

## **Time Scales and Stability in Models of Coevolution**

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V. Krivan and R. Cressman

“On evolutionary stability in predator-prey models with fast behavioural dynamics”,  
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<http://www.wlu.ca/wwwmath/faculty/cressman/rcressman.research.html>

### **Single Species Habitat Selection**

Separation of Time Scales

- a) Fast Migration Dynamics
- b) Fast Population Dynamics

### **Single Habitat Predator Prey Models**

1. Lotka-Volterra with logistic prey

- a) Fast Prey Dynamics
- b) Intermediate Time Scales

2. Holling II with logistic prey

- a) Intermediate Time Scales

### **Two Habitat Predator Prey Models**

1. LV with logistic prey and adaptive predators

- a) Intermediate Time Scales

2. LV with logistic prey and adaptive prey and predators

- a) Intermediate Time Scales

### **Single Species Habitat Selection**

Intermediate Time Scales

## Single Species Habitat Selection

$H$ : Number of habitats

$M$ : Total population size

$p$ : Distribution of population in habitats.

$$p \in \Delta^H = \{(p_1, \dots, p_H) : \sum p_i = 1, p_i \geq 0\}$$

Individuals migrate from patch  $j$  to patch  $i$  at the rate  $I_{ij}(p, M)$ . That is, if there is only migration and no change in population size,

$$\dot{p} = I(p, M)p - p \quad \text{or} \quad \dot{p}_i = \sum_{j=1}^H I_{ij}(p, M)p_j - p_i$$

where  $\sum_{i=1}^H I_{ij}(p, M) = 1$  for all  $1 \leq i \leq H$ .

### Assumptions:

1. The fitness of all individuals in habitat  $i$  is  $F_i(p_i, M)$  which is a decreasing function of both  $p_i$  and  $M$ . Fitness is positive if a habitat is empty and each habitat has a carrying capacity  $K_i$ . That is

$$F_i(0, M) > 0 \text{ and } F_i(K_i/M, M) = 0 \text{ if } M \geq K_i.$$

2. No individuals migrate to a patch with a lower fitness. That is,

$$I_{ij}(p, M) = 0 \text{ if } F_i(p_i, M) < F_j(p_j, M)$$

3. Some individuals migrate to the patch with the highest fitness. That is, for some  $j \neq i$  with  $p_j > 0$ ,

$$I_{ij}(p, M) > 0 \text{ if } F_i(p_i, M) = \max_j F_j(p_j, M).$$

### Separation of Time Scales:

For fast behavioral dynamics, first fix  $M$  and consider the evolution of the population distribution. Then consider the population dynamics assuming that it evolves at a per capita rate given by the mean fitness for the current distribution.

## Fast Behavioral Dynamics

**Theorem 1.** If the three assumptions above are satisfied, then  $p$  evolves to the Ideal Free Distribution (IFD) under the fast behavioral dynamics with fixed  $M$ . Label this IFD as  $p(M)$ .

The population dynamics is  $\dot{M} = M\bar{F}(p(M), M)$  where  $\bar{F} \equiv \sum_{j=1}^H p_j F_j(p(M), M) = F_i(p(M), M)$  for all  $p_i > 0$  and is the mean fitness of the population.

**Theorem 2.** Total population size evolves to  $K \equiv K_1 + \dots + K_H$  with corresponding IFD given by  $p_i = K_i/K$  for  $i = 1, \dots, H$ .

That is, under fast behavioral dynamics, the population evolves to its carrying capacity  $K_i$  in each of its  $H$  habitats.

**Proof 1.** Let  $V(p, M) = \max_j F_j(p_j, M)$ . Since  $p_i$  increases if  $F_i(p_i, M) = \max_j F_j(p_j, M)$ ,  $F_i(p_i, M)$  decreases and so  $V(p, M)$  decreases. Similarly,  $v(p, M) = \min_j \{F_j(p_j, M) : p_j > 0\}$  increases and so eventually,  $F_i(p_i, M) = F_j(p_j, M) = \bar{F}$  for all  $p_i p_j > 0$ . Furthermore, at this limit, if  $F_i(0, M) > \bar{F}$ , then  $p_i > 0$ . This is the unique IFD at fixed  $M$ .

**Proof 2.** If  $M > K$ , then  $M p_i(M) > K_i$  for some  $p_i > 0$ . Thus  $\bar{F}(p(M), M) < 0$  and so  $M$  is decreasing. Similarly, if  $M < K$ , then  $M p_i(M) < K_i$  for some  $p_i$ . Thus  $\bar{F}(p(M), M) > 0$  and so  $M$  is increasing. That is,  $M$  evolves to  $K$ .

## Fast Population Dynamics

First fix  $p$  and consider the evolution of the population size. Then consider the behavioral dynamics assuming that it evolves through migration satisfying our three assumptions.

**Theorem 3.** For fixed  $p$ , the total population size evolves to a unique population size  $M(p)$  satisfying  $\bar{F}(p, M(p)) = 0$ .

