 a_1 u + \alpha_1 v} - \frac{a_2 w}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w}$$

$$(4)^{\sim} \quad \tilde{g}(u,v,w) = \frac{e_1 a_1 u}{1 + h_1 a_1 u + \alpha_1 v} - \frac{a_3 w}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w} - \mu_1 - \omega_2 v$$

$$(5)^{\sim} \quad \tilde{h}(u,v,w) = \frac{e_2 a_2 u + e_3 a_3 v}{1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w} - \mu_2 - \omega_3 w$$

PARAMETERS

d_1: RESOURCE MOTILITY
d_3: IG PREDATOR MOTILITY

$M(u,v,w)$: IG PREY MOTILITY
(TWICE DIFFERENTIABLE WITH $M(u,v,w) \geq d > 0$ FOR ALL $u,v,w \geq 0$)

(PROVE GLOBAL EXISTENCE TO $(1)^{N}$-(2) WITH ONLY ADDITIONAL REQUIREMENT OF $M_v \geq 0$. SPECIFY FORM IN TERMS OF A FITNESS BASED AVOIDANCE STRATEGY.)

$r(x)$: SPATIALLY VARYING RESOURCE PRODUCTIVITY
($r(x) > 0$ ON $\bar{\Omega}$, $r \in C^{\alpha}(\bar{\Omega})$ FOR SOME $\alpha \in (0,1)$)

μ_1, μ_2 : NATURAL MORTALITIES OF IG PREY AND IG PREDATOR

ω_i : LOGISTIC SELF LIMITING COEFFICIENTS

a_i : ATTACK RATES

h_i : HANDLING TIMES

e_i : CONVERSION EFFICIENCIES

α_1, α_2 : MUTUAL INTERFERENCE IN PREDATION

BOUNDARY CONDITIONS

$$\frac{\partial}{\partial \vec{\eta}}(M(u,v,w)v) = M(u,v,w)\frac{\partial v}{\partial \vec{\eta}}$$

$$+ v\frac{\partial M}{\partial u}\frac{\partial u}{\partial \vec{\eta}} + v\frac{\partial M}{\partial v}\frac{\partial v}{\partial \vec{\eta}} + v\frac{\partial M}{\partial w}\frac{\partial w}{\partial \vec{\eta}}$$

$$\frac{\partial u}{\partial \vec{\eta}} = \frac{\partial v}{\partial \vec{\eta}} = \frac{\partial w}{\partial \vec{\eta}} = 0 \Rightarrow \frac{\partial}{\partial \eta}(M(u,v,w)v) = 0$$

$$\frac{\partial u}{\partial \vec{\eta}} = \frac{\partial w}{\partial \vec{\eta}} = \frac{\partial}{\partial \vec{\eta}}(M(u,v,w)v) = 0$$

$$\Rightarrow \left(M + v\frac{\partial M}{\partial v}\right)\frac{\partial v}{\partial \vec{\eta}} = 0$$

SO IF $\frac{\partial M}{\partial v} \geq 0$, NEUMANN BOUNDARY

CONDITIONS ARE EQUIVALENT TO NO-FLUX

IN $(1)^{\sim}-(2)$.

GLOBAL EXISTENCE AND COMPACT ATTRACTOR

$[W^{1,p}(\Omega)]^3$: SPACE OF TRIPLES (u, v, w)

IN $W^{1,p}(\Omega)$

$$\|(u,v,w)\|_{[W^{1,p}(\Omega)]^3} = \|u\|_{W^{1,p}(\Omega)} + \|v\|_{W^{1,p}(\Omega)} + \|w\|_{W^{1,p}(\Omega)}$$

$$p > n \Rightarrow W^{1,p}(\Omega) \hookrightarrow C(\bar{\Omega})$$

WE CAN USE $[W^{1,p}_{+}(\Omega)]^3$, THE CONE

OF TRIPLES OF NONNEGATIVE FUNCTIONS

IN $W^{1,p}(\Omega)$ AS OUR SPACE

Global Existence and Compact Global Attractor (Cont.)

a. **Amann** (Nonlinear Analysis 1988, Mathematische Zeitschrift (1989), Differential and Integral Equations (1990) proved global existence results for a class of quasi-linear parabolic PDE problems that include (1)-(2).

b. Thm 1 of MZ (1989) implies that if $p > n$, there is a unique classical solution to (1)-(2) corresponding to an initial density configuration in our space. This solution exists on maximal interval J. Thm 3 of MZ (1989) implies that if the L^∞ norms of all components are bounded for $t \in J$, then $J = [0, \infty)$.

c. Standard comparison principles for single parabolic equations with coefficients that depend on space and time can be applied to conclude that solution coefficients remain nonnegative in space for $t \in J$.

