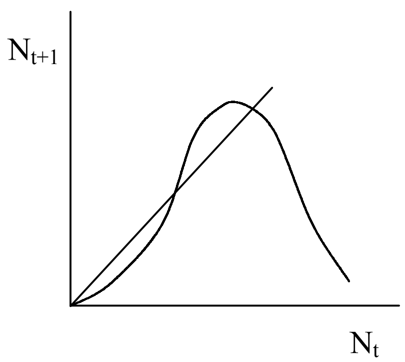
THEORETICAL ECOLOGY - EXERCISES

Note: The order of the exercises is random and does not reflect how difficult the problem is. New exercises are added to the end. You are welcome if you need help!

1. Consider a population that grows according to the continuous-time logistic model. You harvest this population by removing a constant number of individuals per time unit. At what density should you keep the population such that you can take the most individuals away in equilibrium (i.e., without killing the population)?

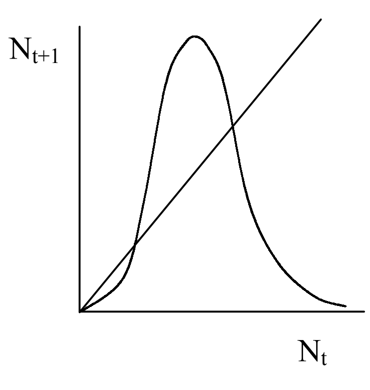
2. Assume an organism survives one year with probability P and produces B offspring each year. Calculate (a) the expected lifetime (=average age at death), (b) the expected number of offspring during the entire life. (*Hint:* You will need a trick we used to calculate an infinite sum.)

3. Find all equilibria and determine their stability in the following discrete-time model:



4. Assume that N_{t+1} is a unimodal function of N_t (i.e., it has a single peak). Show that after some time, population density always remains between a minimum and a maximum value - even if the population is chaotic! How does this range change if N_{t+1} has a higher peak? (*Hint:* Draw N_{t+1} as a function of N_t, and find first the maximum attainable density; the minimum follows from this. "After some time" is needed because we may start the population outside this range, but once density is within the range, it will never go out.)

5. Show that no matter what the initial density is, the population will eventually go extinct in the following model:



6. Show that the Hassell model,

$$N_{t+1} = \frac{aN_t}{(1+bN_t)^{\beta}}$$

is undercompensating if $\beta = 1$ but overcompensating if $\beta > 1$. (In which case are cycles possible?)

7. *Allee-effect.* Most models assume that the population grows fastest at low population densities, when each individual has access to plenty of resources. In sexually reproducing species, however, it may be difficult for females to find a mate when population density is low, and consequently females may fail to reproduce. This is an example for the *Allee-effect*, the notion that the population may experience small or even negative growth rate at very low densities (other examples include social species where individuals suffer from lack of help from conspecifics at low densities).

Assume that the rate of finding a mate is a saturating function of male density (which we take to be equal to female density, N) of the form $\frac{\alpha N}{v+N}$. When the female found a mate, she produces *b* offspring. The death rate is *cN* (density dependent). Altogether, population growth is given by

$$\frac{dN}{dt} = \left(\frac{\alpha Nb}{v+N} - cN\right)N = \left(\frac{u}{v+N} - c\right)N^2$$

with $u = \alpha b$. Find the equilibria and their stability in this model. Draw the bifurcation diagram varying the value of parameter *u*.

8. Assume that in absence of herbivores, plant biomass (*x*) grows linearly in time: In each time interval *dt* a constant amount *a* is added to *x*, leading to *dx/dt=a*). Herbivores consume the plant and their density (*y*) grows similarly to the Lotka-Volterra predator-prey model:

$$\frac{dx}{dt} = a - bxy$$
$$\frac{dy}{dt} = cxy - dy$$

Analyse this model by drawing the phase portrait, and finding the equilibria and their stability.

9. *Volterra's principle*. After World War I, there was an unusual increase in the density of predatory fish in the Adriatic sea, but no such increase in the prey species. The war had disrupted fishing and hence decreased the death rate of all fish. Why was this more beneficial to the predators than to their prey?

In order to explain, Volterra set up the famous predator-prey model

$$\frac{dx}{dt} = (a - by)x$$
$$\frac{dy}{dt} = (cx - d)y$$

and determined the equilibrium densities $\hat{x}$ (prey) and $\hat{y}$ (predator). Less fishing means a higher value of a (faster growth of the prey in absence of the predator) and a lower value of d (less mortality in the predator). Show that increasing a and decreasing d indeed leads to the observed change in $\hat{x}$ and $\hat{y}$. (Note: although x and y are oscillating in the Lotka-Volterra model, but their time averages are $\hat{x}$ and $\hat{y}$. The above result thus explains the change in the average densities of predators and their prey.)

