

Ecology I.

- <http://zeus.nyf.hu/~szept/kurzusok.htm>
- Krebs, C. J. (2014) Ecology, The experimental Analysis of Distribution and Abundance. Harper Int. Ed.
<https://archive.org/details/KrebsCharlesJ.EcologyTheExperimentalAnalysisOfDistributionAndAbundance201440mb/mode/2up>
- M. Begon, J.L. Harper & C.R. Townsend (2021) Ecology, Individuals, Population and Communities. Blackwell Sci. Publ.

Topics

1. Introduction to the Science of Ecology
2. Distribution of living organisms, Factors that limit distributions
3. Populations, Population parameters, Demographic Techniques
4. Population growth
5. Evolution and Ecology
6. Species interactions: Competition, Niche
7. Species interactions: Predation, Herbivory, Mutualism, Parasitism
8. Nature of the Community: structure and change
9. Flux of Energy and Matter through Ecological systems
10. Natural and artificial ecological systems. Biological diversity
11. Climate change and its ecological consequences

1. Introduction to the Science of Ecology

History of Ecology

Primitive tribes, for example—who depended on hunting, fishing, and food gathering—needed detailed knowledge of where and when their quarry might be found.

Ancient Greeks

Aristotle (IV. B.C): high reproductive rate of field mice could produce more mice than natural predators can reduce. Reduce of mouse plagues can be by heavy rain.

Herodotus and Plato: nature is designed to benefit and preserve each species, number of every species essentially constant, outbreak of some population might occur (punishment of evil-doers). Each species had a special place in nature, and extinction did not occur because it would disrupt this balance and harmony of nature

History of Ecology

- Graunt (1662) Father of demography. Importance of measuring in a quantitative way the birth rate, death rate, sex ratio and age structure of human populations. Concluded, that even without immigration, London could double its population in 64 years.
- Leeuwenhoek (1687) studied the reproductive rate of grain beetles, carrion flies and human lice. One pair of carrion flies could produce 746 496 flies in three months. First attempts to calculate theoretical rates of increase for an animal species



History of Ecology

Buffon (1756) Population of man and other living organism subjected to the same processes.

Great fertility of every species was counterbalanced by innumerable agents of destruction.

Plague populations of field mice checked partly by diseases and scarcity of food (biological factors) – not only the heavy rains

He dealt among the first with population regulation.



- Malthus (1798) „The numbers of organisms can increase geometrically, but their food supply may never increase faster than arithmetically.”

Reproduction is checked by food production.

Interest in mathematical aspects of demography increased after Malthus

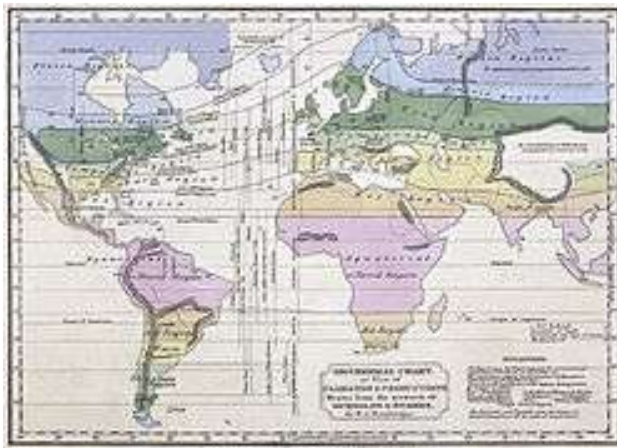


History of Ecology

- Möbius (1877) Biocoenosis

- Cowles (1899) Plant succession

- Humboldt (XIX century) Relation between climate and vegetation



History of Ecology

- Darwin (1859) Natural selection



Ecology, definition

The roots of ecology lie in natural history.

A word used first by Henry Thoreau (1858) without definition



Haeckel (1869) defined first: as the total relations of the animals to both its organic and inorganic environment -> Too wide definition !

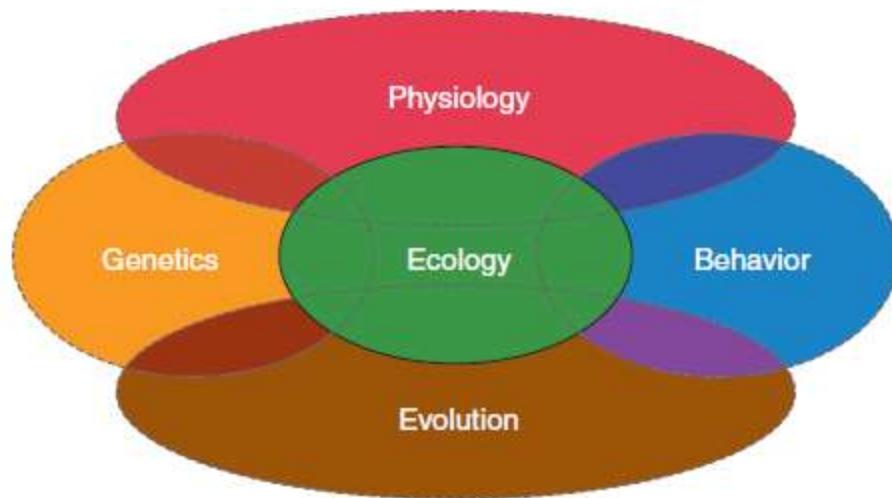
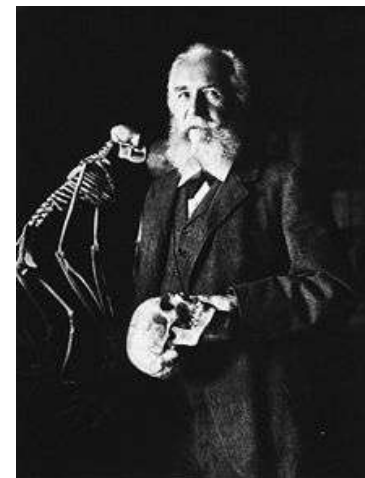


Figure 1 The four biological disciplines closely related to ecology.



Ecology - definition



Elton (1927): Scientific natural history

Odum (1963): Study of the structure and function of nature



Andrewartha (1961): Ecology is the scientific study of the distribution and abundance of organism – problem: this definition is static and leaves out the importance of relationships



Krebs (1985): Ecology is the scientific study of the interactions that determine the distribution and abundance of organism. Where organisms are found, how many occur there, and why



Hungarian approach Juhász-Nagy Pál (1970):



Ecology:

- focusing on supraindividual levels of biological organisation
- Population is the basic unit of it

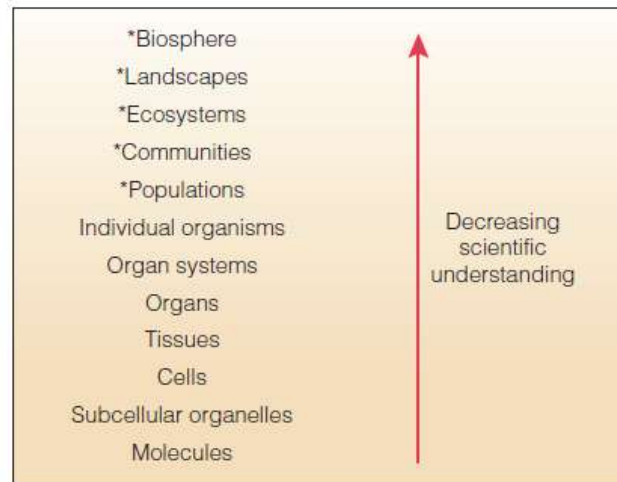
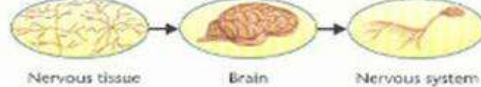


Figure 7 Levels of integration studied in biology.

13 FIGURE 1–21 LEVELS OF ORGANIZATION

Biosphere	The part of Earth that contains all ecosystems	
Ecosystem	Community and its nonliving surroundings	 Hawk, snake, bison, prairie dog, grass, stream, rocks, air
Community	Populations that live together in a defined area	 Hawk, snake, bison, prairie dog, grass
Population	Group of organisms of one type that live in the same area	 Bison herd
Organism	Individual living thing	 Bison
Groups of Cells	Tissues, organs, and organ systems	 Nervous tissue → Brain → Nervous system
Cells	Smallest functional unit of life	 Nerve cell
Molecules	Groups of atoms; smallest unit of most chemical compounds	 Water DNA

Hungarian approach
Juhász-Nagy Pál (1970):



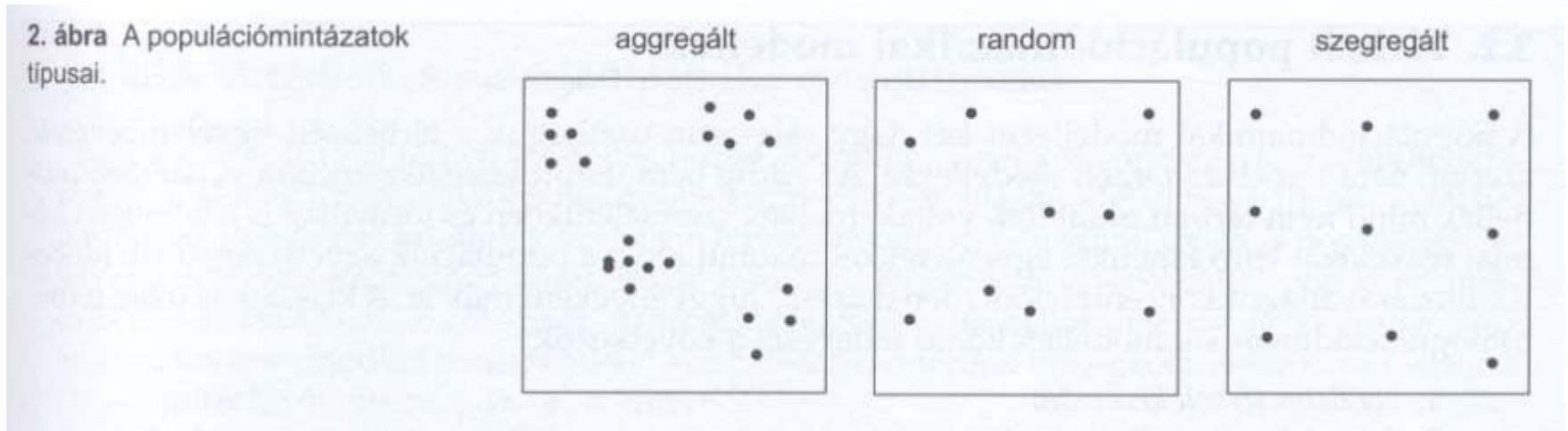
Ecology:

- focusing on supraindividual levels of biological organisation
- Population is the basic unit of it
- Central (null) hypothesis (CH): Any population could find any where, any time, any quantity in the nature – occurrence in space, time and abundance is random
- Central fact: CH could be faulty
- Central problem: How the CH is faulty and Why?

Example: spatial distribution

Three basic distributions:

aggregated random segregated



In the case of non random distribution there is an chance to find factors responsible for the found pattern.

Ecological principles - Opportunities to explain difference from the random distribution

1. Indication principle

- indicators (living organisms)
- indicandum, environmental factor which ones the indicator indicates



2. Complementation principle

- Relation of exterior and interior environments – acting factors and perceptive abilities
- exterior-interior complexes, neighbourhood – living organism
- Exterior complexes, all potentially acting factors in the neighbourhood
- Miliö spectrum, potentially acting factors in the neighbourhood on the base of existing experience
- Miliő, effectively acting factors in the neighbourhood responsible for the found distribution – environment
- Interior complexes, all potentially perceptive abilities
- Tolerance spectrum, potentially perceptive abilities on the base of existing experience
- Tolerance, effectively perceptive abilities responsible for the found distribution

▪
Ecological environment: all factors in the neighbourhood which directly and effectively act on the biological object

Neighbourhood → topological environment

Habitat (biotope): area where the supraindividual biological object occur

3. Multiplural environmental principle

There are several ecological environments in the given topological environment in the given time

4. Limitation principle

- Environmental factors acts together, synergy, any of it which reach range of the tolerance became limiter. Liebig limitation.
„The strength of the chain depend on the weakest chain link”

Type of ecological studies

- **Descriptive**

Natural history, describing populations, communities and their relationships

- **Functional**

Investigations of how the ecological system working. Discovering proximal processes.

- **Evolutionary**

Explanation of how evolution by natural selection has molded the ecological patterns we observe today. Discovering ultimate processes.

Type of ecological studies

Plant and animal ecology

Hydro and terrestrial ecology

Population and Community Ecology

Behavioural ecology

Study methods

- Field observation
- Experiment
- Modeling

Synecology – study of group of organisms

Autecology → individuals organism –
> environmental physiology

Levels of Ecological Research



Global ecology

study of the effects of regional changes in energy and matter exchange on the function and distribution of organisms across the biosphere



Landscape ecology

study of energy and matter (including organisms) exchanges between ecosystems



Ecosystem ecology

study of changes in the community in response to changes in abiotic components of the ecosystem.



Community ecology

study of how interactions between species (symbioses) affect community structure and organization



Population ecology

study of how factors affect population growth and structure through time



Organismal ecology

study of the physiological, evolutionary, and behavioral mechanisms used by individual organisms to meet ecological challenges

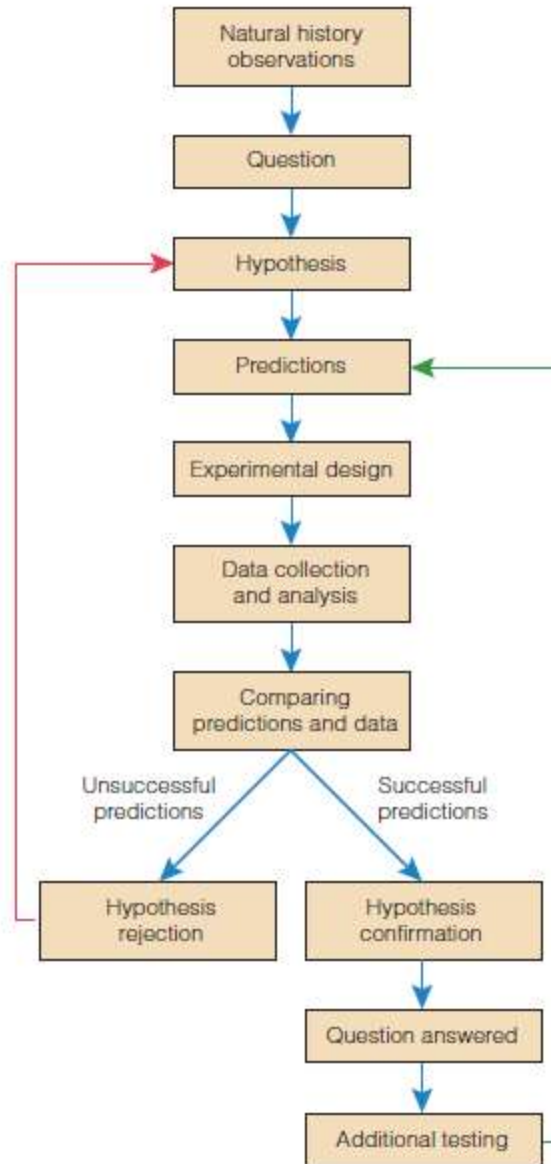
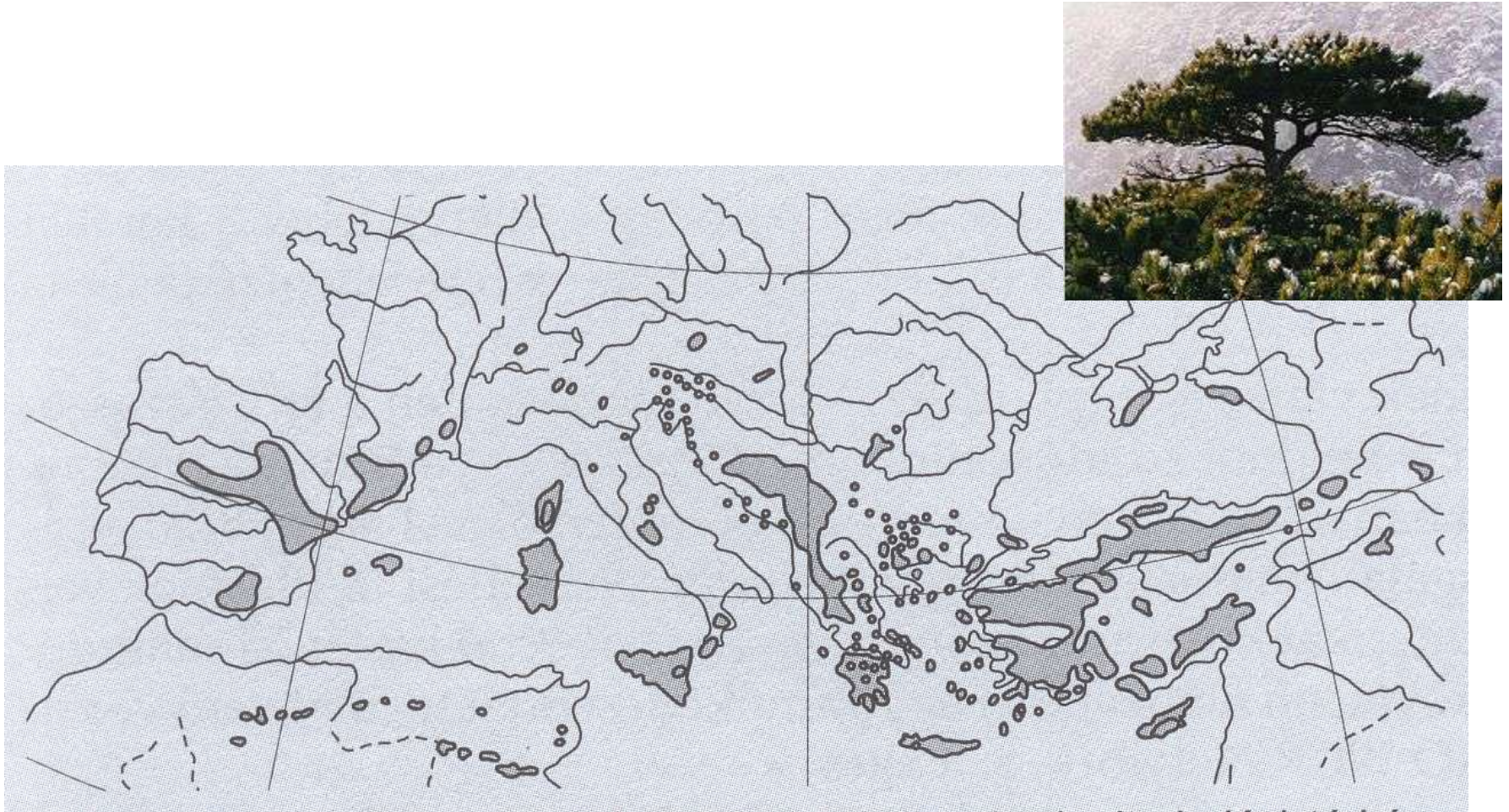


Figure 8 Schematic illustration of the scientific method as applied to ecological questions.

09.16

Methods for analysing distribution

What explains the occurrence of a species in a given place?



Distribution of black pine (*Pinus nigra*) in Europe

What explains the occurrence of a species in a given place?

Area accessible yes ← **Dispersal** → no



Dispersal

- Spread of the African honey bee in South America

Dispersal: undirected movement

Migration: directed movement (e.g. bird migration)

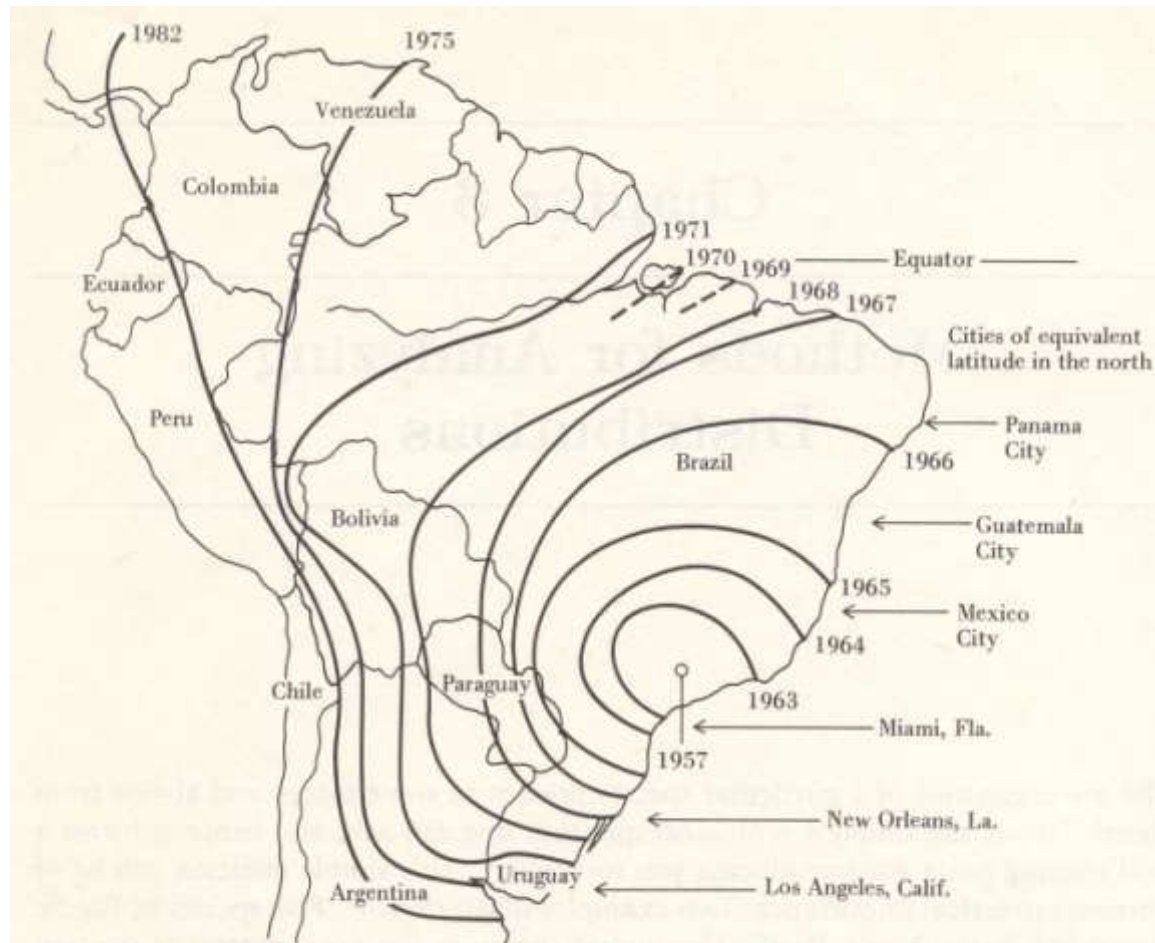


Figure 3.1 Spread of the African honey bee in South America since 1956. Southward and westward expansion has been slight since 1971. Further northward spread is occurring. (After Michener 1975 and personal communication.)

Dispersal

Part of Biogeography

European starling (*Sturnus vulgaris*) introduced to USA

Between 1850-1889 at many sites – no success

Introduced in 1918 at New York 80 males and 80 females,
slow dispersal

Young individuals have the most important role

Types:

- Diffusion
- Jump dispersal
- Secular migration (in evolutionary Scale) (e.g. opossum)

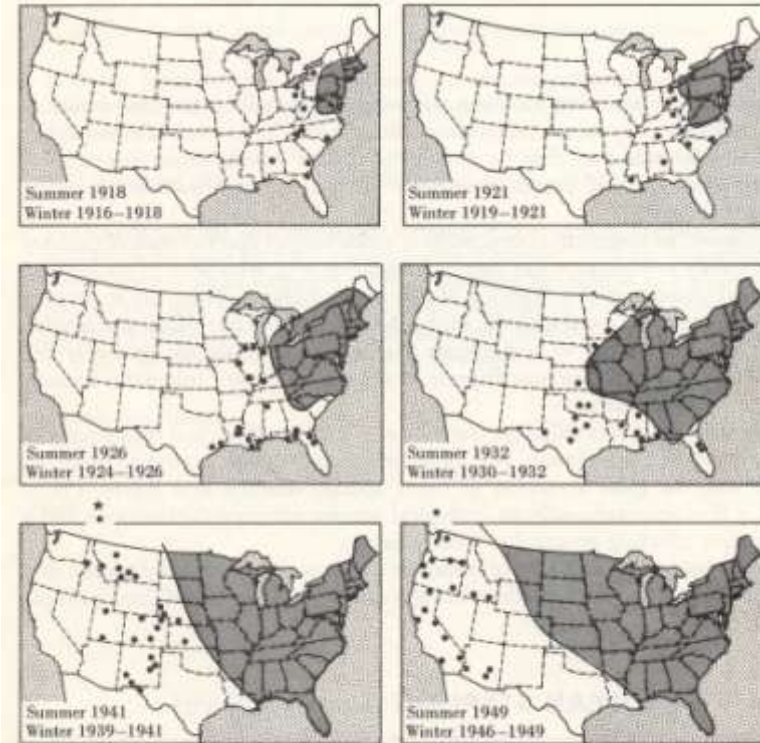


Figure 4.1 Westward expansion of the range of the starling. The shaded area shows the approximate breeding range for a given summer; the dots indicate winter occurrences outside the breeding range for the same year and two or three previous years. The star indicates an unusually advanced breeding record, in 1934, at Camrose, Alberta. (After Kessel 1953.)

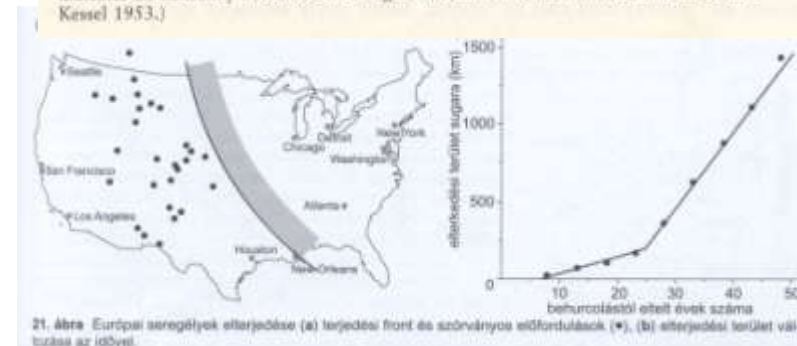
The role of barriers

(Oceans, deserts, high mountains,...e.g.)

