Lecture 8

Population Regulation and Intraspecific Competition continued

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Outline

Exercise 2: calculating λ

The "emigrating unicellulars" problem ($R_0 = 1.6$, $T = 24hr$, $\tau = 48hr$, it takes $5sec$ to refresh the medium):

$$N_t \xrightarrow{R_0^2\ [48hr]} N'_t \xrightarrow{1-e\ [5sec]} N_{t+1} \xrightarrow{R_0^2} N'_{t+1} \xrightarrow{1-e} N_{t+2} \quad \ldots$$

- If we measure right **after** emigration, we measure $N_t,\ N_{t+1},\ N_{t+2},\ \ldots$
- It is the granddaughters that emigrate.
- So if we begin with $N_0 = 100$, we get $N_1 = 192$, $N_2 = 368.64$ etc.
- If we measure right **before** emigration, we measure $N'_t,\ N'_{t+1},\ N'_{t+2},\ \ldots$
- It is the parents that emigrate.
- So if we begin with $N_0 = 100$, we get $N'_0 = 256$, $N'_1 = 491.52$, $N'_2 = 943.72$ etc.

Exercise 2: calculating λ

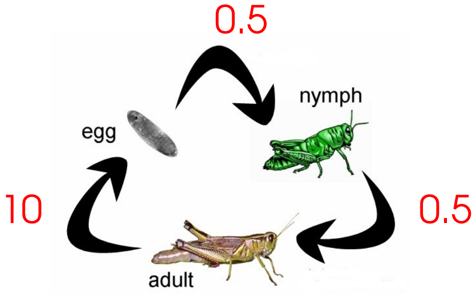
The "emigrating unicellulars" problem ($R_0 = 1.6$, $T = 24hr$, $\tau = 48hr$, it takes $5sec$ to refresh the medium):

$$N_t \xrightarrow{R_0^2\ [48hr]} N_t' \xrightarrow{1-e\ [5sec]} N_{t+1} \xrightarrow{R_0^2} N_{t+1}' \xrightarrow{1-e} N_{t+2} \quad \ldots$$

- If we measure right **after** emigration, we measure $N_t,\ N_{t+1},\ N_{t+2},\ \ldots$
- If we measure right **before** emigration, we measure $N_t',\ N_{t+1}',\ N_{t+2}',\ \ldots$
- Although the measured population sizes/densities are different.
- The ratio of successive values remains the same, whether we measure the N_t or the N_t'.
- I.e., $\lambda = R_0^2(1-e)$ (in this case 1.92), regardless of timing of measurement.

Exercise 2: calculating λ

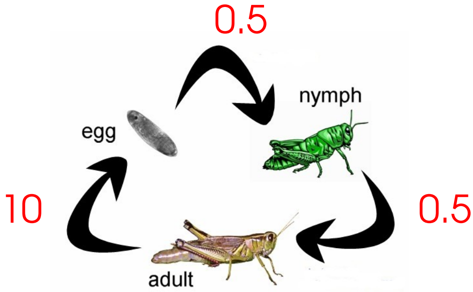
Another example – **annual life cycle of a grasshopper:**



- With no emigration, $\lambda = R_0 = 0.5 * 0.5 * 10 = 2.5$.

Exercise 2: calculating λ

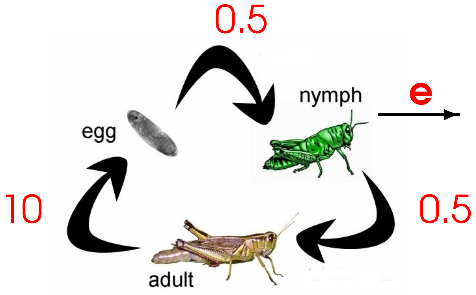
Another example – **annual life cycle of a grasshopper:**



- Starting with 100 eggs,
  1. Egg number will increase to 250, then to 625, etc.
  2. Initially 50 nymphs, then 125, then 312.5 etc.
  3. Initially 25 adults, then 62.5, then 156.25 etc.
- Population numbers will change, depending on what we are measuring (eggs, nymphs, adults).
- But λ is the same in all cases.