Global Existence and Compact Global Attractor (Cont.)

d. **Le** (Indiana University Mathematics Journal 2002) proved stronger results for a two component system with additional assumptions bounding the growth of the flux and reaction terms. **Le**'s system included one component with dispersal described by cross diffusion and one with random dispersal . He shows that if the component incorporating cross diffusion is ultimately uniformly bounded in $L^n(\Omega)$, one can bootstrap to get the L^∞ bounds needed to employ Amann. In a particular example he shows how to get $L^2(\Omega)$ bounds when Ω lies in two dimensional Euclidean space. In the DCDS-A paper we argued how the proof of Thm 2.2 of IUMJ 2002 can be extended and adapted to prove global existence of solutions to (1)-(2) when $p > 2$. Moreover, when viewed as a semi-flow on our space, we showed (1)-(2) will have a compact global attractor. The essence of Le's approach (in the context of (1)-(2)) is to use Gagliardo-Nirenberg type inequalities to get appropriate integral estimates on the gradients of u and w. These estimates work beautifully when $n= 2$. Not so much for $n > 2$.

e. Adding predator mutual self-interference enables us to bound $(\tilde{f})^2$ independent of the density of v which is a key step in getting suitable estimates on the gradients of both u and w without relying on Gagliardo-Nirenberg.

$\boxed{\text{THEOREM 1}}$ Let $n \geq 2$ and consider $(1)^{\sim}$ - (2). Let $(u(x,t), v(x,t), w(x,t))$ denote the unique classical solution to $(1)^{\sim}$ - (2) with initial conditions in $[W^{1,p}_{+}(\Omega)]^3$ where $p > n$ and Ω is a smooth bounded domain in $\mathbb{R}^n$. Assume that $M_v \geq 0$ for $u \geq 0$, $v \geq 0$, $w \geq 0$. Then the solution exists for all $t \geq 0$, and moreover, there is a $\gamma \in (0,1)$ so that

$$\|u(\cdot,t)\|_{C^{1+\gamma}(\bar{\Omega})}, \|v(\cdot,t)\|_{C^{1+\gamma}(\bar{\Omega})}, \|w(\cdot,t)\|_{C^{1+\gamma}(\bar{\Omega})}$$

are ultimately uniformly bounded. In particular, $(1)^{\sim}$ - (2) defines a semi-flow on $[W^{1,p}_{+}(\Omega)]^3$ and this semi-flow possesses a compact attractor.

Motility Functions Modeling Avoidance

a. The condition that $\tilde{M}_v$ be nonnegative for all nonnegative u,v, and w can be relaxed to having $\tilde{M}_v(u(x,t),v(x,t),w(x,t))$ nonnegative for all x in Ω and $t > t_0$.

b. We assume IG prey is able to assess local density of resources and frequency of predator attacks. This assumption is reasonable for a variety of species (**Durant**, Behavioral Ecology 2000; **Palomares** and **Ferrerras**, Journal of Applied Ecology 1996; **Sergio** et al, Journal of Animal Ecology 2003; **Thomson** and **Gese**, Ecology 2007). It uses resource availability and frequency of predator attacks as a means of judging local environmental quality to increase its motility in regions judged to bad with a lower base rate of motility in regions judged to be good.

c. The fitness function g(u,v,w) is a good candidate to measure local environmental quality. So we think of M~(u,v,w) as M(g(u,v,w)) where M is a function of a single variable, so that $M\sim_v$ is (DM/dg) * (g_v)

d. We think of embedding M(g) into a family $M_\lambda(g)$ to capture a varying strength of the avoidance response. $\{M_\lambda(g\ )\}_{\lambda \geq 0}$ satisfies

(6a) $d_2 \geq M_\lambda(g) \geq d$ for all λ, $g^* \geq 0$

(6b) $M_\lambda(g) \geq d_2$ for all λ, $g^* < 0$

(6c) $M_\lambda(g) \to \infty$ as $\lambda \to \infty$ for all $g^* < 0$

e. ONE MAY CALCULATE THAT

$$g_v(u,v,w) = \frac{a_3 w h_3 a_3}{(1 + h_2 a_2 u + h_3 a_3 v + \alpha_2 w)^2} - \omega_2$$

$$\leq a_3^2 h_3 w - \omega_2$$

LET $W_0 = \left(\max\left\{\frac{e_2}{h_2}, \frac{e_3}{h_3}\right\} - \mu_1\right) / \omega_3$

THEN $\limsup_{t \to \infty} \| w(\cdot, t) \|_\infty \leq W_0$

SO IF $a_3^2 h_3 W_0 < \omega_2$, WE GET THAT

FOR SOME t_0,

$$g_v(u(x,t), v(x,t), w(x,t)) \leq 0$$

FOR $x \in \Omega$ AND $t \geq t_0$.