As a function of  $p$ ,  $M(p)$  is called the  $((H - 1)$ -dimensional) stationary density surface (SDS).

The behavioral dynamics is now

$$\dot{p} = I((p, M(p)))p - p.$$

**Theorem 4.** Total population distribution evolves to  $p_i = K_i/K$  with corresponding total population size  $K$ .



**Proof 3.** For fixed  $p$ , the population dynamics is  $\dot{M} = M\bar{F}(p, M)$  where  $\bar{F}(p, M)$  is a decreasing function of  $M$ . If  $M = 0$ ,  $\dot{M} > 0$  since  $F_i(p, 0) > 0$  for all  $i$ . Also if  $M > \sum_{\{i: p_i > 0\}} K_i/p_i$ , then each occupied habitat is above its carrying capacity and so  $\dot{M} < 0$ . Thus, there exists a unique  $M(p) > 0$  such that  $\dot{M} = 0$  and  $M$  evolves to it.

**Proof 4.** Let  $V(p, M(p)) = \max_j F_j(p_j, M(p)) = F_{i_0}$ . Then  $V(p, M(p)) \geq 0$  since  $\bar{F} = 0$ . If  $V(p, M(p)) > 0$ , then  $\dot{p}_{i_0} > 0$  by our assumptions on the migration dynamics and so  $F_{i_0}$  is decreasing. Thus,  $V(p, M(p))$  evolves to zero. At every limit point  $p^*$  of the trajectory,  $p_i^* > 0$  and  $F_i = \bar{F} = 0$  for all  $i$ . The proof is complete since the only such limit point  $p^*$  is the IFD with each habitat at its carrying capacity.

### Summary for Single-Species Habitat Selection:

Under either fast behavioral dynamics or fast population dynamics, the system evolves to carrying capacity in each of the  $H$  patches.

Question: What about intermediate time scales?  
Return to this later.

## Single Habitat Predator Prey Models

1. Lotka-Volterra with logistic prey growth.

$x$ : prey density

$y$ : predator density

$$\begin{aligned}\dot{x} &= ax \left(1 - \frac{x}{L}\right) - \lambda xy \\ \dot{y} &= y(e\lambda x - m)\end{aligned}$$

Prey carrying capacity  $L$ ;  
intrinsic growth rate  $a$ .

Predator search rate  $\lambda$ ; mortality rate  $m$ .

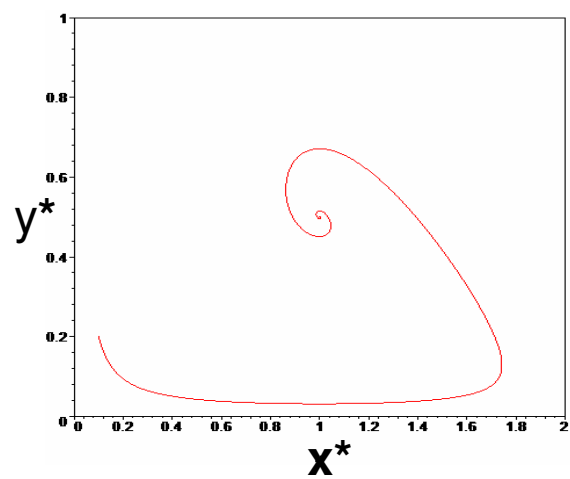
Consumed prey converted to new predators  
with efficiency  $e$ .

The equilibrium is  $(x^*, y^*) = \left(\frac{m}{e\lambda}, \frac{a(eL\lambda - m)}{eL\lambda^2}\right)$  provided the prey carrying capacity is larger than its equilibrium value (i.e.  $L > x^*$ ). By standard techniques,  $(x^*, y^*)$  is globally asymptotically stable.

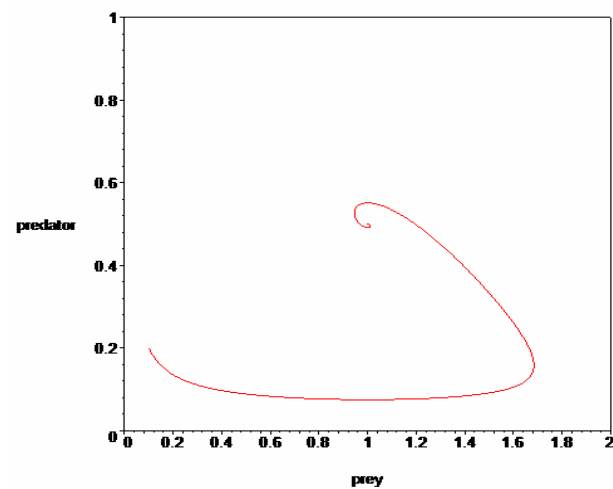
Note: If  $L \leq x^*$ , the predator goes extinct and the prey evolve to their carrying capacity. That is,  $(L, 0)$  is globally asymptotically stable.