Exercise 2: calculating λ

Another example – **annual life cycle of a grasshopper:**



- With nymph emigration, $\lambda = 0.5 * (1 - e) * 0.5 * 10 = R_0(1 - e) = 2.5(1 - e)$.

Exercise 2: calculating λ

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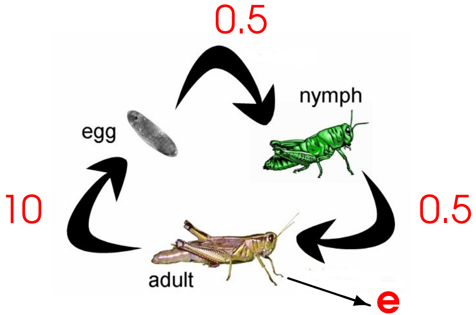
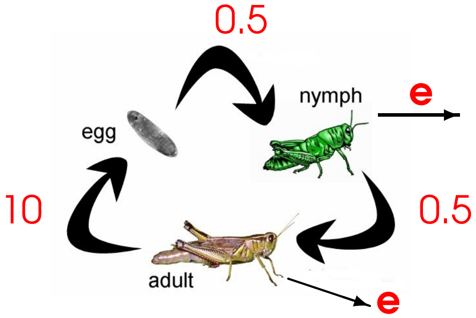


- With nymph emigration,
  $\lambda = 0.5 * (1 - e) * 0.5 * 10 = R_0(1 - e) = 2.5(1 - e)$.
- With adult emigration,
  $\lambda = 0.5 * 0.5 * (1 - e) * 10 = R_0(1 - e) = 2.5(1 - e)$.

Exercise 2: calculating λ

Another example – **annual life cycle of a grasshopper:**

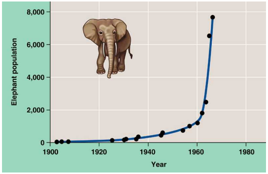


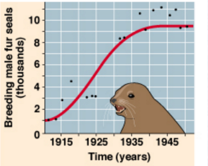
- As long as effects are multiplicative, the order does not matter.
- The exact timing of emigration will affect observed numbers of nymphs or adults.
- But will not affect λ, as long as e is the same in both cases.

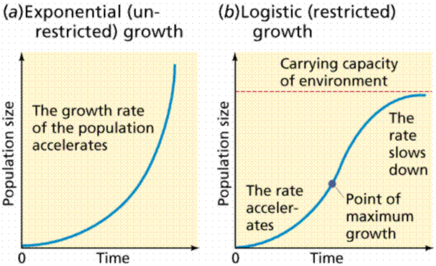
Outline

J-curves and S-curves

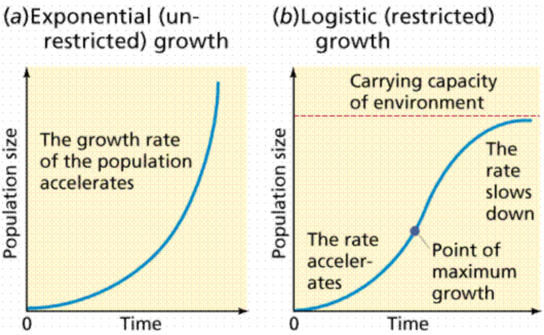
- Typically, unregulated populations have growth curves that are exponential (shaped like the letter J).
- Typically, regulated populations have growth curves that are **sigmoidal** (shaped like the letter S).