Colonisation and extinction -> part of dispersal

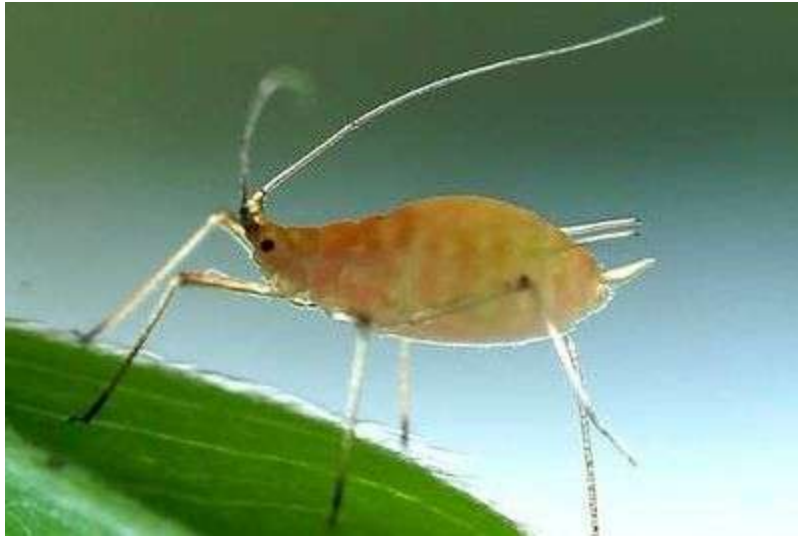
What is the function of the dispersal ?

- Option to invade new habitats



21. ábra: Európai seregélyek elterjedése (a) terjedési front és szóróvízosi előfordulások (*), (b) elterjedési terület változása az idővel.

Aphids



Aphids

Different forms:

- winged, sexual reproduction, high dispersal
- wingless, partenogenetic reproduction



Primary host plant—
Spindle tree

Secondary host plant—
Bean, sugar beet, and so on.

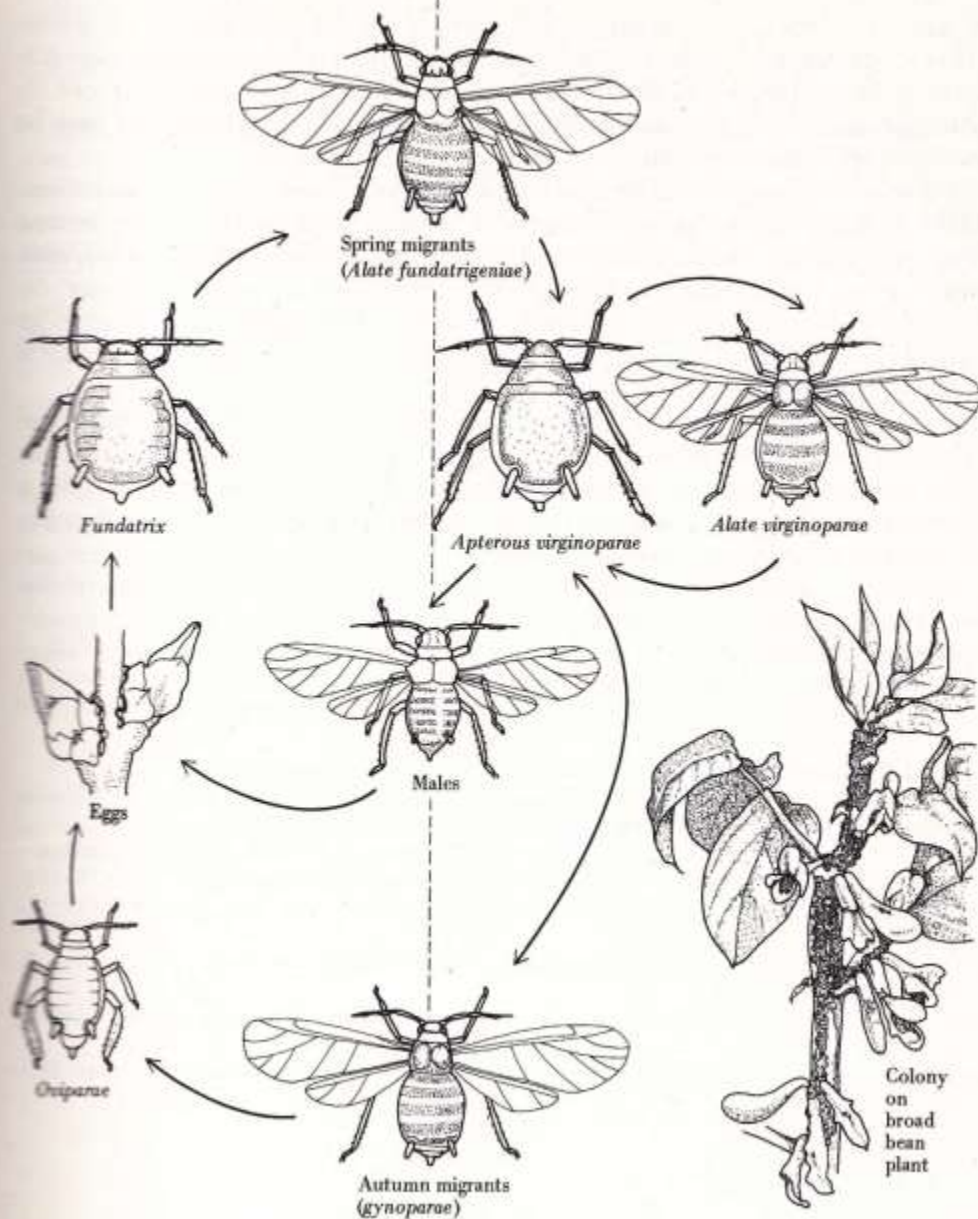


Figure 4.7 Life cycle of the black bean aphid (*Aphis fabae*). (From Blackman 1974.)

Speed of dispersal

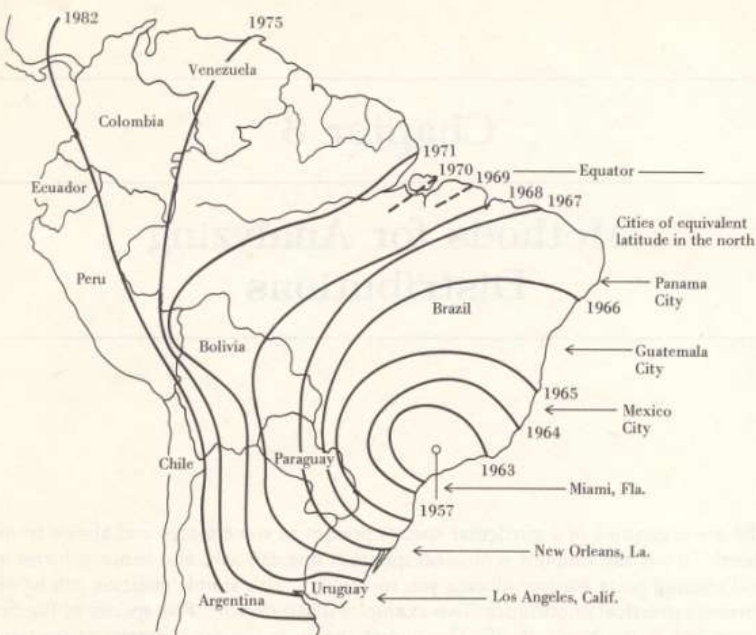
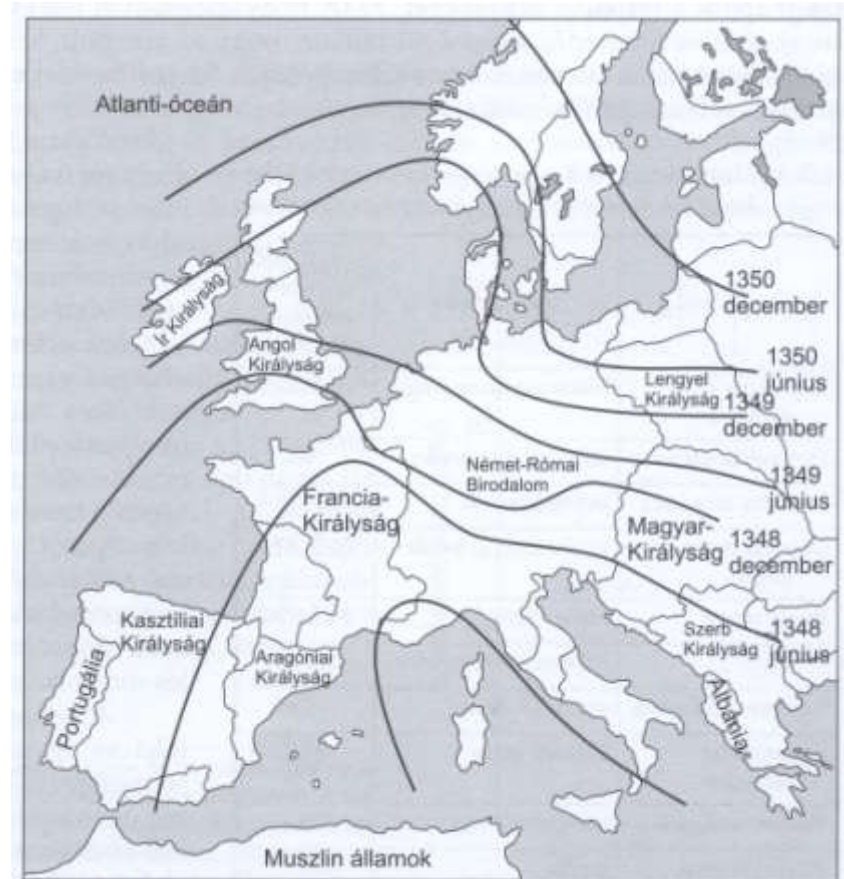


Figure 3.1 Spread of the African honey bee in South America since 1956. Southward and westward expansion has been slight since 1971. Further northward spread is occurring. (After Michener 1975 and personal communication.)

Latin	Hungarian	Megfigyelt speed km/year
<i>Impatiens glandulifera</i>	bíbor nebáncsvirág	9,4–32,9
<i>Lymantria dispar</i>	erdei gyapjaslepke	9,6
<i>Ondatra zibethica</i>	pézsmapocok	0,9–25,4
<i>Oulema melanopus</i>	vetésfehérítő bogár	26,5–89,5
<i>Pieris rapae</i>	répapillangó	14,7–170
	róka veszettség vírus	30–60
<i>Sciurus caroliensis</i>	szürke mókus	7,66
<i>Streptopelia decaocto</i>	balkáni gerle	43,7
<i>Sturnus vulgaris</i>	seregély	200
<i>Yersinia pestis</i>	pestis	400



Spread of pestis (*Yersinia pestis*) plague in Europe

Dispersal

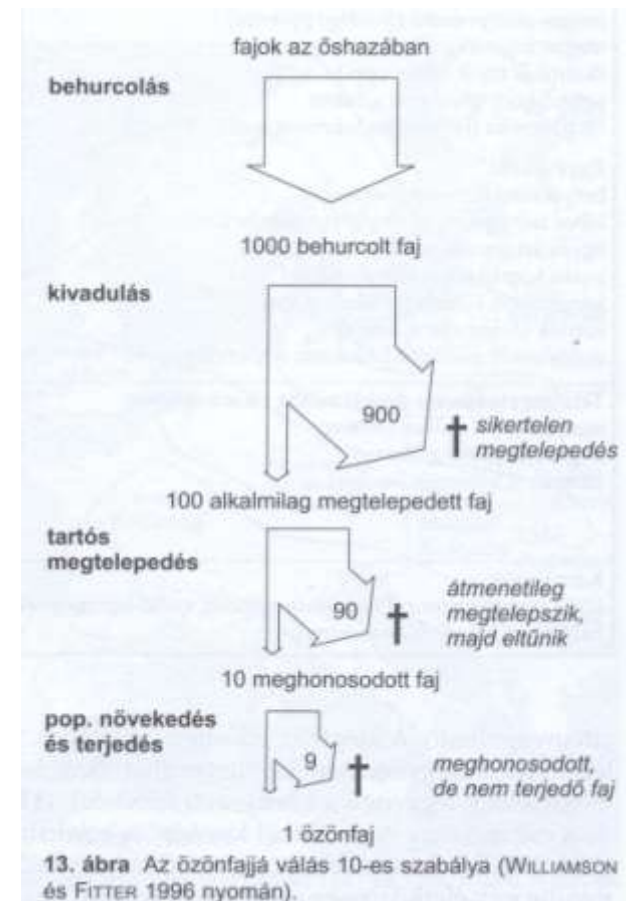
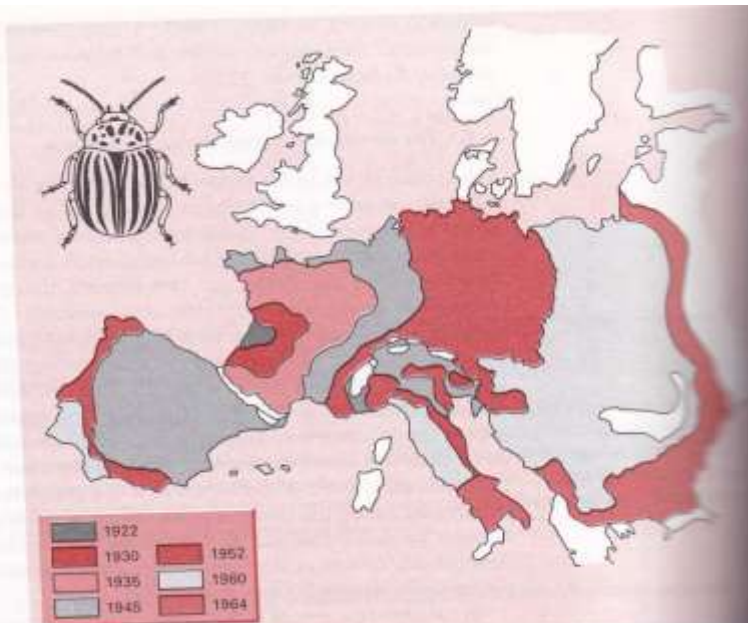
Invasive species -> economic, health and conservation problems

„10% role”

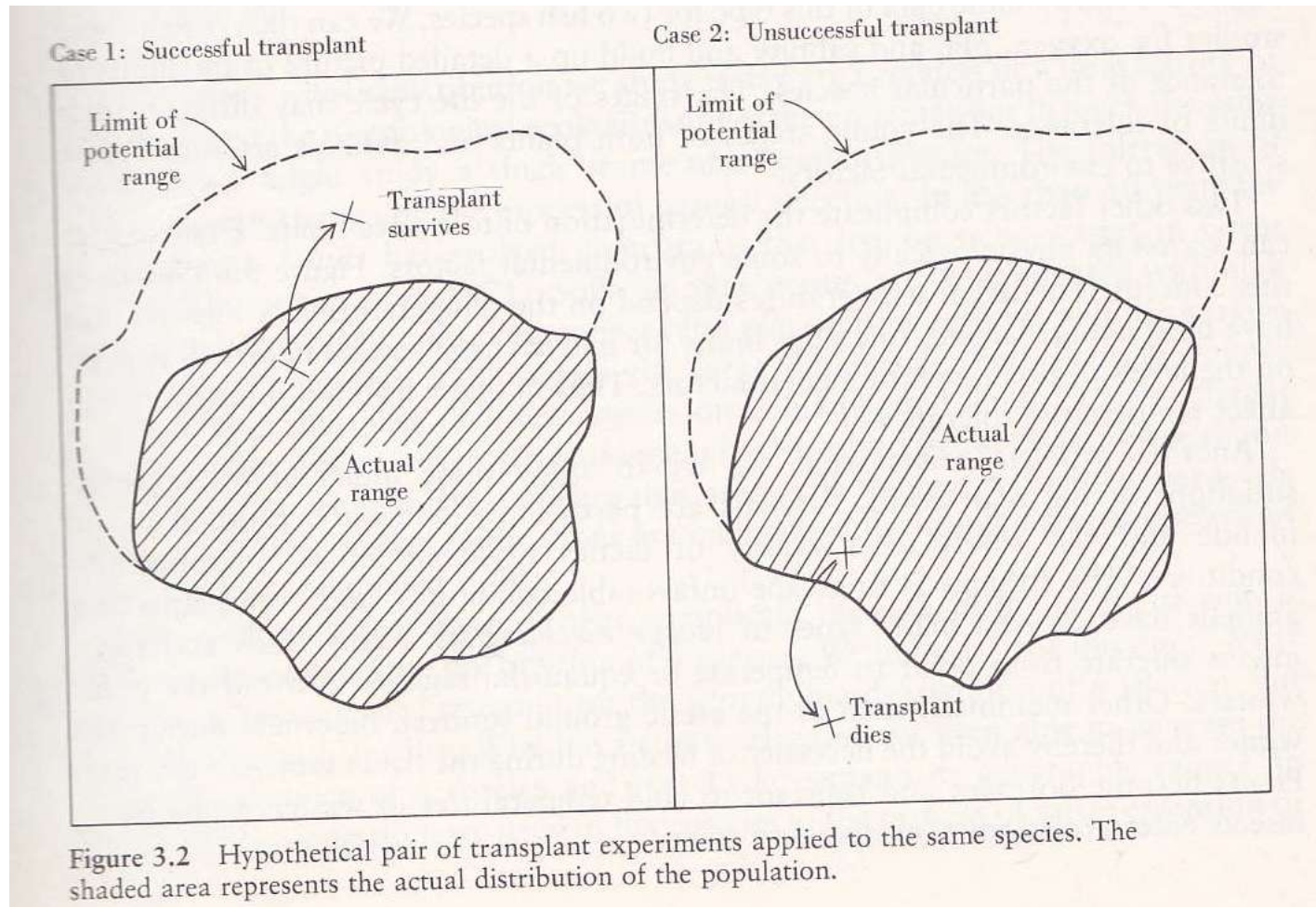
An average 10% of an introduced alien species survive in the new area

↑ An average 10% of these species could live longer in the new area

↑ An average 10% of these species could reproduce extremely-> invasive species



Transplantation experiments



What explains the occurrence of a species in a given place?

Area accessible

yes ← **Dispersal** → no



Habitat yes ← **Behaviour** → no
selection ↓

Habitat selection

Several animals do not occupy all their potential range even though they are able to disperse into the unoccupied area

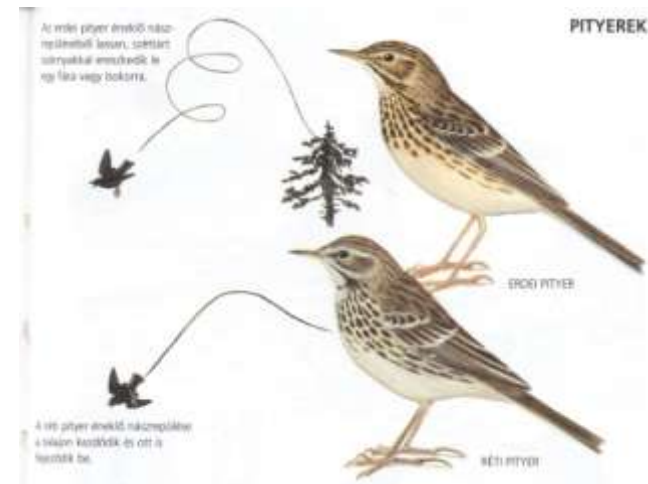
Anopheline mosquitoes – malaria infection – the mosquitoes lay eggs in much smaller areas as they are able to do – height of vegetation above the surface of water influence the egg-laying habit of the female mosquitoes – they prefer the open surface to during ovipositing dance



Lapwing (*Vanellus vanellus*) prefer the brown colored grassland in spring against the green one for nesting -> proper height of the vegetation during incubation

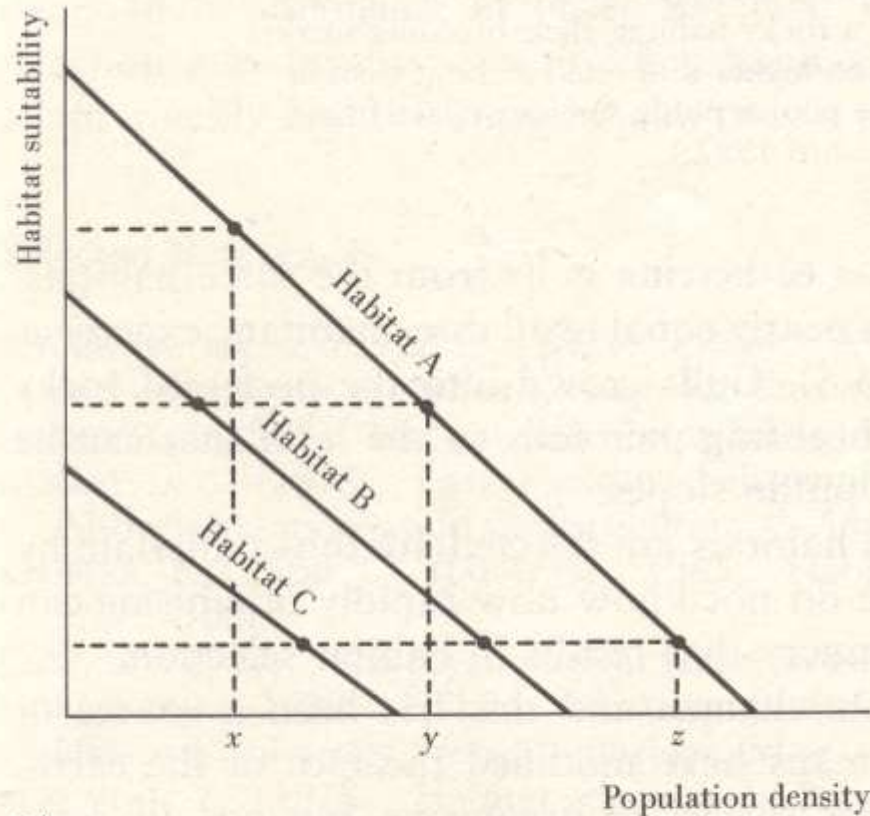
Two pipit bird species (*Anthus trivialis*, *Anthus pratensis*)

A. *trivialis* need trees in the habitat – important during pair-formation



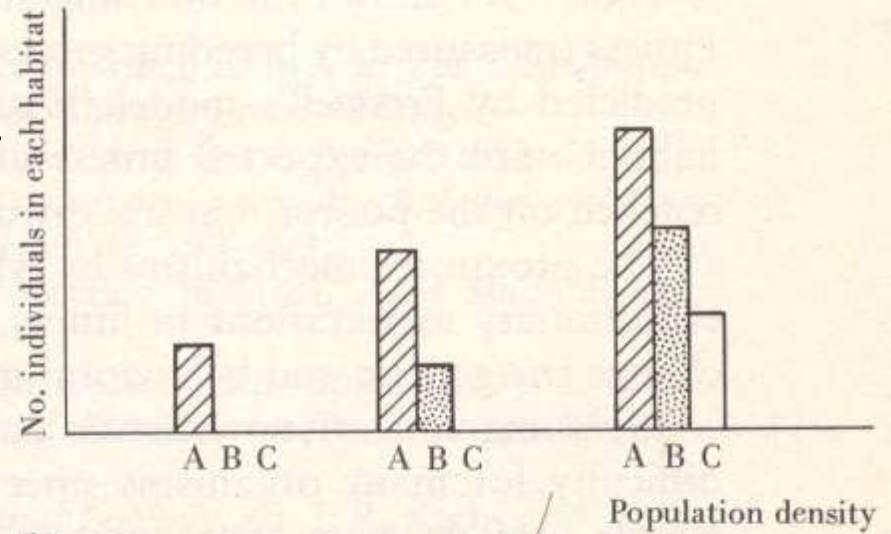
Habitat selection

Fretwell (1972) Ideal free distribution model



(a)

a



(b)

Figure 5.3 A simple model of habitat selection. Three habitats are used for illustration (A = good habitat, C = poor habitat). Habitat suitability is measured by the fitness of individuals living in that habitat. For illustrative purposes, three levels of population density are indicated (x , y , z). At low density x , all individuals live in favored habitat A. At high density z , all three habitats are occupied. (Modified from Fretwell 1972.)

What explains the occurrence of a species in a given place?