SO $\tilde{M}_v(u(x,t), v(x,t), w(x,t)) \geq 0$ FOR $x \in \Omega$

AND $t \geq t_0$ SO LONG AS $dM/dg \leq 0$

f. A SUITABLE CHOICE OF M_λ IS

GIVEN BY :

$$M_\lambda(g) = \begin{cases} d_2 & \text{IF } g \geq 0 \\ -\lambda g \exp(d_2/\lambda g) + d_2 & \text{IF } g < 0 \end{cases}$$

WHERE $\lambda \geq 0$ AND $d_2 > 0$. THEN FOR ANY $\lambda \geq 0$

$\frac{dM_\lambda}{dg} \leq 0$. (HERE M_λ IS INFINITELY

DIFFERENTIABLE AT $g = 0$.)

g. IN THE DCDS-A PAPER WE HAD USED AN

APPROXIMATE FITNESS $g^*(u, w) = g(u, 0, w)$

WHICH WAS REASONABLE WHEN THINKING

IN TERMS OF WANTING THE IG PREY TO INVADE

FROM LOW DENSITIES.

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE

$Y = [W^{1,p}_{+}(\Omega)]^3$

$\pi : Y \times [0, \infty) \to Y$ SEMI-FLOW INDUCED BY (1)-(2)

A : COMPACT GLOBAL ATTRACTOR FROM THM 1

$\overset{\circ}{Y}$: INTERIOR OF Y (TUPLES OF FUNCTIONS POSITIVE ON $\overline{\Omega}$)

∂Y : TUPLES WITH AT LEAST ONE COMPONENT ZERO SOMEWHERE IN $\overline{\Omega}$

TAKE $t_1, t_2 > 0$, $\varepsilon > 0$

$\tilde{X} = \overline{\pi(\mathcal{B}(A, \varepsilon), t_1)}$

$X = \pi(\tilde{X}, t_2)$ $\qquad S = X \cap \partial Y^{\circ}$

X, S COMPACT

$X, S, X \setminus S$ FORWARD INVARIANT UNDER π

(IF A COMPONENT OF AN ELEMENT IN S IS ZERO SOMEWHERE IN $\overline{\Omega}$, IT IS IDENTICALLY ZERO ON $\overline{\Omega}$.)

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

S_{uw} : SUBSET OF S WITH $V \equiv 0$

$A_{uw} = A \cap S_{uw}$

$$\omega(S_{uw}) = \bigcup_{(u,0,w) \in S_{uw}} \omega(u,0,w) \qquad \text{(NONSTANDARD DEFINITION)}$$

$$(7) \qquad \frac{\partial u}{\partial t} = d_1 \Delta u + u\left(r(x) - \omega_1 u - \frac{a_2 w}{1 + h_2 a_2 u + d_2 w}\right)$$

$$\frac{\partial w}{\partial t} = d_3 \Delta w + w\left(\frac{e_2 a_2 u}{1 + h_2 a_2 u + d_2 w} - \mu_2 - \omega_3 w\right)$$

IN $\Omega \times (0,\infty)$

$$\frac{\partial u}{\partial \vec{\eta}} = \frac{\partial w}{\partial \vec{\eta}} = 0 \qquad \text{ON } \partial\Omega \times (0,\infty)$$

(7) HAS BOUNDARY EQUILIBRIA $(u^*, 0)$ AND $(0,0)$

WHERE u^* IS THE UNIQUE POSITIVE SOLUTION OF

$$0 = d_1 \Delta u + u(r(x) - \omega_1 u) \qquad \text{IN } \Omega$$

$$\frac{\partial u}{\partial \vec{\eta}} = 0 \qquad \text{ON } \partial\Omega$$

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

IF THE PRINCIPAL EIGENVALUE σ_1 OF

$$d_3 \Delta w_1 + \left(\frac{e_2 a_2 u^*}{1 + h_2 a_2 u^*} - \mu_2 \right) w_1 = \sigma w_1 \qquad \text{IN } \Omega$$

$$\frac{\partial w_1}{\partial \vec{\eta}} = 0 \qquad \text{ON } \partial\Omega$$

IS POSITIVE, (7) IS UNIFORMLY PERSISTENT (PERMANENT) AND THERE IS A COMPACT INVARIANT SET A_1 BOUNDED AWAY FROM THE BOUNDARY OF S_{uw}, ATTRACTING ALL INITIAL DATA OF THE FORM (u_0, w_0) WITH $u_0 \not\equiv 0$, $w_0 \not\equiv 0$.