**Example:** Take  $a = \lambda = e = m = 1$  and  $L = 2$ . Then  $L > x^* = 1$  and so  $(x^*, y^*) = \left(1, \frac{1}{2}\right)$  is globally asymptotically stable.

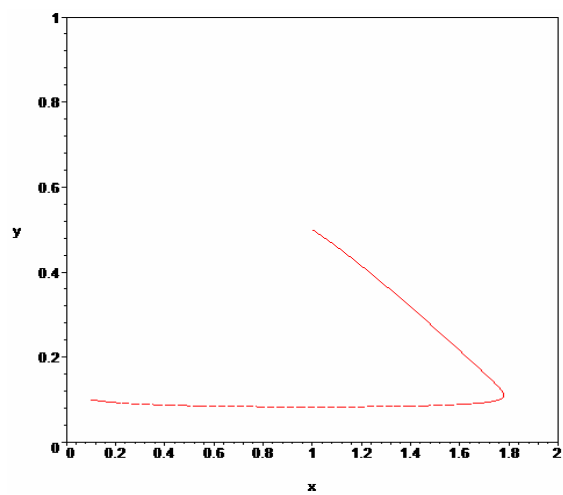
A sample trajectory is shown on the next slide labeled  $r = 1$ .



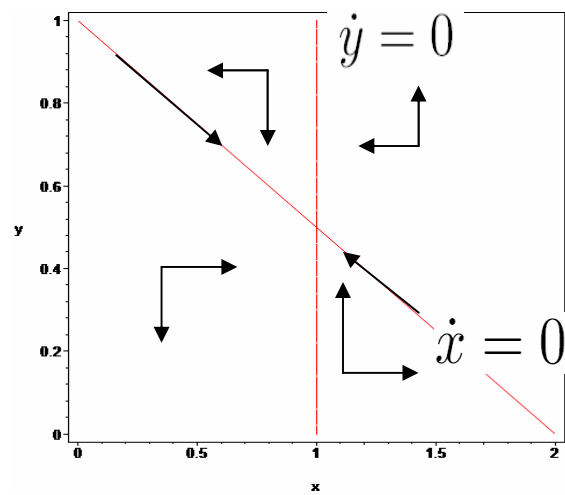
**$r=1$**



**$r=2$**



**$r=10$**



## Fast Prey Dynamics

First fix  $y$  and consider the evolution of the prey population. Then consider the predator dynamics assuming that the prey are at their limiting behavior for each  $y$ .

$$\text{For fixed } y, x \rightarrow \begin{cases} \frac{L}{a}(a - \lambda y) & \text{if } y < \frac{a}{\lambda} \\ 0 & \text{if } y \geq \frac{a}{\lambda} \end{cases}.$$

Thus, the predator dynamics is

$$\dot{y} = \begin{cases} y \left( \frac{e\lambda L}{a}(a - \lambda y) - m \right) & \text{if } y < \frac{a}{\lambda} \\ -my & \text{if } y \geq \frac{a}{\lambda} \end{cases}.$$

$$\dot{y} = \begin{cases} (e\lambda L - m) y \left( 1 - \frac{y}{a(e\lambda L - m)/eL\lambda^2} \right) & \text{if } y < \frac{a}{\lambda} \\ -my & \text{if } y \geq \frac{a}{\lambda} \end{cases}.$$

If  $L \leq x^*$ , then  $y \rightarrow 0$  and  $x \rightarrow L$ .

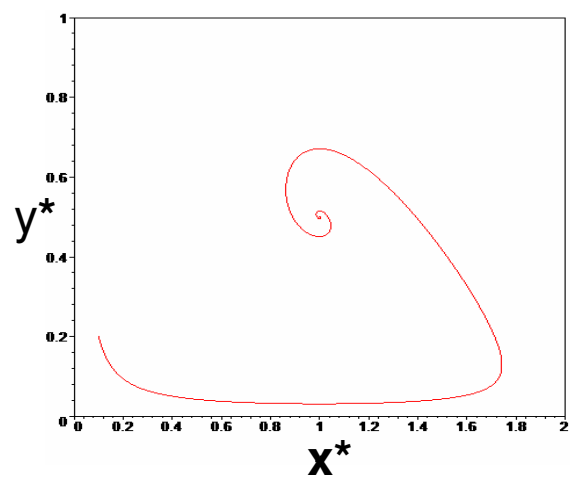
If  $L > x^*$ , then  $y \rightarrow \frac{a(eL\lambda - m)}{eL\lambda^2} = y^*$  since  $y^* < \frac{a}{\lambda}$ . Also  $x \rightarrow x^*$ .

