The Ideal Free Distribution: from hypotheses to tests

Vlastimil Krivan

Biology Center
and
Faculty of Science
Ceske Budejovice
Czech Republic

vlastimil.krivan@gmail.com

www.entu.cas.cz/krivan

Talk outline

1. Distribution of a single species among two habitats: Swans and Fish

2. Distribution of a two fish species: A test with fish

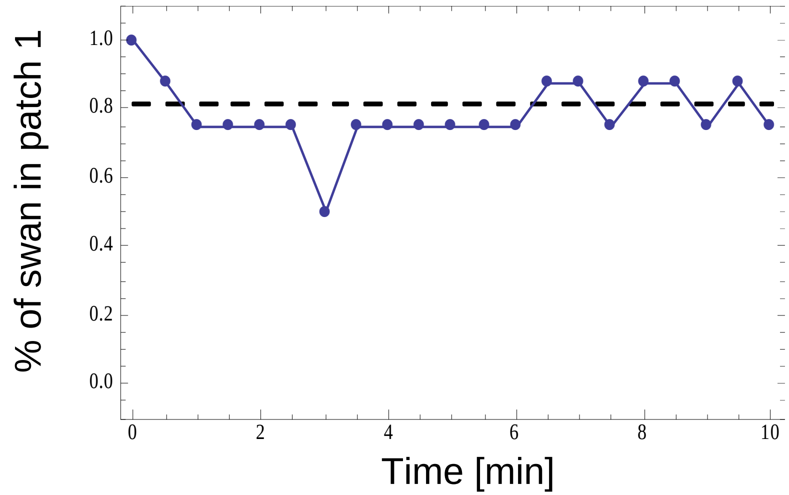
3. Population dynamics and distribution of a single population: A test with bacteria growing on two sugars

1. How does a single population of a fixed size distribute in a heterogeneous space?

Swan distribution

Distribution of 8 swans

among two feeding patches



Fish distribution (Milinski, 1979)

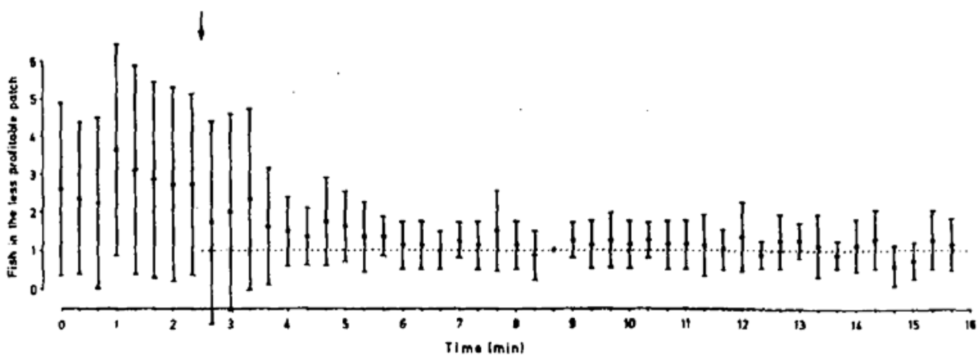


Fig. 1: First experiment (profitability ratio 5 : 1): Number of fish in the less profitable half of the tank; dots are means of 8 trials with 6 fishes each measured at a 20 s clock signal; bars give standard deviations (included to give some indication of variance, though data are not normally-distributed); arrow points to start of feeding; dotted line indicates the number of fish predicted according to profitability ratio

The Parker matching principle

(Parker 1978)

m_i = abundance in the $i-$th patch

$M = m_1 + m_2$ is the total abundance

r_i = resource input rate in patch i

$$V_i = \frac{\text{resource input rate}}{\text{animal abundance in the patch}} = \frac{r_i}{m_i}$$

The population distribution: $p_i = \frac{m_i}{M} = \frac{r_i}{r_1+r_2}$

The Ideal Free Distribution

Definition (Fretwell and Lucas 1969). *Population distribution* $p = (p_1, \ldots, p_n)$ *is called* the Ideal Free Distribution *if payoffs in the occupied habitats are the same and maximal.*

$$V_1(p_1) = \cdots = V_k(p_k) =: V^\star \geq V_j(0) \text{ for } j = k+1, \cdots, n.$$

Dual meaning of $p = (p_1, \ldots, p_n)$, $p_1 + \cdots + p_n = 1$:

1. Population distribution

2. For a monomorphic population it is a strategy of an individual (p_i is the proportion of the lifetime an individual spends in patch i)

The IFD as a game theoretical concept: The Habitat Selection Game (Cressman and Krivan, 2006)

$$V_1(p_1) = \cdots = V_k(p_k) =: V^\star \geq V_j(0) \text{ for } j = k+1, \cdots, n.$$

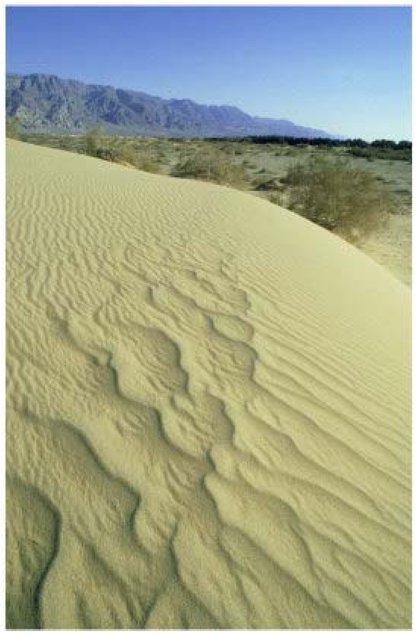
Proposition. *Let payoffs be negatively density dependent. Then the strategy corresponding to the Ideal Free Distribution is the Nash equilibrium of the Habitat selection game.*