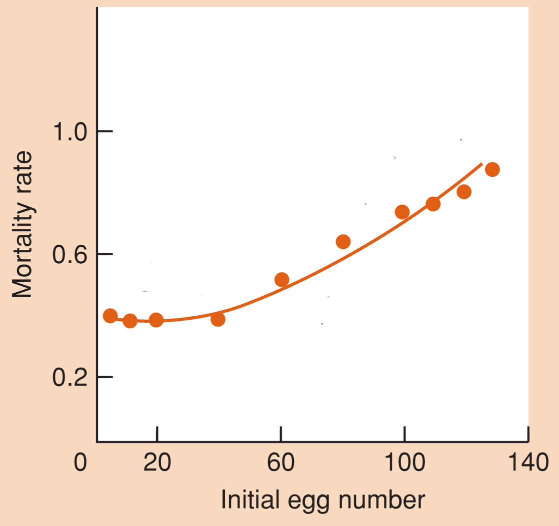
J-curves and S-curves



- Exponential or geometric growth cannot produce sigmoidal curves.
- We are obviously missing something – some mechanism that causes population growth to slow down.
- Time to modify our models.

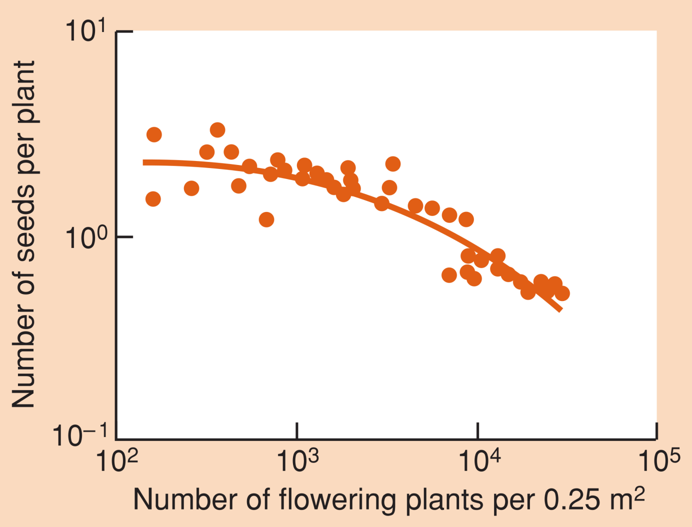
Density-dependent birth and death rates

Density-dependent mortality in flour beetle (*Tribolium*).

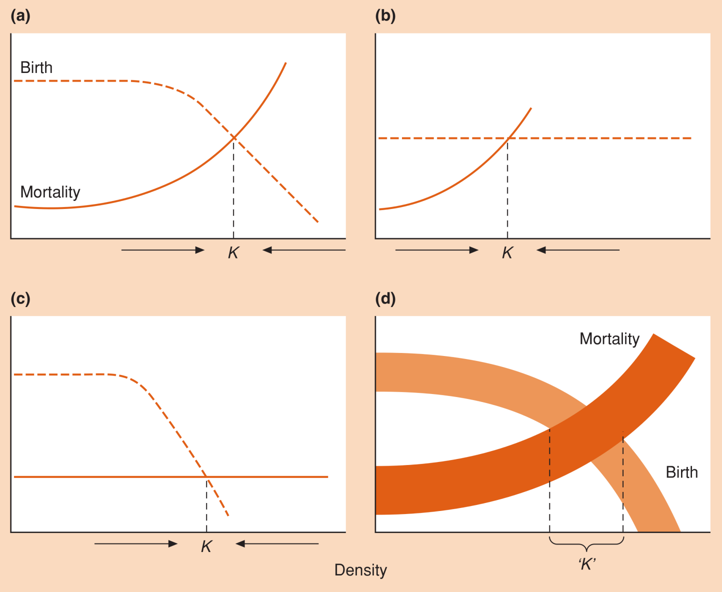


Density-dependent birth and death rates

Density-dependent seed production in an annual plant.