We have shown the following result:

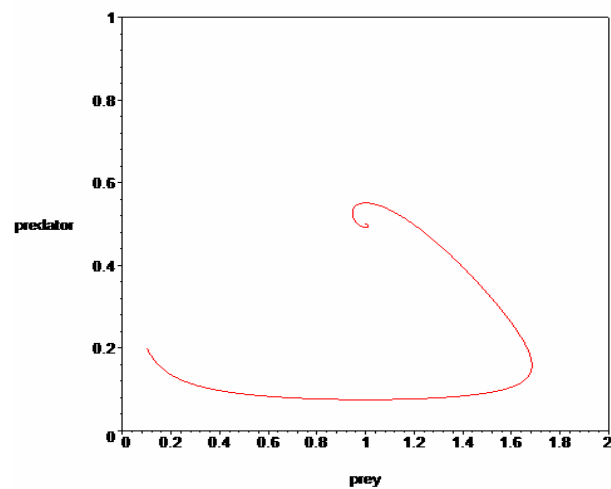
**Theorem 5.** With fast prey dynamics, the system evolves to the same equilibrium as the original predator-prey system. In fact, this equilibrium is globally asymptotically stable for any choice of time scales (i.e. any choice of  $r > 0$ ) in the system

$$\begin{aligned}\dot{x} &= r \left[ ax \left( 1 - \frac{x}{L} \right) - \lambda xy \right] \\ \dot{y} &= y (e\lambda x - m) .\end{aligned}$$

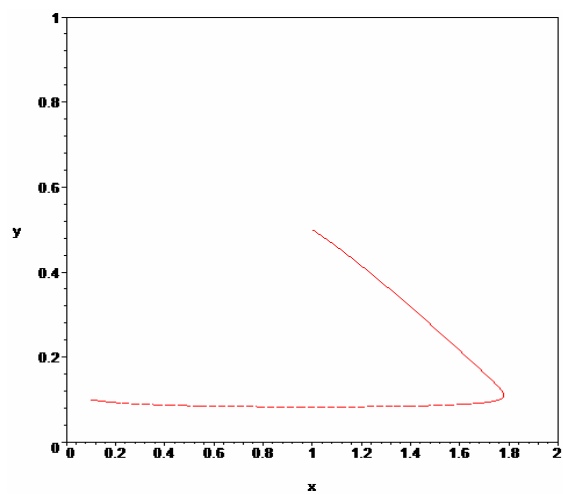
Thus, for long term behavior of the system, it is not important to know the time scale of the prey dynamics compared to the predator dynamics. This long term outcome is determined by completely separating the time scales and analyzing the predator dynamics on the prey null cline (which I will also call the stationary prey density surface).



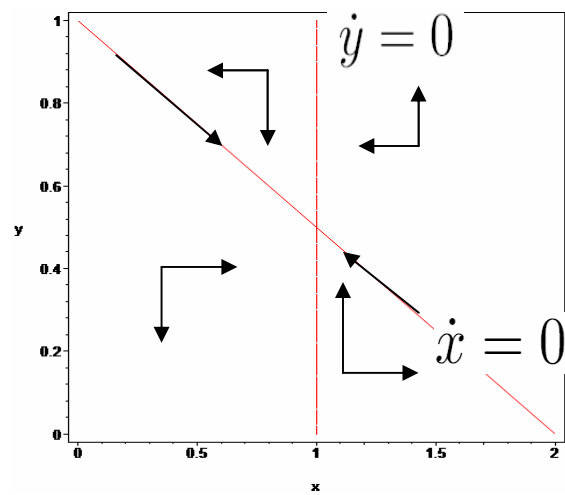
**$r=1$**



**$r=2$**



**$r=10$**





## Single Habitat Predator Prey Models

### 2. Holling II with logistic prey growth.

With  $h$  the predator handling time to process a single prey, we have the the following model (Rosenzweig and MacArthur, 1963)

$$\begin{aligned}\dot{x} &= ax \left(1 - \frac{x}{L}\right) - \frac{\lambda x}{1 + \lambda h x} y \\ \dot{y} &= y \left( \frac{e \lambda x}{1 + \lambda h x} - m \right)\end{aligned}$$

The equilibrium is

$$(x^*, y^*) = \left( \frac{m}{(e - mh)\lambda}, \frac{ae(L\lambda(e - mh) - m)}{L\lambda^2(e - hm)^2} \right)$$

provided  $e > mh$  and prey carrying capacity is larger than its equilibrium value ( $L > x^*$ ).

We will assume these two inequalities hold from now on.

Stationary Prey Density Surface:  $\dot{x} = 0$  when

$$y = \frac{a}{\lambda} \left( \left( 1 - \frac{x}{L} \right) \right) (1 + h\lambda x)$$

This is a downwards parabola with vertex at  $\hat{x} \equiv \frac{h\lambda L - 1}{2h\lambda}$ . If  $\hat{x} > x^*$ , then  $(x^*, y^*)$  is unstable and a stable limit cycle attracts all initial conditions. If  $\hat{x} < x^*$ , then  $(x^*, y^*)$  is globally asymptotically stable.

