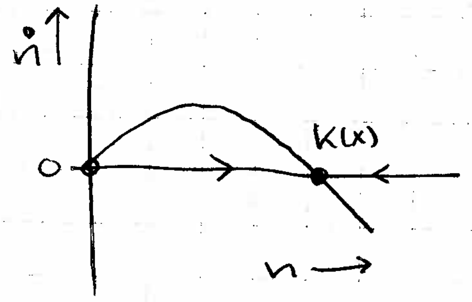
II Lotka-Volterra competition model

Resident dynamics

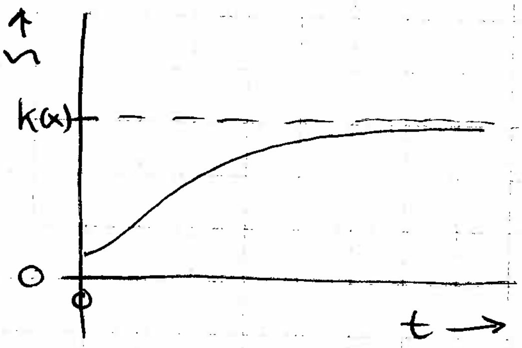
x strategy (food preference)

n population density.

① $\dot{n} = r(x)\, n \left(1 - \dfrac{n}{K(x)}\right)$ (logistic equ.)

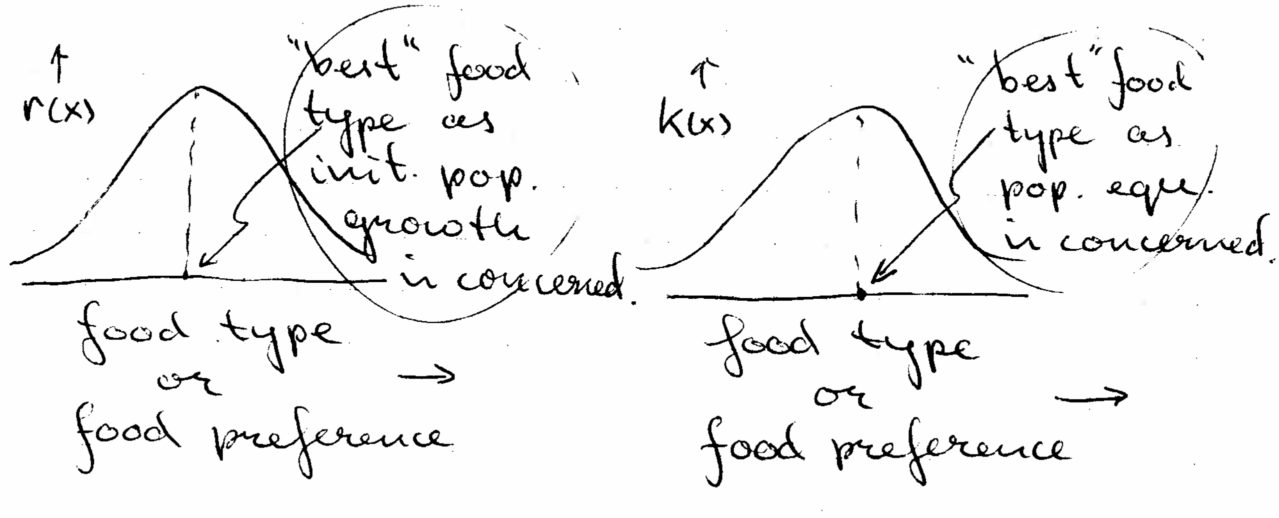


⇒



Why should r and K depend on food preference x?

- Different kinds of food occur in different abundances, have different nutritial values, or are more or less easy to access, etc.



Resident - mutant dynamics.

x , n : resident strat., pop. dens.

y, m : mutant " , " " .

$$
② \begin{cases} \dot{n} = r(x)\, n \left(1 - \dfrac{n + a(x,y)\, m}{K(x)}\right) \\[2ex] \dot{m} = r(y)\, m \left(1 - \dfrac{m + a(y,x)\, n}{K(y)}\right) \end{cases}
$$

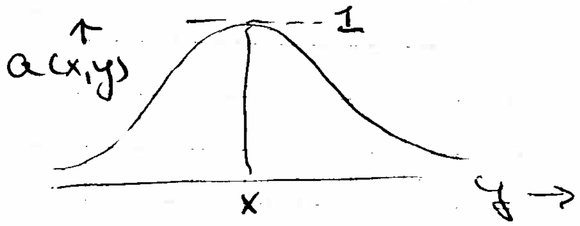
Note that if $m=0$, then ② reduces to the resident dynamics ① on page 1.