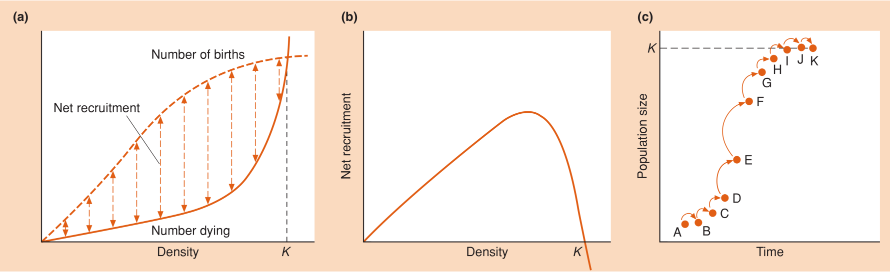


Density-dependent birth and death rates



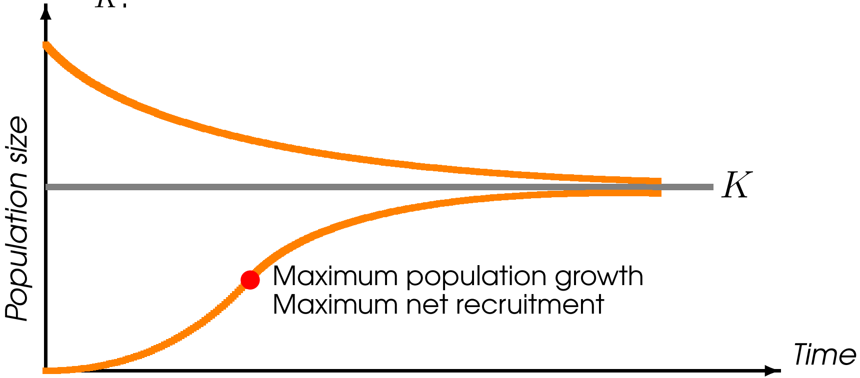
Density-dependent birth and death rates

- Net recruitment (total births minus total deaths) is usually humped-shaped.
- Having maximum at intermediate densities ⟶ population growth is maximal at intermediate densities.
- ⟶ resulting in S-shaped growth curve.



The carrying capacity, K

- The carrying capacity, K, is the long-term stable population size – i.e., where births and deaths cancel each other.
- If starting below, population size will increase towards K.
- If starting above, population size will decrease towards K.



Population growth vs. Relative/Per-capita growth

- **Population growth rate (PGR)** is the rate or increment of change in population size/density.

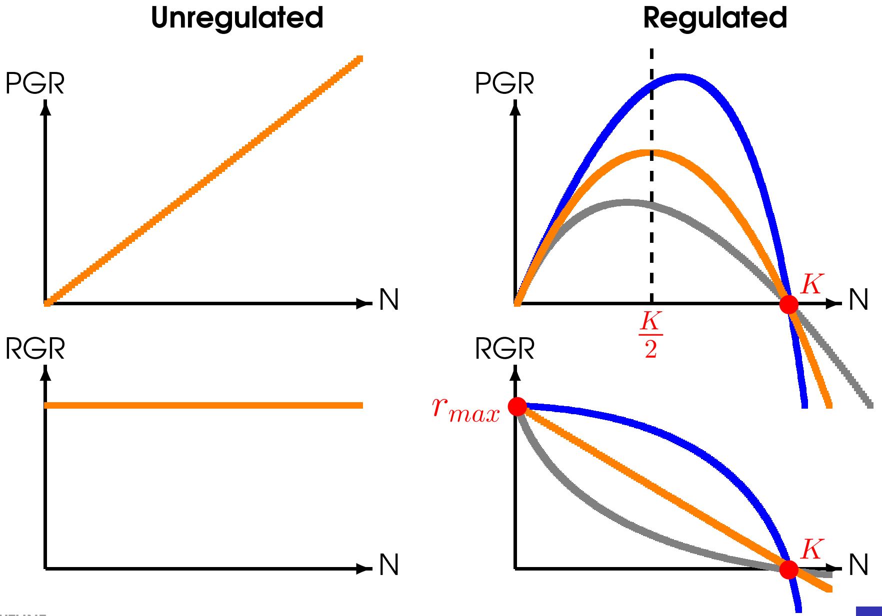
$$\frac{dN}{dt}, \quad \frac{dn}{dt}, \quad \Delta N, \quad \Delta n$$