Area accessible

yes ← **Dispersal** → no



Habitat selection yes ← **Behaviour** → no



yes ← **Other species** → no

Predation

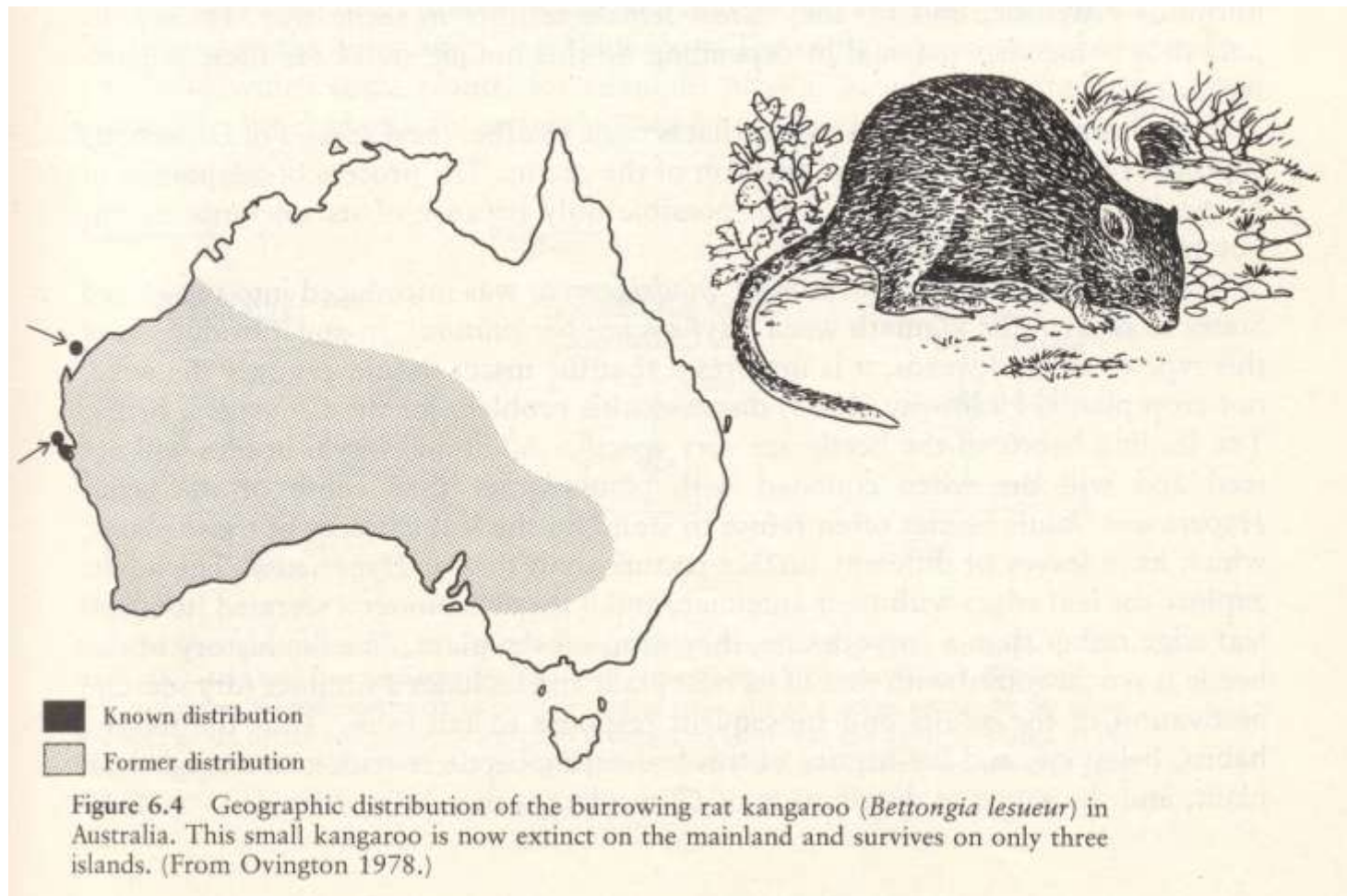
Competition

Parasitism

Mutualism

Interrelations with other organisms

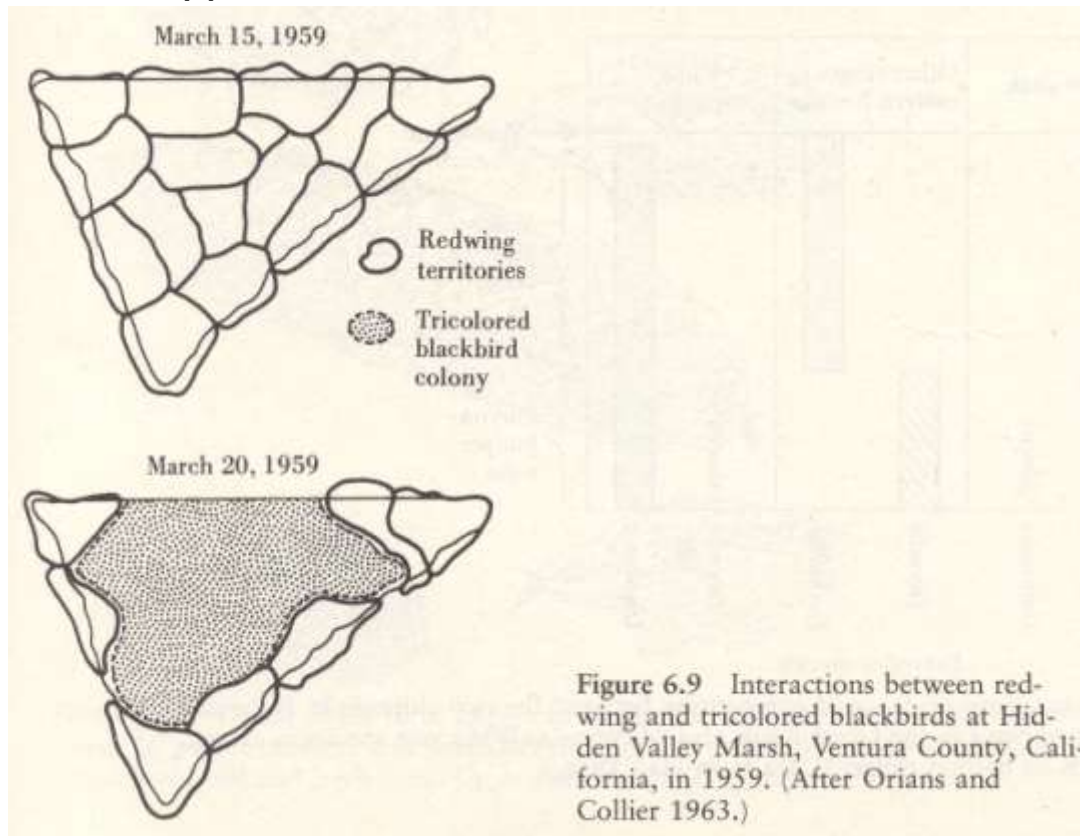
Burrowing rats distribution before discovering by European (grey area) and recently (black dots) – cause: fox (predatio) és rabbit (competition)



Interrelations with other organisms

Competition

Redwing territories (upper map) before the Tricolored blackbird arrival in spring and territories of these two species after arrival of Tricolored blackbird (lower map).



Interrelations with other organisms

Allelopathy

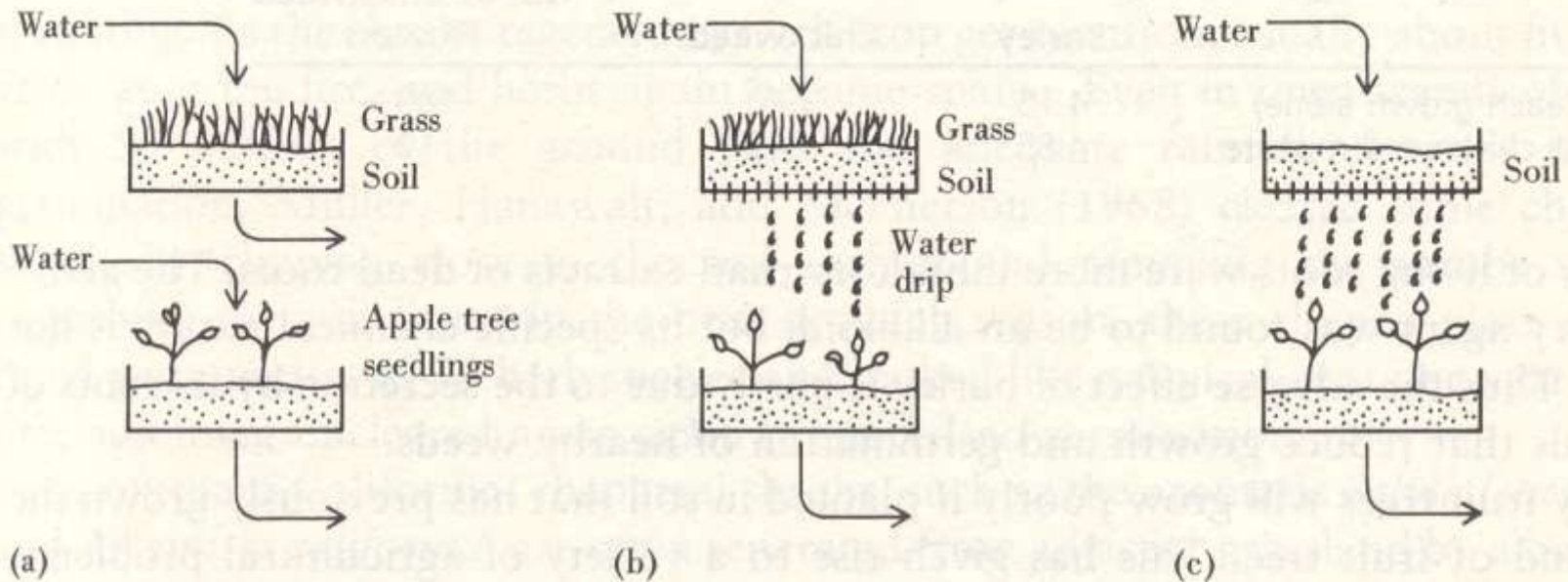


Figure 6.5 Experiments that demonstrated the detrimental effects of grass on apple tree seedlings. Grass and tree seedlings are grown in separate flats in a greenhouse. Water is provided either (a) independently to both grass and trees, (b) as a single source to the grass and soil, or (c) to the soil alone. Water drip provides moisture for the apple seedlings in (b) and (c). Apple tree seedlings do not grow properly when the water has passed through grass first (b).

Interrelations with other organisms

Parasitism

e.g. Mosquitoes and reindeer in the tundra

Mutualism

e.g. Fungies and Pine trees

e.g.

Ant species (*Pseudomyrmex triplarinus*) and a tree (*Triplaris americana*) in South America

What explains the occurrence of a species in a given place?

Area accessible

yes ← **Dispersal** → no



Habitat selection yes ← **Behaviour** → no



yes ← **Other species** → no

Predation

Competition

Parasitism

Mutualism

Physical and Chemical factors

Temperature

Water

Light

Oxygen

Soil structure

Salinity

Fire

pH

Currents

Soil nutrients

etc.

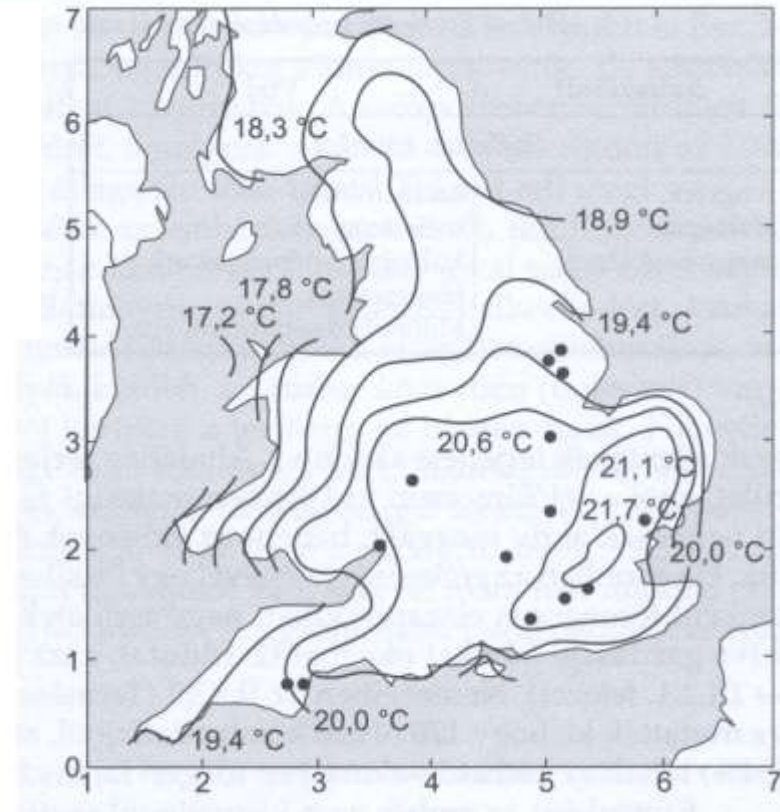
Etc.

Physical and Chemical factors

Tree species (*Tilia cordata*) distribution in UK
Lines- daily maximum temperature in August
Points – occurrence of the tree species

Effects:

- Survival
- Reproduction
- Development of young organisms
- Competition



Temperature

e.g. Mynah (*Sturnus cristatellus*) – not able to breed in (Vancouver, USA) because of the very low hatching rate of eggs

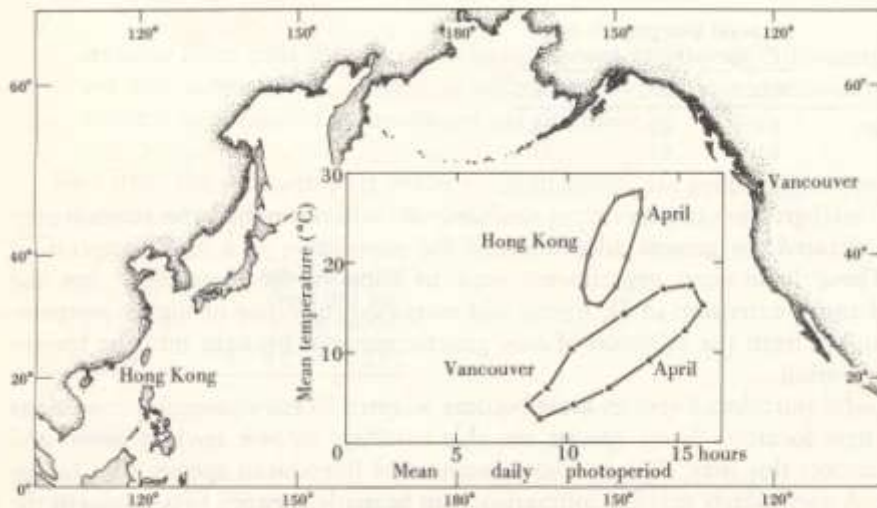


Figure 7.15 Comparison of native (Hong Kong) and introduced (Vancouver) home of the crested mynah (*Sturnus cristatellus*). The climatograms are constructed by connecting means (air temperature and photoperiod) for succeeding calendar months. Egg laying starts in April at both localities. (After Johnson 1971.)

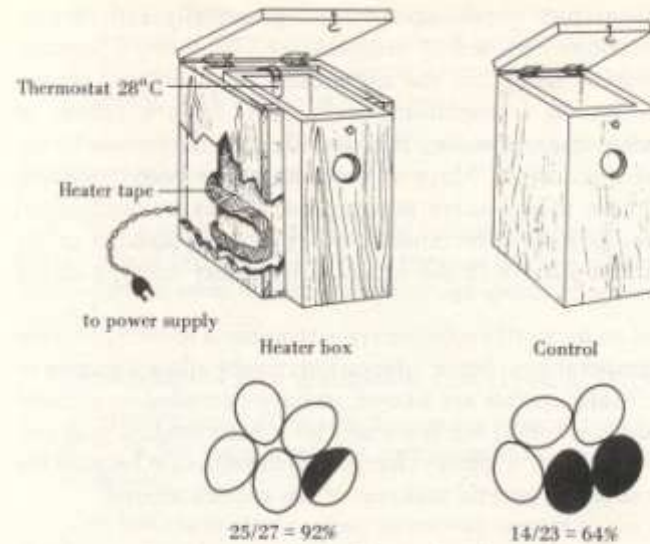
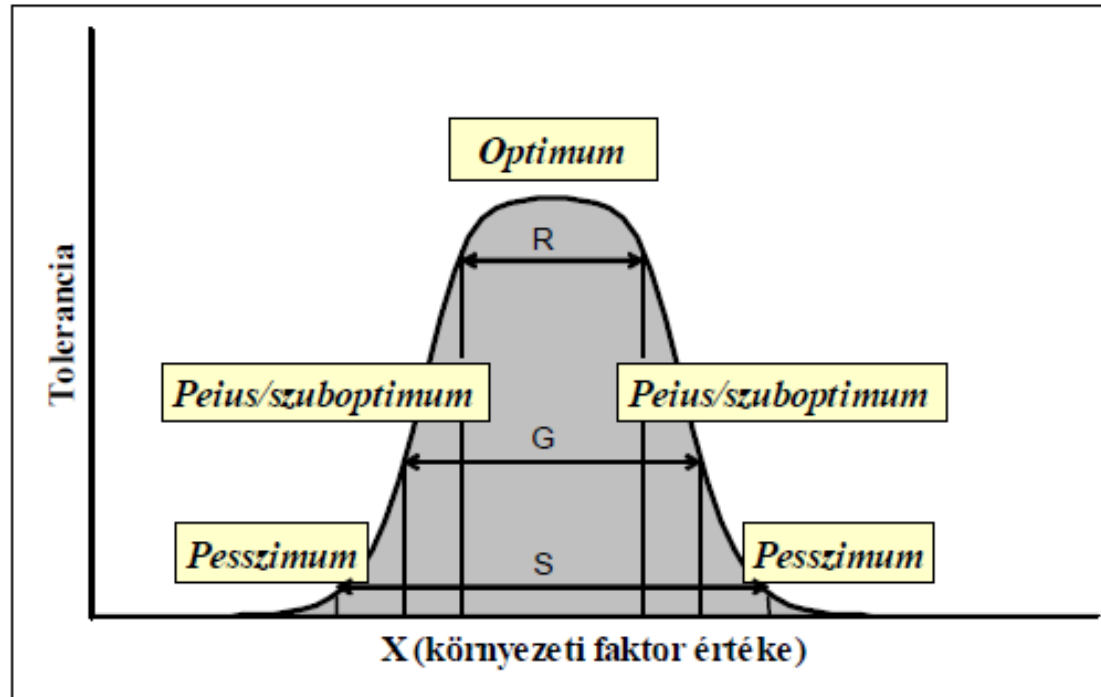


Figure 7.16 Experiment with altered nest microclimate in Vancouver; at five crested mynah nests, a heater was installed and nest temperature was maintained at Hong Kong levels (28°C). Hatching success at these nests is contrasted with the controls exposed to natural temperature fluctuations. (After Johnson 1971.)



Physical and Chemical factors



Tolerance curve and intervalls in relation to an X environmental factors

optimum (reproduction)

peiusz – suboptimum (only growing without reproduction)

pesszium (only surviving)

Physical and Chemical factors

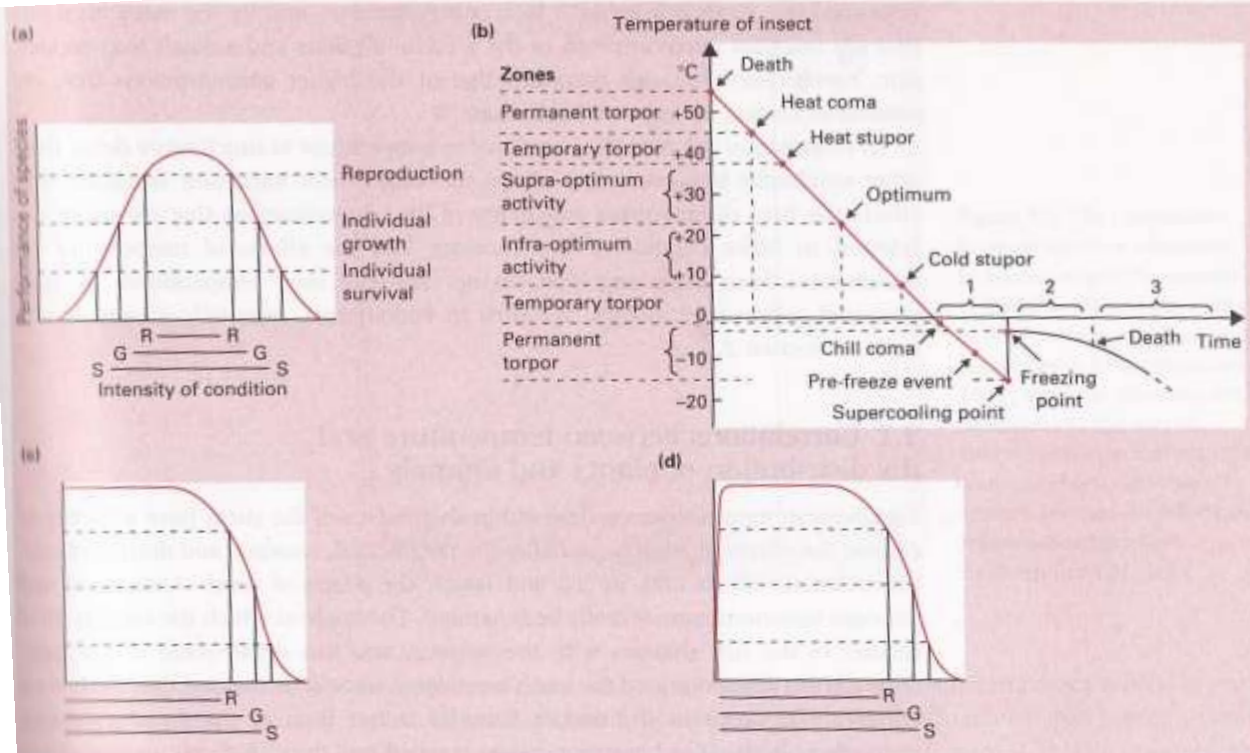
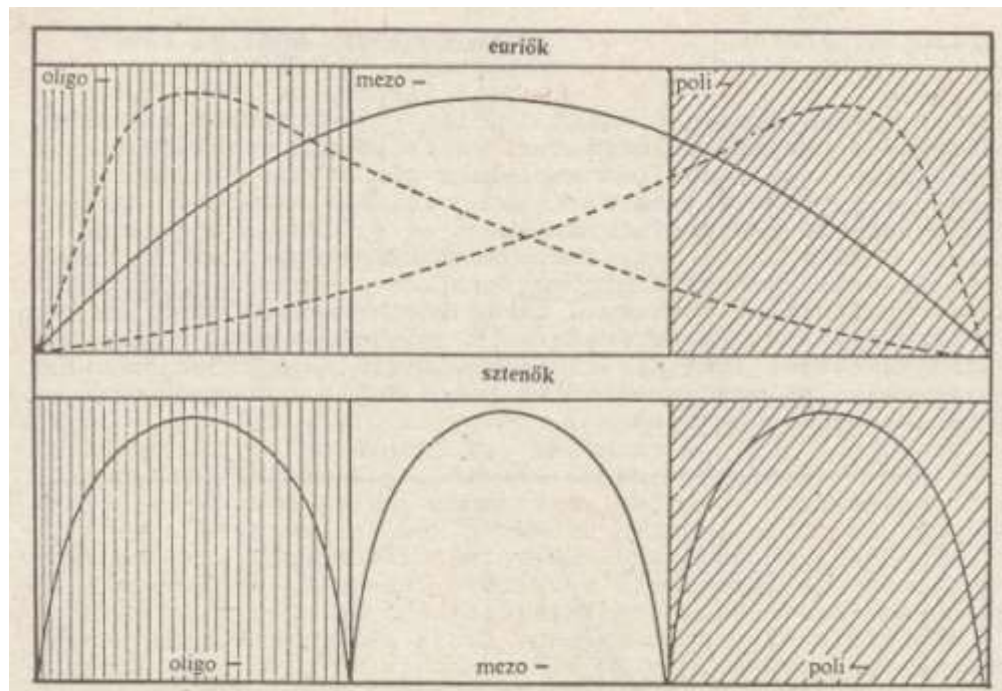


Figure 2.1 (a) A generalized graphical representation of the manner in which the activities of an organism may relate to the intensity of an environmental condition, such as temperature or pH. The narrow range over which reproduction can occur (R-R) usually dictates where continued existence of the species is possible (although the patterns of distribution of some species may be maintained by the repeated dispersal and recruitment of individuals into areas where they could not otherwise maintain themselves). (b) The thermobiology of an arthropod which does not tolerate freezing. Note that a symmetrical sequence of physiological states is recognized passing through stupor into temporary torpor and coma to permanent torpor and death as conditions become much hotter or cooler than the optimum. (After Vannier, 1987; Block, 1990.) (c) A generalized response curve of the form that relates the activities of an organism to the level, concentration or intensity of a condition (e.g. toxin, radioactive emission or pollutant which is harmful only at high levels). (d) As (c) but as the level, concentration or intensity of a condition is increased it changes from being an essential resource for growth at low levels to becoming damaging or lethal at higher concentrations (e.g. micronutrients such as copper and zinc).

Physical and Chemical factors

.growing

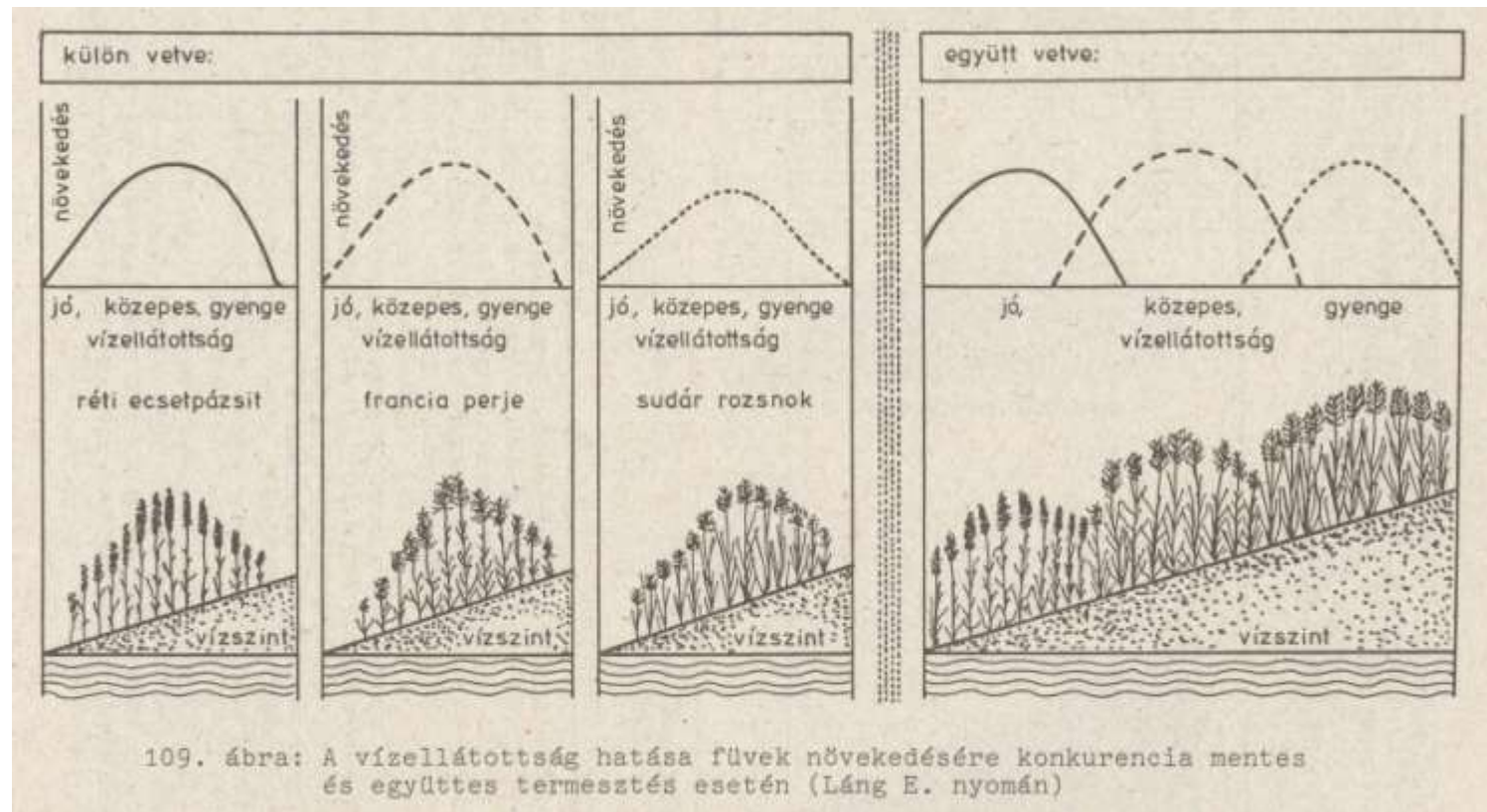


quantity of an environmental factor

Euriök - generalist

sztenők - specialist

Physical and Chemical factors



physiological – ecological optimum

Growth of three grass species

réti ecsetpázsit: Meadow Foxtail (*Alopecurus pratensis*),

francia perje: Perennial Ryegrass (*Lolium perenne*)

sudár roznok: Upright Brome (*Bromus erectus*)

in relation to water availability when it was seeding separately (left part) and mixed way (right part).