Proposition. *Let payoffs be negatively density dependent. Then the strategy corresponding to the IFD is an ESS of the Habitat selection game.*

2. How do two interacting populations of a fixed size distribute in a heterogeneous space consisting of two patches?

Gerbillus pyramidum

Gerbillus allenbyi



Northern Collared Lemming

American Brown Lemming

Tests with rodents (Rosenzweig 1979,…, Morris 1987,…)

Isolegs (Rosenzweig 1979) and Isodars (Morris 1987)

An *isoleg* is a curve in the species 1-species 2 density phase space that separates regions with qualitatively different species distributions (e.g., species 1 occupies habitat A only, species 2 occupies both habitats and similarly for species B)

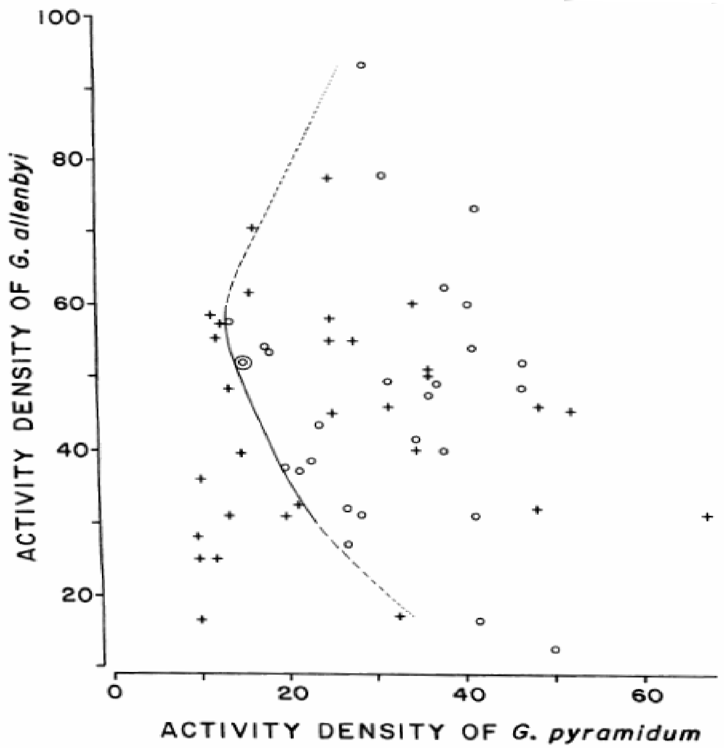
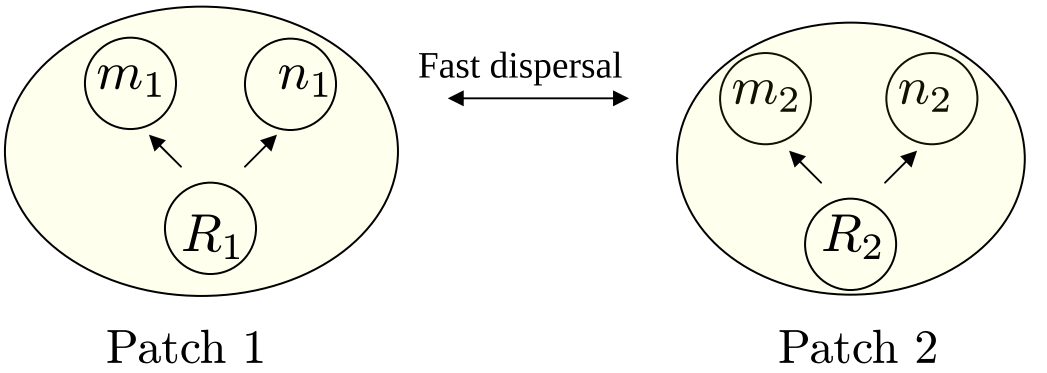


FIG. 5. Preferences of *Gerbillus allenbyi* for the semistabilized dune (SA) drawn in a state space of activity densities of the two species (AGA, AGP). Data with AGP < 10 were excluded since, in this region, all *G. allenbyi* preferences for the semistabilized dune were >0.40. Preferences were divided into either SA > 0.40 (+) or 0 ≤ SA ≤ 0.40 (0). The broken fading lines show our lack of confidence in the actual shape or slope of the isoleg in the regions where AGA > 60 or AGA < 30. For further information see *Results: The isolegs: G. allenbyi.*

The IFD for two competing species (Krivan and Sirot 2002)



$$M = m_1 + m_2 \qquad m_i = p_i M$$

$$N = n_1 + n_2 \qquad n_i = q_i N$$

Species 1 payoff in habitat i : $V_i(p, q; M, N) \quad = r_i \left(1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i}\right) \quad i = 1, 2$