- **Relative/per-capita growth rate (RGR)** is the mean per-capita contribution of an individual to population growth.

$$\frac{1}{N}\frac{dN}{dt}, \quad \frac{1}{n}\frac{dn}{dt}, \quad \frac{\Delta N}{N}, \quad \frac{\Delta n}{n}$$

- Unregulated (exponential or geometric) population growth and regulated (density-dependent) growth show different patterns of change in PGR and RGR as density increases.

Population growth vs. Relative/Per-capita growth



Density-independent vs. Density-dependent regulating factors

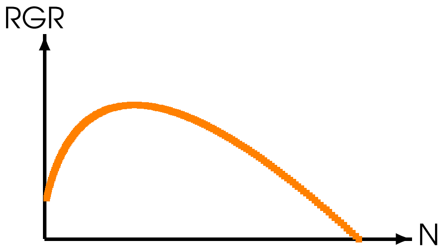
- Some regulating factors are density-independent: seasonal frosts or droughts, fires, storms or other catastrophes.
- Other mortality factors are density-dependent: increased starvation risk, increased risk of injury or death through competitive interactions, risk of disease or predation, etc.
- We can write total death rate as sum of density-independent terms and density-dependent terms.
- For example, $d = d_0 + d_1 N$ (d_0 and d_1 are constants.)
- Of course, density-dependence does not have to be linear (other functional forms are possible).

Density-independent vs. Density-dependent regulating factors

- Similarly, fecundity / birth rate can be written as $b = b_0 + b_1 N$. (Typically, b_1 is negative, as we expect per-capita fecundity to decrease as density rises).
- Density-dependent population regulation is the result of biotic interactions:
    - Intraspecific competition – more conspecifics, less resources per-capita.
    - Interspecific competition – more competitors (from any species), less resources per-capita.
    - Predation – more predators, higher mortality.
    - Outbreaks of disease – a kind of predation.

Density-independent vs. Density-dependent regulating factors

- Sometimes (at least for some range of densities) density-dependence can be positive – i.e., RGR would increase with rising density.
- This is called Allee effect.
- For example, wind-pollinated plants suffer reduced fecundity at very low densities, because many flowers remain unpollinated due to limited pollen availability.



Outline

Intraspecific competition

- Individuals of the same species have similar needs and behavior in terms of resources, habitat, timing of lifecycle events etc.

- Therefore, individuals should suffer strong competition from conspecifics, under conditions of crowding.

- These competition effects eventually manifest themselves as reduced fecundity and survival rates.

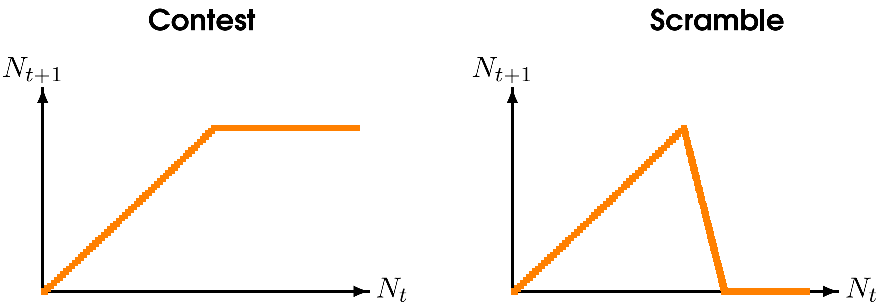
Intraspecific competition

Types of intraspecific competition

1. **Scramble vs. Contest**
   - In scramble competition all individuals suffer more or less the same reduction in fecundity or same increase in mortality.
   - In contest competition there are "winners" and "losers" – all or nothing.
     "Winners" do not suffer reduction in survival or fecundity.
     "Losers" suffer maximum reduction.