**Theorem 6.** Assume that  $e > mh$  and  $\hat{x} < x^* < L$ . With fast prey dynamics, the system evolves locally to the same equilibrium as the original predator-prey system (i.e. to  $(x^*, y^*)$ ). In fact, this equilibrium is globally asymptotically stable for any choice of time scales (i.e. any choice of  $0 < r < \infty$ ) in the system

$$\begin{aligned} \dot{x} &= r \left[ ax \left( 1 - \frac{x}{L} \right) - \frac{\lambda x}{1 + \lambda h x} y \right] \\ \dot{y} &= y \left( \frac{e\lambda x}{1 + \lambda h x} - m \right) \end{aligned}$$

**Proof** of local stability for  $0 < r < \infty$ .

Linearization about  $(x^*, y^*)$  is 
$$\begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} = J \begin{bmatrix} x - x^* \\ y - y^* \end{bmatrix}$$

where

$$J(x^*, y^*) = \begin{bmatrix} rx^* \left[ -\frac{a}{L} + \frac{\lambda^2 hy^*}{(1+h\lambda x^*)^2} \right] & -rx^* \frac{\lambda}{1+h\lambda x^* y^*} \\ \frac{e\lambda y^*}{(1+h\lambda x^*)^2} & 0 \end{bmatrix}.$$

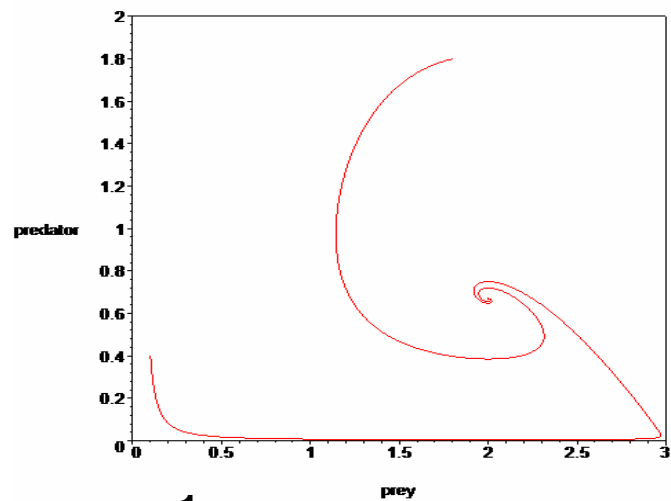
Since  $\det J > 0$ ,  $(x^*, y^*)$  is locally asymptotically stable if  $\frac{a}{L} > \frac{\lambda^2 hy^*}{(1+h\lambda x^*)^2}$  (i.e.  $\text{tr} J < 0$ ) and unstable if this inequality is reversed.

Now  $\frac{a}{L} = \frac{\lambda^2 hy^*}{(1+h\lambda x^*)^2}$  if and only if

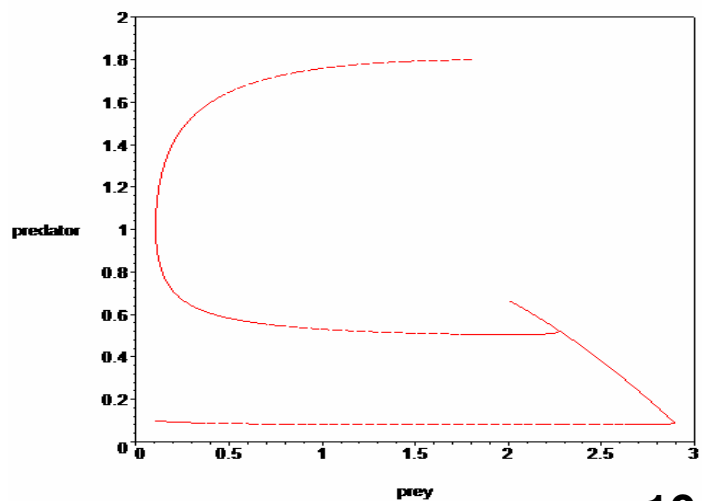
$a(1+h\lambda x^*)^2 = L\lambda^2 hy^*$  if and only if

$L = \frac{e+mh}{h\lambda(e-mh)}$  if and only if  $\hat{x} = x^*$ .

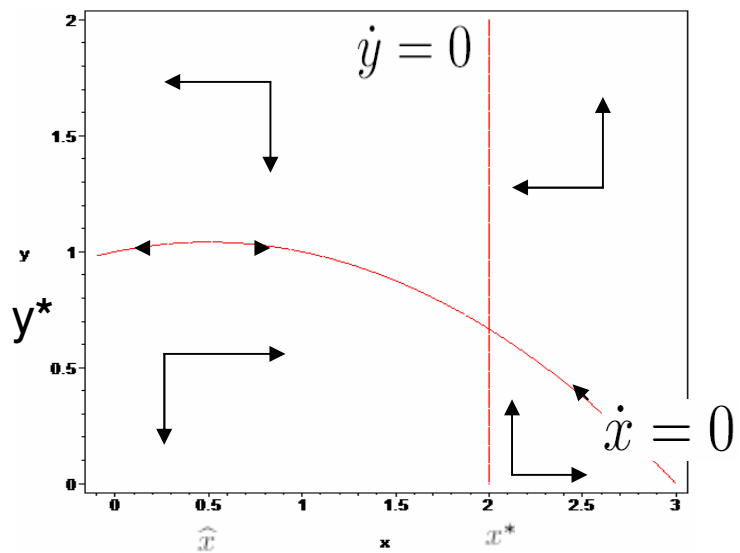
The remainder of the proof is straightforward.



