# On evolutionary stability of optimal foraging

**Vlastimil KRIVAN**

**Biology Center & Faculty of Science**
**Ceske Budejovice**
**Czech Republic**

vlastimil.krivan@gmail.com

www.entu.cas.cz/krivan

Talk outline:

1. Two paradigmas of the optimal foraging theory: patch and diet choice models.

2. Derivation of frequency dependent fitness functions

3. Calculation of ESS, emergence of partial preferences

# Optimal foraging theory

(MacArthur and Pianka, 1966; Emlen 1966)

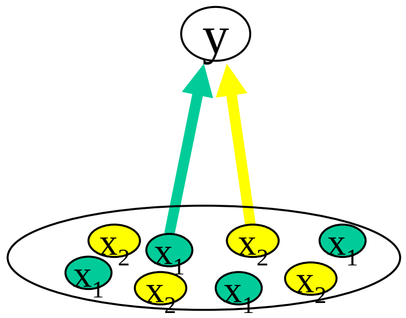
Two paradigms:

**Patch model** (Charnov 1976a) – heterogeneous environments consisting of foraging patches. When a forager should leave its current patch and start to search for a new patch?

**Diet choice model** (Charnov 1976b) - homogeneous environments with several resource types, strategy is defined as the probability with which a resource is included in the consumer diet

***Question:*** *What is the ``optimal'' foraging strategy?*

# Fitness function for the diet choice model




Energy gained during search time $T_s$: $(u_1 e_1 \lambda_1 x_1 + u_2 e_2 \lambda_2 x_2) T_s$

Total time spent by handling and searching food: $(1 + u_1 h_1 \lambda_1 x_1 + u_2 h_2 \lambda_2 x_2) T_s$

$$\text{Fitness} = \frac{\text{Energy gained}}{\text{Total time}}$$

$$W(\tilde{u}, u) = \frac{e_1 \lambda_1 \tilde{u}_1 x_1 + e_2 \lambda_2 \tilde{u}_2 x_2}{1 + h_1 \lambda_1 \tilde{u}_1 x_1 + h_2 \lambda_2 \tilde{u}_2 x_2}$$

# Optimal strategy for the diet choice

Assumption: Prey 1 is more profitable than prey 2, (i.e., $\frac{e_1}{h_1} > \frac{e_2}{h_2}$)

$$W = \frac{e_1\lambda_1\tilde{u}_1x_1 + e_2\lambda_2\tilde{u}_2x_2}{1 + h_1\lambda_1\tilde{u}_1x_1 + h_2\lambda_2\tilde{u}_2x_2} \mapsto \max_{(\tilde{u}_1,\tilde{u}_2)}$$

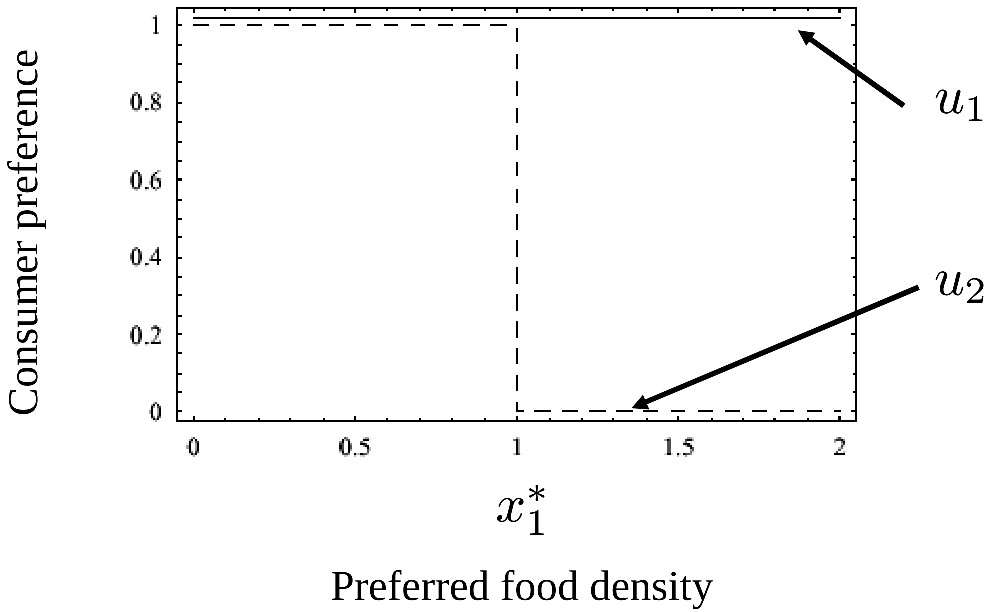
Zero-one rule:

(1) The preferred food 1 is always included in diet ($\tilde{u}_1 = 1$)

(2) The alternative food 2 is included when the abundance of the preferred food type 1 is lower than the threshold

$$x_1^\star = \frac{e_2}{\lambda_1(e_1h_2 - e_2h_1)}$$

otherwise it is excluded.