Climatic, edafic (soil), and hydrological factors

Light

Photoperiodism

- long-day plants, wheat
- short-day plants, rice
- spektrum

Light intensity

- heliophile, Maize
- sciophilous, leaf frogs
- scotophil, earthworm

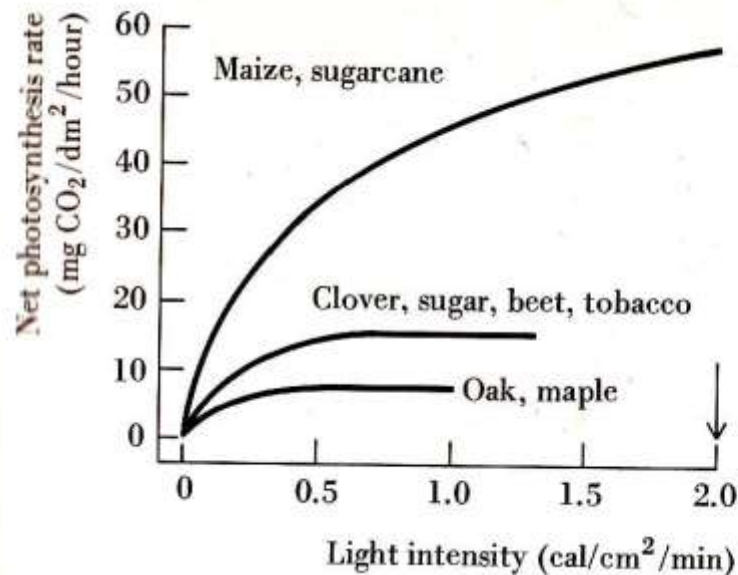


Figure 9.1 The effect of light intensity on the rate of photosynthesis in several species of plants. Photosynthesis was measured by CO₂ uptake at 30°C and 300 ppm CO₂ in air. The arrow on the light axis marks the approximate equivalent of full summer sunlight. (After Zelitch 1971.)

Water

- hydrophytes, lemna
- heliophytes, reed
- mezophytes, violet
- xerophytes, succulent
- halophytes, sea lavender



Soil

- Structure
- Nutrients

Salinity

pH

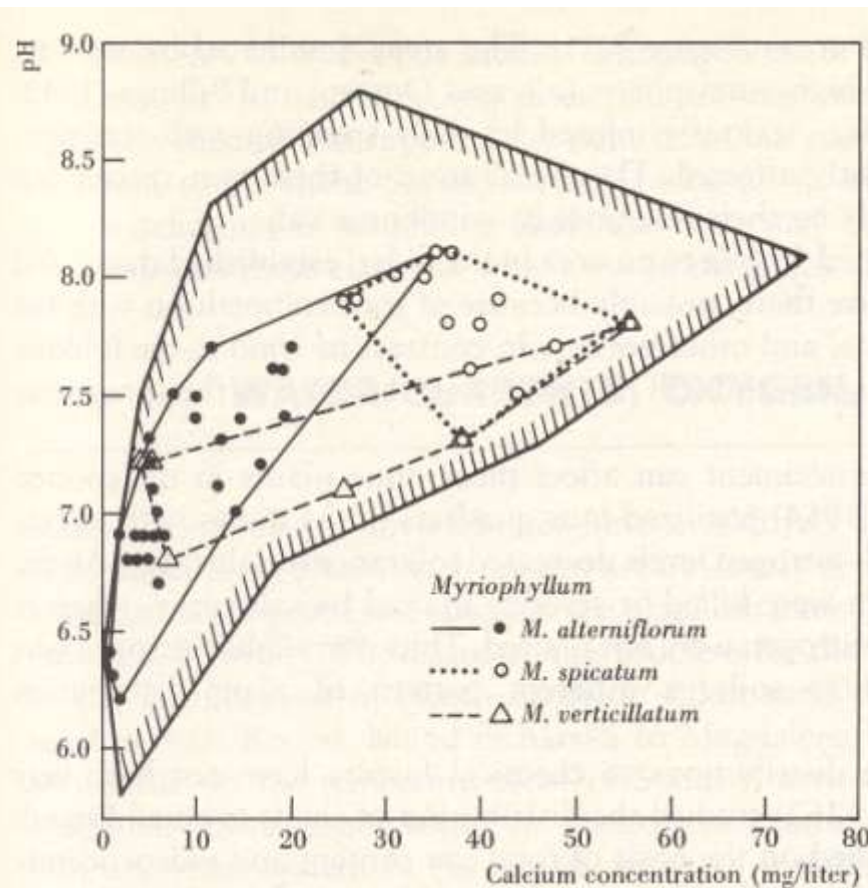
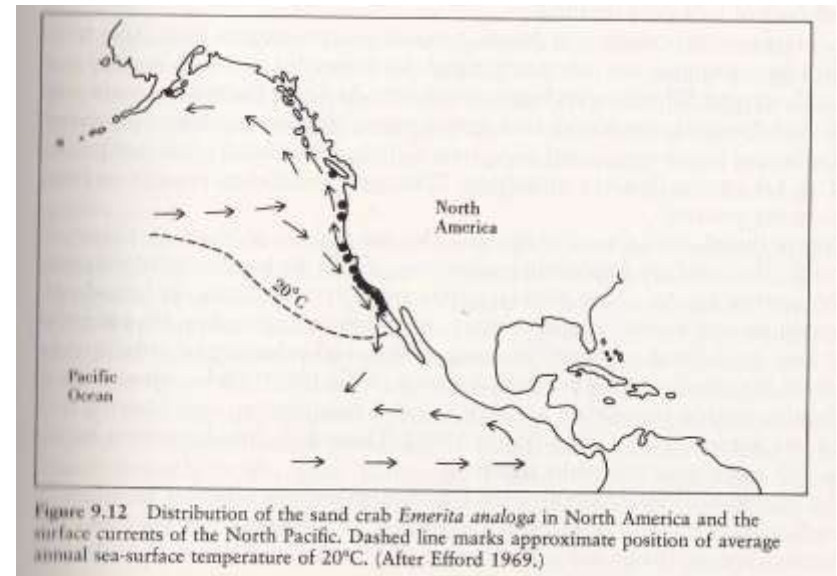


Figure 9.10 Occurrences of the three species of *Myriophyllum* in the lakes of central Sweden in relation to calcium concentration and pH. The shaded envelope encloses the points for all the lakes studied in the region. (After Hutchinson 1970.)

Water currents

Oxygen

- Its level vary hardly in freshwaters



Fire

- Occurrence is important for several Species/communities



What explains the occurrence of a species in a given place?

Area accessible

yes ← **Dispersal** → no



Habitat selection yes ← **Behaviour** → no



yes ← **Other species** → no

Predation

Competition

Parasitism

Mutualism

Physical and Chemical factors

Temperature

Water

Light

Oxygen

Soil structure

Salinity

Fire

pH

Currents

Soil nutrients

etc.

Etc.

Populations, Population parameters, Demographic Techniques

Population ecology

- Biological and statistical definitions

Biological: A population is the number of organisms of the same species that live in a particular geographic area at the same time, with the capability of interbreeding

Statistical: A group of organisms of the same species occupying a particular space at a particular time

- Abundance (N)

individuals, pairs, biomass (genet-clonal plants), colonies (eusocial insects)

- Density (D)

- Abundance/Area, Abundance/Volume

Estimation Abundance/Density

Absolute methods

- total counts (census)

Count all individuals of the population

(human, rare or very low density species)

Sampling methods

- estimation of density in sampling area

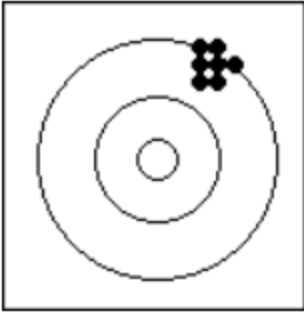
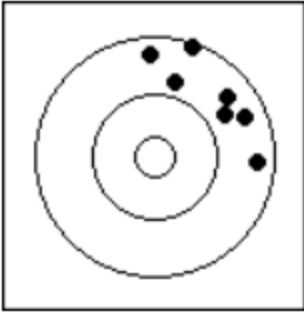
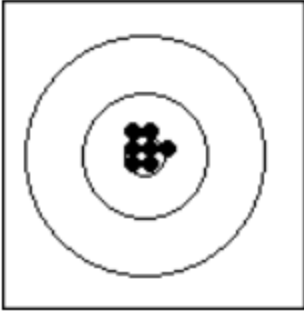
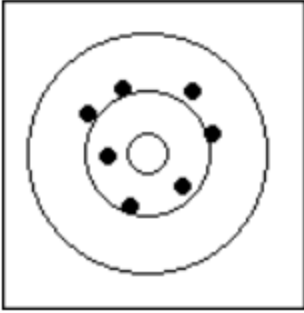
Count all individuals in the sampled areas (quadrats), estimate the density and estimate the abundance for the entire area of the population

Condition:

- Total counts in the samples area
- Known the size of the sampled area
- Sampled areas must be representative to the entire area of the population -> proper sampling strategy to minimize the bias and precision

Accuracy of an Estimation

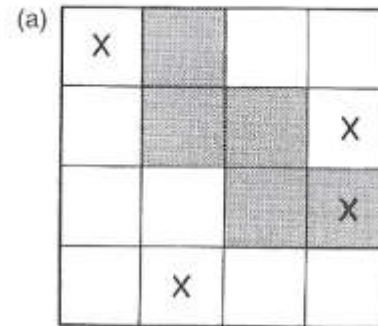
Accuracy, Precision, and Bias

	Precise	Imprecise
Biased		
Unbiased		

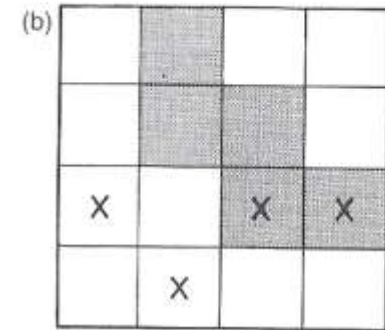
Sampling strategy

27

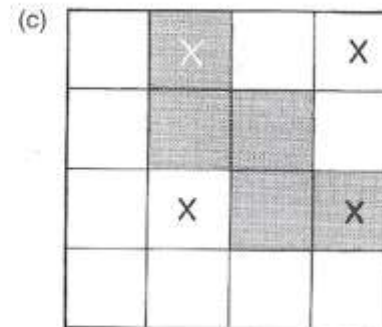
Random (a)



Stratified random (b)



Regular (c)



09.19.

Estimation Abundance/Density

Sampling methods

- Capture-recapture method

e.g. Lincoln index:

$$\frac{m_2}{n_2} = \frac{n_1}{N}$$

N: abundance of the population

n_1 : # of caught and marked individuals during the first capture, released back to the population

n_2 : # of caught and marked individuals during the second capture, released back to the population

m_2 : # of marked individuals among individuals caught in the second capture

N': estimated abundance of the population

$$N' = \frac{n_1 * n_2}{m_2}$$

Estimation Abundance/Density

Relative methods – Population indices

- # of trapped individuals
- # of fecal pellets
- Vocalisation frequency
- Pelt records
- # of artifacts
- Questionnaires
- Cover
- Feeding capacity
- Roadside counts



Hungarian Common Bird Monitoring scheme since 1999

Mindennapi Madaraink Monitoringja (MMM)

Started with the help of RSPB and EBCC

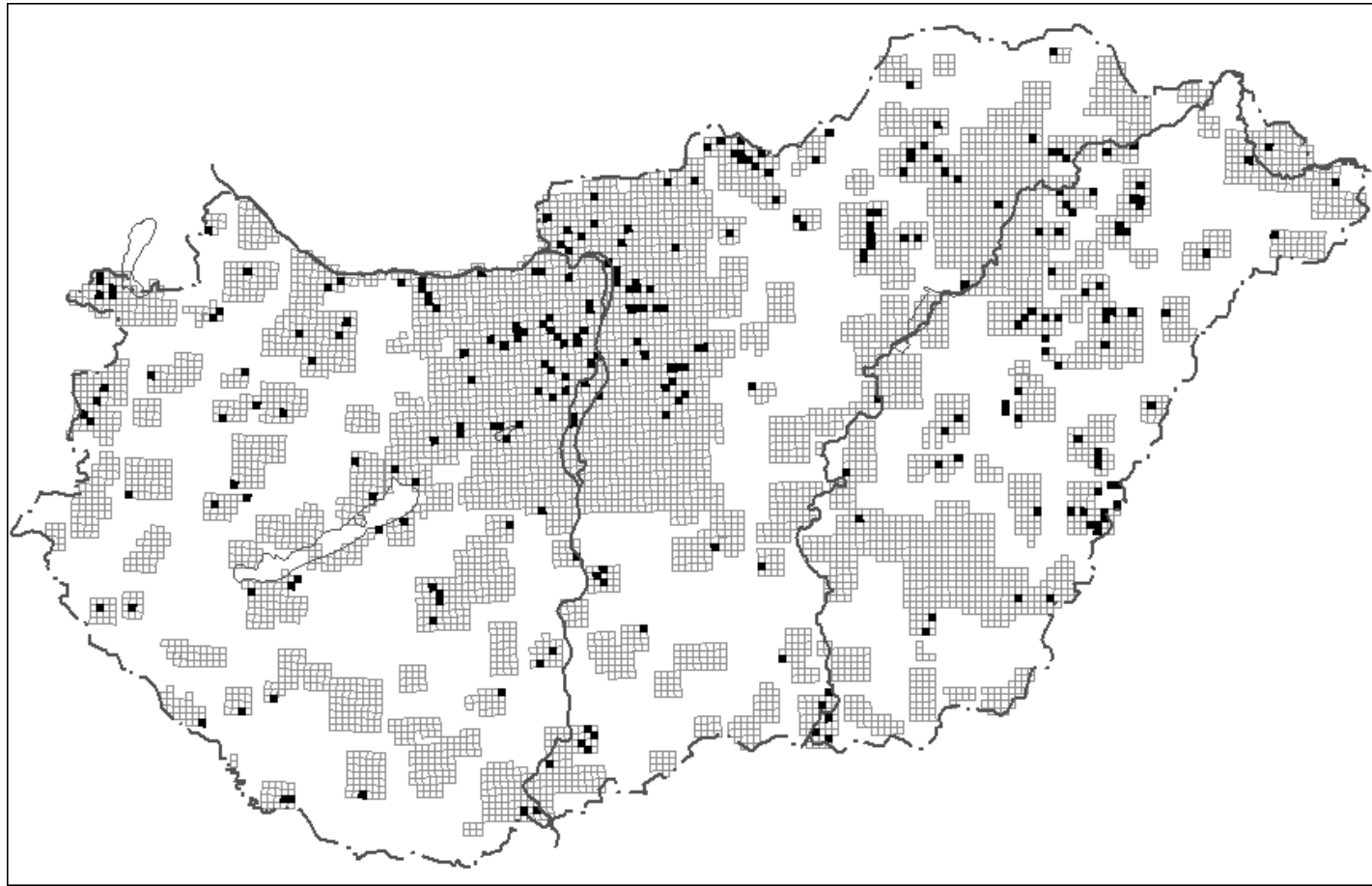
- Szép, T. and Gibbons, D. 2000. Monitoring of common breeding birds in Hungary using a randomised sampling design. The Ring 22: 45-55.

- <http://mmm.mme.hu>

Sampling design

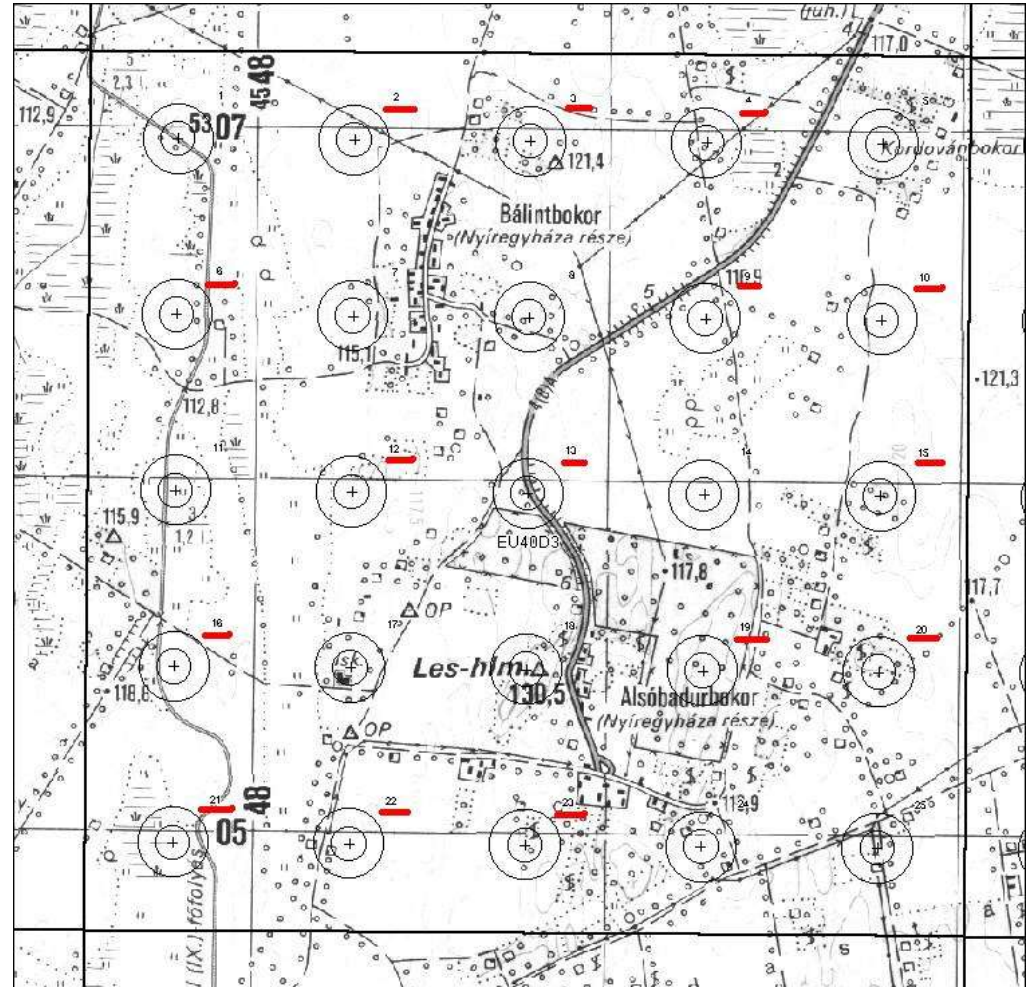
Semi-random selection of the surveyed 2.5*2.5km UTM squares

- Unit: 2.5*2.5 km UTM square
- randomly selected within the minimum 100 km² large area indicated by the observers



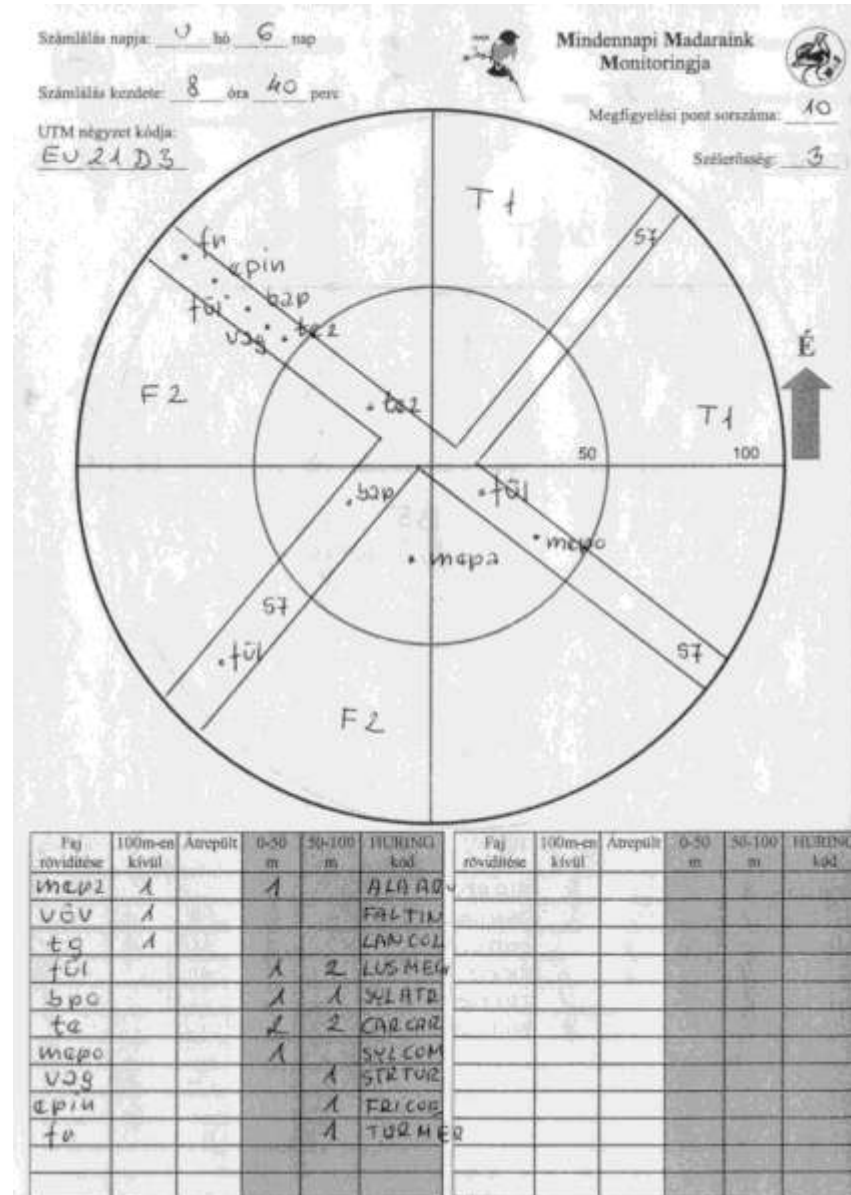
Sampling design

- Randomly selected 15 observation points within the selected 2.5*2.5 km UTM squares
- Map (coordinates) with exact position of the observation points provided



Standard Method

- 5 minutes point counts two times per breeding season (early, late) between 5-10 am
- Distance (0-50m, 51-100m, 101-200m, fly over), habitat and wind recorded



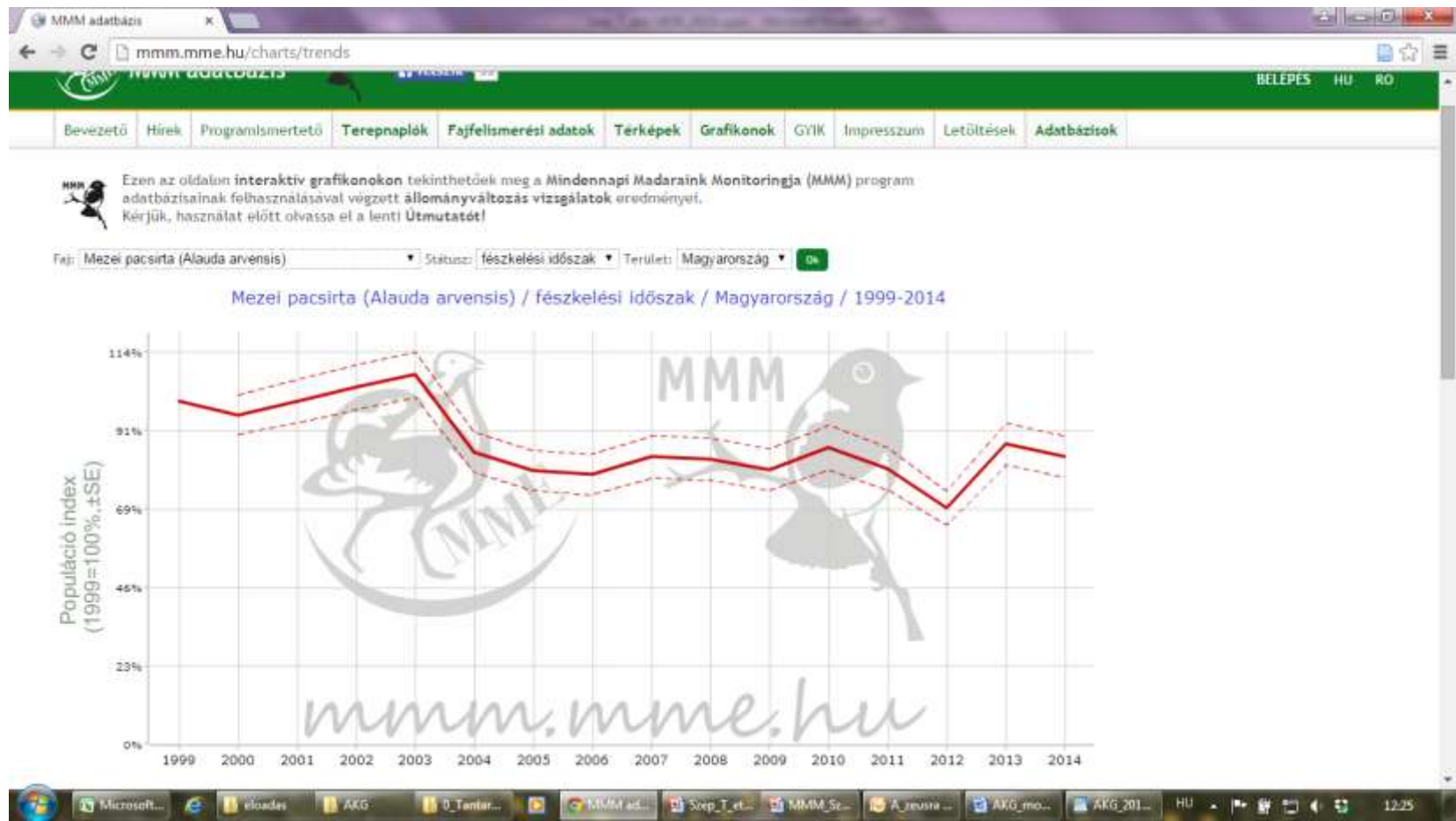
Identification skill of the observers

- Annual survey of the species identification skill of the observers for each species occurring in Hungary
 - „How can you identify the given species?”
 - only by view
 - only by sound
 - by view and sound
 - I'm uncertain to identify
 - Control the cause of the absence of the given species in the given squares – real absence or identification problems of the observers