Remark: Volterra's principle remains valid in more realistic models as well: An indiscriminate increase in the death rates of both the prey and the predator will lead to more prey and less predator. This has important consequences in pest control. Many insect pest species are prey to some natural enemies. The insecticide used against the pest (prey) often harms the enemy (predator) as well, and therefore using the insecticide can lead to *more* pest (and less natural enemy).

10. Consider the spruce budworm system, and assume that we keep the budworms at a low density by using an insecticide (which does not affect the birds that feed on the budworms). What will happen if, after some decades, we shall be forced to stop using the chemical?

11. Draw the phase portrait of the predator-prey model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - bxy$$
$$\frac{dy}{dt} = cxy - dy$$

if $K < d/c$. Can you explain verbally why the predator goes extinct?

12. Consider the prey-predator model where the prey has logistic growth in absence of predators and the predators have Holling II functional response (same as in the lecture),

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \frac{bxy}{\beta + x}$$
$$\frac{dy}{dt} = \frac{cxy}{\beta + x} - dy$$

(a) Verify that the equilibrium is given by $\hat{x} = \frac{\beta d}{c-d}$ and $\hat{y} = \frac{r}{b}\left(1 - \frac{\hat{x}}{K}\right)(\beta + \hat{x})$.

(b) By computing *T* and *D*, verify that the equilibrium is stable if $\frac{K-\beta}{2} < \frac{\beta d}{c-d}$.

(*Hint:* this is a bit laborious but just follow the recipe.)

13. Consider the prey-predator model where the prey has logistic growth in absence of predators and the predators have Holling II functional response (same as in the lecture and in exercise 12). Suppose that we would like to protect the predator: We want to increase its equilibrium density and keep it away from occasional low densities, i.e., we do not want cycles. Would you recommend increasing *K*? Decreasing *d*? (*Hint:* draw the isoclines on the phase plane; watch out for arrangements on both sides of the Hopf bifurcation. The answer should come in a form "yes but only if... and not more than...".)

14. (*perhaps a bit more demanding*) Consider the prey-predator model with Holling II functional response but no density dependence in the prey:

$$\frac{dx}{dt} = ax - \frac{bxy}{\beta + x}$$
$$\frac{dy}{dt} = \frac{cxy}{\beta + x} - dy$$

(a) Draw the isoclines of this model.

(b) Show that the equilibrium is never stable. (*Hint:* You can show this analytically by performing the local stability analysis; but on a heuristic level, you can also argue by comparing the vicinity of the equilibrium in the isocline plots of this model and of the model where the prey has density dependence.)

(c) Argue graphically that this model will produce ever increasing cycles, periodically leading to ever increasing densities (thus it cannot be ecologically realistic; prey density dependence is a must). Explain verbally, why cannot the predator alone keep prey density in check? (*Hint:* remember that predators are limited by time in the Holling II functional response.)

15. Argue graphically that three consumer species cannot coexist on two resources in equilibrium.

16. Consider the Lotka-Volterra competition model

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right)$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right)$$

(a) Show that if the two species have the same carrying capacity ($K_1 = K_2$), then they can coexist only if $\alpha_{12} < 1$ and $\alpha_{21} < 1$. Biologically, this means that competition between species must be weaker than competition within species (e.g. in the first equation, adding one individual of species 1 harms species 1 more than adding one individual of species 2).

(b) Show that the simple condition $\alpha_{12} < 1$ and $\alpha_{21} < 1$ is not necessary for coexistence if the carrying capacities are not equal; in particular, the two species can coexist even if $\alpha_{21} > 1$ (species 2 is strongly affected by species 1) provided that species 2 has higher carrying capacity (or vice versa).

(c) Show that the two species cannot coexist if both $\alpha_{12} > 1$ and $\alpha_{21} > 1$, irrespectively of their carrying capacities. (*Hint:* this is based on the result of (b).)

17. Consider the resource (R) - consumer (N) - predator (P) model

$$\frac{dR}{dt} = sR\left(1 - \frac{R}{L}\right) - bRN$$
$$\frac{dN}{dt} = (cR - d)N - \beta NP$$
$$\frac{dP}{dt} = (\gamma N - \delta)P$$

Suppose that we increase the carrying capacity of the resource (L). What will be the effect in the equilibrium densities of the resource, of the consumer, and of the predator?