Intraspecific competition

Schematic representation of scramble and contest competition.



Example of contest: A fixed number of territories that individuals compete for.

Example of scramble: Food divided equally, but there is a minimum requirement to survive and reproduce successfully. If not enough food per individual, all starve to death.

Intraspecific competition

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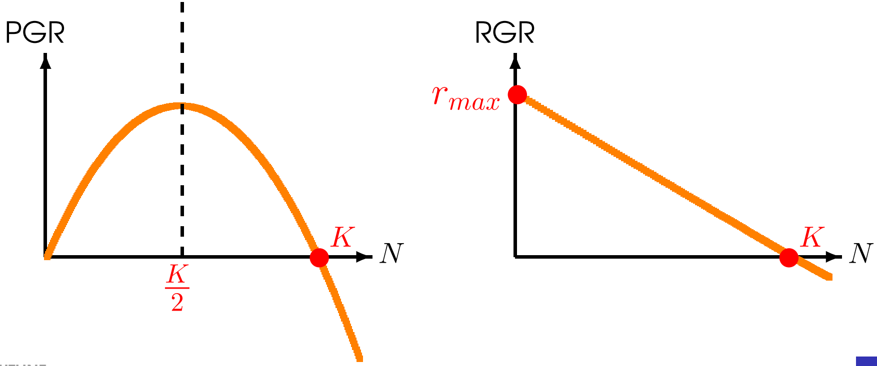
     "Winners" do not suffer reduction in survival or fecundity.
     "Losers" suffer maximum reduction.
2. **Interference vs. Exploitation**
   - In Interference competition there is direct interaction (aggression) among individuals, where one individual prevents or reduces access to resources from the other.
   - In exploitation competition there are no direct interactions – individuals affect each other by depleting a common resource.

Of course these are just extremes of a spectrum of types of intraspecific competition.

Outline

Logistic growth

- Simplest form of density-dependence is linear.
- Always start with a simple model – otherwise it is difficult to draw conclusions.
- Recruitment is a quadratic function – i.e., a parabola.
- Maximum recruitment (maximum PGR) occurs at $K/2$.



Logistic growth

- Continuous time model is given by

$$\frac{dN}{dt} = r_{max} N \left(1 - \frac{N}{K}\right)$$

- I.e., the expression for exponential growth, multiplied by a competition factor that is increasingly smaller than 1, as population size/density increases.
- RGR or per-capita growth rate is not constant, but given by the linear density-dependence relation

$$r(N) = r_{max} \left(1 - \frac{N}{K}\right)$$

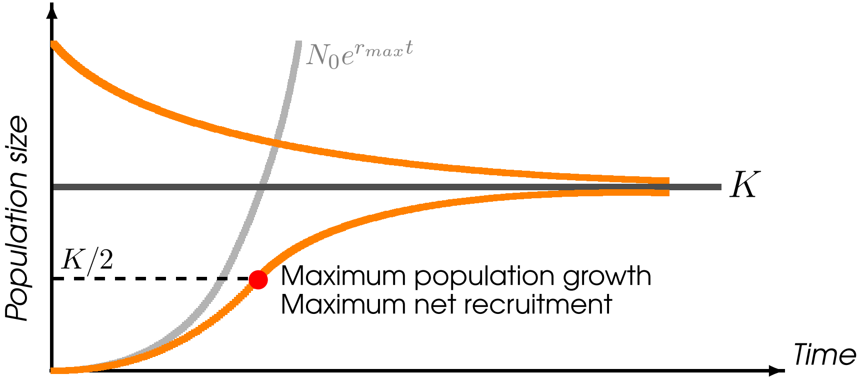
- An analogous discrete time model is given by

$$\lambda(N_t) = 1 + r_{max} \left(1 - \frac{N_t}{K}\right)$$

Logistic growth

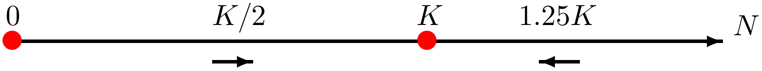
The logistic growth curve (continuous time):