**r=1**



**r=10**

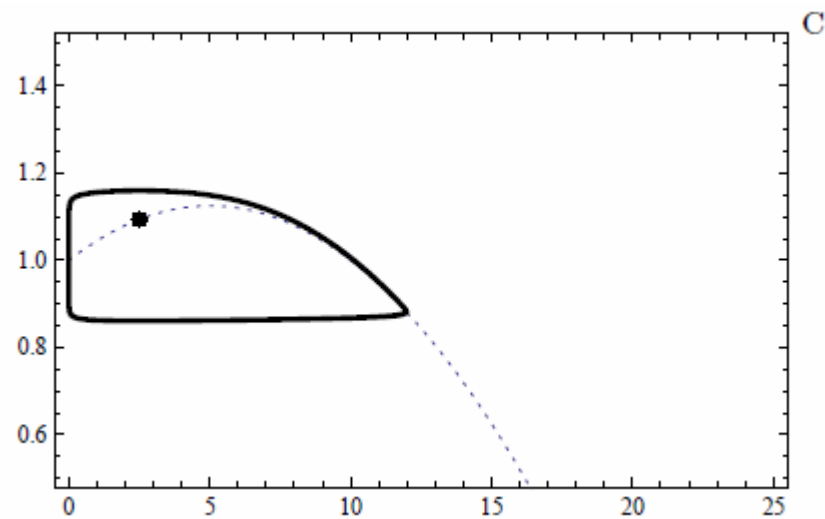


**Example:** Take  $a = \lambda = e = m = 1$ ,  $h = 0.5$  and  $L = 3$ . Then  $L > x^* = 1$  and so  $(x^*, y^*) = (2, \frac{2}{3})$  is globally asymptotically stable.

Two sample trajectories are shown on the previous slide labeled  $r = 1$ . Also shown are two trajectories with  $r = 10$  as well as the phase diagram with the parabolic stationary prey density surface. The prey dynamics quickly approaches the stationary prey density surface and then follows along this curve to the equilibrium. For still larger  $r$ , this occurs for initial points above and to the left of  $(x^*, y^*)$  as well.

We again find that, to understand the long term behavior of this system, it is not important to know the time scale of the prey dynamics compared to the predator dynamics.

On the other hand, if  $x^* < \hat{x}$  as in the diagram below,  $(x^*, y^*)$  is unstable and a stable limit cycle emerges with part of its trajectory along the stationary prey density surface as  $r$  gets large.



## Two Habitat Predator Prey Models

1. LV with logistic prey and adaptive predators

$x_i$ : prey density in habitat  $i$  ( $i = 1, 2$ )

$u_i$ : predator preference for habitat  $i$

Here  $u_1 + u_2 = 1$ .

$$\dot{x}_1 = a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - u_1 \lambda_1 x_1 y$$

$$\dot{x}_2 = a_2 x_2 \left(1 - \frac{x_2}{L_2}\right) - u_2 \lambda_2 x_2 y$$

$$\dot{y} = (e_1 \lambda_1 x_1 - m_1) u_1 y + (e_2 \lambda_2 x_2 - m_2) u_2 y$$

$$\dot{u}_1 = u_1(1 - u_1) [(e_1 \lambda_1 x_1 - m_1) - (e_2 \lambda_2 x_2 - m_2)]$$

Provided  $x_1^* = \frac{m_1}{e_1 \lambda_1}$  and  $x_2^* = \frac{m_2}{e_2 \lambda_2}$  are less than their respective prey carrying capacities  $L_1$  and  $L_2$ , the equilibrium  $(x_1^*, x_2^*, y^*, u_1^*)$  exists.

The equilibrium is  $x_1^* = \frac{m_1}{e_1\lambda_1}$ ,  $x_2^* = \frac{m_2}{e_2\lambda_2}$ ,

$$y^* = \frac{a_1(e_1L_1\lambda_1 - m_1)}{e_1L_1\lambda_1^2} + \frac{a_2(e_2L_2\lambda_2 - m_2)}{e_2L_2\lambda_2^2}$$

and  $u_1^*$  given by

$$u_1^* = \frac{a_1e_2\lambda_2^2L_2(e_1L_1\lambda_1 - m_1)}{a_1e_2\lambda_2^2L_2(e_1L_1\lambda_1 - m_1) + a_2e_1\lambda_1^2L_1(e_2L_2\lambda_2 - m_2)}.$$

**Theorem 7** Assume  $x_1^* > \frac{m_1}{e_1\lambda_1}$  and  $x_2^* > \frac{m_2}{e_2\lambda_2}$ . Then  $(x_1^*, x_2^*, y^*, u_1^*)$  is asymptotically stable. In fact, it is locally asymptotically stable for any choice of time scales for the three density dynamics and behavioral dynamics.