IF $\sigma_1 < 0$, $A_1 = \emptyset$

$$\omega(S_{uw}) = \{(0,0,0)\} \cup \{(u^*,0,0)\} \cup A_1$$

$\boxed{\text{ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)}}$

IF U IS A COMPACT INVARIANT SUBSET OF X,

$$W^s(U) = \{u \in X \mid \omega(u) \neq \phi,\ \omega(u) \subseteq U\}$$
$$W^u(U) = \{u \in X \mid \omega(u) \neq \phi,\ \alpha(u) \subseteq U\}$$

<u>LEMMA 1</u>: LET $U \subseteq S_{uw}$ BE A COMPACT INVARIANT SET. SUPPOSE THERE IS A CONTINUOUS FUNCTION $b(x)$ SO THAT

$$b(x) \leq \frac{g(u,0,w)}{M(u,0,w)}$$

FOR ALL $(u,0,w) \in U$ AND THAT THE PRINCIPAL EIGENVALUE σ_2 OF

$$\Delta v_2 + b(x) v_2 = \sigma_2 v_2 \qquad \text{IN } \Omega$$

$$\frac{\partial v_2}{\partial \vec{n}} = 0 \qquad \text{ON } \partial\Omega$$

IS POSITIVE. THEN $W^s(U) \cap (X \setminus S_{uw}) = \phi$. $\square$

UTILIZING THE FITNESS BASED AVOIDANCE STRATEGY $M_\lambda(g(u,v,w))$ WE DERIVE CONDITIONS THAT GENERATE THE EXISTENCE OF A $b(x)$ SATISFYING THE REQUIREMENTS OF LEMMA. WE NEED THE FOLLOWING LEMMA.

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

LEMMA 2: SUPPOSE U IS A COMPACT SUBSET OF $[C(\bar{\Omega})]^n$ AND $\phi : \mathbb{R}^n \to \mathbb{R}$ IS A CONTINUOUS FUNCTION. THEN THE FUNCTION $F : \bar{\Omega} \to \mathbb{R}$ DEFINED BY

$$F(x) = \min_{f \in U} \phi(f(x))$$

IS CONTINUOUS. $\square$

GIVEN ANY COMPACT SUBSET U OF $[C(\bar{\Omega})]^3$, DEFINE

$$\underline{g}_U(x) = \min_{(u,v,w) \in U} g(u(x), v(x), w(x))$$

$$b_{\lambda,U}(x) = \min_{(u,v,w) \in U} \frac{g(u(x), v(x), w(x))}{M_\lambda(g(u(x), v(x), w(x)))}.$$

THEN $\underline{g}_U$ AND $b_{\lambda,U}$ ARE CONTINUOUS BY LEMMA 2.

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

LEMMA 3: LET $U \subseteq S_{ww}$ BE COMPACT, AND $\underset{\sim}{g}_U(x)$ AND $b_{\lambda,U}(x)$ BE AS ABOVE. DEFINE

$$\Omega_1 = \{ x \in \Omega \mid \underset{\sim}{g}_U(x) > 0 \}$$

IF $(\tilde{1})-(2)$ IS SUCH THAT Ω_1 HAS POSITIVE MEASURE AND $\{M_\lambda\}_{\lambda \geq 0}$ SATISFIES (6a - 6c), THEN THERE IS $\Lambda > 0$ SO THAT $\int_\Omega b_{\lambda,U}(x)\,dx > 0$ FOR ALL $\lambda \geq \Lambda$.