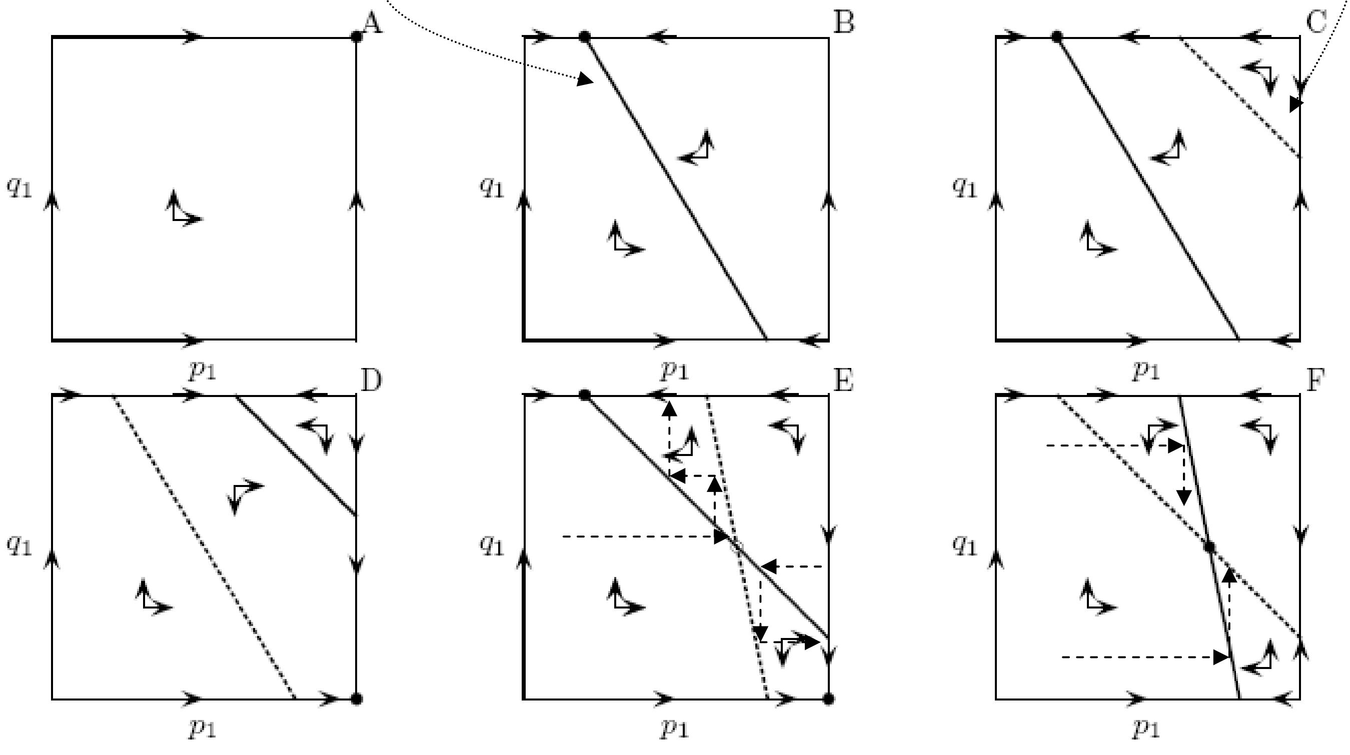
Species 2 payoff in habitat j: $W_j(p, q; M, N) \quad = s_j \left(1 - \frac{q_j N}{L_j} - \frac{\beta_j p_j M}{L_j}\right) \quad j = 1, 2.$

Equal fitness lines for two competing Lotka-Volterra model

Equal payoff lines at fixed population abundances:

$$V_1(p,q;M,N) = V_2(p,q;M,N)$$ Solid line

$$W_1(p,q;M,N) = W_2(p,q;M,N)$$ Dotted line

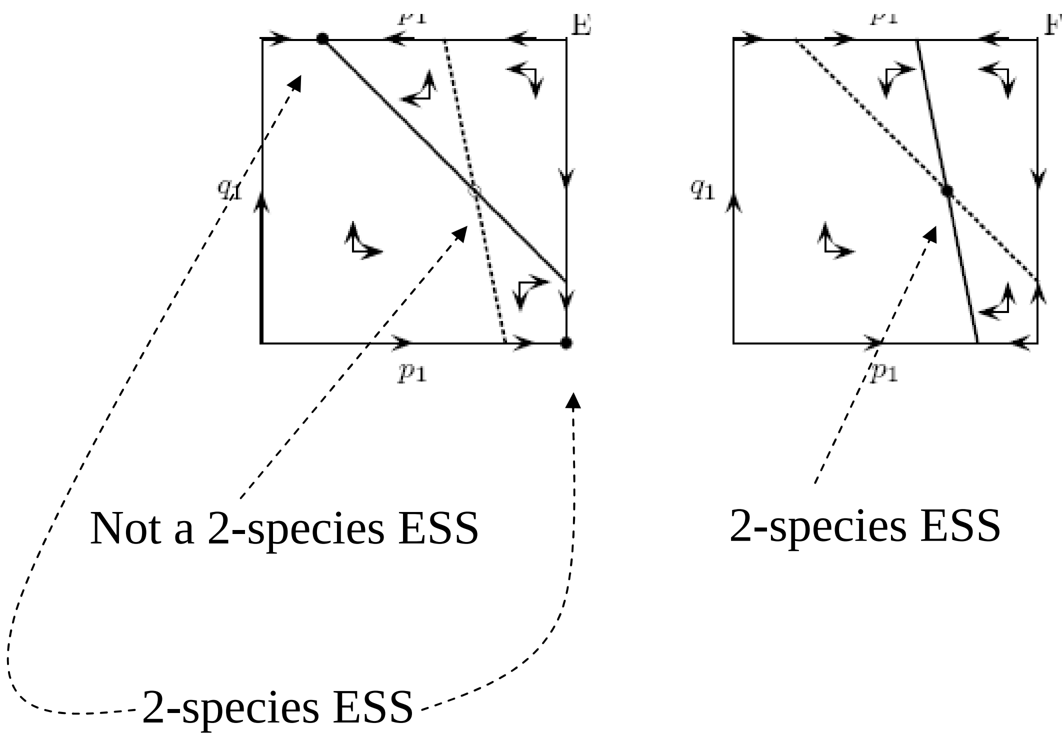


Two species ESS (Cressman 1992)