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-r_{max}t}}$$

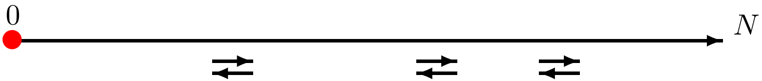


Stationarity and stability

- **Stationary points** represent special values of the variable that do not change over time.
- I.e., if we start at a stationary point, we remain on it on subsequent times.
- Therefore, stationary points are defined zero rate of change: $\Delta N = 0$ or $dN/dt = 0$.
- E.g., for the logistic growth model we have two stationary points, $N = 0$ and $N = K$:

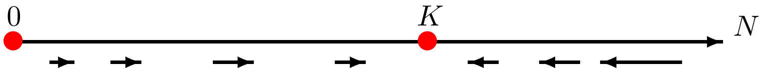


- For exponential growth, only $N = 0$:



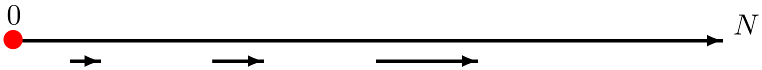
Stationarity and stability

- A stationary point can be either **stable** or **unstable**.
- Any deviation from a stable stationary point would tend to decrease over time – i.e., a restoring "force" operating towards the point.
- Any deviation from an unstable stationary point would tend to increase over time – i.e., a repelling "force" away from the point.
- We can determine stability graphically.
- E.g., for the logistic model $N = 0$ is unstable, and $N = K$ is stable:

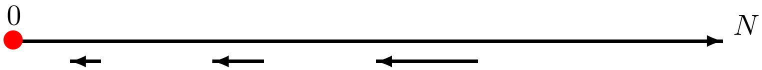


Stationarity and stability

- For the exponential model, $N = 0$ is unstable, if $r > 0$:



- And stable, if $r < 0$:

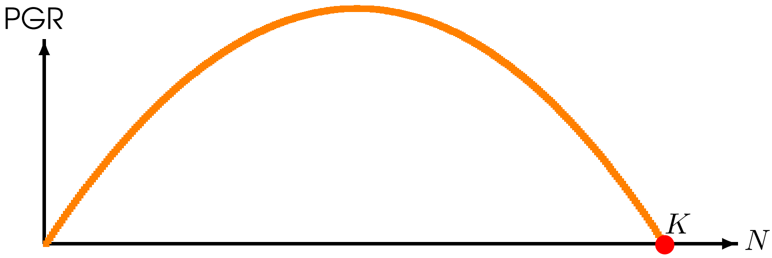


- Ultimately, checking for stability requires mathematical analysis using methods of linear algebra and nonlinear dynamics.
- But the graphical method is sufficient for our purposes.
- We will return to this subject when we talk about interspecific competition.

Application to sustainable harvesting

- If we harvest a logistically growing population at a constant rate (i.e., individuals or kilos per unit time) – the stationary population size will decrease.
- For example, commercial fishing depletes natural fish populations.
- Denoting harvest rate by H, the dynamics is given by

$$\frac{dN}{dt} = r_{max} N \left(1 - \frac{N}{K}\right) - H$$



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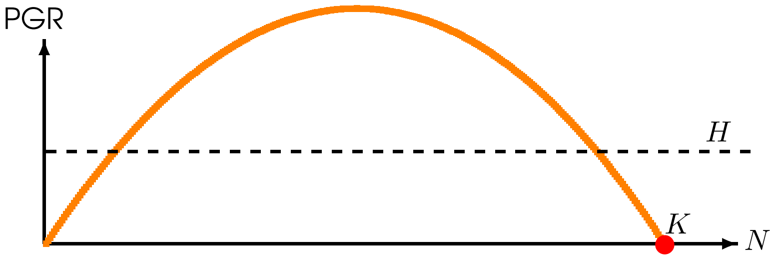

