

- 9.1. Suppose: - a bird of type  $i$  lays  $n_i$  eggs  
 - probability of surviving first year of life  $s$  is a decreasing function of  $n$ .  
 - assume birds get adult in age 1 and survive then each year with probability  $p$ , which also decreases with  $n$ .  
 - assume  $s$  also depends on  $N$  (the total population density)

We have population dynamics:

$$N_i(t+1) = [n_i s(n_i, N(t)) + p(n_i)] N_i(t)$$

a.) Show: Generically only one type can be present in equilibrium, i.e. there exists an optimal fecundity  $n^*$  and it maximizes the equilibrium population density.

Assume type 1 is at equilibrium, i.e.  $N_1(t+1) = N_1(t) = \hat{N}_1$

$$1 = n_1 s(n_1, \hat{N}_1) + p(n_1)$$

$$\Rightarrow s(n_1, \hat{N}_1) = \frac{1 - p(n_1)}{n_1}$$

If type 2 was at equilibrium (alone)

$$s(n_2, \hat{N}_2) = \frac{1 - p(n_2)}{n_2}$$

Assume 1 is now at equilibrium. Type 2 can then invade, if:

$$n_2 s(n_2, \hat{N}_1) + p(n_2) > 1$$

$$\Rightarrow s(n_2, \hat{N}_1) > \frac{1 - p(n_2)}{n_2} = s(n_2, \hat{N}_2) \quad (*)$$

since  $s$  decreases with  $\hat{N}$ ,  $\hat{N}_1 < \hat{N}_2$ .

From this it also follows that type 1 cannot invade back: if it could, we would have

$$n_1 s(n_1, \hat{N}_2) + p(n_1) > 1$$

$$s(n_1, \hat{N}_2) > s(n_1, \hat{N}_1), \text{ which contradicts } (*) \rightarrow$$

Coexistence of types would be possible if  $\hat{N}_1 = \hat{N}_2$ , which generically is not true.

b.) suppose juvenile survival is of the form  $s(n, N) = s(n)f(N)$ , where  $f(0) = 1$ .

Show that optimal fecundity  $n^*$  also maximizes function  $R_0(n) = \frac{n s(n)}{1 - p(n)}$

assume again type 1 at equilibrium. Type 2 can invade if:

$$n_2 s(n_2) f(\hat{N}_1) + p(n_2) > 1$$

$$\underbrace{f(\hat{N}_1)}_{= \frac{1 - p(n_1)}{n_1 s(n_1)}} > \frac{1 - p(n_2)}{n_2 s(n_2)}$$

$$\Rightarrow \frac{1 - p(n_1)}{n_1 s(n_1)} > \frac{1 - p(n_2)}{n_2 s(n_2)}$$

$$\Rightarrow \frac{n_1 s(n_1)}{1 - p(n_1)} < \frac{n_2 s(n_2)}{1 - p(n_2)} = R_0(n_2)$$

Evolution goes towards larger values of  $R_0$ .



$$9.2 \quad \dot{R} = rR(1 - \frac{R}{K}) - \sum_i \beta_i N_i R$$

$$\dot{N}_i = (\gamma \beta_i R - \mu_i - b_i P) N_i$$

$$\dot{P} = (\sum_i c b_i N_i - \delta) P$$

(a) For coexistence,  $\gamma \beta_i R - b_i P = \mu_i \quad i=1, \dots, n$   
overdetermined if  $n > 2$

(b)  $\gamma \beta_1 R - b_1 P = \mu_1$   
 $\gamma \beta_2 R - b_2 P = \mu_2$

$$R = \frac{\begin{vmatrix} \mu_1 & -b_1 \\ \mu_2 & -b_2 \end{vmatrix}}{\gamma \begin{vmatrix} \beta_1 & -b_1 \\ \beta_2 & -b_2 \end{vmatrix}} = \frac{1}{\gamma} \frac{b_1 \mu_2 - b_2 \mu_1}{b_1 \beta_2 - b_2 \beta_1}$$

$$P = \frac{\gamma \begin{vmatrix} \beta_1 & \mu_1 \\ \beta_2 & \mu_2 \end{vmatrix}}{\gamma \begin{vmatrix} \beta_1 & -b_1 \\ \beta_2 & -b_2 \end{vmatrix}} = \frac{\beta_1 \mu_2 - \beta_2 \mu_1}{b_1 \beta_2 - b_2 \beta_1}$$

suppose  $b_1 \beta_2 - b_2 \beta_1 > 0 \Leftrightarrow \frac{b_1}{\beta_1} > \frac{b_2}{\beta_2}$

$$R > 0 \Leftrightarrow \frac{b_1}{\mu_1} > \frac{b_2}{\mu_2}$$

$$P > 0 \Leftrightarrow \frac{\beta_1}{\mu_1} > \frac{\beta_2}{\mu_2}$$

or the opposite case  $\rightarrow \frac{b_2}{\mu_2} > \frac{b_1}{\mu_1} \quad \& \quad \frac{\beta_2}{\mu_2} > \frac{\beta_1}{\mu_1}$