Equal payoff lines at fixed population abundances:

$$V_1(p,q;M,N) = V_2(p,q;M,N)$$ Solid line

$$W_1(p,q;M,N) = W_2(p,q;M,N)$$ Dotted line



Condition for the 2-species ESS for the Lotka-Volterra competition model (Krivan and Sirot, 2002; Cressman et al. 2004)

$$\text{Species 1 payoff in habitat } i: \; V_i(p,q;M,N) = r_i\left(1 - \frac{p_i\,M}{K_i} - \frac{\alpha_i\,q_i\,N}{K_i}\right) \quad i = 1,2$$

$$\text{Species 2 payoff in habitat } j: \; W_j(p,q;M,N) = s_j\left(1 - \frac{q_j\,N}{L_j} - \frac{\beta_j\,p_j\,M}{L_j}\right) \quad j = 1,2.$$

Proposition. *Let us assume that the interior Nash equilibrium for the distribution of two competing species at population densities M and N exists. If*

$$r_1 s_1 K_2 L_2 (1-\alpha_1\beta_1) + r_1 s_2 K_2 L_1 (1-\alpha_1\beta_2) + r_2 s_1 K_1 L_2 (1-\alpha_2\beta_1) + r_2 s_2 K_1 L_1 (1-\alpha_2\beta_2) > 0$$

Then this distributional equilibrium is a 2-species ESS.

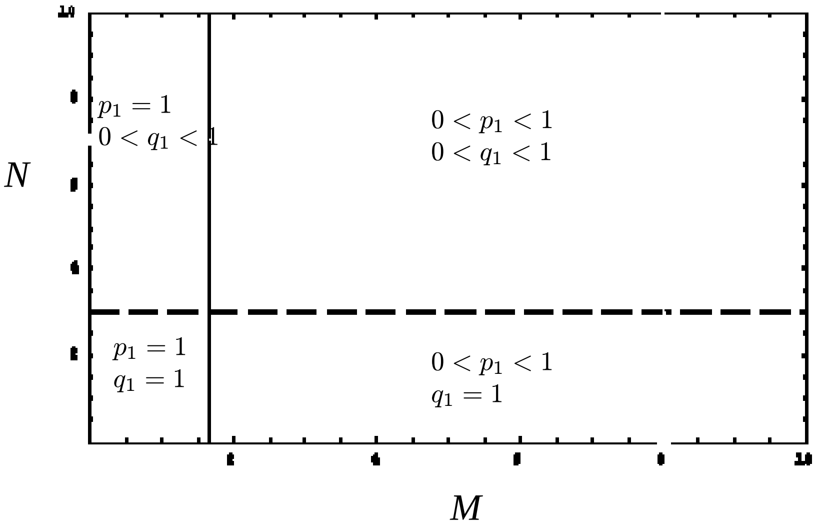
The two species IFD (Krivan and Sirot, 2002)

σ = the relative strength of intraspecific competition to interspecific competition
σ=0: interspecific competition only;
σ=1: intraspecific competition only

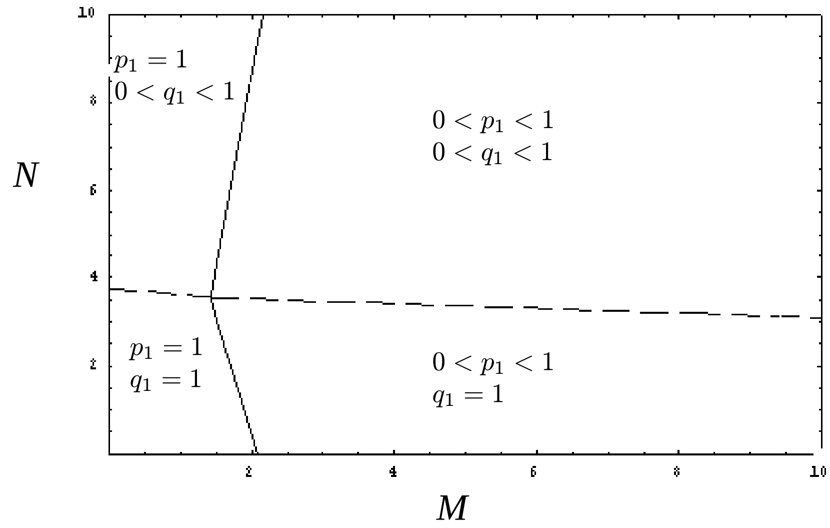
$$V_i(p,q;M,N) = r_i\left(1 - \frac{p_i\sigma M}{K_i} - \frac{\alpha_i q_i(1-\sigma)N}{K_i}\right) \quad i = 1,2$$

$$W_j(p,q;M,N) = s_j\left(1 - \frac{q_j\sigma N}{L_j} - \frac{\beta_j p_j(1-\sigma)M}{L_j}\right) \quad j = 1,2.$$

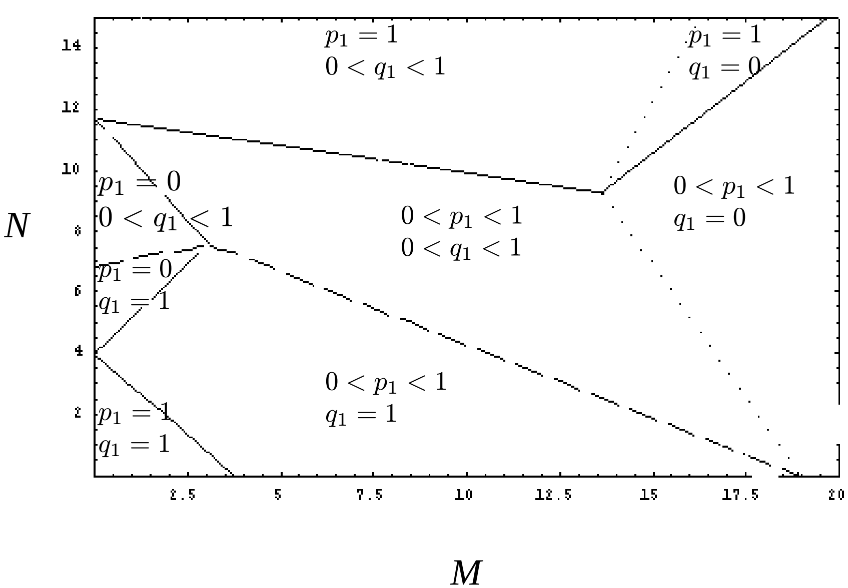
$\sigma = 1$ (Intraspec.comp.only)