1. When $x_1 = x_1^*$ the strategy is not uniquely defined.
2. The optimal strategy does not depend on the number of foragers.

# Experiments with great tits

Krebs et al. (1977) | Berec et al. (2003)

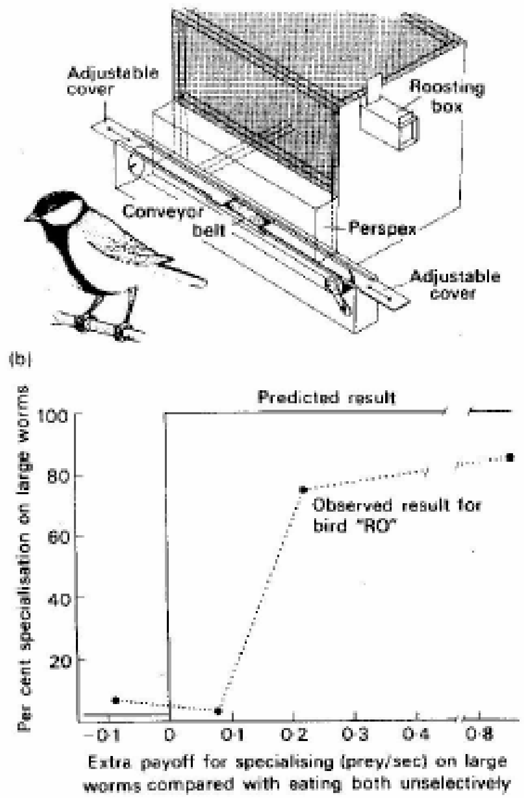
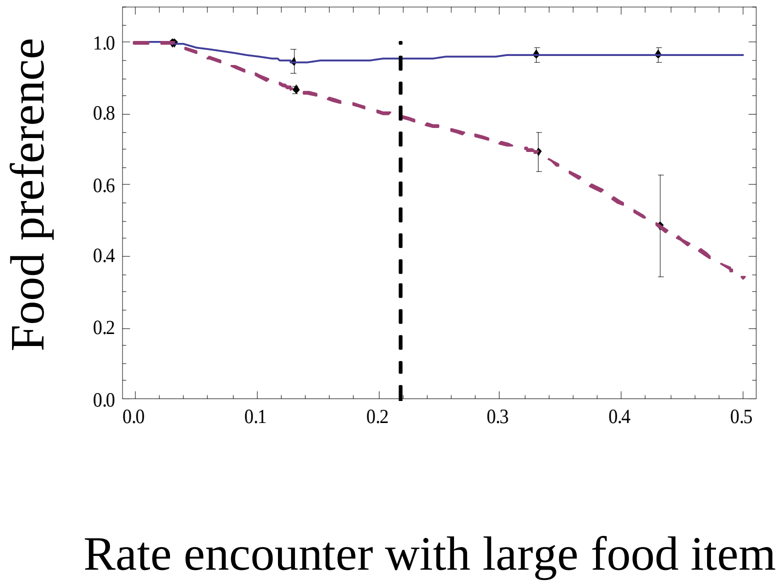
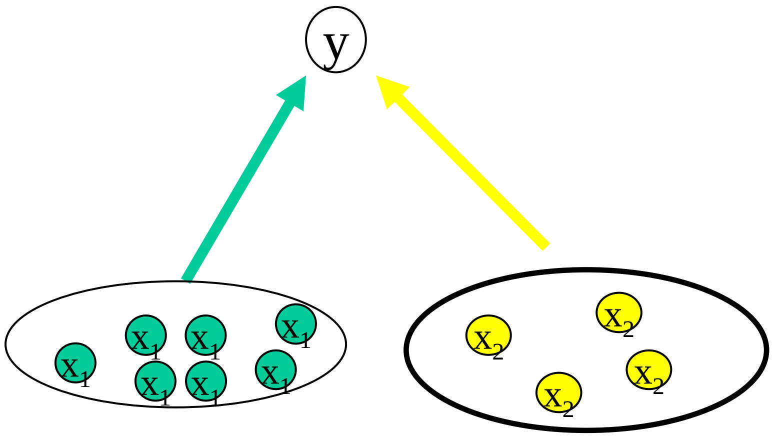