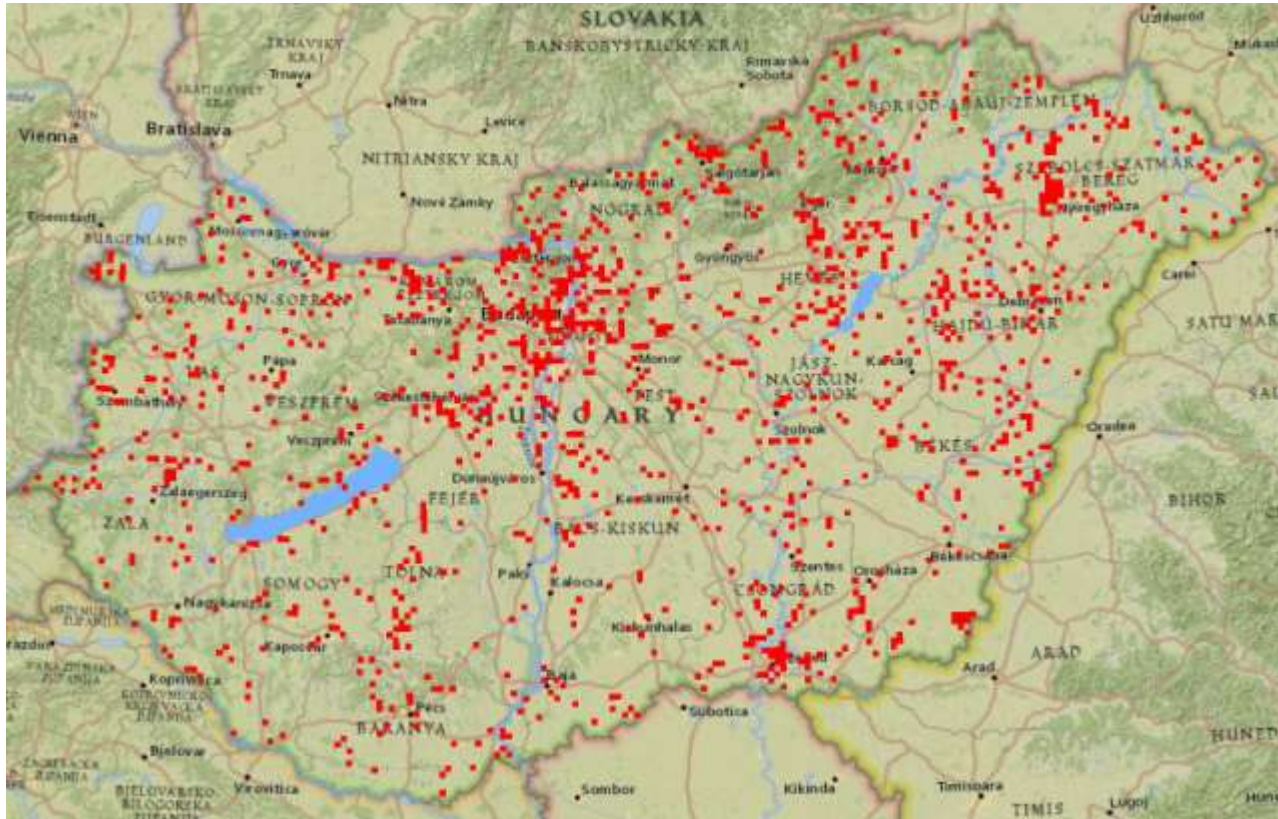
On-line database

<http://mmm.mme.hu>

- Input and verification of field data
- Maps, Results, Additional information for observers



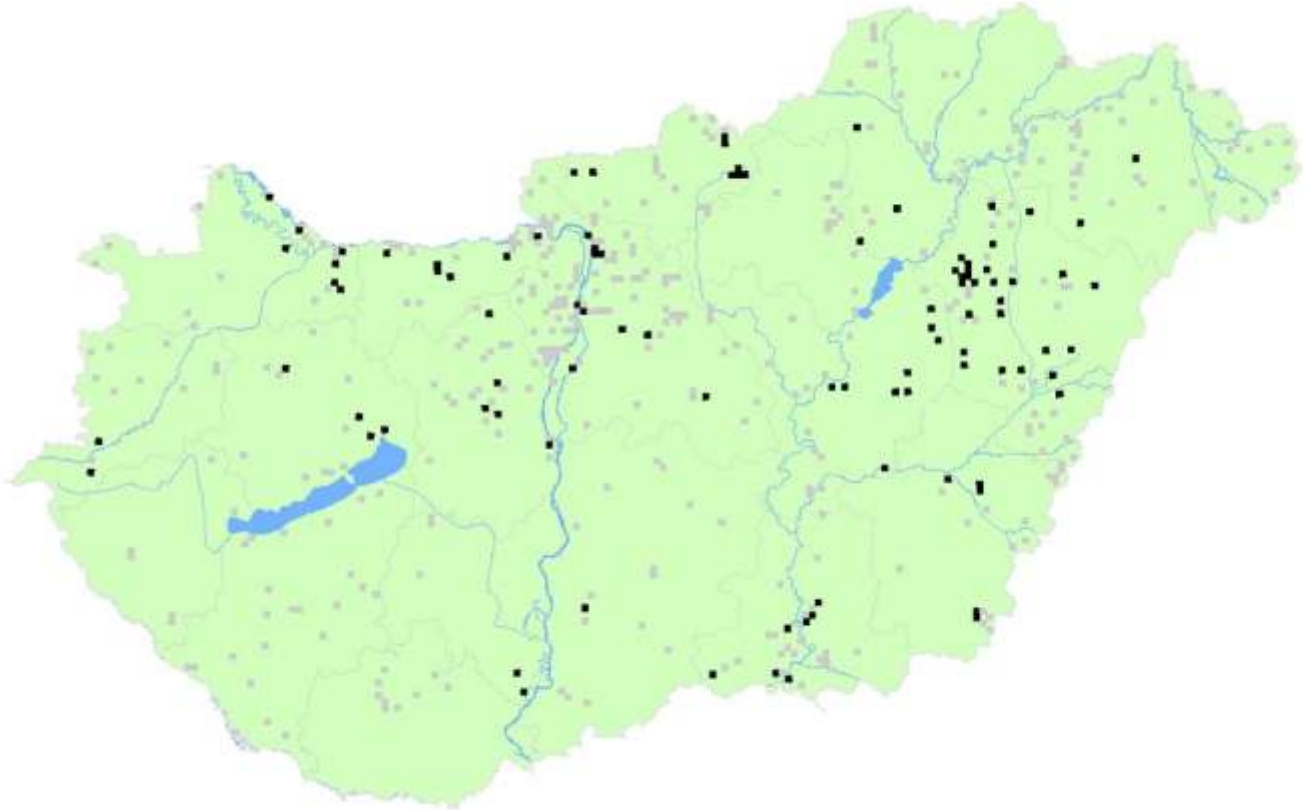
Surveyed UTM squares between 1999-2021 during the breeding season



Surveyed UTM squares

- More than 1000 squares surveyed minimum in two years
- More than 1000 participating observers
- One of the largest database on common birds in Central-Eastern Europe, based on random sampling design, 44,5 million records (UTM, point, species, date, number)
- 200-300 UTM surveyed annually (~2% of the country territory)

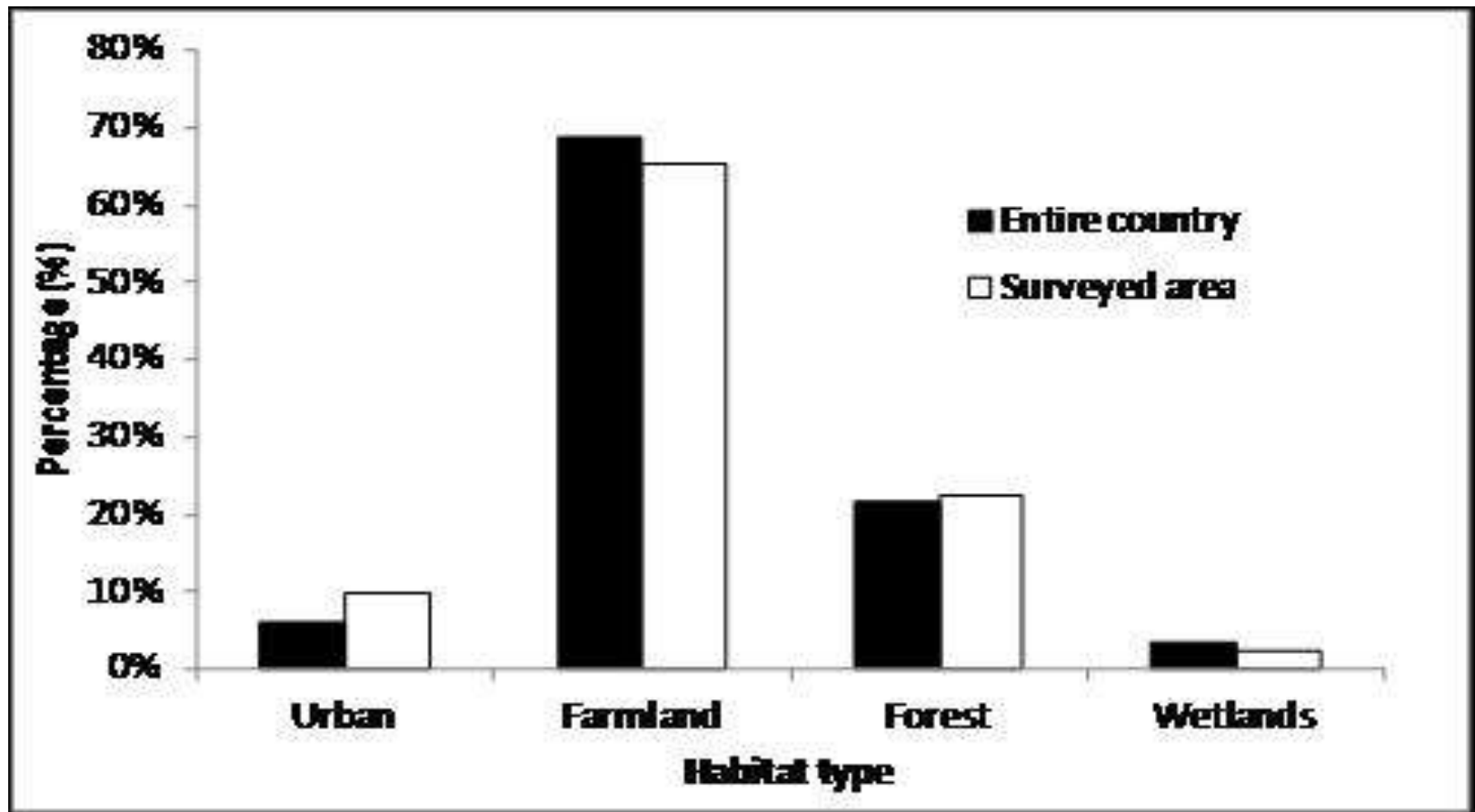
Surveyed UTM squares between 2000-2021 during the wintering season (January)



Colors of the UTM
squares indicate the
number of surveyed
years

- Standard survey during the wintering season for monitoring occurrence and abundance of species
- Use of similar field protocol as during the breeding season (but: only one visit in January, during daylight period)

Distribution of habitats in Hungary and in the area surveyed (Corine)



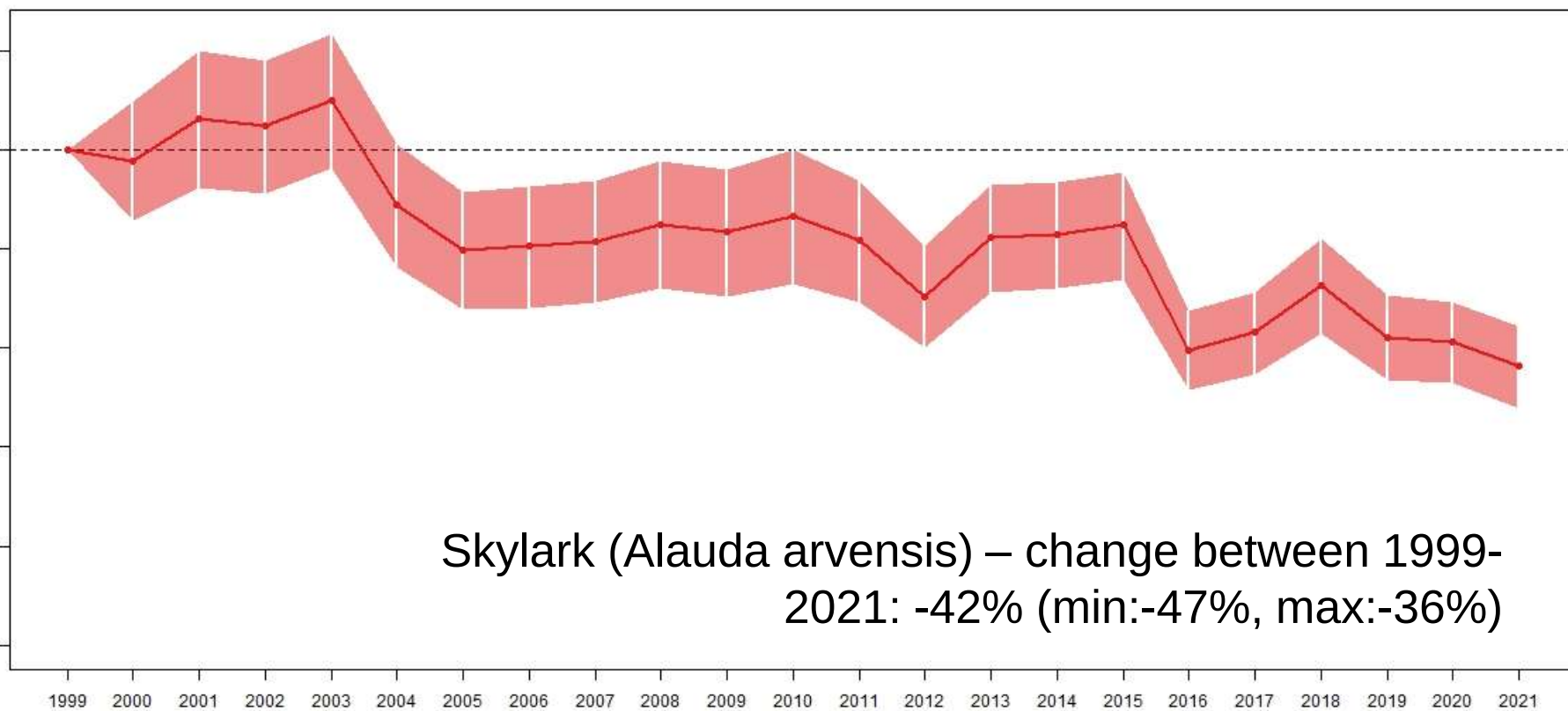
Size of the country: 93 000 km²



ALAARV állományindex, éves változás: -2.4% (-2.9%, -2%), csökkenő trend ($p < 0.01$)

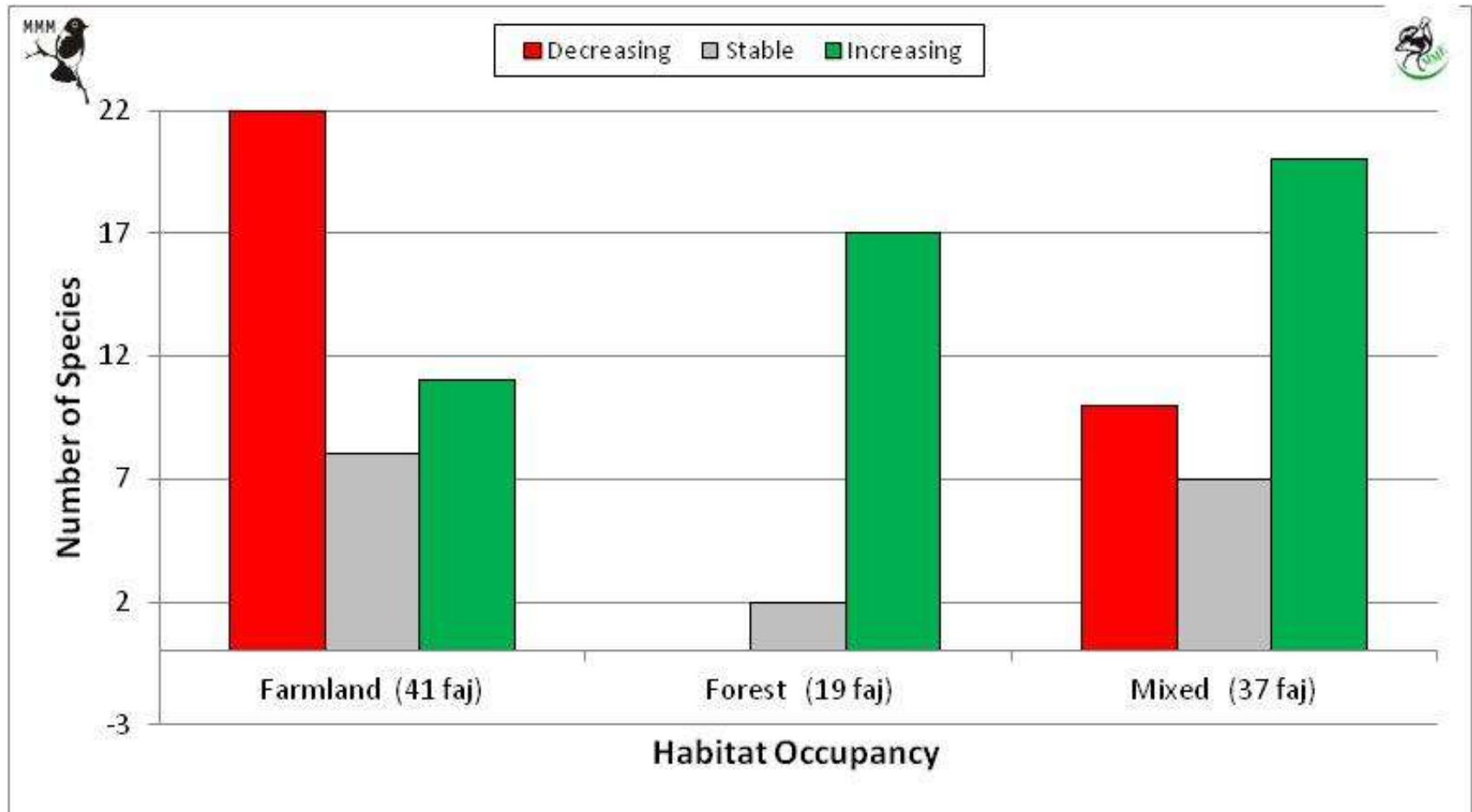
Population index (1999:100%)

Skylark (*Alauda arvensis*) – change between 1999-2021: -42% (min:-47%, max:-36%)



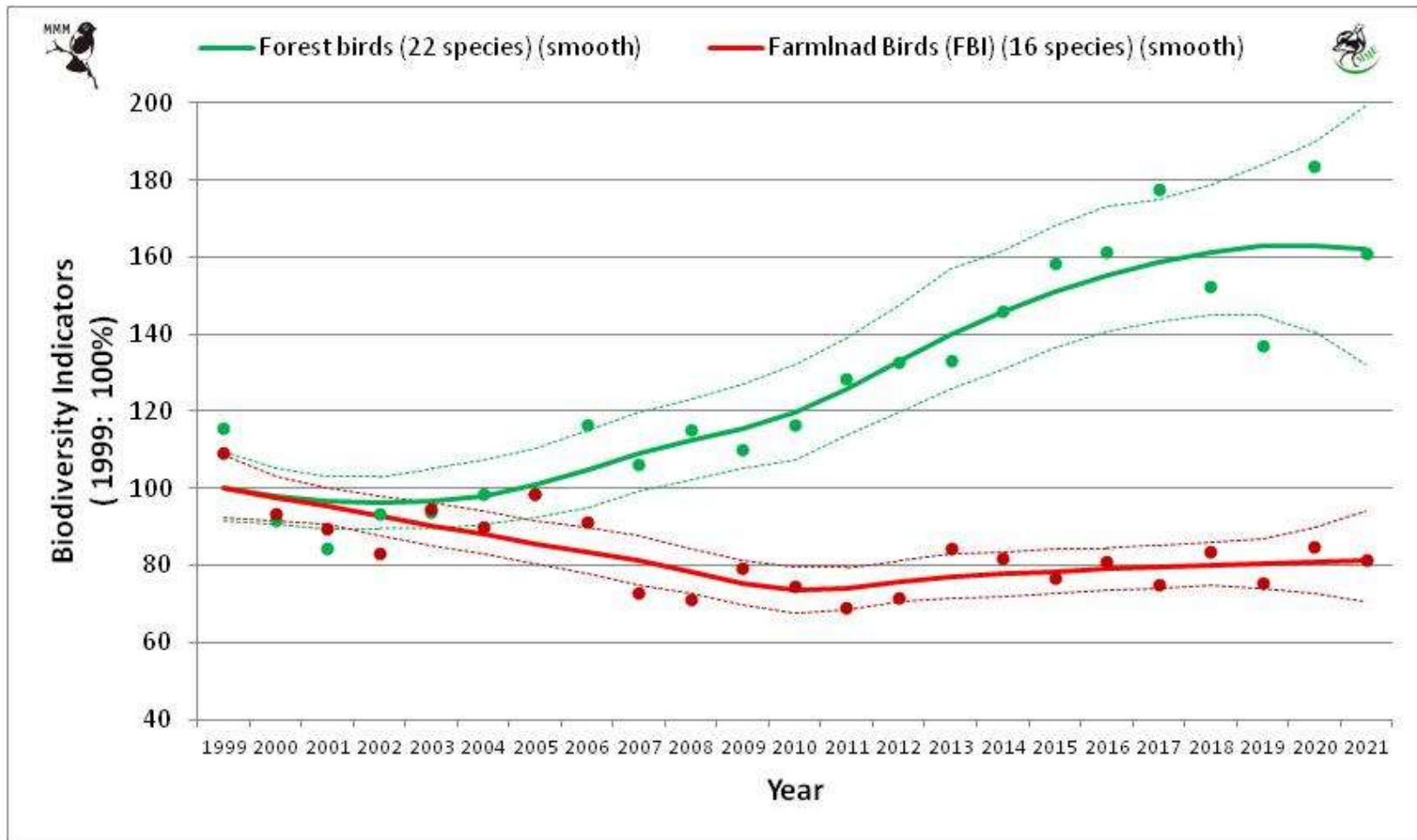
Year

Trends of 100 breeding species were identified by TRIM between 1999-2021, habitats



54% of farmland bird species has significant declining trend during 1999-2021

Recent trends of Bird Indicators in Hungary, MMM habitat



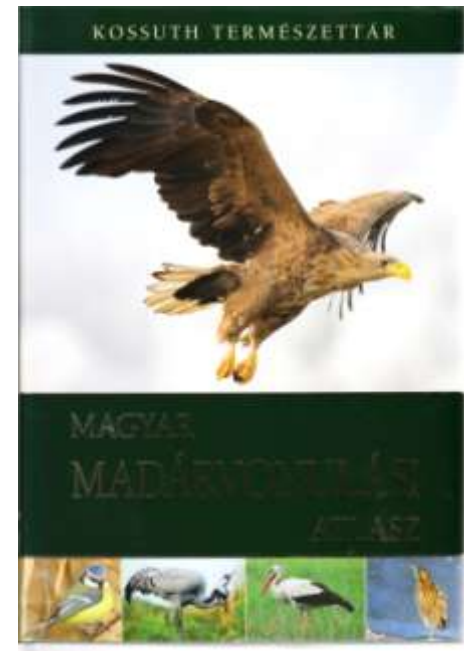
Farmland biodiversity (FBI) show a marked decline between 1999-2021
(slope: -0.9% (SE=0.3%, P<0.01))

There is an opposite trend for the forest (slope=3.1%, SE=0.4, P<0.01)

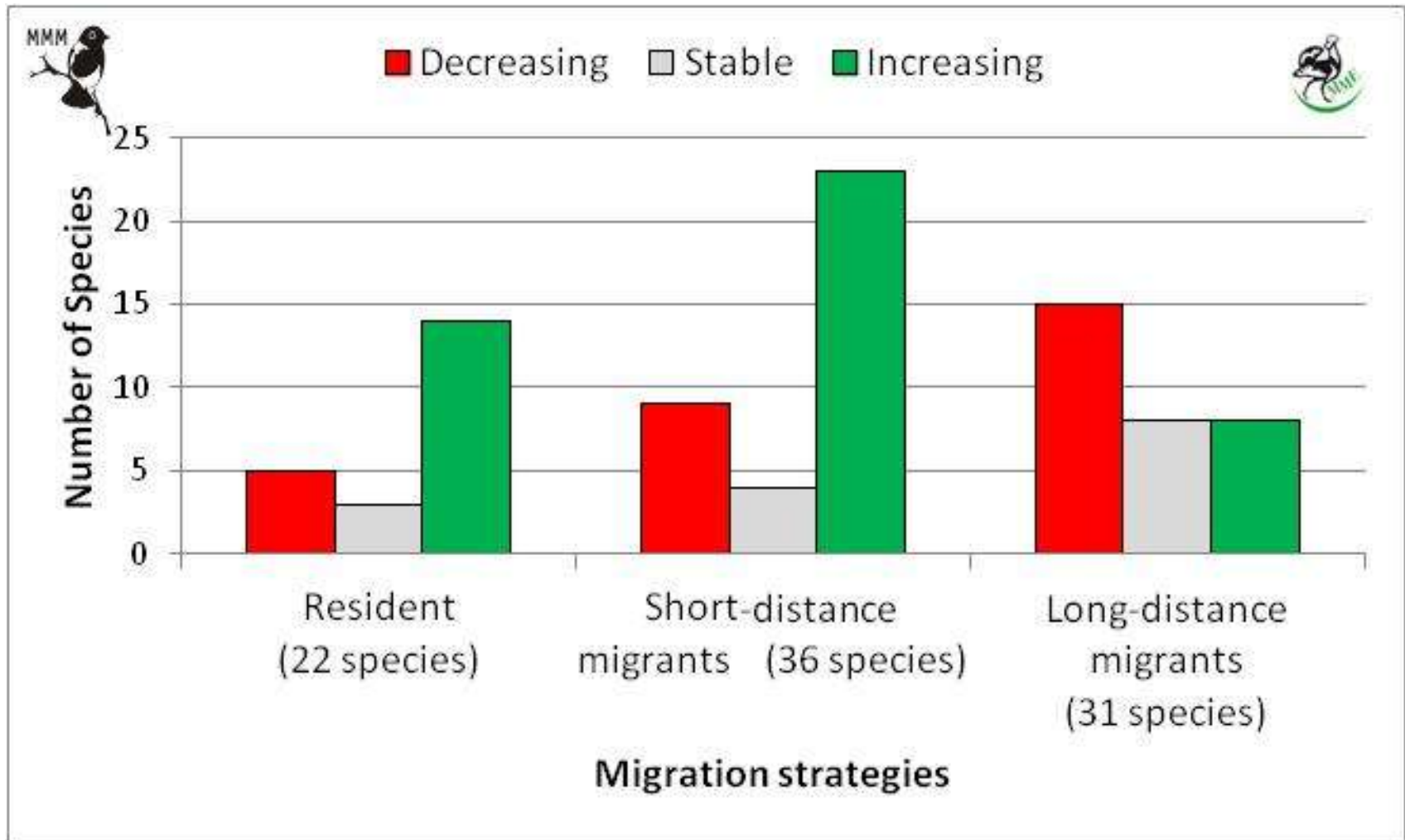
Classification species on migration strategy

Breeding species in Hungary was classified on the base of recent Hungarian Bird Migration Atlas (Csörgő et al. 2009)