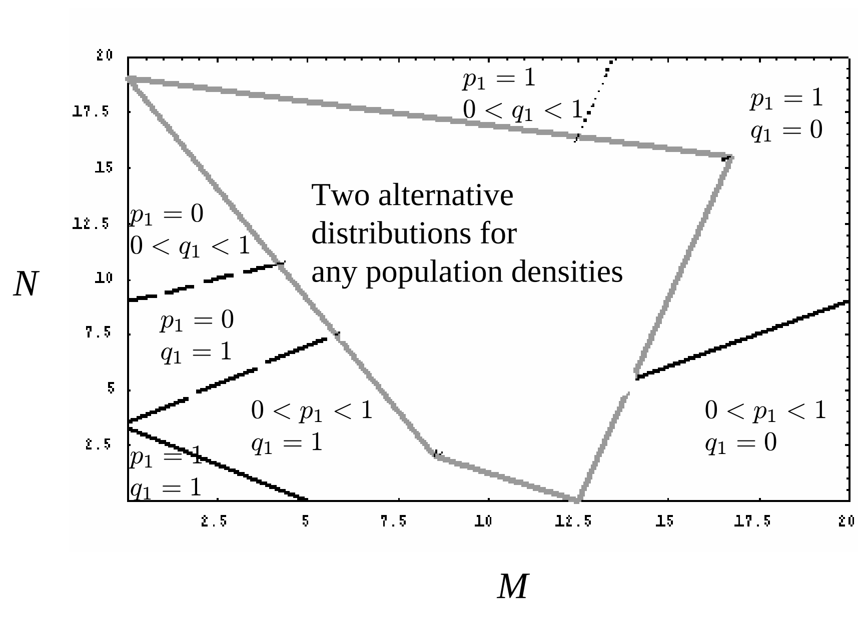
$\sigma = 0.8$



$\sigma = 0.44$

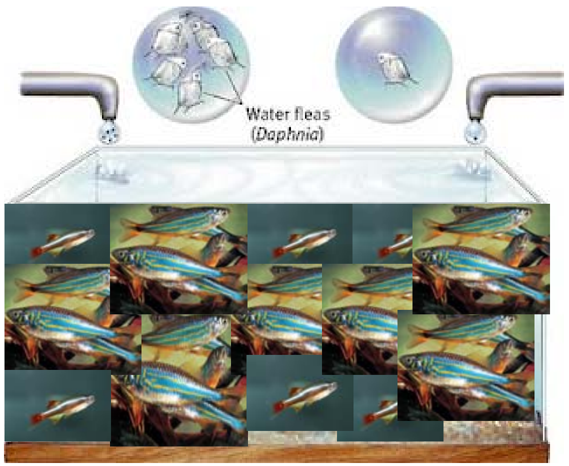


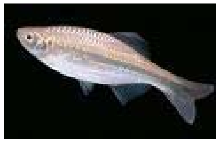
$\sigma = 0.33$



Joint distribution of two fish species (Berec et al. 2006)

r_1 r_2





Species M: Minnow (*Tanichthys albonubes*)

Species D: Danio (*Danio aequipinnatus*)

Joint distribution of two fish species (Berec et al. 2006)

Species M: Minnow

Species D: Danio

R_i $(i = 1, 2)$: standing food density at patch i

r_i $(i = 1, 2)$: rate of feeding in patch i

$$\frac{dR_1}{dt} = r_1 - (\lambda_M p_1 R_1 M + \lambda_D R_1 q_1 D)$$

$$\frac{dR_2}{dt} = r_2 - (\lambda_M p_2 R_2 M + \lambda_D R_2 q_2 D)$$

Equal fitness lines:

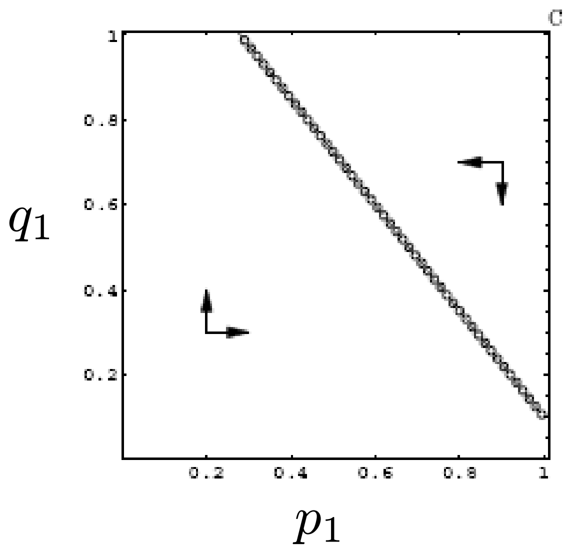
$$\left.\begin{array}{l} \lambda_M R_1 = \lambda_M R_2 \\ \lambda_D R_1 = \lambda_D R_2 \end{array}\right. \iff R_1 = R_2$$

At the resource equilibrium the fish distribution satisfies:

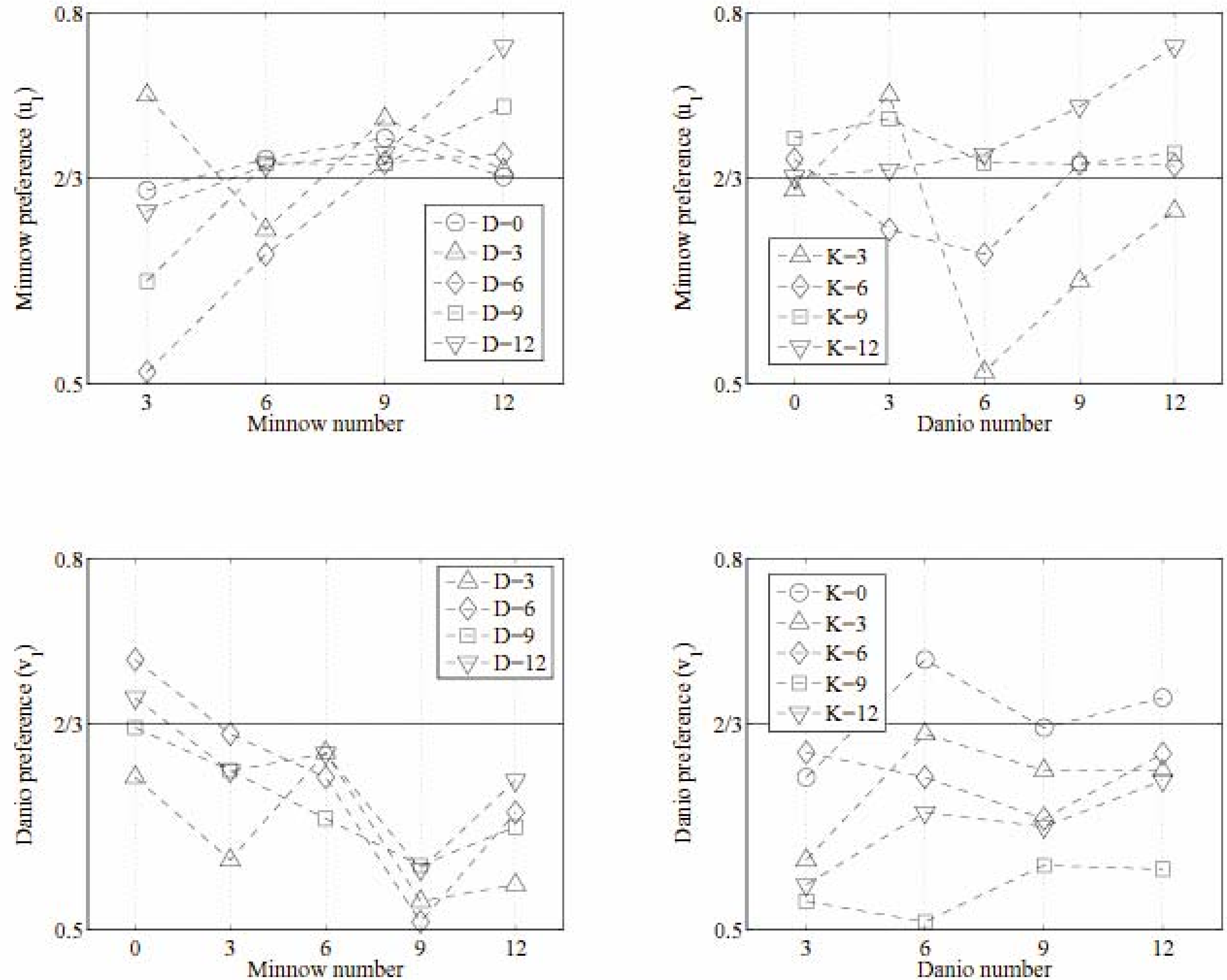
$$\frac{r_1}{\lambda_M p_1 M + \lambda_D q_1 D} = \frac{r_2}{\lambda_M p_2 M + \lambda_D q_2 D}$$

And the corresponding distribution satisfies:

$$(p_1 - \frac{r_1}{r_1 + r_2})\lambda_M M + (q_1 - \frac{r_1}{r_1 + r_2})\lambda_D D = 0$$



Distribution of two fish species (Berec et al. 2006)



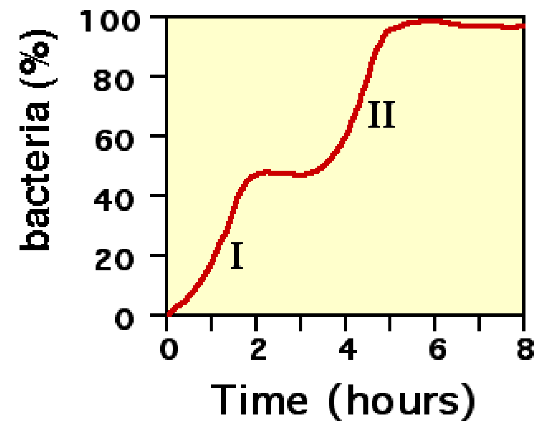
Joint distribution of two fish species (Berec et al. 2006)

Observation:

1. Minnows are stronger competitors than Danios, because they move faster ($\lambda_M > \lambda_D$). Thus, Minnows is competitively dominant species
2. Minnows quickly distribute following their own single-species IFD, i.e., $p_i = \frac{r_i}{r_1+r_2}$, $i = 1, 2$
3. This balances the resources at both patches, i. e., $R_1 = R_2$
4. Danios distribute 50:50 because both patches are equally profitable for them

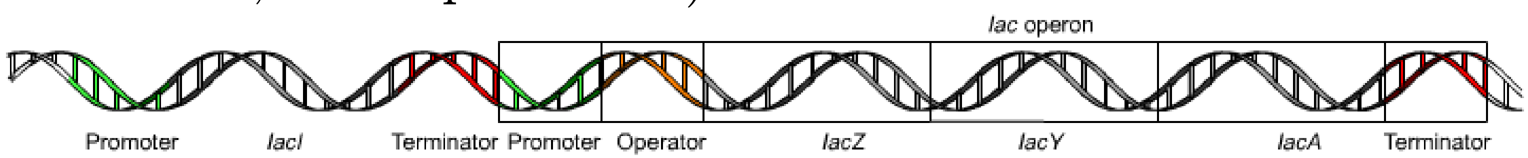
3. How does a single population distribute in a heterogeneous space when it undergoes demographic changes?