Fig. 3.6 (a) The apparatus used to test a model of choice between big and small worms in great tits (*Parus major*). The bird sits in a cage by a long conveyor belt on which the worms pass by. The worms are visible for half a second as they pass a gap in the cover over the top of the belt and the bird makes its choice in this brief period. If it picks up a worm it misses the opportunity to choose ones that go by while it is eating. (b) An example of the results obtained. As the rate of encounter with large worms increases the birds become more selective. The x-axis of the graph is the extra benefit obtained from selective predation. As shown in Box 3.2, the benefit becomes positive at a critical value of $S_1$, the search for worms. The bird becomes more selective about the predicted point, but in contrast with the model's prediction this change is not a step function. From Krebs *et al.* (1977).



# Fitness function for the patch model




$$W(\tilde{u}, u) = (e_1\lambda_1 x_1 - m_1)\tilde{u}_1 + (e_2\lambda_2 x_2 - m_2)\tilde{u}_2$$

Optimal strategy

$$\tilde{u}_1 = \begin{cases} 1 & \text{if} \;\; e_1\lambda_1 x_1 - m_1 > e_2\lambda_2 x_2 - m_2 \\ 0 & \text{if} \;\; e_1\lambda_1 x_1 - m_1 < e_2\lambda_2 x_2 - m_2 \end{cases}$$

$$\tilde{u}_2 = 1 - u_1$$

What is the optimal strategy when $e_1\lambda_1 x_1 - m_1 = e_2\lambda_2 x_2 - m_2$?

Is it possible to define the strategy when maximization of fitness functions does not predict a unique optimal strategy?

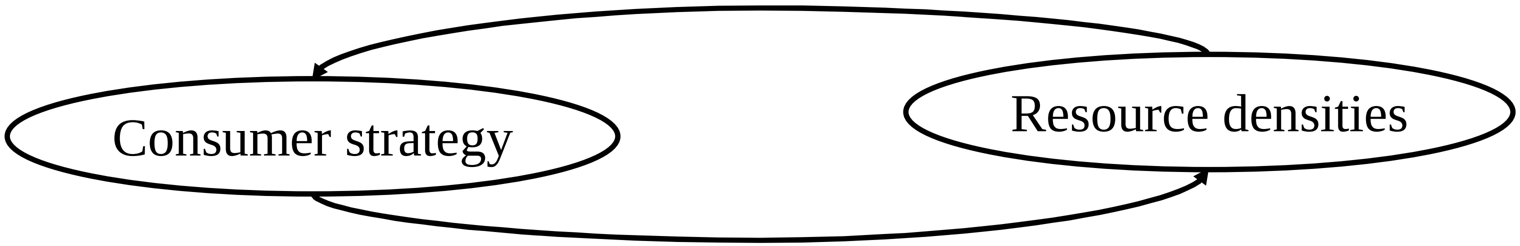
For the patch model this happens when both patches provide the same payoff $(e_1\lambda_1 x_1 - m_1 = e_2\lambda_2 x_2 - m_2)$

For the prey model this happens when the more profitable prey density reaches the switching threshold $x_1 = x_1^*$

Both fitness functions are missing:

1. the ecological feedback, i.e., the effect of consumers on resources and resources on consumer strategy