$\boxed{\text{THEOREM 2:}}$ SUPPOSE THAT $\{M_\lambda\}_{\lambda \geq 0}$ SATISFIES (6a) - (6c) AND THAT $(u^*, 0, 0)$ AND A_1 ARE AS PRECEDING. IF

THERE EXISTS $x_0 \in \Omega$ SO THAT $g(u(x_0), 0, w(x_0)) > 0$

FOR ALL $(u, 0, w) \in \{(u^*, 0, 0)\} \cup A_1$ AND

$\tilde{M}(u,v,w) = M_\lambda(g(u,v,w))$ FOR SUFFICIENTLY

LARGE λ, THEN v WILL BE UNIFORMLY PERSISTENT IN $(\tilde{1})-(2)$ FOR ALL INITIAL CONDITIONS (u_0, v_0, w_0) WITH NEITHER u_0 NOR v_0 IDENTICALLY ZERO.

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

ELEMENTS OF PROOF: BASED ON THE ACYCLICITY THEOREM OF PERSISTENCE THEORY, WE NEED:

(i) NO SUBSET OF $C = \{(0,0,0), (u^*,0,0), A_1\}$ CAN FORM A CYCLE IN S.

(ii) NO ISOLATED COMPACT INVARIANT SET IN $A \cap (S \setminus S_{uw})$ IS CHAINED TO AN ELEMENT OF C.

(iii) $W^s(M) \cap (X \setminus S) = \phi$ FOR $M \in C$.

(i): FOLLOWS FROM OUR DISCUSSION OF (7)

(ii): ACYCLICITY APPLIES TO S_{uv} $(w \equiv 0)$ PROVIDED

$W^s((u^*,0,0)) \cap \text{int}\, S_{uv} = \phi$. HERE ANALOGUES TO LEMMAS 1 AND 3 FOR $b_\lambda(x) = \dfrac{g^*((u^*(x),0,0)}{M_\lambda(g^*(u^*(x),0,0))}$

IMPLY SUCH WILL BE THE CASE FOR λ SUFFICIENTLY LARGE. ONE GETS A COMPACT INVARIANT SET A_2 IN INT S_{uv} WHICH ATTRACTS ALL INITIAL DATA OF THE FORM $(u_0,v_0,0)$ WITH $u_0 \not\equiv 0$, $v_0 \not\equiv 0$.

ACYCLICITY ARGUMENT FOR UNIFORM PERSISTENCE (CONT.)

FOR S_{vw} $(u \equiv 0)$, ONE MAY SHOW (VIA A SOMEWHAT DELICATE ARGUMENT) THAT ALL INITIAL DATA ARE DRAWN TO $(0,0,0)$.

CONSEQUENTLY A_2 IS THE ONLY ISOLATED COMPACT INVARIANT SET IN $A \cap (S \setminus S_{uw})$. A_2 IS NOT CHAINED TO ANY ELEMENT OF $\mathcal{C}$. SO (ii) HOLDS.

(iii): SET $U = \{(u^*,0,0)\} \cup A_1$. APPLY LEMMAS 1 AND 3.

(ARGUMENT AT $\{(0,0,0)\}$ SIMPLER.)

COMMENTS

a. ECOLOGICALLY, THM 2 SAYS THAT AS LONG AS THERE IS A LOCATION IN THE HABITAT WHERE CONDITIONS ARE FAVORABLE (FOR THE IG PREY) FOR ALL ASYMPTOTICALLY FEASIBLE RESOURCE - IG PREDATOR CONFIGURATIONS, APPLYING A STRONG ENOUGH FITNESS BASED AVOIDANCE STRATEGY WILL ALLOW THE IG PREY TO BE UNIFORMLY PERSISTENT IN THE SYSTEM.

b. AS NOTED, A FAMILY OF MOTILITY FUNCTIONS $\{M_\lambda(g^*)\}_{\lambda \geq 0}$ SATISFYING (6a)-(6c) WITH M_λ TWICE DIFFERENTIABLE IS