Bacterial growth on two substrates



Diauxie (J. Monod): microbial cells consume two or more substrates in a sequential pattern, resulting in two separate growth phases (phase I and II). During the first phase, cells preferentially metabolize the sugar on which it can grow faster (often glucose). Only after the first sugar has been exhausted do the cells switch to the second. At the time of the "diauxic shift", there is often a lag period during which cells produce the enzymes needed to metabolize the second sugar.

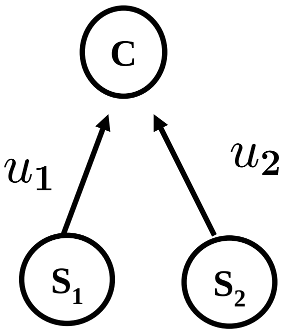
Lac operon: Molecular mechanism that regulates diauxic growth (F. Jacob and J. Monod, Nobel prize 1965)



Adaptation: Evolution should result in optimal timing of the diauxic switch so that bacterial fitness maximizes

Question: Is the lac operon evolutionarily optimized?

Michaelis-Menten batch population kinetics



$$\begin{cases} \dfrac{dS_1}{dt} &= -\dfrac{1}{Y_1}\dfrac{S_1}{K_1+S_1}u_1 C \\ \dfrac{dS_2}{dt} &= -\dfrac{1}{Y_2}\dfrac{S_2}{K_2+S_2}u_2 C \\ \dfrac{dC}{dt} &= \left(\dfrac{\mu_1 S_1}{K_1+S_1}u_1 + \dfrac{\mu_2 S_2}{K_2+S_2}u_2\right) C \end{cases}$$

S_1, S_2 - sugar concentration (eg. glucose and lactose)

C - bacterial population

u_i -bacterial preference for the $i-$th ($u_1 + u_2 = 1$, $i = 1, 2$) sugar

Optimal bacterial strategy

Fitness= per capita bacterial population growth rate i.e.,

$$\frac{1}{C}\frac{dC}{dt} = \frac{\mu_1 S_1}{K_1 + S_1} u_1 + \frac{\mu_2 S_2}{K_2 + S_2} u_2 \mapsto \max_{u_i}$$

The optimal strategy:

$$\frac{\mu_1 S_1}{K_1 + S_1} > \frac{\mu_2 S_2}{K_2 + S_2} \implies u_1 = 1$$

$$\frac{\mu_1 S_1}{K_1 + S_1} < \frac{\mu_2 S_2}{K_2 + S_2} \implies u_1 = 0$$

Michaelis-Menten batch population kinetics with optimal sugar switching

$$
\begin{cases}
\dfrac{dS_1}{dt} = -\dfrac{1}{Y_1}\dfrac{S_1}{K_1+S_1}u_1 C \\[2ex]
\dfrac{dS_2}{dt} = -\dfrac{1}{Y_2}\dfrac{S_2}{K_2+S_2}u_2 C \\[2ex]
\dfrac{dC}{dt} = \left(\dfrac{\mu_1 S_1}{K_1+S_1}u_1 + \dfrac{\mu_2 S_2}{K_2+S_2}u_2\right) C \\[2ex]
u_1 = \begin{cases} 1 & \text{when} \quad \frac{\mu_1 S_1}{K_1+S_1} > \frac{\mu_2 S_2}{K_2+S_2} \\ 0 & \text{when} \quad \frac{\mu_1 S_1}{K_1+S_1} < \frac{\mu_2 S_2}{K_2+S_2} \end{cases}
\end{cases}
$$

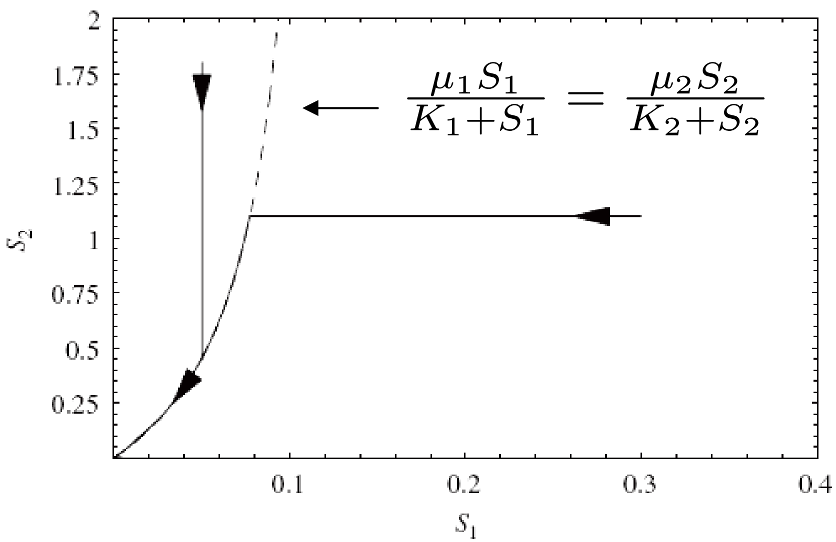


Fig. 1. Switching curve (dashed line) for the growth of *K. oxytoca* on a mixture of glucose ($\mu_1 = 1.08$, $K_1 = 0.01$, $Y_1 = 0.52$) and arabinose ($\mu_2 = 1.00$, $K_2 = 0.05$, $Y_2 = 0.5$). The two solid lines are solutions of model (1) for batch bacterial growth ($D = 0$). Parameters taken from Kompala et al. (1986).