2. The effect of consumer numbers on consumer strategy (i.e., consumer density dependence)



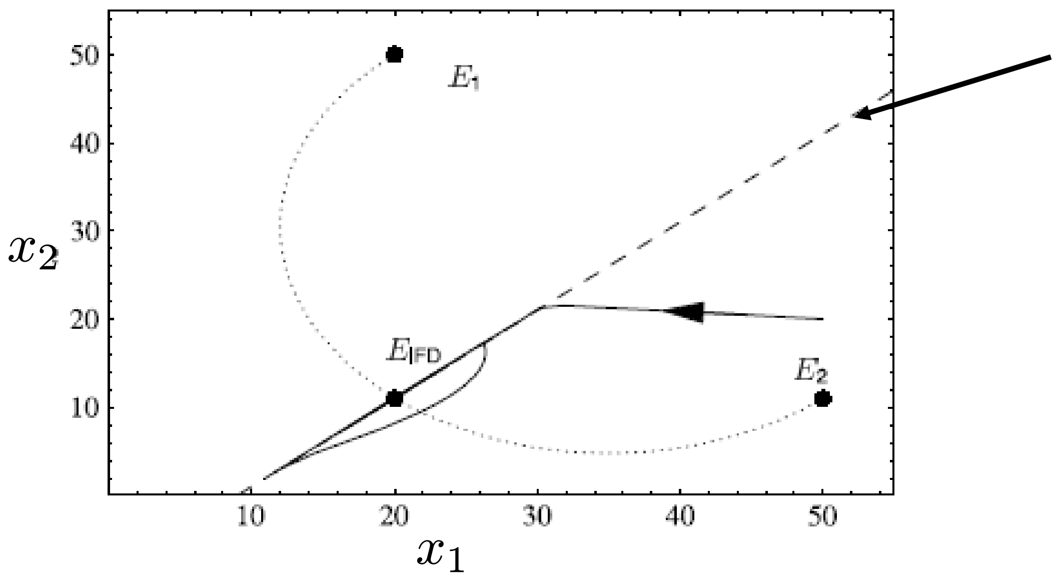
# Ecological feedback for the patch model

(Krivan and Schmitz 2003)

$$\frac{dx_1}{dt} = a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - u_1 \lambda_1 x_1 y$$

$$\frac{dx_2}{dt} = a_2 x_2 \left(1 - \frac{x_2}{L_2}\right) - u_2 \lambda_2 x_2 y$$

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




$$e_1 \lambda_1 x_1 - m_1 = e_2 \lambda_2 x_2 - m_2$$

# Time scale separation

Assumption: Resource population dynamics run on a fast time scale when compared with consumer population dynamics, i.e., resources equilibrate quickly with current consumer numbers

$$\frac{dx_1}{dt} = a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - u_1 \lambda_1 x_1 y$$
$$\frac{dx_2}{dt} = a_2 x_2 \left(1 - \frac{x_2}{L_2}\right) - u_2 \lambda_2 x_2 y$$
$$\frac{dy}{dt} = (e_1 \lambda_1 x_1 - m_1) u_1 y + (e_2 \lambda_2 x_2 - m_2) u_2 y$$

Resource equilibrium:

$$x_i = L_i \left(1 - \frac{\lambda_i u_i y}{r_i}\right)$$

Frequency dependent fitness function:

$$W(\tilde{u}, u) = \tilde{u}_1 (e_1 \lambda_1 x_1 - m_1) + \tilde{u}_2 (e_2 \lambda_2 x_2 - m_2) = \tilde{u}_1 r_1 \left(1 - \frac{u_1 y}{K_1}\right) + \tilde{u}_2 r_2 \left(1 - \frac{u_2 y}{K_2}\right)$$

where

$$r_i = e_i \lambda_i L_i - m_i \qquad K_i = \frac{a_i (e_i \lambda_i L_i - m_i)}{e_i L_i \lambda_i^2}$$