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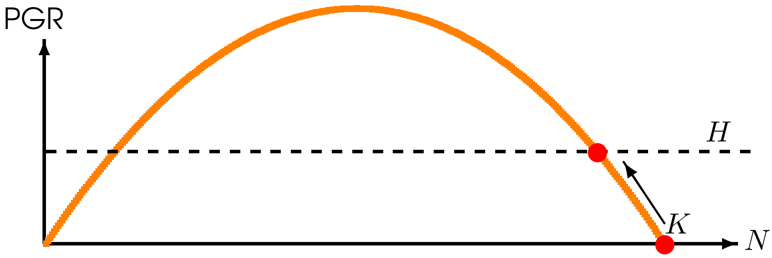

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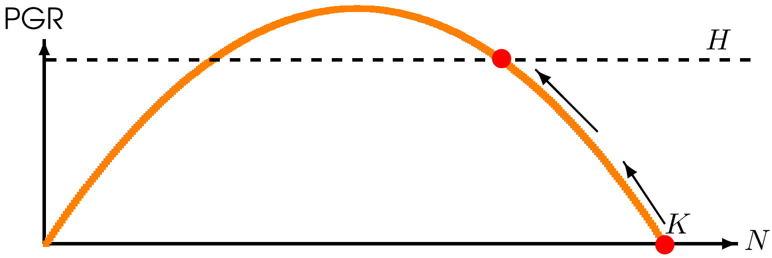

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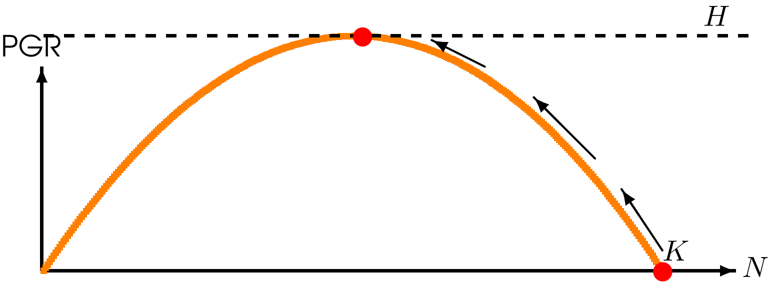

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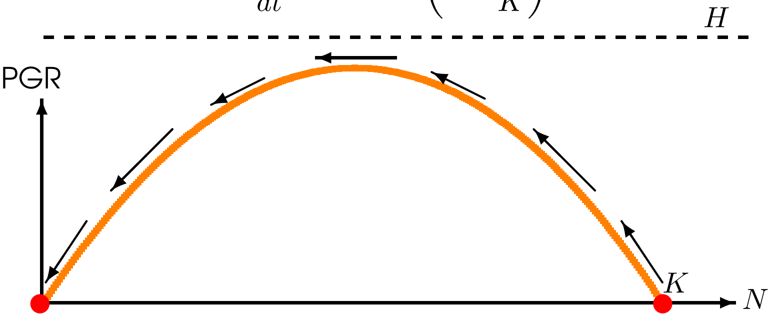

Application to sustainable harvesting

- Overharvesting (e.g., overfishing) occurs when H exceeds the maximal possible net recruitment rate (PGR).
- The natural population collapses, resulting in loss of the natural resource.
- For example,
  - Fisheries collapse – resulting not only in damage to nature, but also economic collapse of industries and human communities.
  - Overgrazed grasslands/pastures (grazed by livestock) turn into deserts – again resulting in subsequent collapse of human societies.
  - Overhunted animals go extinct.

Application to sustainable harvesting

- Following collapse of the resource, harvesting must be stopped for a long period, to allow the natural population to recover and exceed the maximum PGR point (in logistic growth, to exceed $K/2$).

- **Sustainable harvesting** can then be achieved if H is lower than the maximal PGR.