- Resident – spend entire year in the breeding area
- Partial and/or short-distance migrants – migrate only until the Mediterranean region
- Long-distance migrants – migrate over the Sahara

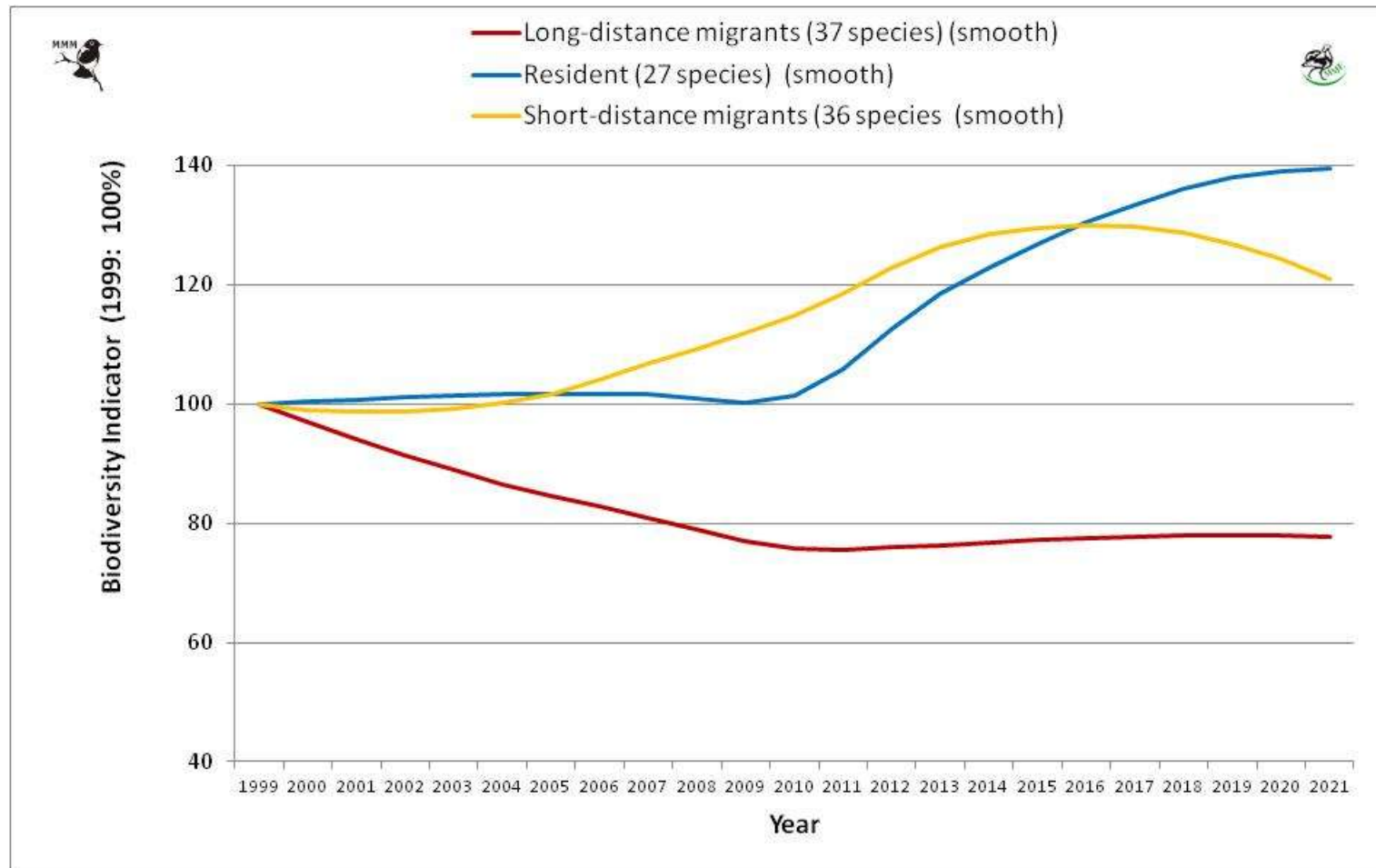


Trends of 100 breeding species were identified by TRIM between 1999-2021



48% of long-distance migrants bird species has significant declining trends, while other two groups has increasing trends during 1999-2021

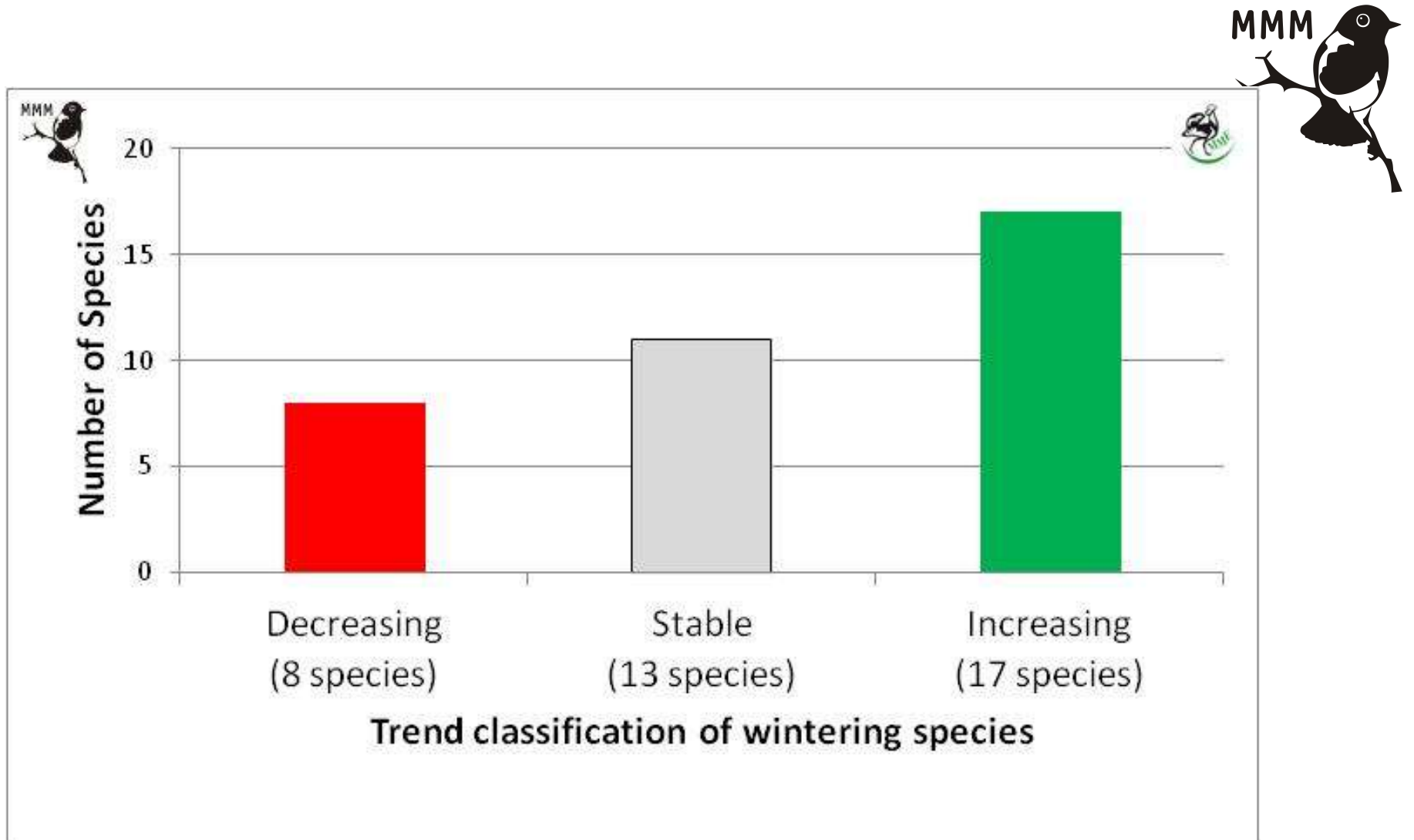
Recent trends of Bird Indicators in Hungary, migration strategy



Long-distance migrant species show decline between 1999-2021 (slope= -1.0%, (SE=0.3%, $P<0.01$))

In contrast, short-distance migrants (slope=1.5%, SE=0.3%, $P<0.05$) and resident (slope=1.8%, SE=0.4%, $P<0.01$) has increasing trends,

Recent trends of wintering common species in Hungary



44% of common wintering species in Hungary has significant increasing wintering population size

Recent tendencies in the biodiversity, based on common birds in Hungary

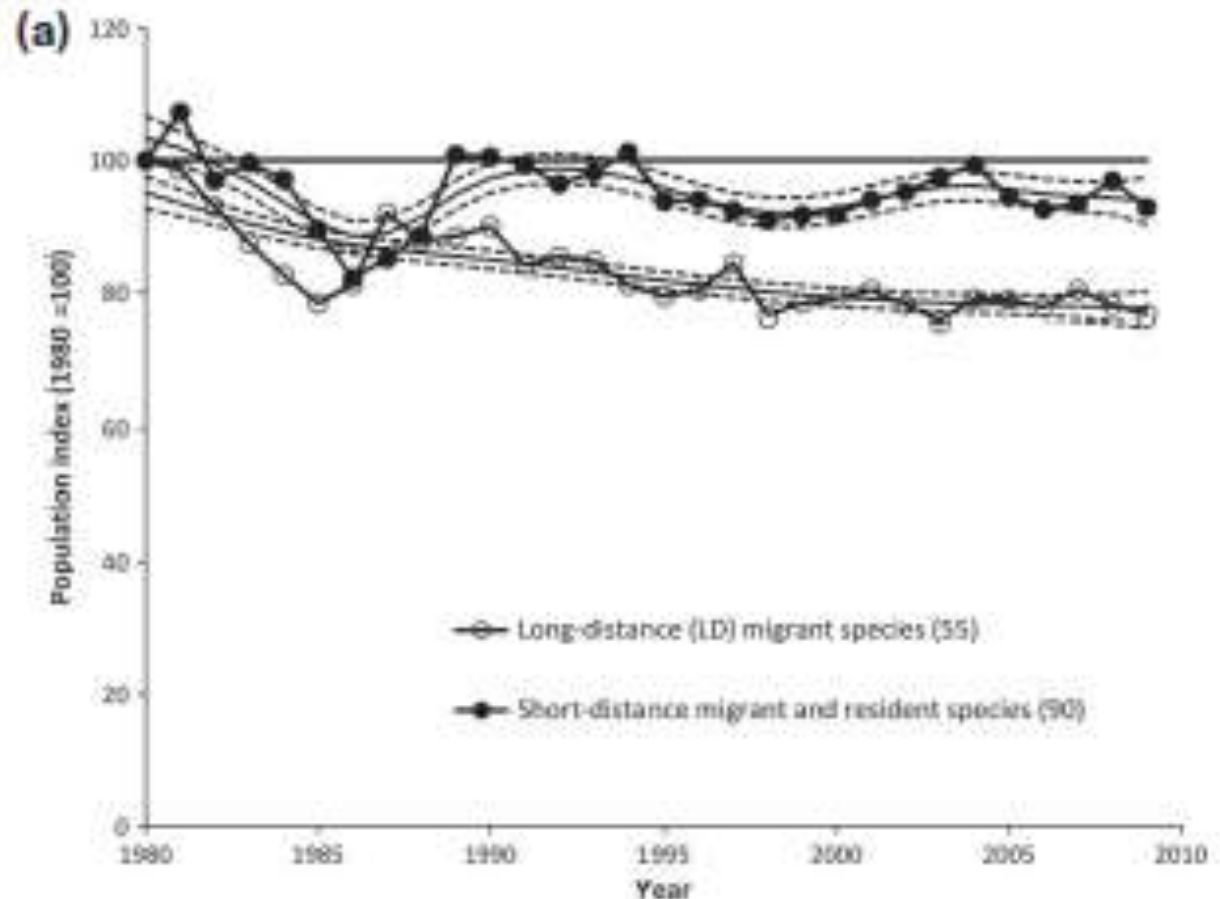


- Farmland biodiversity show marked decline since EU CAP has implemented in Hungary!
- Contrasting population trends of long distance migrants versus resident and partially/short migrants since start of the monitoring indicate climate related processes (Stephens et al. 2016, Science)
- Increasing trends of wintering populations indicate climate related processes as well (warmer winter, lower mortality)
- Behind the increasing trends of forest birds, climate change could have important influence because dominant part of this species resident and/or partially or short distance migrants

Long distance migrants in Europe

There is growing evidence that long distance (Afro-Palaeartic, (A-P)) migrants are in decline throughout Europe, with declines often being more pronounced than those of either short-distance migrants or sedentary (Sanderson et al. 2006, Vickery et al. 2014)

These declines are of growing conservation concern in both scientific and political arenas



Study of Bird Migration, long-term study of Sand Martin in Hungary



Tibor Szép

Environmental Institute, University of Nyíregyháza &
MME/BirdLife Hungary



Why Sand Martin?

Weight 12-13 g

Socially monogamous

Insectivorous



Wintering areas, south from the Sahara

Long-distance migratory species

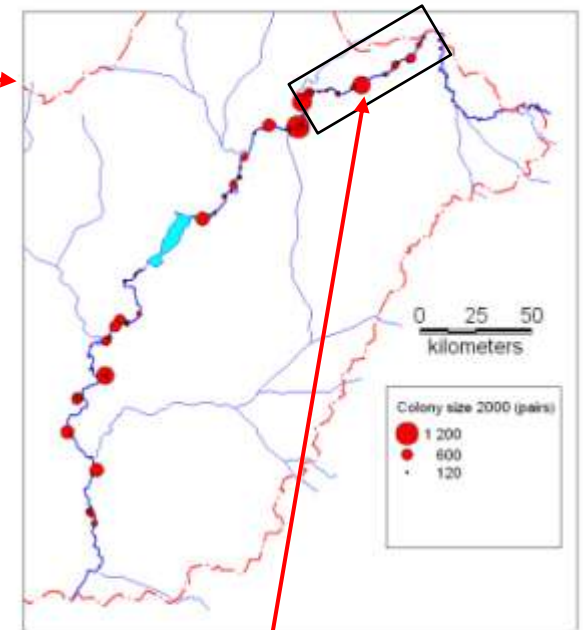
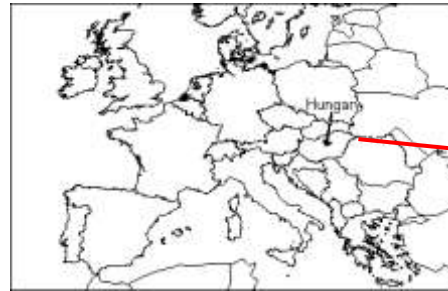
Bre(e)d in large colonies in Hungary in natural habitat



Easy to catch in large numbers without adverse effect – usage of capture-recapture methods

Easy to survey breeding habitats and populations

Start of integrated monitoring of Sand Martin along Tisza river, Eastern Hungary, 1986-1994



- Annual survey of **breeding habitat**, perpendicular walls
breeding colonies along the 70km long section of the river
- **Ringling adult and fledged juveniles** at the largest colony at Tiszatelek colony during the fledging period (June-July)
~ 1000-2000 ind./year









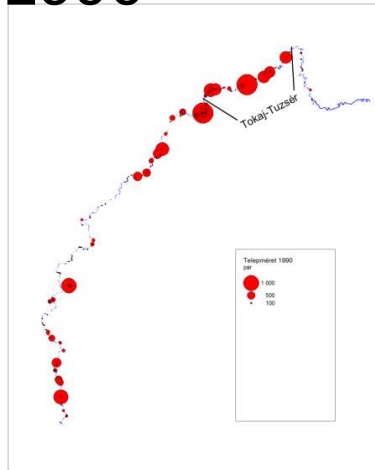


Opportunity for censusing breeding habitats, colonies and its sizes along the river

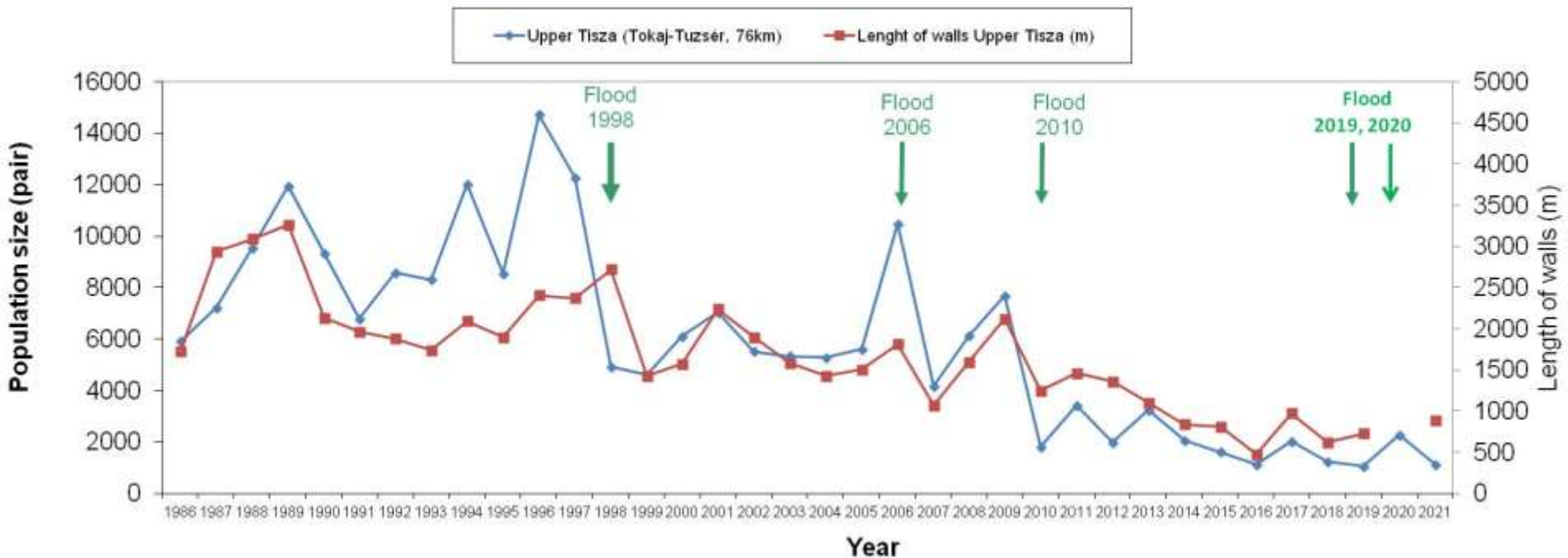
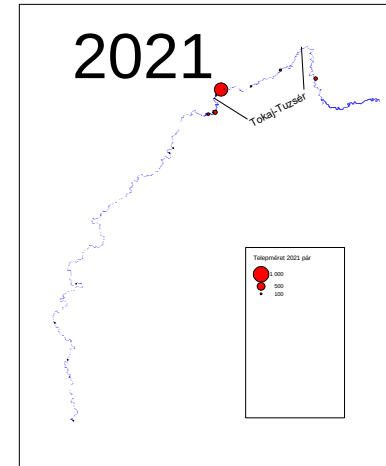
Population along the Hungarian section of river Tisza (600 km)