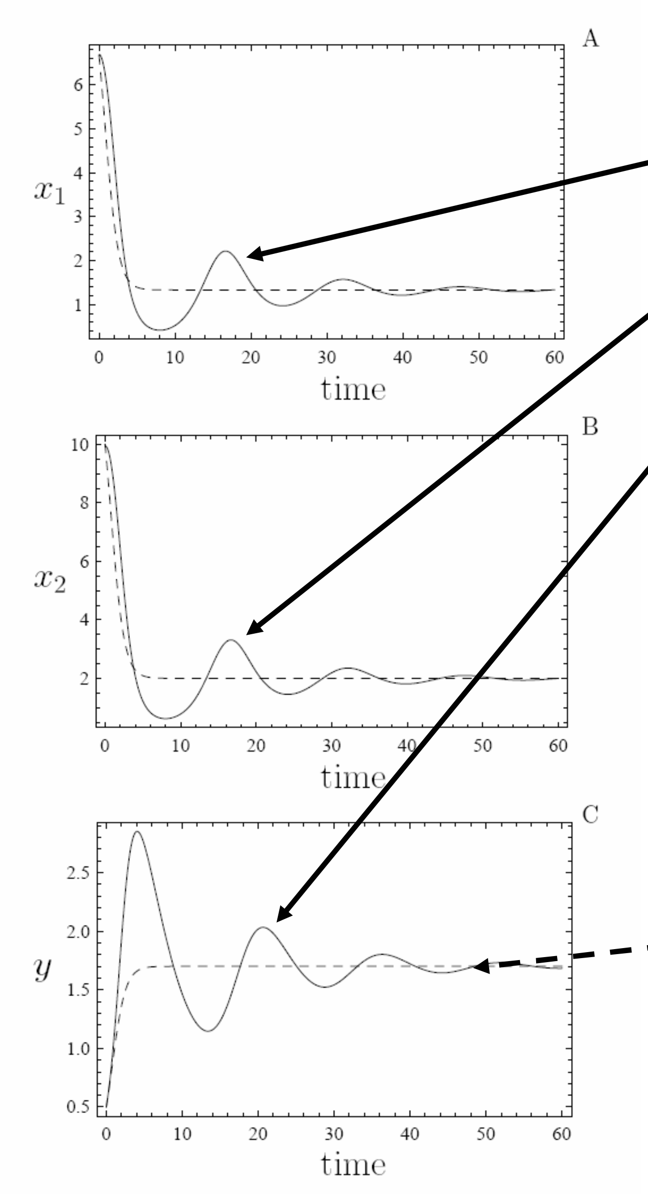
# ESS for the patch model

(Cressman et al. 2004)

$$u_1^* = \begin{cases} \dfrac{K_1 r_2}{K_1 r_2 + K_2 r_1} + \dfrac{K_1 K_2 (r_1 - r_2)}{(K_1 r_2 + K_2 r_1) y} & \text{if} \quad y > \frac{(r_1 - r_2) K_1}{r_1} \\ 1 & \text{if} \quad y \leq \frac{(r_1 - r_2) K_1}{r_1} \end{cases}$$

$$\frac{dy}{dt} = \begin{cases} r_1 y \left(1 - \dfrac{y}{K_1}\right) & \text{if} \quad y \leq \frac{(r_1 - r_2) K_1}{r_1} \\ \dfrac{r_1 r_2 (K_1 + K_2)}{K_2 r_1 + K_1 r_2} y \left(1 - \dfrac{y}{K_1 + K_2}\right) & \text{if} \quad y > \frac{(r_1 - r_2) K_1}{r_1} \end{cases}$$

# Comparision of unscaled (solid line) and scaled (dashed line) population dynamics




$$
\begin{aligned}
\frac{dx_1}{dt} &= a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - u_1(x_1, x_2)\lambda_1 x_1 y \\
\frac{dx_2}{dt} &= a_2 x_2 \left(1 - \frac{x_2}{L_2}\right) - u_2(x_1, x_2)\lambda_2 x_2 y \\
\frac{dy}{dt} &= (e_1\lambda_1 x_1 - m_1)u_1(x_1, x_2)y + (e_2\lambda_2 x_2 - m_2)u_2(x_1, x_2)y
\end{aligned}
$$

$$x_i = L_i(1 - \lambda_i u_i y / a_i)$$

$$
\frac{dy}{dt} = \begin{cases} r_1 y \left(1 - \frac{y}{K_1}\right) & \text{if } \ y \le \frac{(r_1 - r_2)K_1}{r_1} \\ \frac{r_1 r_2 (K_1 + K_2)}{K_2 r_1 + K_1 r_2} y \left(1 - \frac{y}{K_1 + K_2}\right) & \text{if } \ y > \frac{(r_1 - r_2)K_1}{r_1}, \end{cases}
$$