Growth rate parameters of Klebsiela oxytoca on single substrate (Kompala et. al. 1986)

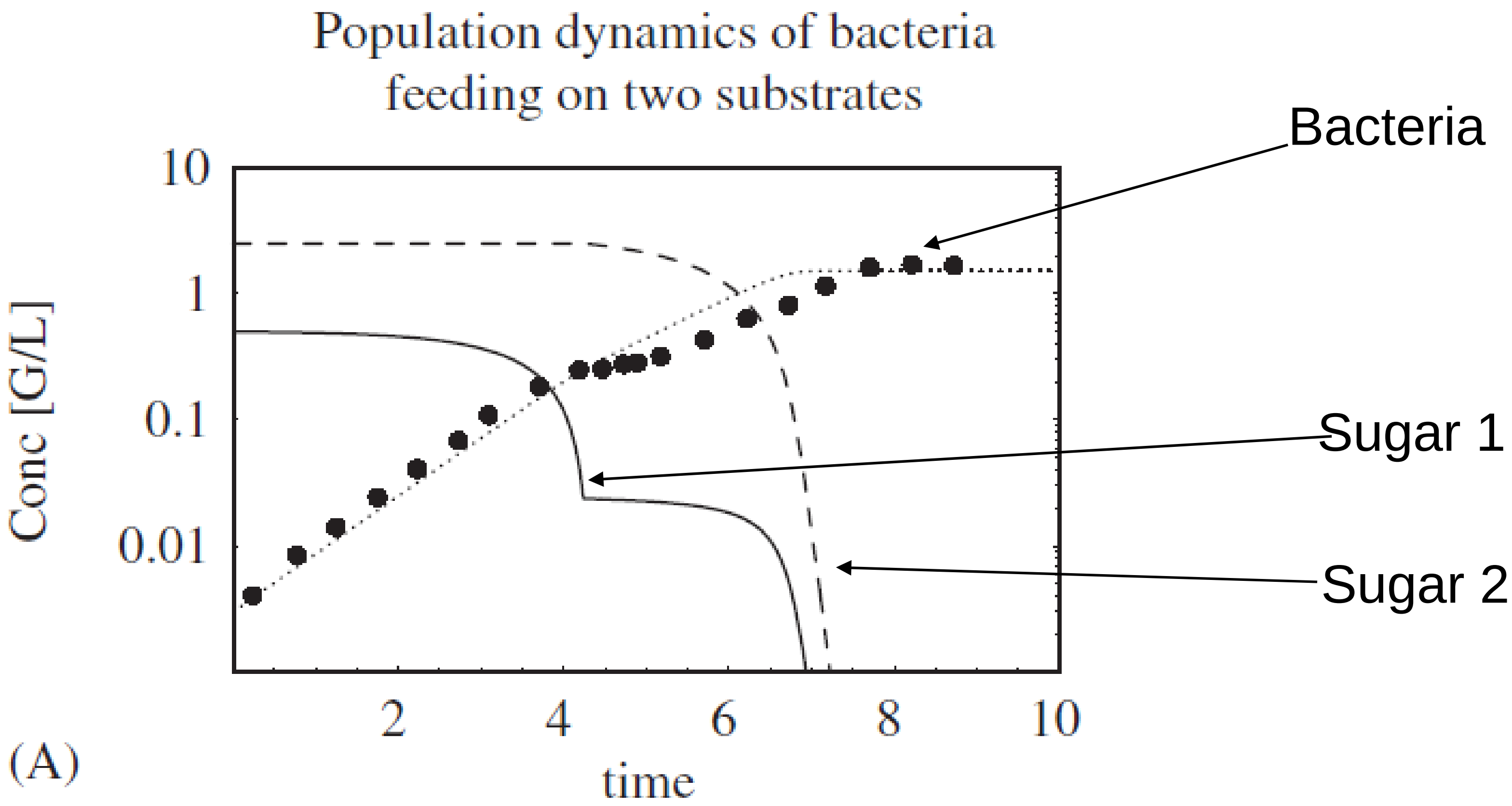
	μ	K	Y
glucose	1.08	0.01	0.52
arabinose	1.00	0.05	0.5
fruktose	0.94	0.01	0.52
xylose	0.82	0.2	0.5
lactose	0.95	4.5	0.45

Predicted and observed switching times

Substrates	Estimated switch time	Predicted switch time
glucose–xylose	4.2	4.2
glucose–xylose	1.7	1.6
glucose–xylose	2	1.8
glucose–lactose	5	4.1
glucose–lactose	4.2	3.8
glucose–lactose	4.2	3.8
glucose–lactose	4.6	4.2
glucose–arabinose	4	3.7
glucose–arabinose	4	3.8
glucose–fructose)	4.5	4.8

Estimated time of switching from data given in Kompala et al (1986) and predicted time of switching from model.

Conclusion: There is no significant difference between observed times of switching and predicted times of switching. Thus, bacteria switch between different sugars at times at which their fitness is maximized. This shows that the lac operon is evolutionarily optimized.


Population dynamics of bacteria
feeding on two substrates
Bacteria
Sugar 1
Sugar 2
Conc [G/L]
10
1
0.1
0.01
2
4
6
8
10
time
(A)

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