Note: In fact, this equilibrium is globally asymptotically stable when the time scale of the fast behavioral dynamics is separated from the population dynamics.  
(Krivan and Schmitz, 2003).



**Proof** of local stability for  $0 < r_i < \infty$ .

Linearization about  $(x_1^*, x_2^*, y^*, u_1^*)$  yields the  $4 \times 4$  Jacobian matrix  $J(x_1^*, x_2^*, y^*, u_1^*)$

$$\begin{bmatrix} -r_1 x_1^* \frac{a_1}{L_1} & 0 & -r_1 \lambda_1 u_1^* x_1^* & -r_1 \lambda_1 y^* x_1^* \\ 0 & -r_2 x_2^* \frac{a_2}{L_2} & -r_2 \lambda_2 u_2^* x_2^* & r_2 \lambda_2 y^* x_2^* \\ r_3 e_1 \lambda_1 u_1^* y^* & r_3 e_2 \lambda_2 u_2^* y^* & 0 & 0 \\ r_4 e_1 \lambda_1 u_1^* u_2^* & -r_4 e_2 \lambda_2 u_1^* u_2^* & 0 & 0 \end{bmatrix}$$

The Routh-Hurwitz stability criteria are satisfied for all choices of  $0 < r_i < \infty$ .

Mathematically,  $J$  is called a **D-stable** matrix. In such cases, time scales are not important.

2. LV with logistic prey and adaptive prey and predators

$v_i$ : prey preference for habitat  $i$  ( $v_1 + v_2 = 1$ )

$$\begin{aligned}\dot{x} = & \left[ a_1 \left( 1 - \frac{v_1 x}{L_1} \right) - \lambda_1 u_1 y \right] v_1 x \\ & + \left[ a_2 \left( 1 - \frac{v_2 x}{L_2} \right) - \lambda_2 u_2 y \right] v_2 x\end{aligned}$$

$$\dot{y} = (e_1 \lambda_1 v_1 x - m_1) u_1 y + (e_2 \lambda_2 v_2 x - m_2) u_2 y$$

$$\dot{v}_1 = v_1(1 - v_1) \left[ \begin{array}{c} \left( a_1 \left( 1 - \frac{v_1 x}{L_1} \right) - \lambda_1 u_1 y \right) \\ - \left( a_2 \left( 1 - \frac{v_2 x}{L_2} \right) - \lambda_2 u_2 y \right) \end{array} \right]$$

$$\dot{u}_1 = u_1(1 - u_1) [(e_1 \lambda_1 v_1 x - m_1) - (e_2 \lambda_2 v_2 x - m_2)]$$

Provided  $L_1 > \frac{m_1}{e_1 \lambda_1}$  and  $L_2 > \frac{m_2}{e_2 \lambda_2}$ , the

equilibrium is  $(x^*, y^*, v_1^*, u_1^*)$  where

$$x^* = \frac{m_1}{e_1 \lambda_1} + \frac{m_2}{e_2 \lambda_2}$$

$$v_1^* = \frac{m_1}{e_1 \lambda_1 x^*}$$

$$y^* = \frac{a_1}{\lambda_1} \left( 1 - \frac{v_1^* x^*}{L_1} \right) + \frac{a_2}{\lambda_2} \left( 1 - \frac{v_2^* x^*}{L_2} \right)$$

$$u_1^* = \frac{a_1}{\lambda_1 y^*} \left( 1 - \frac{v_1^* x^*}{L_1} \right)$$

The  $4 \times 4$  Jacobian matrix  $J(x^*, y^*, v_1^*, u_1^*)$

$$\begin{bmatrix} -\left(\frac{a_1 v_1^2}{L_1} + \frac{a_2 v_2^2}{L_2}\right)x & -\left(\lambda_1 u_1 v_1 + \lambda_2 u_2 v_2\right)x & \left(-\frac{a_1 v_1}{L_1} + \frac{a_2 v_2}{L_2}\right)x^2 & \left(-\lambda_1 v_1 + \lambda_2 v_2\right)xy \\ \left(e_1 \lambda_1 u_1 v_1 + e_2 \lambda_2 u_2 v_2\right)y & 0 & \left(e_1 \lambda_1 u_1 - e_2 \lambda_2 u_2\right)xy & 0 \\ \left(-\frac{a_1 v_1}{L_1} + \frac{a_2 v_2}{L_2}\right)v_1 v_2 & \left(-\lambda_1 u_1 + \lambda_2 u_2\right)v_1 v_2 & -\left(\frac{a_1 x}{L_1} + \frac{a_2 x}{L_2}\right)v_1 v_2 & -\left(\lambda_1 + \lambda_2\right)v_1 v_2 y \\ \left(e_1 \lambda_1 v_1 - e_2 \lambda_2 v_2\right)u_1 u_2 & 0 & \left(e_1 \lambda_1 x - e_2 \lambda_2 x\right)u_1 u_2 & 0 \end{bmatrix}.$$

The Routh-Hurwitz stability criteria are satisfied for this matrix but not for all choices of  $0 < r_i < \infty$ .