# The ecological feedback mechanism for the prey model

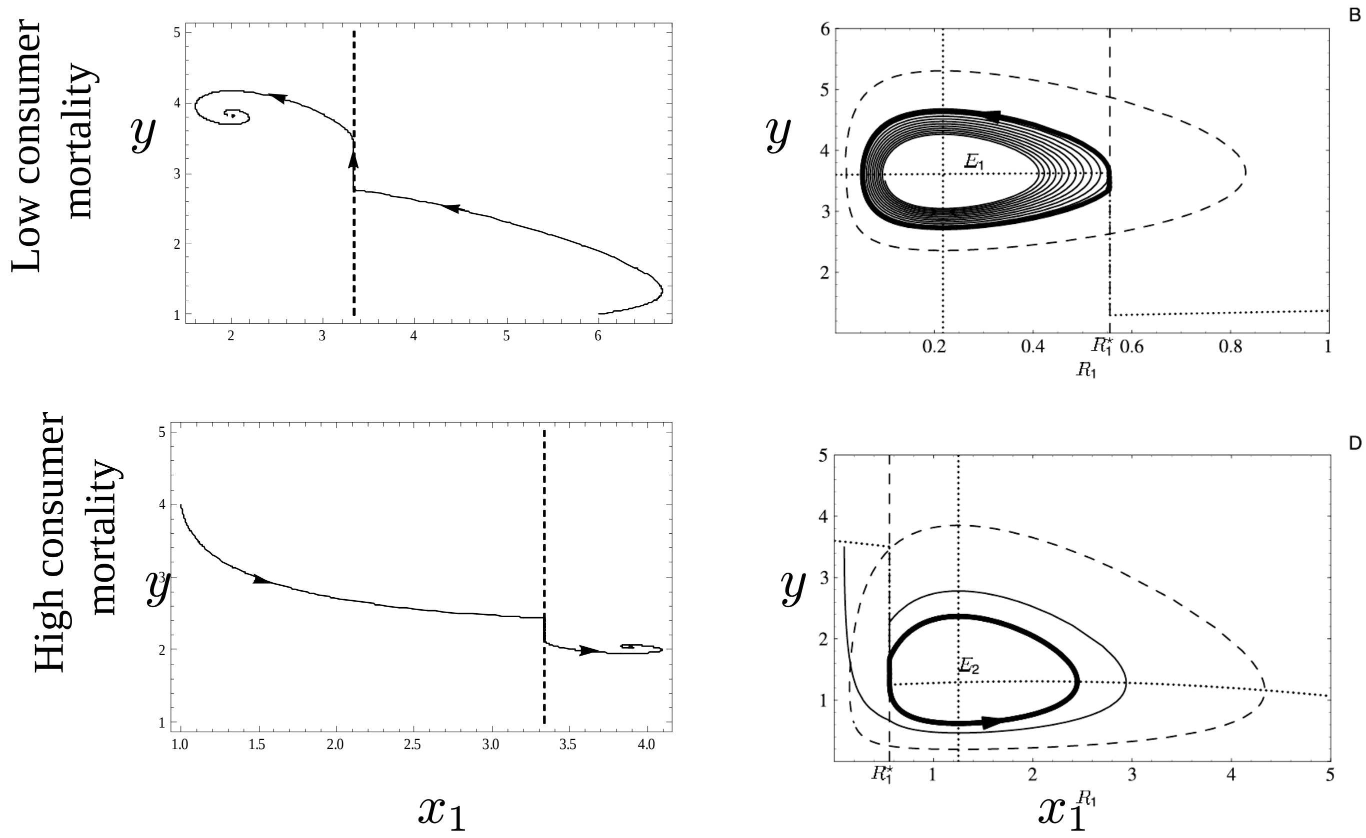
(Krivan and Schmitz 2003):

$$\frac{dx_1}{dt} = a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - \frac{\lambda_1 x_1 y}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2(x_1) x_2}$$

$$\frac{dy}{dt} = \left(\frac{e_1 \lambda_1 x_1 + e_2 \lambda_2 u_2(x_1) x_2}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 u_2(x_1) x_2} - m\right) y$$

Low resource carrying capacity

High resource carrying capacity



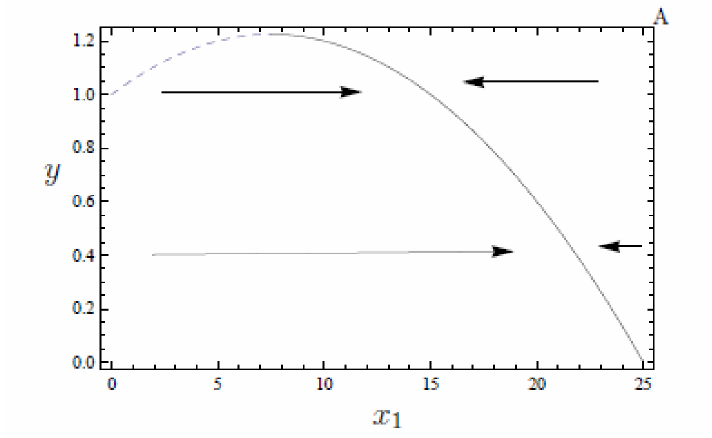
The ecological feedback mechanism for the prey model

$$\frac{dx_1}{dt} = a_1 x_1 \left(1 - \frac{x_1}{L_1}\right) - \frac{\lambda_1 x_1 y}{1 + h_1\lambda_1 x_1 + h_2\lambda_2 u_2(x_1)x_2}$$

$$\frac{dy}{dt} = \left(\frac{e_1\lambda_1 x_1 + e_2\lambda_2 u_2(x_1)x_2}{1 + h_1\lambda_1 x_1 + h_2\lambda_2 u_2(x_1)x_2} - m\right) y$$