Strong decline, in 2021 only 6% of the population of 1990 remained

1990

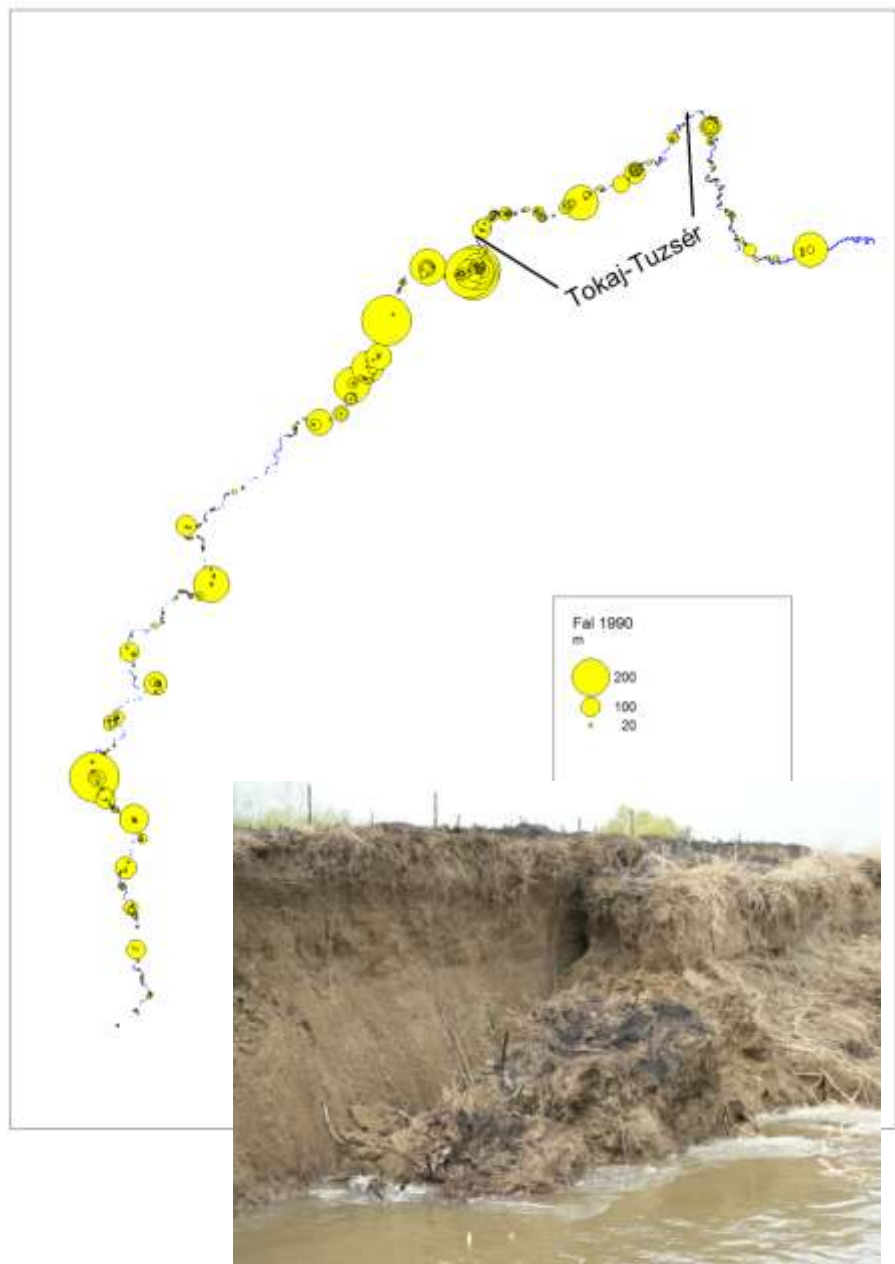


2021

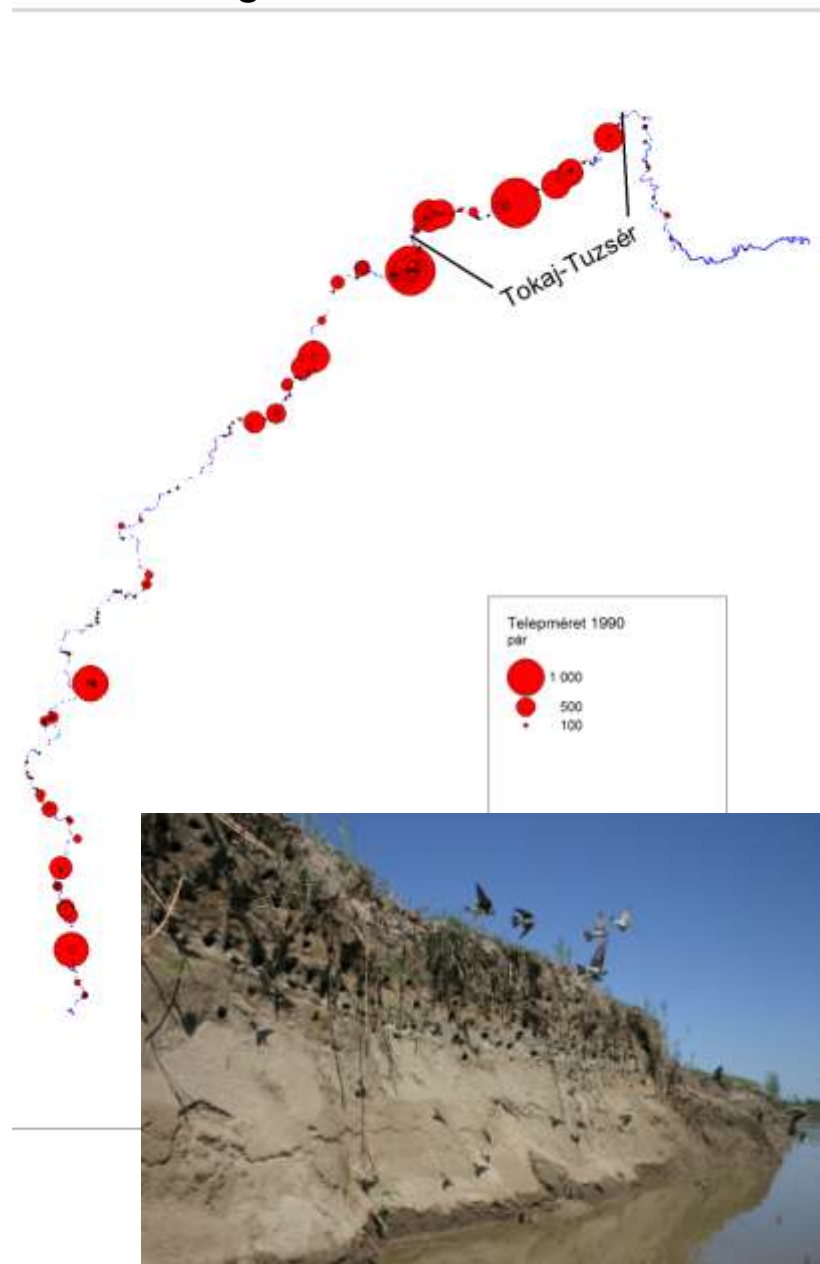


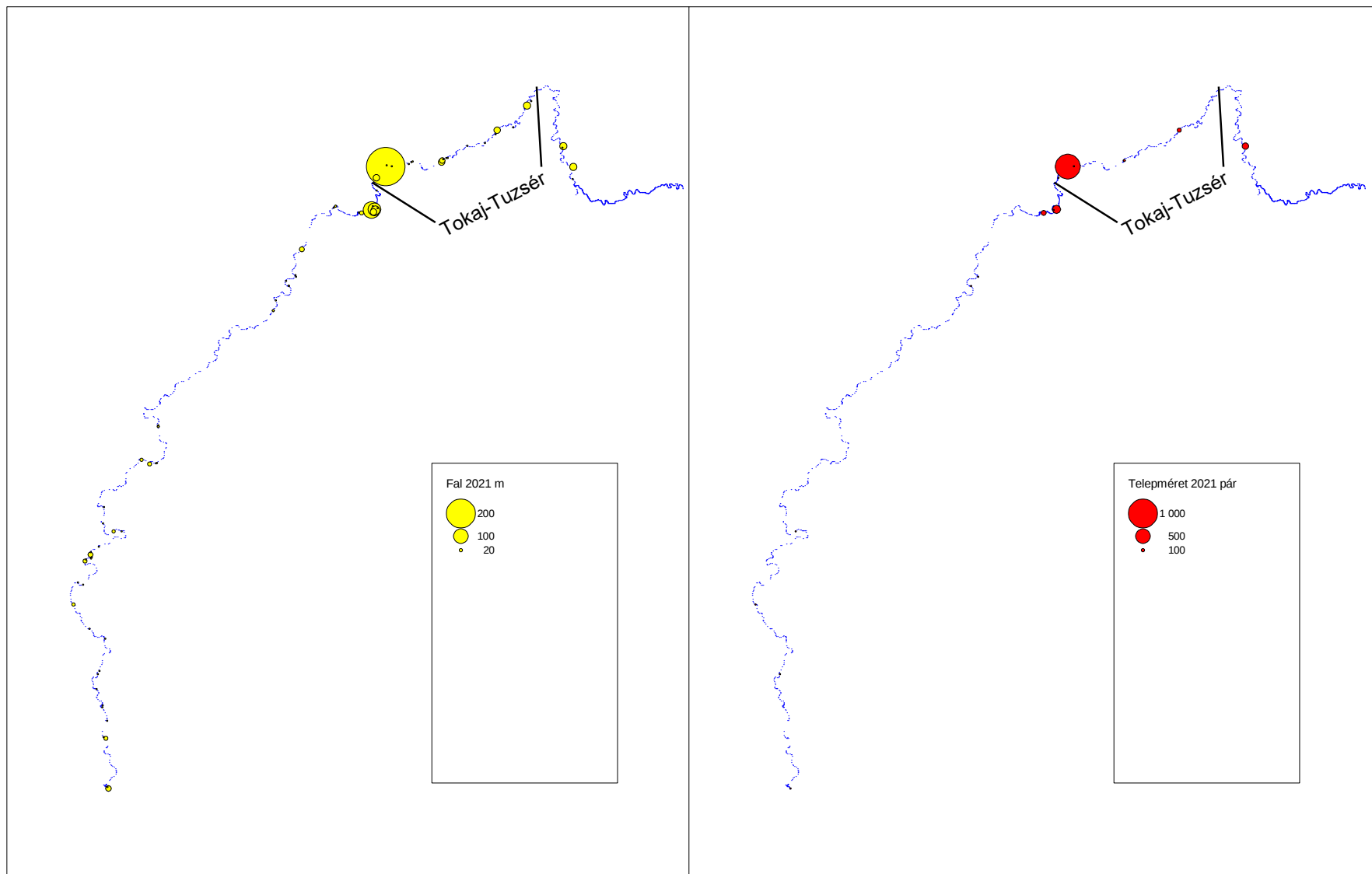
1990

Potential breeding walls and its sizes

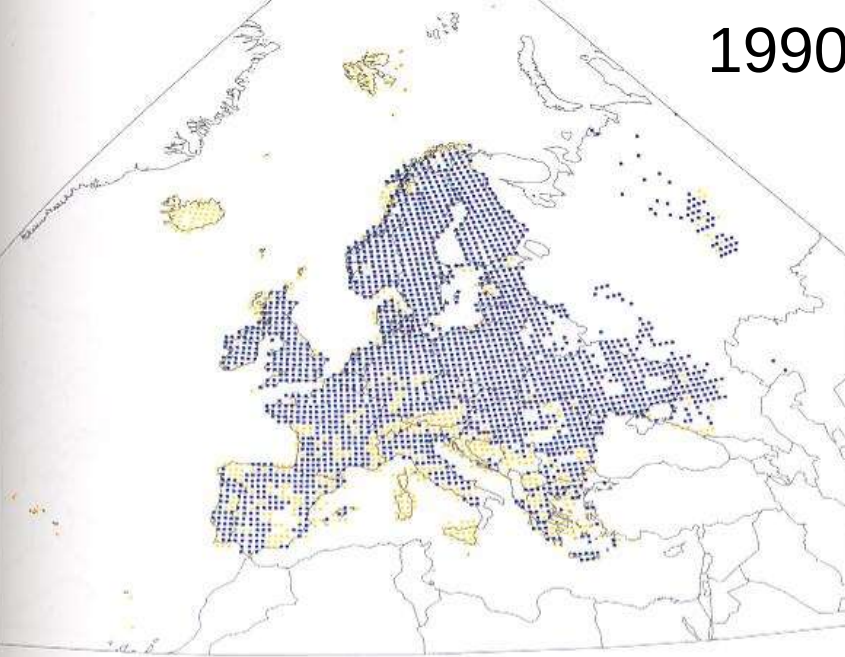


Breeding colonies and its sizes





1990

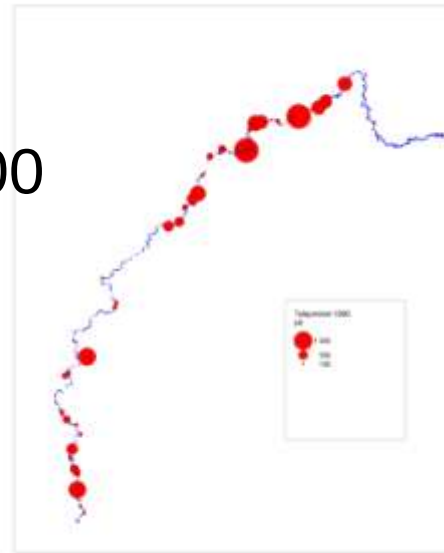


Present recorded distribution

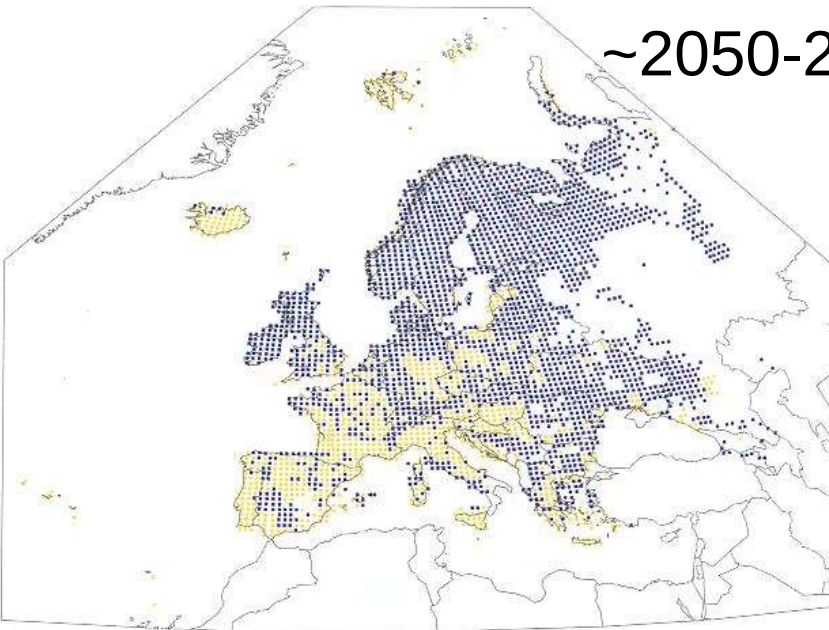
Marked change is predicted
within Hungary for Sand
Martin - mainly in the
southern part

Huntley et al. 2007. A Climatic Atlas
of European Breeding Birds.

1990

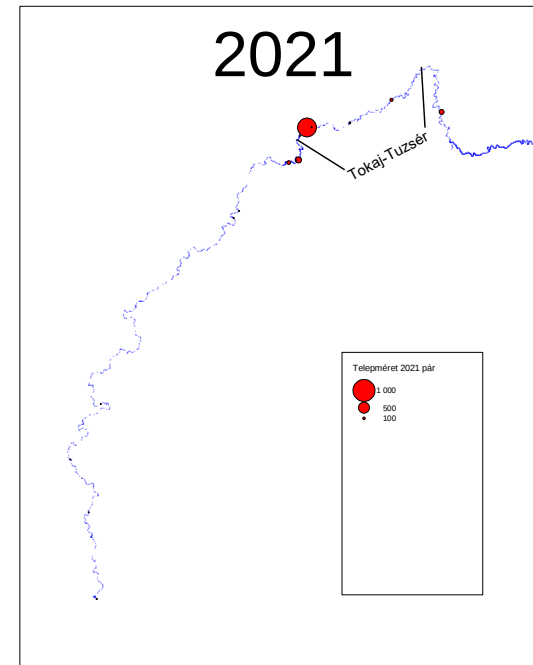


~2050-2100



Simulated potential late 21st century distribution ($R = 0.81$; $O = 0.73$)

2021





Long-distance migrants – birds of several worlds

- 4 months breeding (May.-Aug.)
- 0.5 months migration in autumn (Aug.-Sept.) 4-6 thousands km
- 7 months wintering (Oct.-April.)
- 0.5 months spring migrations (Apr.-May) 4-8 thousands km



Why the Sand Martin population size is decreasing ?

- Higher mortality during migration and/or wintering ?
- Lower reproduction in the breeding area?
- Higher emigration toward North?

Survival rate – most direct proxy to detect influence of migration/wintering event

Immigration from other breeding population

+

+

**Size of
Breeding population**

-

Mortality/Survival
Death between
breeding seasons

-

Emigration to other breeding population

Reproduction

Development of integrated monitoring of Sand Martin 1994-

Annual survey of the ~600 km long Hungarian section of the river, since 1990

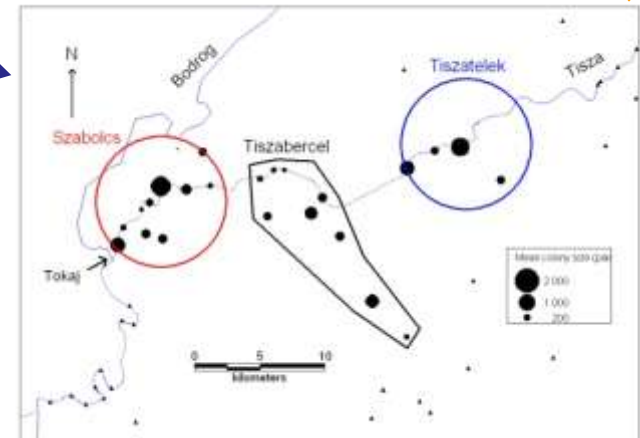
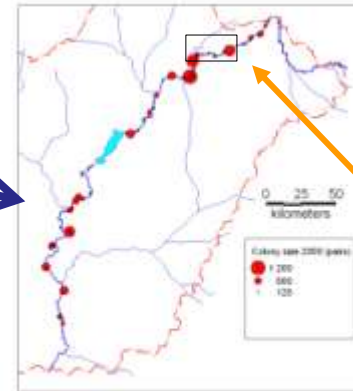
Regular ringing of all riverside and sand pit colonies in an standard studied area, along a 40km section of the river (Tokaj-Tiszatelek), since 1994

~2000-6000 ringed ind./year

~260-1300 recaptures/year
ringed during former years

Regular survey of breeding success at randomly selected section(s) of colonies in the studied area using videoendoscope, since 1995

(~800-2000 burrows/year)





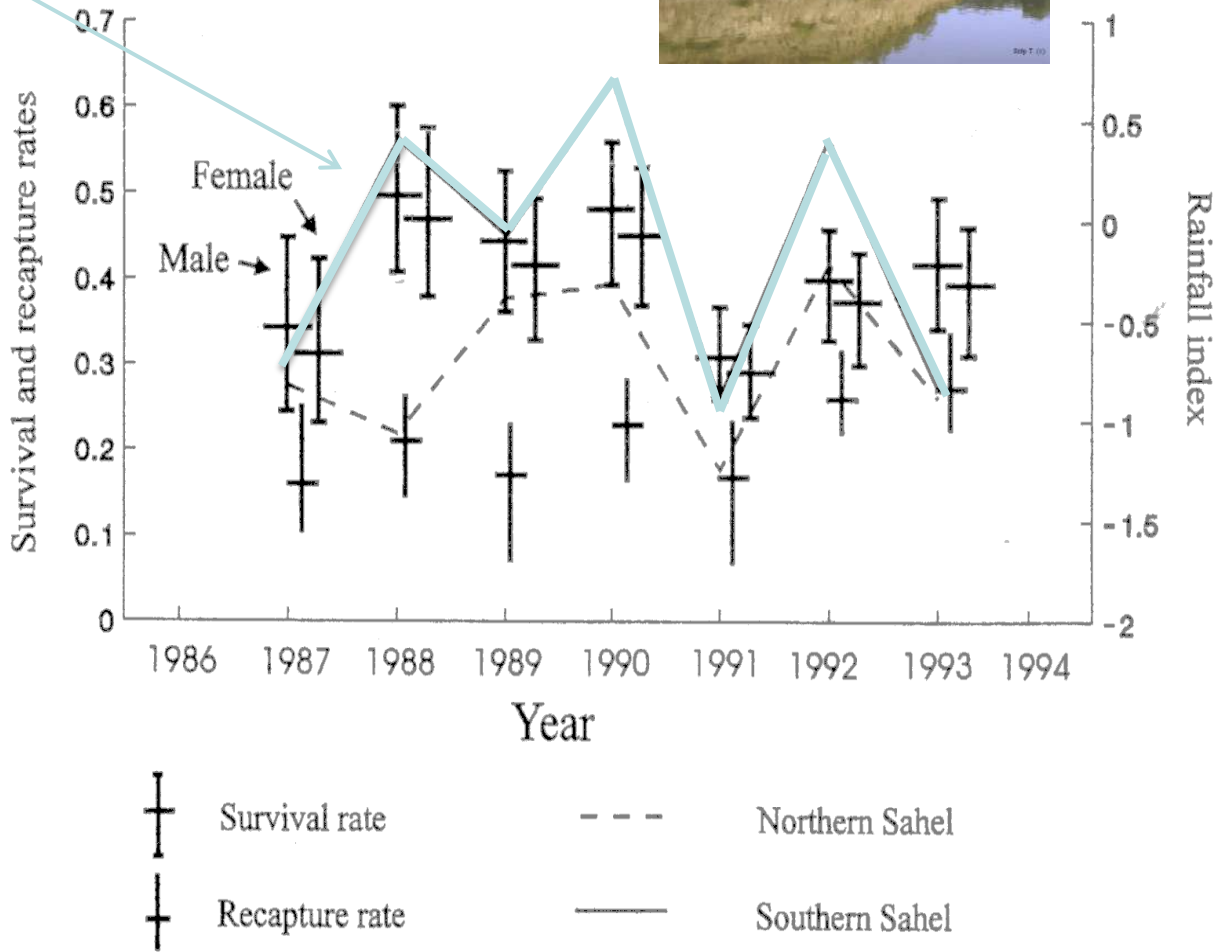






- Survival rate highly depend on the rainfall (Sahel, Western part) condition in Africa (Szép 1995, *Ibis*), one could model the survival rate with Sahelian rainfall for short term (1986-1994, Tiszatelek colony)

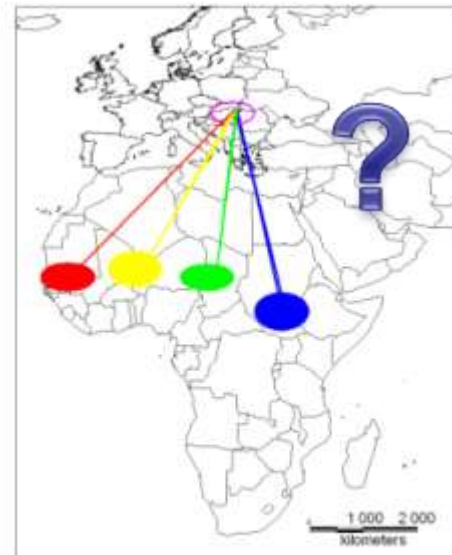
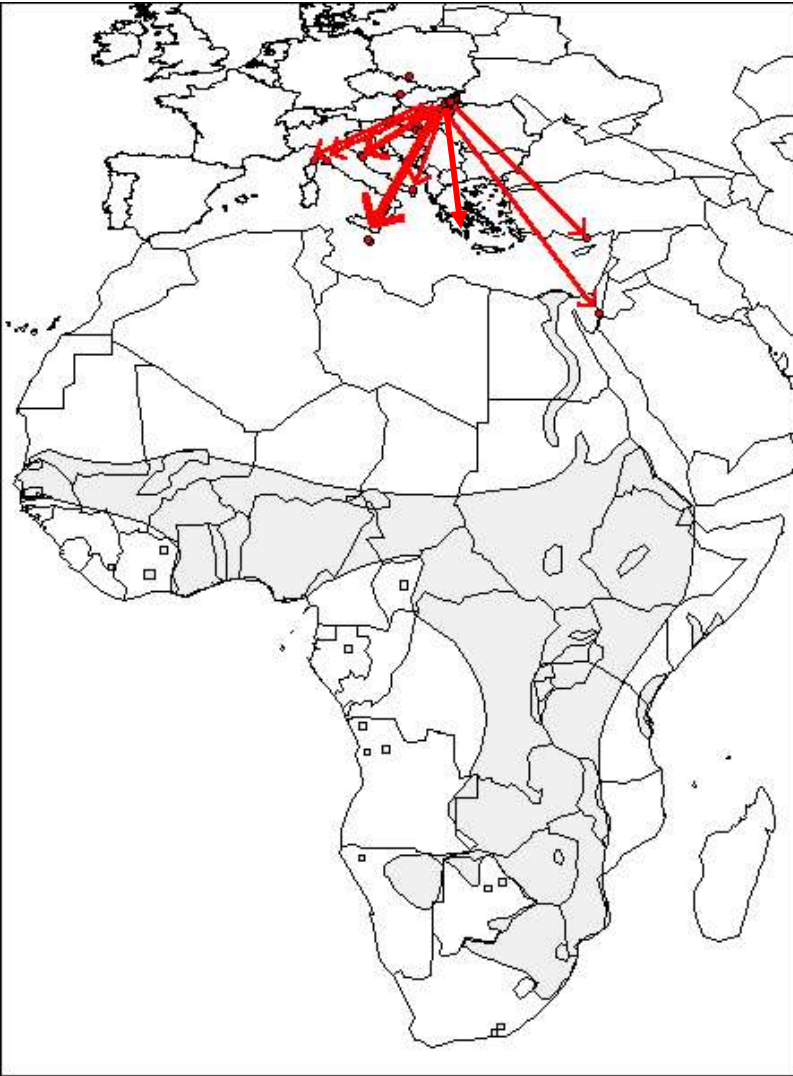
Sahelian rainfall index



Limited or no information about the all migration and wintering areas of sand martin breeding in Eastern Hungary until 2013



- ~190 thousand ringed breeding birds since 1985,
 - No any African recoveries/recaptures !



Application of geolocators in cooperation with Swiss Ornithological Institutes (2012/13) – first success !!!

Szép, T., Liechti, F., Nagy, K., Nagy, Zs., Hahn, S. 2017. Discovering the migration and non-breeding areas of Sand Martins and House Martins breeding in the Pannonian basin (central-eastern Europe). *Journal of Avian Biology* 48: 114-122



Recent project using geolocators, 2017-2020

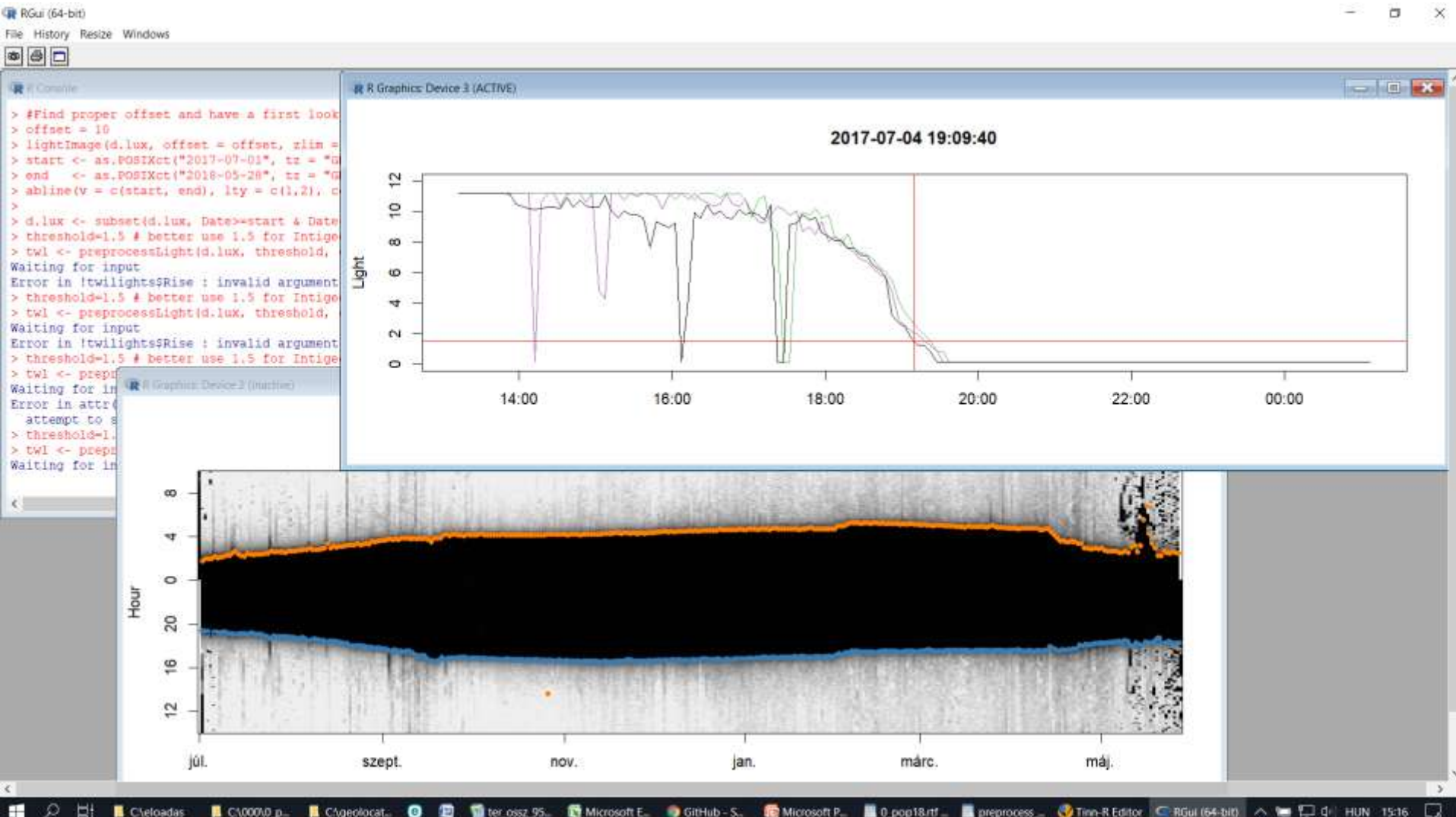
- 100-100 geolocators deployed in 2017 and in 2018

- (Migratech, 14 months lifespan, measure light in wide range – option to use template fit)

- Opportunity to investigate in details the entire non-breeding period

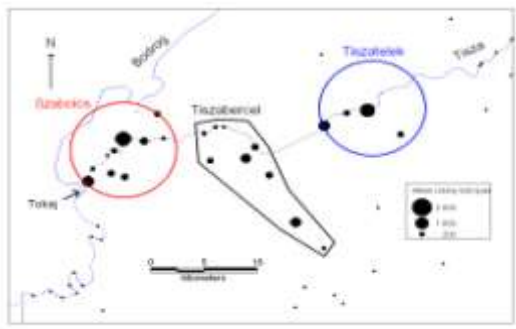


Geolocation - Flight_R - template fit method, more detailed information about post breeding/autumn migration period , less sensitivity to equinox



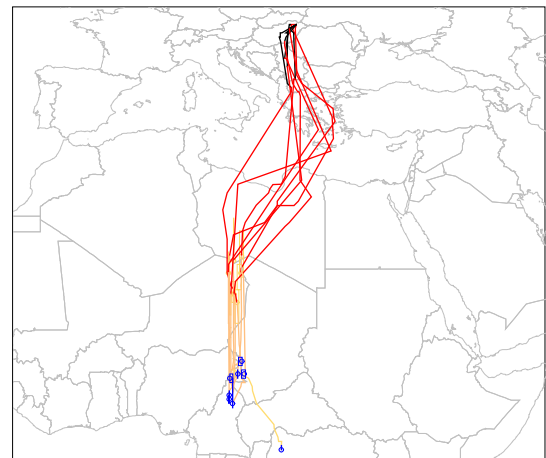
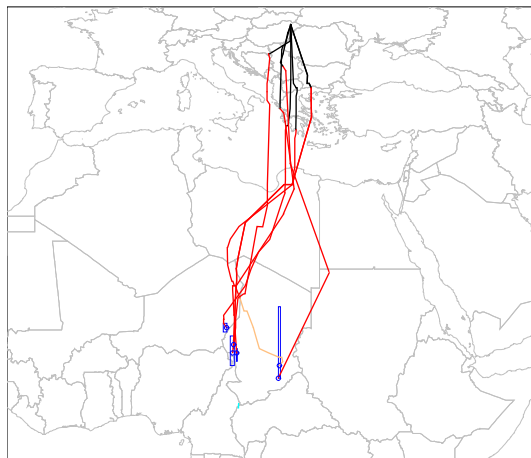
Sand Martin is a long-distance migrant species

Study area in Hungary

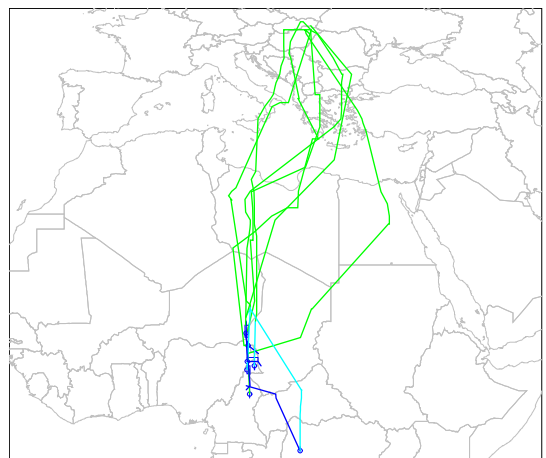
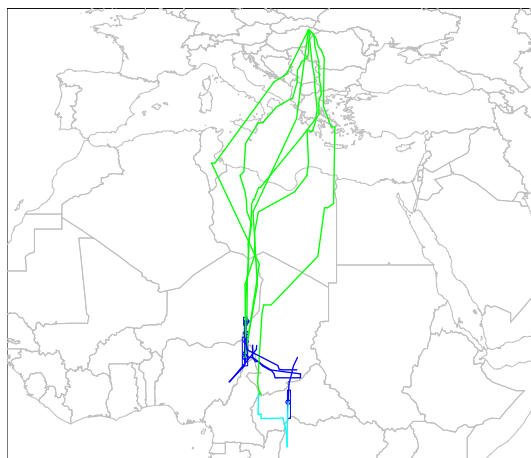