Reasonable properties of the competition kernel $a(x,y)$:

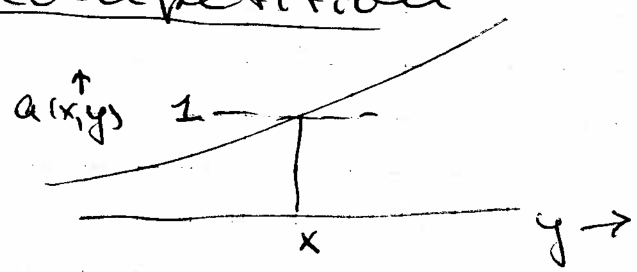
$a(x,x) = 1 \quad \forall x$

$a(x,y) \geq 0 \quad \forall x, y$.

If in addition $a(x,y) < 1$ for $x \neq y$, then we speak of symmetric competition:



If, however, $a(x,y)$ is monotonic in y, then we have asymmetric competition



Invasion & invasion fitness

Can in initially rare mutant with strategy y invade a resident population with strategy x when it is near its equilibrium $K(x)$?

(remember the basic assumptions of adaptive dynamics ...)

From the resident-mutant dyn. (2) on page 2:

$$(3) \quad \boxed{S_x(y)} := \lim_{\substack{m \to 0 \\ n \to K(x)}} \frac{d \log m}{dt} = r(y)\left(1 - \frac{a(y,x)K(x)}{K(y)}\right)$$

- $S_x(y)$ is called the <u>invasion fitness</u> of strategy y in a resident pop. of strategy x.
- $S_x(y)$ is the <u>exponential growth rate</u> of the mutant population in an ~~establis~~ established resident population at its equilibrium while the mutant is still rare.
- $S_x(y) > 0 \implies$ mutant can invade

  $S_x(y) < 0 \implies$ mutant cannot invade.
- Notice that

$$(4) \quad S_x(y) \underset{(<)}{>} 0 \iff K(x) \underset{(>)}{<} \frac{K(y)}{a(y,x)}.$$