Time scale separation: Resource population dynamics run on a fast time scale when compared with consumer population dynamics, i.e., resources equilibrate quickly with current consumer numbers

$$x_{1+} = \frac{-1 + h_1 L_1 \lambda_1 - h_2 u_2 x_2 \lambda_2 + H(u_2)\sqrt{1 - c(u_2)y}}{2h_1\lambda_1}$$



Frequency dependent fitness function for the prey model

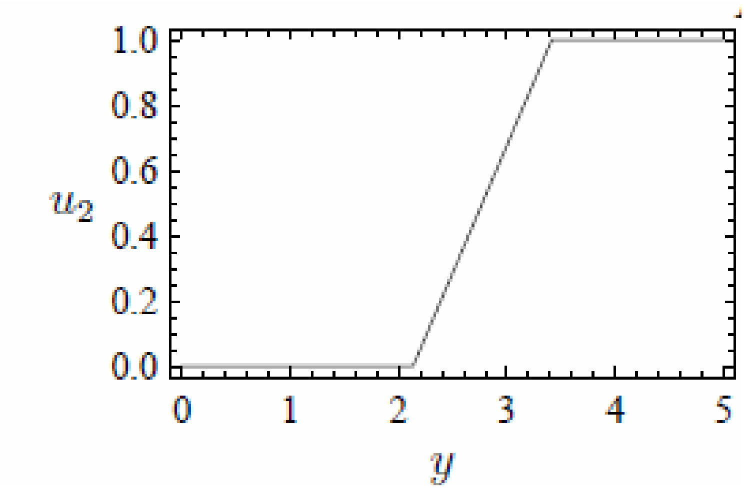
$$W = \frac{e_1 \lambda_1 x_1 + e_2 \lambda_2 \tilde{u}_2 x_2}{1 + h_1 \lambda_1 x_1 + h_2 \lambda_2 \tilde{u}_2 x_2}$$

$$W(\tilde{u}_2, u_2) = \frac{2h_1(e_1 L_1 \lambda_1 + e_2 x_2 \tilde{u}_2 \lambda_2) - e_1 H(u_2)(1 - \sqrt{1 - c(u_2)y})}{2h_1 H(\tilde{u}_2) - h_1 H(u_2)(1 - \sqrt{1 - c(u_2)y})}.$$

Strategy

$$u_2^* = \frac{L_1 \lambda_1^2 (e_1 h_2 - e_2 h_1)}{a_1 h_2 \lambda_2 x_2 (L_1 \lambda_1 (e_1 h_2 - e_2 h_1) - e_2)} y - \frac{e_1}{\lambda_2 x_2 (e_1 h_2 - e_2 h_1)}$$

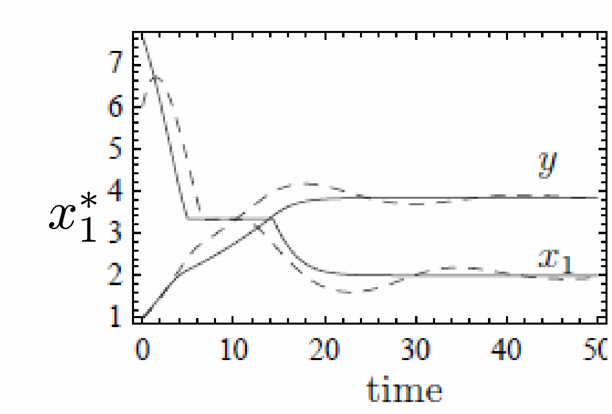
is a convergence stable ESS (Krivan, subm.).