(i)  $\beta_1 N_1 + \beta_2 N_2 = r(1 - \frac{R}{K})$

(iii)  $b_1 N_1 + b_2 N_2 = \delta/c$

$$N_1 = \frac{\begin{vmatrix} r(1 - \frac{R}{K}) & \beta_2 \\ \delta/c & b_2 \end{vmatrix}}{\begin{vmatrix} \beta_1 & \beta_2 \\ b_1 & b_2 \end{vmatrix}}, \quad N_2 = \frac{\begin{vmatrix} \beta_1 & r(1 - \frac{R}{K}) \\ b_1 & \delta/c \end{vmatrix}}{\begin{vmatrix} \beta_1 & \beta_2 \\ b_1 & b_2 \end{vmatrix}}$$

suppose  $\beta_1 b_2 - \beta_2 b_1 > 0$  "opposite case", then  $N_i > 0$  iff  
 $\Leftrightarrow \frac{\beta_1}{b_1} > \frac{\beta_2}{b_2}$

$$\frac{\beta_1}{b_1} \delta/c > r(1 - \frac{R}{K}) > \frac{\beta_2}{b_2} \delta/c$$

$$\frac{\beta_1}{b_1} > \frac{c}{\delta} r(1 - \frac{R}{K}) > \frac{\beta_2}{b_2}$$

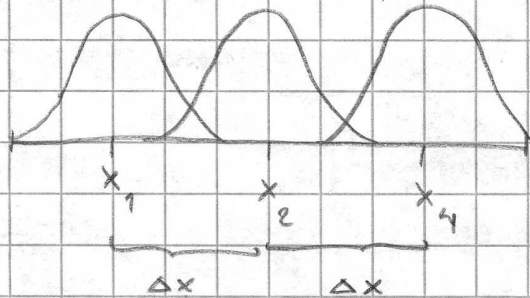
$c/\delta$  can be chosen to satisfy this  
if  $R < K \leftarrow \gamma$  large enough

### 9.3. Limiting similarity of competing species

$$\frac{dN_i}{dt} = rN_i \left( 1 - \sum_{j=1}^3 \frac{\alpha(x_j - x_i) \hat{N}_j}{K} \right)$$

competition coefficient is:  $\alpha(\Delta x) = \exp\left(-\frac{(\Delta x)^2}{2\sigma^2}\right)$

We want to look at limiting similarity, i.e. minimum  $\Delta x$  such that three species can coexist within equal distances:



Let's find the condition for  $\Delta x$  such that the species 2 can invade the equilibrium of species 1 & 3. (This condition is enough, since it is competing most strongly).

Having 1 & 3 <sup>First</sup> at equilibrium, we have equations:

$$\begin{aligned} \hat{N}_1 + \alpha(2\Delta x) \hat{N}_3 &= K \\ \hat{N}_3 + \alpha(2\Delta x) \hat{N}_1 &= K \end{aligned} \Rightarrow \dots \Rightarrow \hat{N}_1 = \hat{N}_3 = \frac{K}{1 + \alpha(2\Delta x)}$$

Now species 2 can invade if:

$$1 - \frac{\alpha(\Delta x) \hat{N}_1 + \alpha(\Delta x) \hat{N}_3}{K} > 0$$

$$\Leftrightarrow \frac{\alpha(\Delta x) \hat{N}_1 + \alpha(\Delta x) \hat{N}_3}{K} < 1$$

$$\Leftrightarrow \frac{\alpha(\Delta x) \hat{N}_1 + \alpha(\Delta x) \hat{N}_1}{\hat{N}_1 + \alpha(2\Delta x) \hat{N}_1} < 1$$

$$\Leftrightarrow 2\alpha(\Delta x) < 1 + \alpha(2\Delta x)$$

$$\Leftrightarrow -(\alpha(\Delta x))^4 + 2\alpha(\Delta x) - 1 < 0 \quad (*)$$

use  $\hat{N}_1 = \hat{N}_3$  &  
 $K = \hat{N}_3 + \alpha(2\Delta x) \hat{N}_1$

$$\alpha(\Delta x) = \exp\left(-\frac{(\Delta x)^2}{2\sigma^2}\right)$$

$$\Rightarrow \alpha(2\Delta x) = \alpha(\Delta x)^4$$



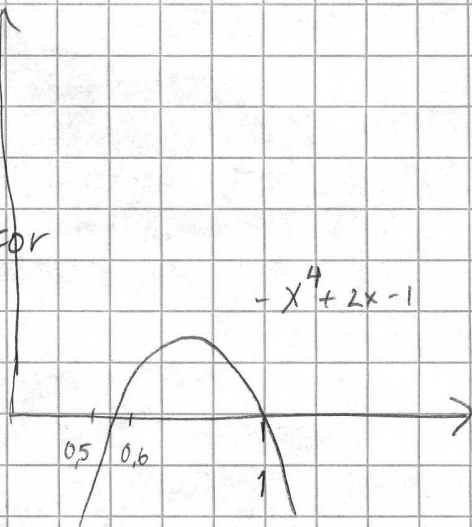
9.3 continues.

We want the solutions

Because  $\alpha(\Delta x) = \exp\left(-\frac{(\Delta x)^2}{2\sigma^2}\right)$

we want the solutions of (\*) for which  $\alpha(\Delta x) < 1$ .

Numerically one can see that smallest solution of (\*) is between 0,5 and 0,6.



We say  $\alpha(\Delta x) < 0.5$

$$\exp\left(-\frac{(\Delta x)^2}{2\sigma^2}\right) < 0.5$$

$$\Rightarrow -\frac{\Delta x^2}{2\sigma^2} < \ln 0.5$$

$$(\Delta x)^2 > -2\sigma^2 \ln 0.5$$

$$\underline{\underline{\Delta x > \sqrt{-2 \ln 0.5} \cdot \sigma}}$$