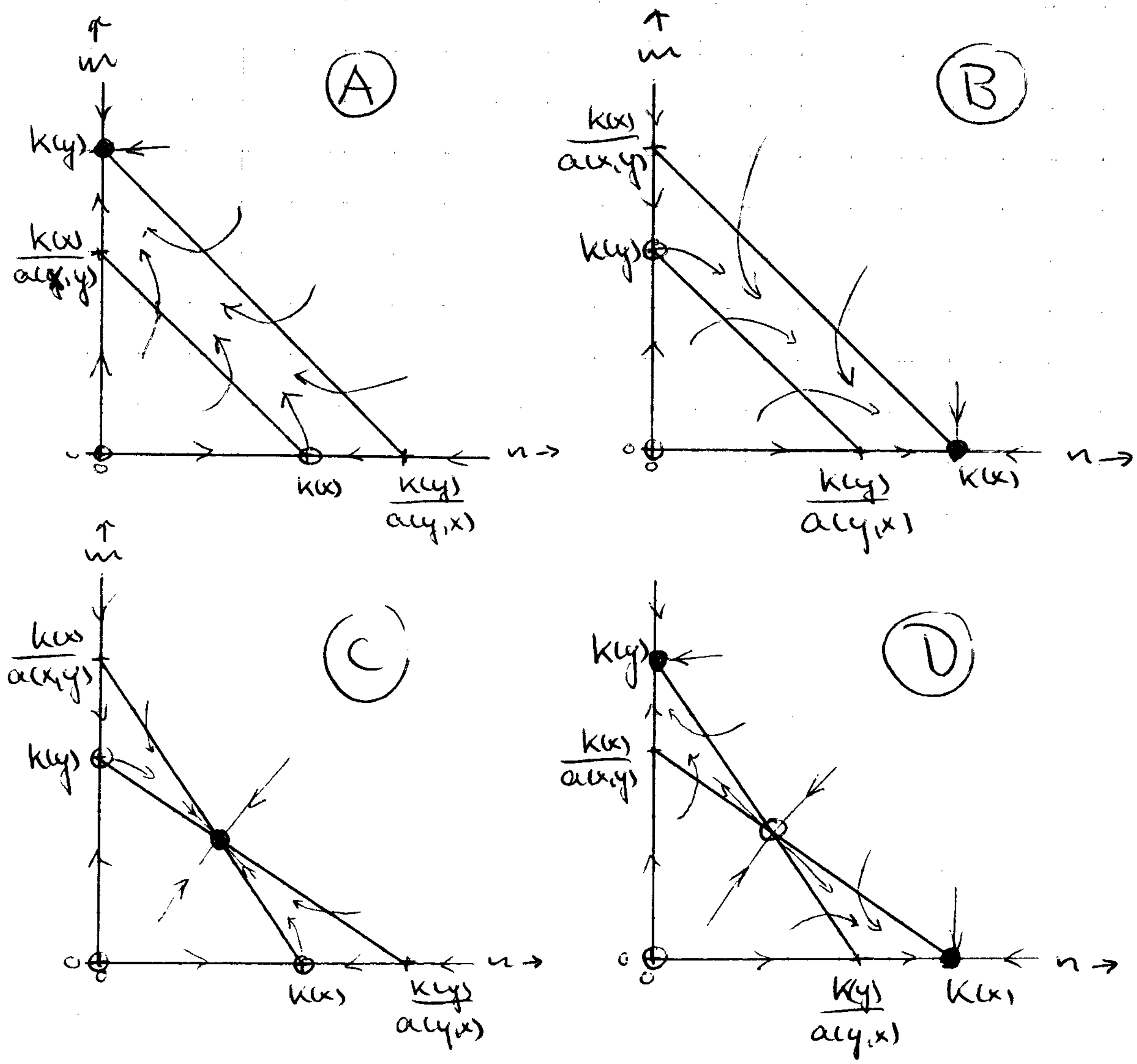
So, we know now under what conditions the mutant can invade ($s_x(y) > 0$) and when not ($s_x(y) < 0$)

(The case $s_x(y) = 0$ is left as an exercise).

But what will happen after an invasion?

To answer that question, we look at the full resident-mutant dyn.:

<u>Phase-plane analysis of the Lotka-Volterra competition model:</u>



In the L.V. comp. model there are only four (generic) configurations of the phase-plane

(see figure on previous page)

One immediately sees from the figures:

Ⓐ Mutant invades and takes over the population from the resident. (="substitution")

Ⓑ Mutant cannot invade.

Ⓒ mutant invades and coexists with the resident.

Ⓓ Mutant cannot invade.

The four cases can be fully characterized by the invasion fitness:

Ⓐ $s_x(y) > 0$ & $s_y(x) < 0$ (~~"substitution"~~)

Ⓑ $s_x(y) < 0$ & $s_y(x) > 0$

Ⓒ $s_x(y) > 0$ & $s_y(x) > 0$ ("mutual invadability")

Ⓓ $s_x(y) < 0$ & $s_y(x) < 0$ ("mutual noninvadability")

In particular, we have:

- Mutual invadability leads to coexistence.
- Otherwise, invasion leads to substitution.

Conclusion.

The sign-structure of the invasion fitness $S_x(y)$ as a function of x and y tells us whether or not invasion can occur and also what will be the outcome of an invasion event.

(Later we will see how this important results generalizes to other models)

Strategy dynamics in the Lotka-Volterra competition model

The sign of $S_x(y)$ tells us all we need to know about the possibility of invasion and the outcome of an invasion event.

Graphical tools:

Pairwise invadability plot (PIP) is a sign-plot of $S_x(y)$ in the (x,y)-plane.