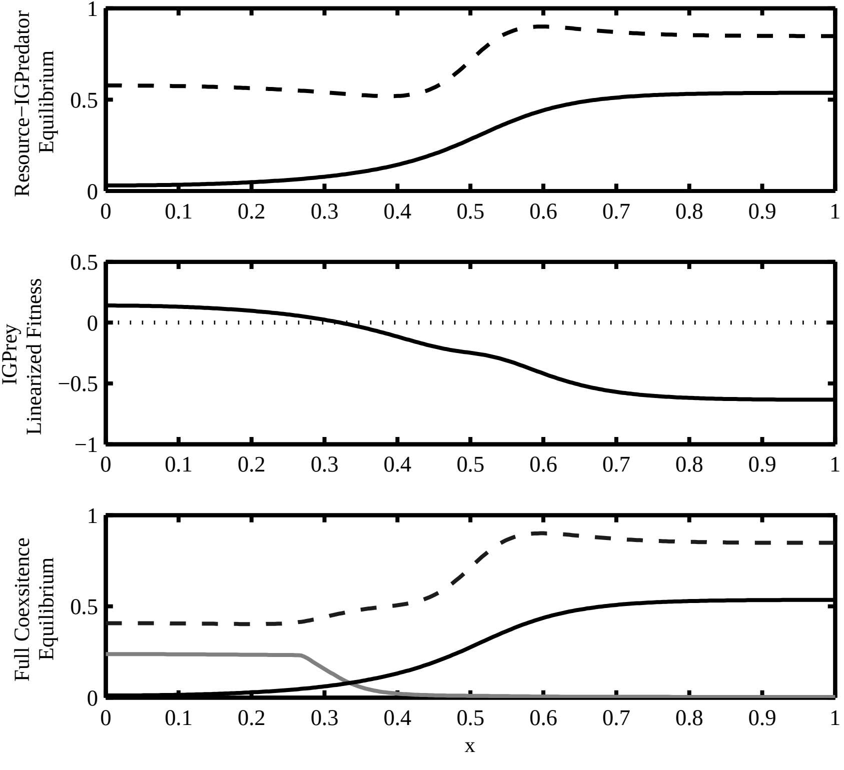
$$M_\lambda(g^*) = \begin{cases} d_2 & g^* \geq 0 \\ -\lambda g^* e^{d_2/(\lambda g^*)} + d_2 & g^* < 0 \end{cases}$$

Numerical Examples

Scenarios: Related to **Holt** and **Polis**, American Naturalist 1997

Scenario One: IG Predator does not gain significantly from consumption of IG prey (e_3 small or zero)

Scenario Two: IG prey is an inferior competitor for the shared resource ($e_1 < e_2$) but is able to invade and persist using fitness based avoidance by exploiting areas where the IG predator has under exploited the available resources due to over dispersion. IG predator has a moderate random diffusion rate and is only mildly aggressive toward the IG prey (a_3 small).


Resource−IGPredator
Equilibrium
IGPrey
Linearized Fitness
Full Coexsitence
Equilibrium
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0.5
0
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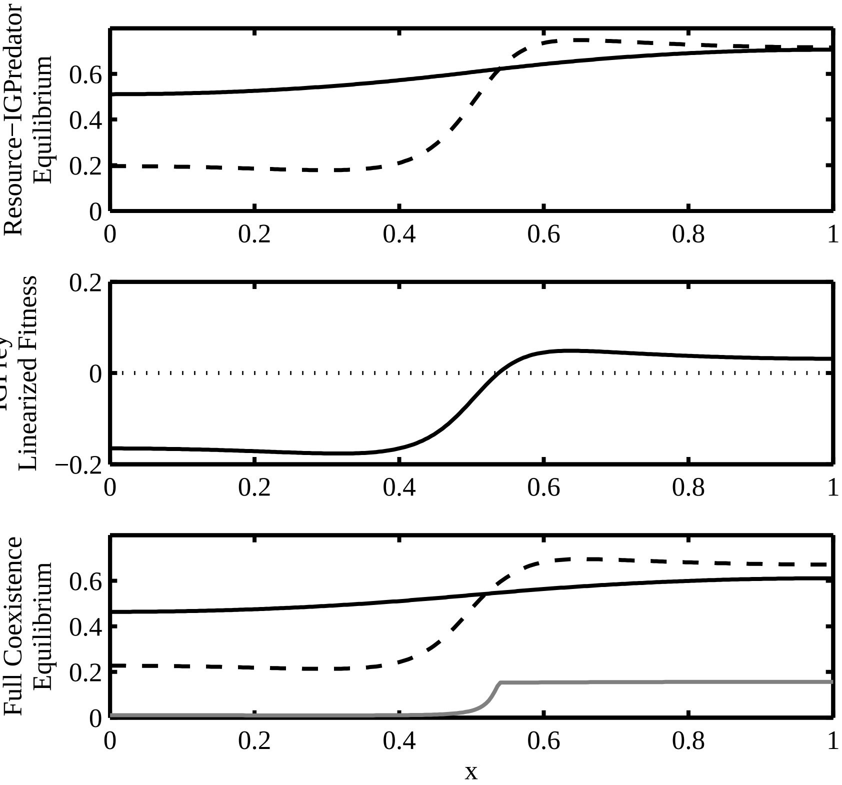
Resource−IGPredator
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Full Coexistence
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THANKS !