That is, this is not always a D-matrix and so time-scales are important.

**Example.** Take  $a_1 = 1; a_2 = 2; L_1 = L_2 = 2;$   
 $\lambda_1 = 1; \lambda_2 = 2; e_1 = m_1 = 4; e_2 = 1; m_2 = 2.$

Then  $v_1^* = u_1^* = \frac{1}{2}, x^* = 2$  and  $y^* = 1.$

The  $4 \times 4$  Jacobian matrix  $J(x^*, y^*, v_1^*, u_1^*)$  is

$$\begin{bmatrix} -\frac{3}{8}x & -\frac{3}{4}x & \frac{1}{4}x^2 & \frac{1}{2}xy \\ \frac{3}{2}y & 0 & xy & 0 \\ \frac{1}{16} & \frac{1}{8} & -\frac{3}{8}x & -\frac{3}{4}y \\ \frac{1}{4} & 0 & \frac{3}{2}x & 0 \end{bmatrix}.$$

The Routh-Hurwitz stability criteria are satisfied for this matrix but if  $r_1$  and  $r_4$  are large,

the corresponding  $2 \times 2$  matrix  $\begin{bmatrix} -\frac{3}{8}x & \frac{1}{2}xy \\ \frac{1}{4} & 0 \end{bmatrix}$   
 has negative determinant  $-\frac{1}{8}xy = -\frac{1}{4}$  and so  
 the system is not stable with this time scale.

For this model, we can completely separate the behavioral dynamics from the population dynamics.

### **Results**

1. For fast behavioral dynamics,  $(x^*, y^*, v_1^*, u_1^*)$  is asymptotically stable (Cressman, Krivan and Garay, 2004).
2. For fast population dynamics (also called adaptive dynamics),  $(x^*, y^*, v_1^*, u_1^*)$  is asymptotically stable.

We can also completely separate the prey dynamics (i.e. the combined population and behavioral dynamics of the prey) from that of the predator.

### **Results**

3. For fast prey dynamics in this example, the linearized system is neutrally stable at  $(x^*, y^*, v_1^*, u_1^*)$

## Single Species Habitat Selection Intermediate Time Scales

When there is no migration, the population dynamics is  $\dot{m}_i = m_i F_i(p_i, M)$  in habitat  $i$ .

When there is only migration, the behavioral dynamics is  $\dot{m}_i = \sum_{j=1}^H I_{ij}(p, M) m_j - m_i$ .

### Intermediate Time Scales (Case 1):

$\dot{m}_i = m_i F_i(p_i, M) + r \left[ \sum_{j=1}^H I_{ij}(p, M) m_j - m_i \right]$ .  
which can be rewritten as

$$\dot{M} = M \bar{F}(p(M), M)$$

$$\dot{p}_i = p_i \left[ F_i(p_i, M) - \bar{F} \right] + r \left[ \sum_{j=1}^H I_{ij}(p, M) p_j - p_i \right].$$

where  $\bar{F} \equiv \sum_{j=1}^H p_j F_j(p(M), M)$  is the mean fitness of the population.

**Theorem 8** (Cressman and Krivan, 2006).  
 Suppose that the three assumptions on  $F_i$  and  $I_{ij}$  are satisfied. Then, for all  $r > 0$ , the population evolves to its carrying capacity  $K_i$  in each of its  $H$  habitats  $i$  where  $1 \leq i \leq H$ .

Note that, in Case 1,  $p_i$  is evolving when there is no migration (i.e. when  $r = 0$ ).

### Intermediate Time Scales (Case 2):

$$\begin{aligned}\dot{M} &= M\overline{F}(p(M), M) \\ \dot{p}_i &= r p_i [F_i(p_i, M) - \overline{F}].\end{aligned}$$

If  $r > 1$ , then we are in Case 1 since  
 $\dot{p}_i = p_i [F_i(p_i, M) - \overline{F}] + (r - 1)p_i [F_i(p_i, M) - \overline{F}]$   
 and the conclusion of Theorem 8 remains valid.

**Conjecture.** For all  $0 < r \leq 1$ , the population evolves to its carrying capacity  $K_i$  in each of its  $H$  habitats  $i$  where  $1 \leq i \leq H$ .

Note: This conjecture is true for  $H = 2$  and  $H = 3$  using the D-stable matrix approach.



**Thank You**

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