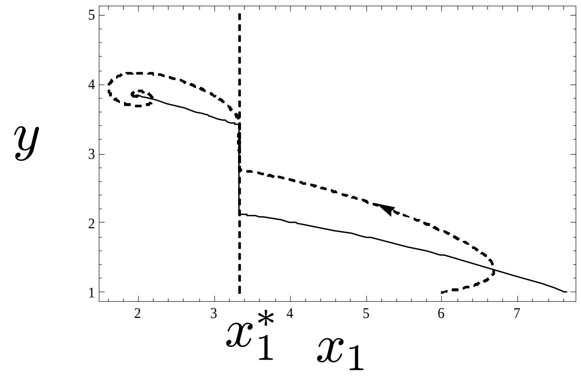


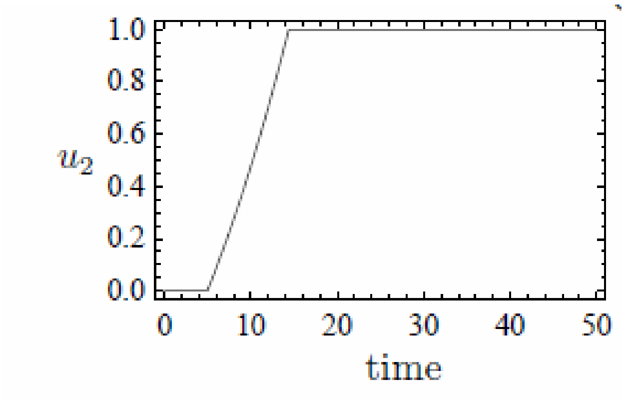
Consumer population dynamics driven by the singular strategy

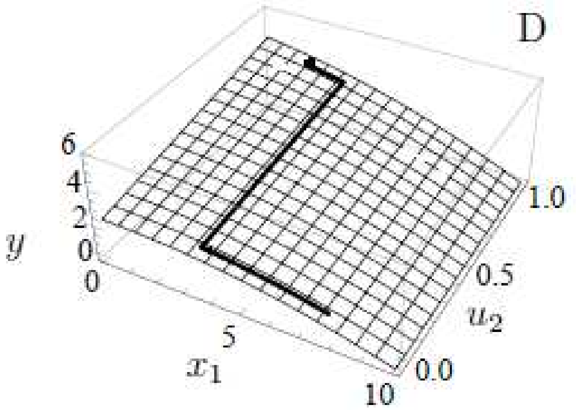
$$u_2^* = \begin{cases} 0 \\ \frac{L_1\lambda_1^2(e_1h_2-e_2h_1)}{a_1h_2\lambda_2x_2(L_1\lambda_1(e_1h_2-e_2h_1)-e_2)}y - \frac{e_1}{\lambda_2x_2(e_1h_2-e_2h_1)} \\ 1 \end{cases}$$

$$\frac{dy}{dt} = \begin{cases} y\frac{e_2-h_2m}{h_2} & \text{if } \ 0 < u_2^* < 1 \\ \\ ry\left(1 - \frac{K(u_2)}{1+\sqrt{1-c(u_2)y}}\right) & \text{if } \ u_2^* = 0 \ \text{ or } u_2^* = 1 \end{cases}$$




$$\left\{\begin{aligned}\frac{dx_1}{dt} &= a_1 x_1\left(1-\frac{x_1}{L_1}\right)-\frac{\lambda_1 x_1 y}{1+h_1\lambda_1 x_1+h_2\lambda_2 u_2(x_1)x_2}\\ \frac{dy}{dt} &= \left(\frac{e_1\lambda_1 x_1+e_2\lambda_2 u_2(x_1)x_2}{1+h_1\lambda_1 x_1+h_2\lambda_2 u_2(x_1)x_2}-m\right)y\end{aligned}\right.$$

$$\left\{\begin{aligned}&\frac{dy}{dt}=\begin{cases} y\frac{e_2-h_2 m}{h_2} & \text{if } \ 0<u_2<1\\ ry\left(1-\frac{K(u_2)}{1+\sqrt{1-c(u_2)y}}\right) & \text{if } \ u_2=0 \ \text{ or } u_2=1\end{cases}\\ &x_{1+}=\frac{-1+h_1L_1\lambda_1-h_2u_2x_2\lambda_2+H(u_2)\sqrt{1-c(u_2)y}}{2h_1\lambda_1}\end{aligned}\right.$$

Conclusions:

1. Frequency dependent fitness functions can be derived from population models using time scale argument.

2. The resulting models can be analyzed using the static methods of evolutionarily game theory

4. For  optimal foraging models this approach can predict partial consumer preferences for various food types.

Krivan, V. Evolutionarily stability of optimal foraging: partial preferences in the diet and patch models, submitted.

Cressman, R., Krivan, V., Garay, J. 2004. Ideal free distributions, evolutionary games and population dynamics in multiple species environments. American Naturalist, 164:473-489.

Krivan, V., Schmitz, O. J. 2003. Adaptive foraging and flexible food web topology. Evolutionary Ecology Research 5:623-652.

Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. American Naturalist 149:164-178.

References & articles at www.entu.cas.cz/krivan

**Thank you!**