Recap:

$$S_x(y) = r(y)\left(1 - \frac{a(y,x)\,K(x)}{K(y)}\right)$$

$$r(x) > 0 \quad \forall x$$

$$K(x) = \exp\{-x^2\}$$

$$a(y,x) = \exp\{-\alpha(x-y)^2\}.$$

$$\Rightarrow \boxed{S_x(y) = 0} \iff K(y) = a(y,x)K(x) \iff$$

$$\iff e^{-y^2} = e^{-\alpha(x-y)^2} \cdot e^{-x^2} \iff y^2 = \alpha(x-y)^2 + x^2 \iff$$

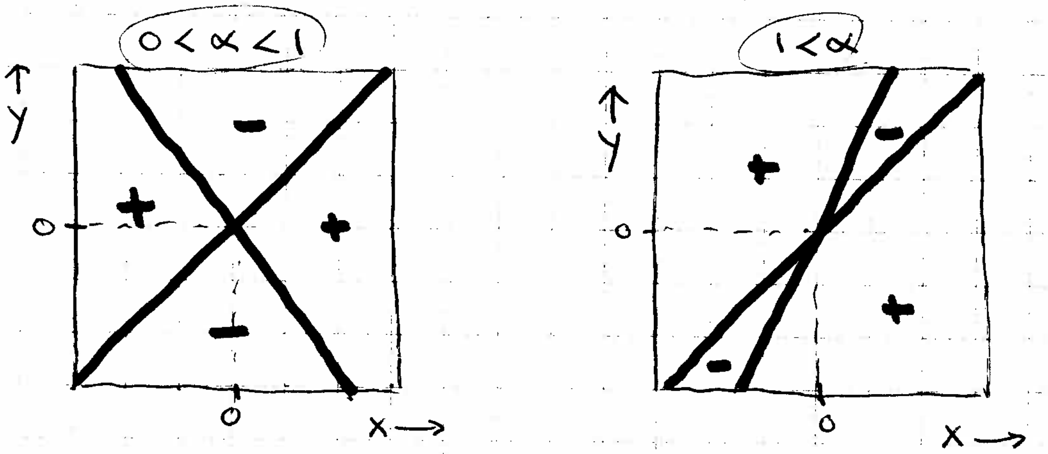
$$\iff 0 = \alpha(x-y)^2 + (x+y)(x-y) \iff$$

$$\iff 0 = (x-y)\left[\alpha(x-y) + x + y\right] \iff$$

$$\iff 0 = (x-y)\left[(\alpha+1)x - (\alpha-1)y\right] \iff$$

$$\iff \boxed{x = y \quad \text{or} \quad y = \frac{\alpha+1}{\alpha-1}\cdot x}$$

⇒ Pairwise invadability plots:



(To find the sign distribution, take the test cases $x=0$ or $y=0$).

- **Who can invade whom? (Demonstrate)**

→ Notion of evolutionary stability.

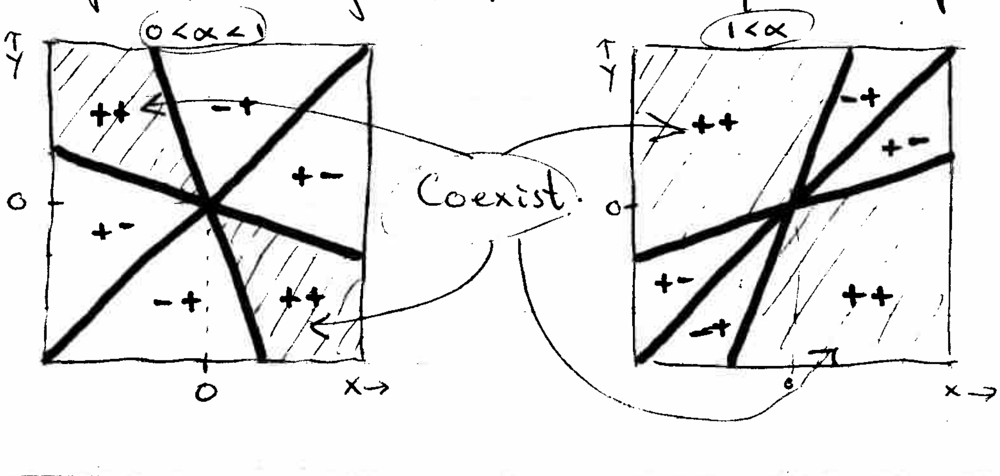
> Def. a strategy x is evolutionarily stable if no $y \neq x$ can invade

Conclusion

- If $0<\alpha<1$, then $x=0$ is evol. stable.
- If $\alpha>1$, then there is no value of x that is evol. stable.

- **Substitution or coexistence? (Demonstrate)**

Sign-plot of $S_x(y)$ and $S_y(x)$ superimposed

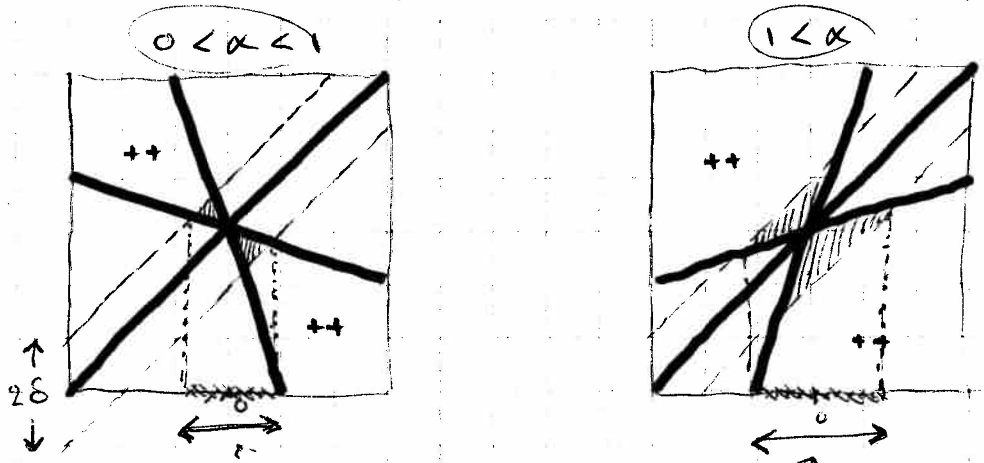


Small mutation steps

(Remember the adaptive dynamics assumptions).

Suppose $|x-y|<\delta$ for every feasible pair of mutant and resident strategies.

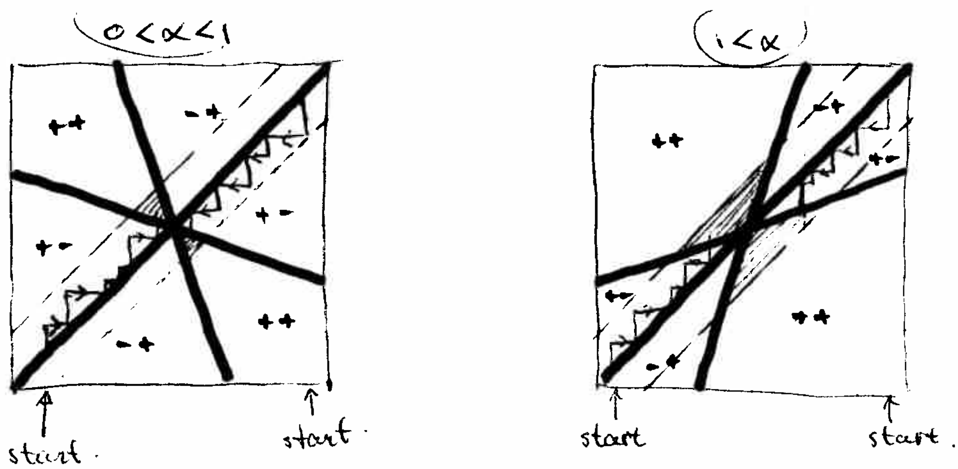
Then we need only consider a narrow band along the diagonal of the PIP:



Coexistence possible only in a neighborhood of $x=0$

(The size of that neighborhood depends on α and the mutation stepsize δ)

Outside this neighborhood, invasion implies substitution:



Remarks.

- Obviously, $x=0$ is *attracting* or *stable* in some sense for sequences of substitutions, both for $\alpha<1$ and $\alpha>1$.

(Remember, however, that $x=0$ is *evolutionary stable* only for $\alpha<1$).

- Notice that we have now made the step from *population* dynamics to *strategy* dynamics.

- Also notice that we have used all four basic assumptions of adaptive dynamics as given in the Introduction (Exercise).

- Now we can explain the initial convergence of the "evolutionary tree" of the simulation experiment in the introduction (Exercise).

- Obviously (from previous figure), once close to $x=0$, the population sooner or later will become *dimorphic* when resident and mutant can mutually invade and hence coexist.

What happens after the pop. has become dimorphic in a neighborhood of $x=0$, is our next question.