- 6 recaptured individuals in 2018
- 8 recaptured individuals in 2019

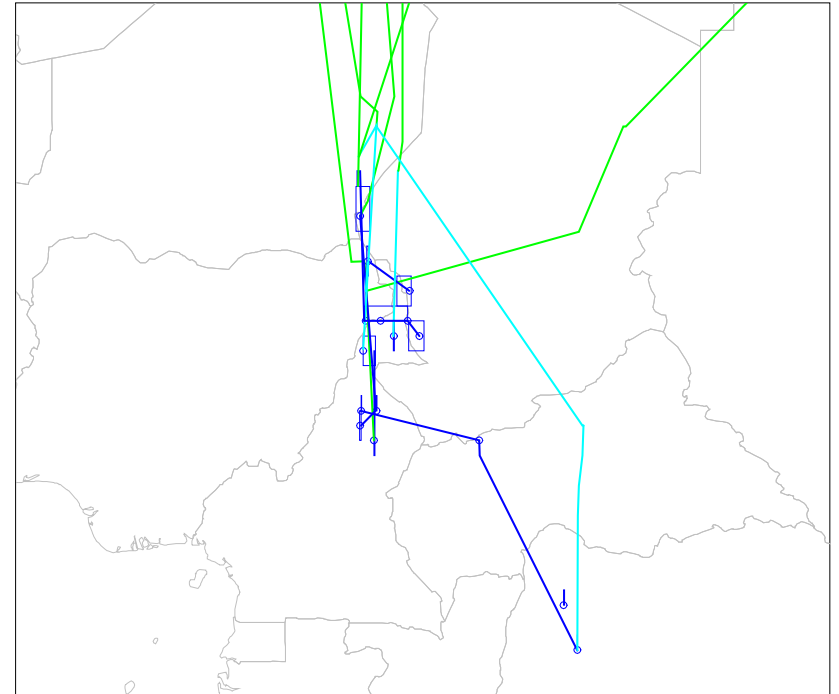
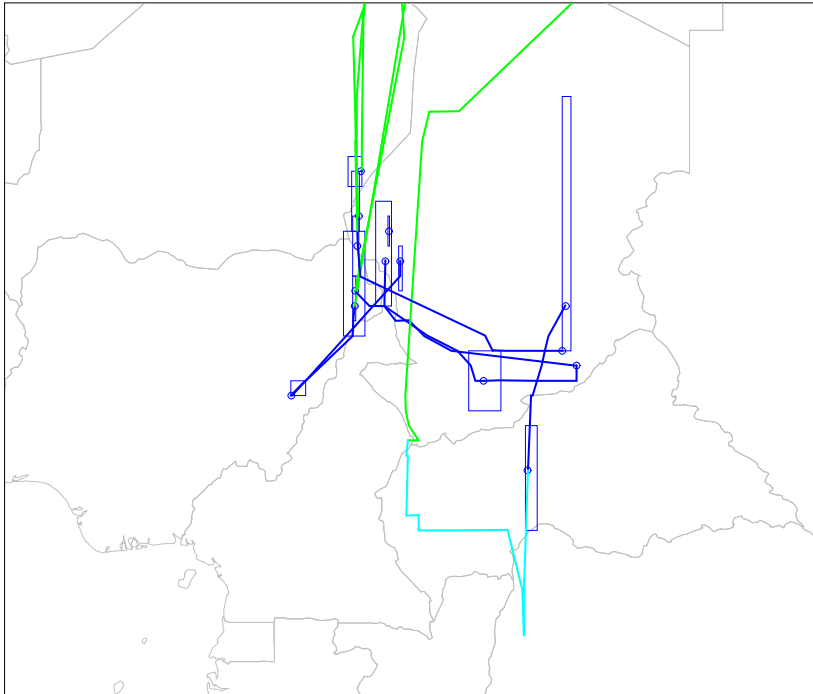
Autumn migration in 2017 and 2018 by geolocators



Spring migration in 2018 and 2019



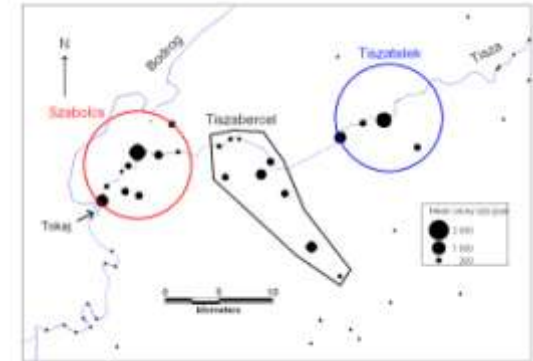
Wintering period



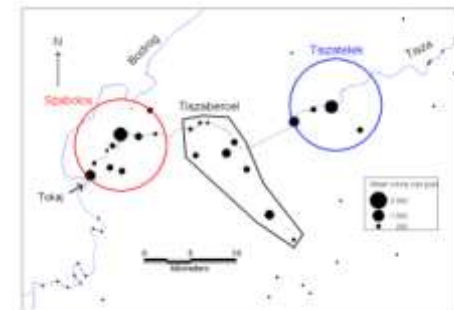
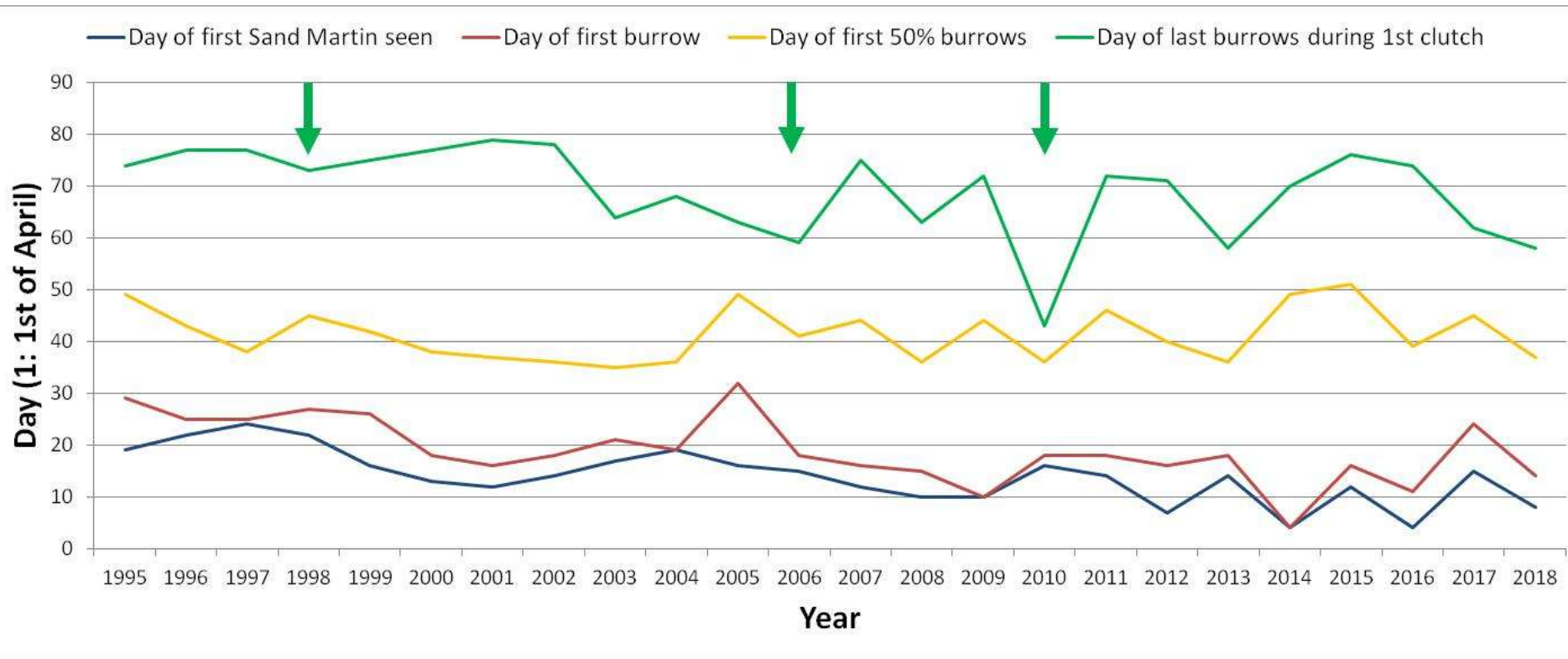
The studied individuals dominantly used the Lake Chad basin as the main non-breeding residence area (Fig. 5), similar to the other two former studies of this population (Szép et al. 2017, Hahn et al. 2021), there were only four individuals (29%) which used different areas in eastern direction (two in SE Chad/Central African Republic) and southern east direction (two in NW Congo).

Regular survey of breeding since 1995

- Annually control 800-2000 burrows, at least once a week, since 1995 in the studied area with videoendoscope (~ 10% of all burrows)
- All burrows in randomly selected 2 meters wide section(s) of colonies
- 478 sections
- 29 753 burrows
- 18 691 nests

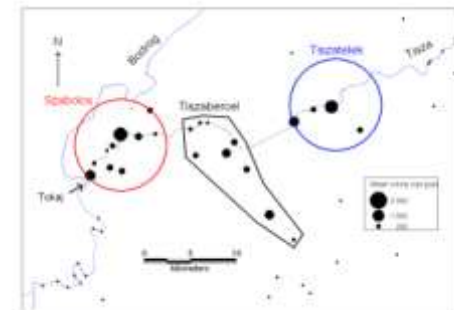
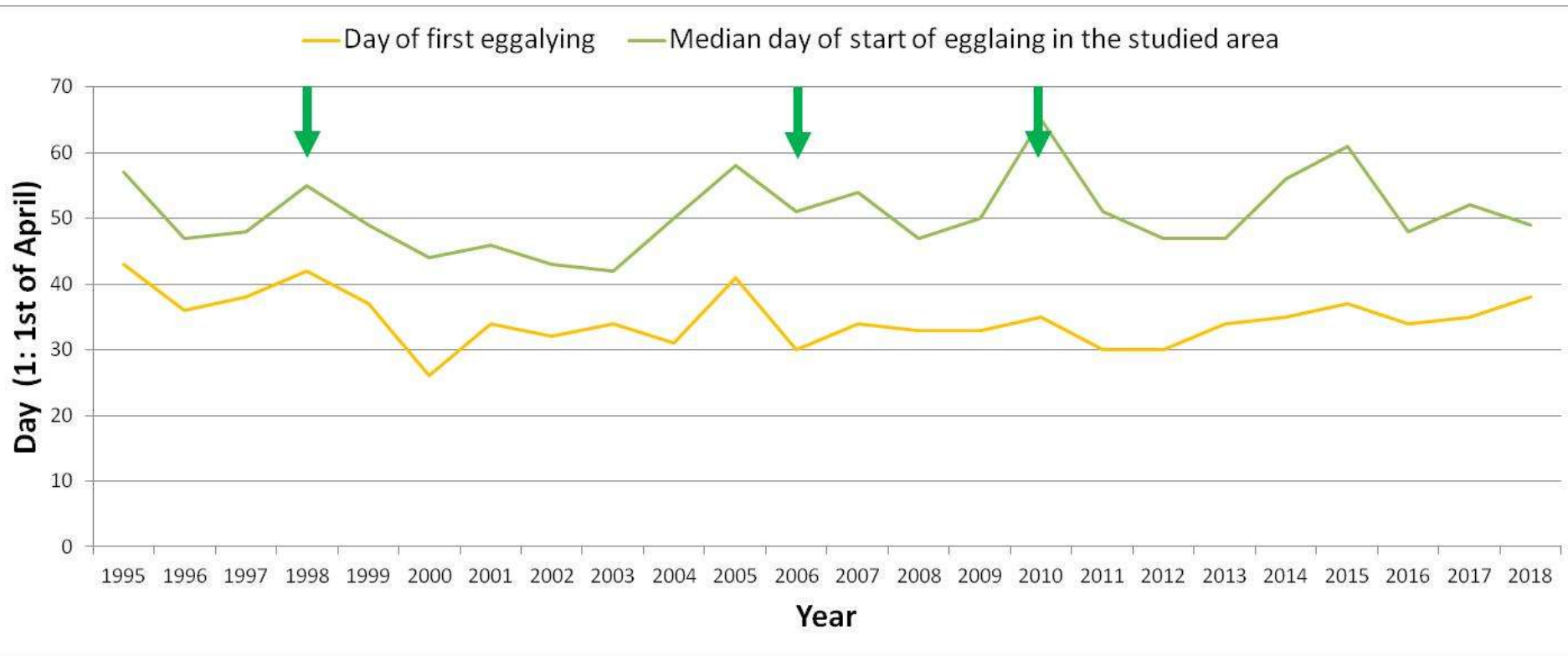


- First Sand Martin arrive ~ 10 days earlier since 1995
- **Arrival of the main part of the population has not changed**
- The day of last arrival occur ~ 10 days earlier

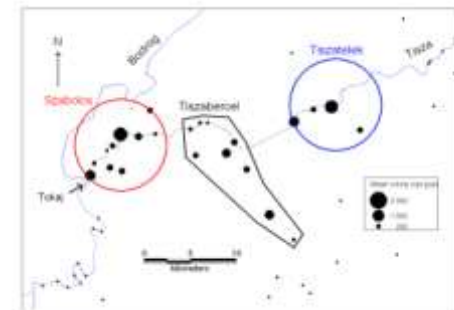
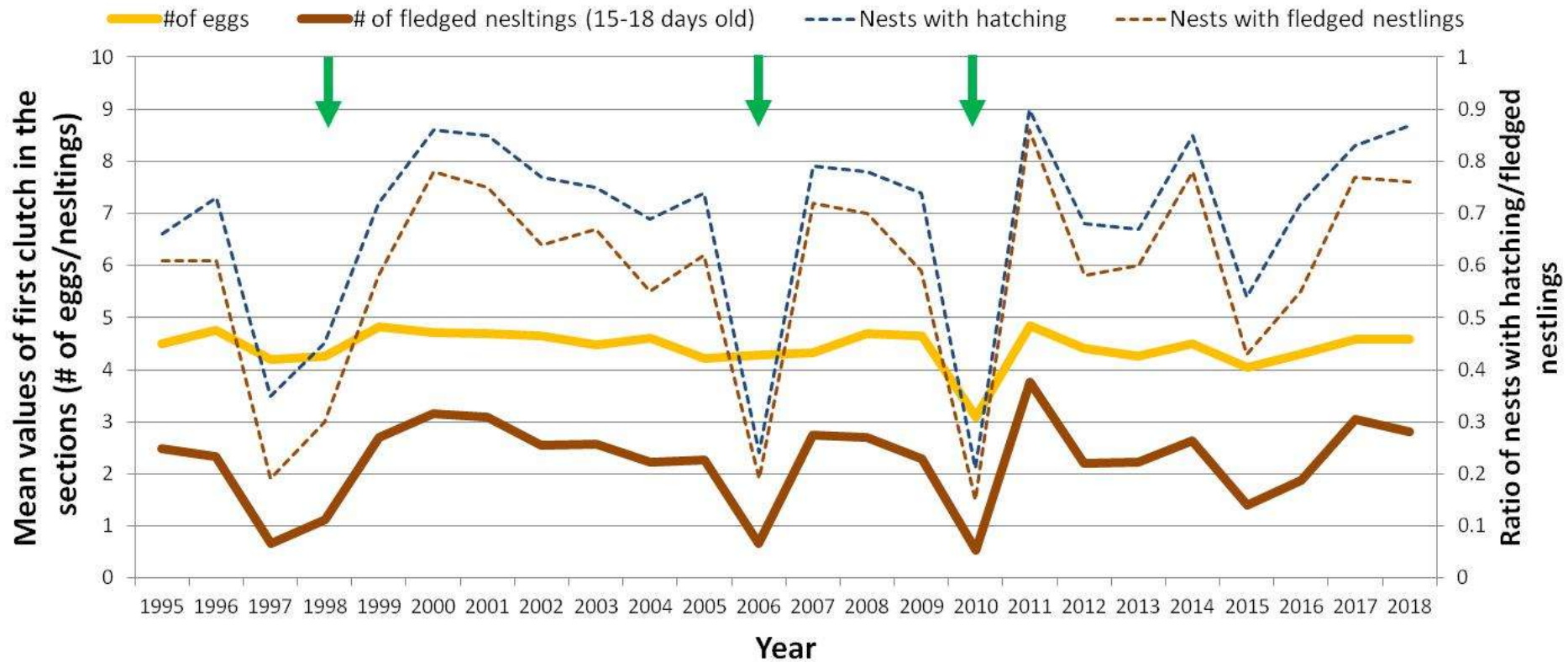


The day of egg laying started ~ 5 days earlier in the case of first breeder

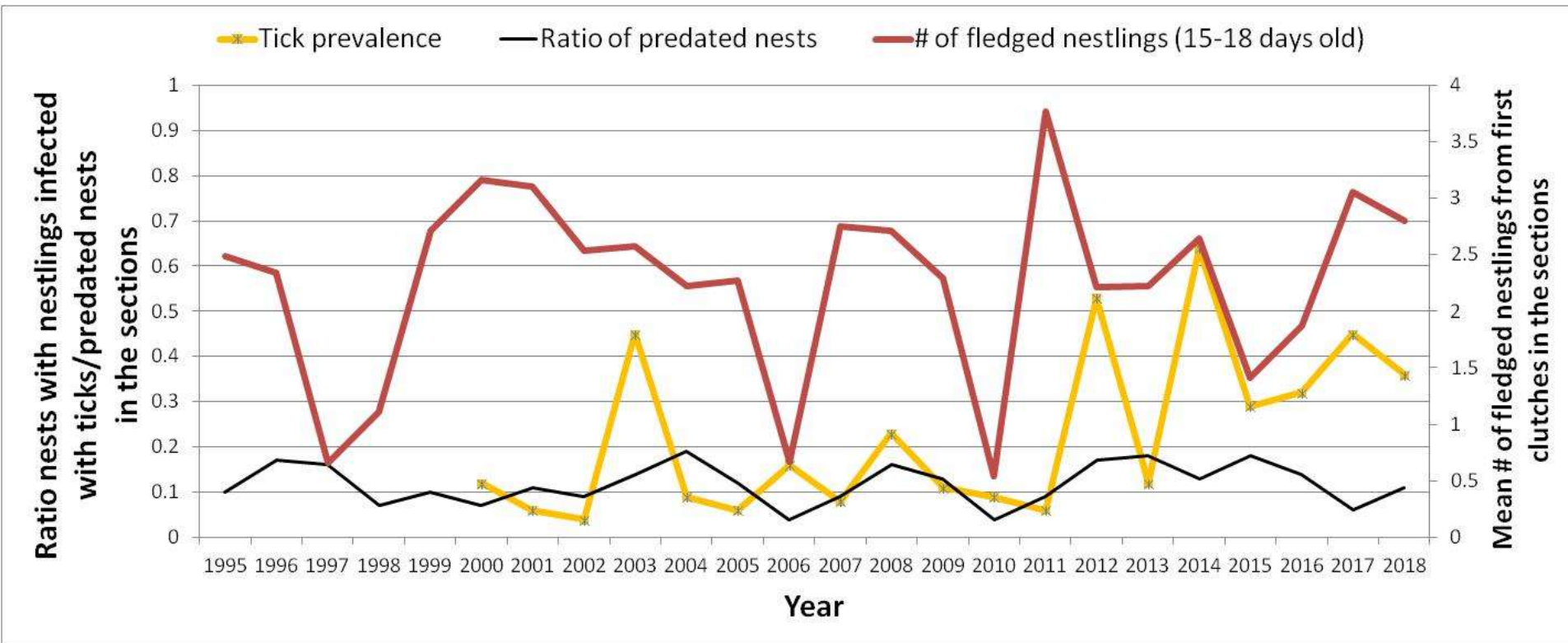
Day of start of egg laying has not changed in the main part of the population



There is no declining trends in the annual breeding values

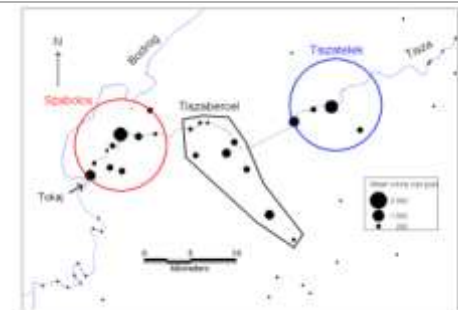
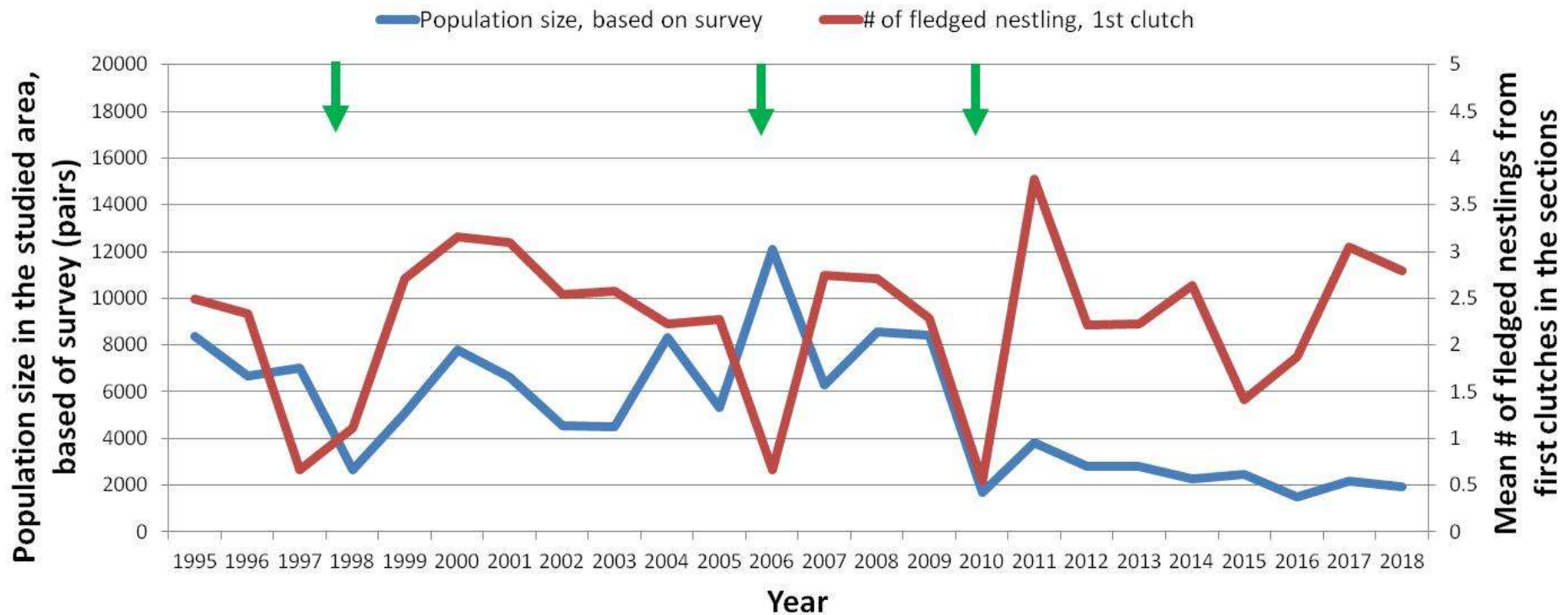


Only the tick prevalence showing increasing tendency during the last decade



Host specific tick species, *Ixodes lividus*, – live and breed only in the Sand Martin nest and individuals and has significant effect on condition of nestlings Szép & Møller (1999, 2000 *Oecologia*)

The mean number of nestlings before fledging did not explain the population decline – importance of postfledging condition/survival, emigration/immigration !?



Which factors potentially responsible behind the decline ?



- Changing intensity of flood intensity – changing quantity and quality breeding habitats?
- Increasing parasite pressure?
- Changing quantity and quality postbreeding/premigratory/wintering habitats by seasonal/transseasonal (carry-over) effects?
- Phenological mismatch?
- Importance to identify used nonbreeding areas, spatial/temporal characteristics
- Investigation of postfledging condition/survival
- Investigation of natal/breeding dispersals, direction/level of emigration/immigration – other populations
- Investigation on levels of individual/population, IPM
- Opportunity to use new methods for difficult to measure parameters, geolocators, MOTUS network with traditional radiotransmitters, LifeTags, Icarus project
- Opportunity to use remote sensing data, chemical/physical characteristics of feathers

09.30

Primary population parameters

$$\begin{array}{c} \text{Immigration} \\ + \\ \text{natality} + N - \text{mortality} \\ - \\ \text{Emigration} \end{array}$$

- **natality**

potential fecundity, human (9-11 months)

realized - " —, human (8 per years)

natality rate – offspring/unit time

- **mortality**

potential longevity

realized - " -

human girls (Rome 21 years, 1780 UK 39 years, 1976 USA 77 years)

- **immigration-emigration**

Secondary population parameters

- Sex ratio
- Age composition
- Distribution
- Genetical composition

Population demography

- Examines and measures the dimensions and dynamics of populations

Life table

Table 3 Cohort life table for the song sparrow on Mandarte Island, British Columbia.^a

Age in years (x)	Observed no. of birds alive (n_x)	Proportion surviving at start of age interval x (l_x)	No. dying within age interval x to $x + 1$ (d_x)	Rate of mortality (q_x)
0	115	1.0	90	0.78
1	25	0.217	6	0.24
2	19	0.165	7	0.37
3	12	0.104	10	0.83
4	2	0.017	1	0.50
5	1	0.009	1	1.0
6	0	0.0	—	—

^a Males hatched in 1976 were followed from hatching until all had died six years later.

SOURCE: From Smith (1988).

Life table (mortality) of women in Canada

Table 4 Static life table for the human female population of Canada, 2006.

Age group (yr)	No. in each age group	Deaths in each age group	Mortality rate per 1000 persons (1000 q_x)
0-4	829,300	911	1.10
5-9	899,500	70	0.08
10-14	1,016,500	136	0.13
15-19	1,055,500	317	0.30
20-24	1,100,200	370	0.34
25-29	1,101,200	377	0.34
30-34	1,101,100	511	0.46
35-39	1,168,400	853	0.73
40-44	1,341,700	1481	1.10
45-49	1,336,900	2364	1.77
50-54	1,193,800	3338	2.80
55-59	1,054,000	4775	4.53
60-64	805,500	5729	7.11
65-69	636,800	7253	11.39
70-74	554,300	10,210	18.42
75-79	490,800	15,221	31.01
80-84	389,200	21,236	54.56
85-90	227,900	22,256	97.66
90 and above	125,300	38,742	309.19

SOURCE: Statistics Canada (2007).

Survivorship curve

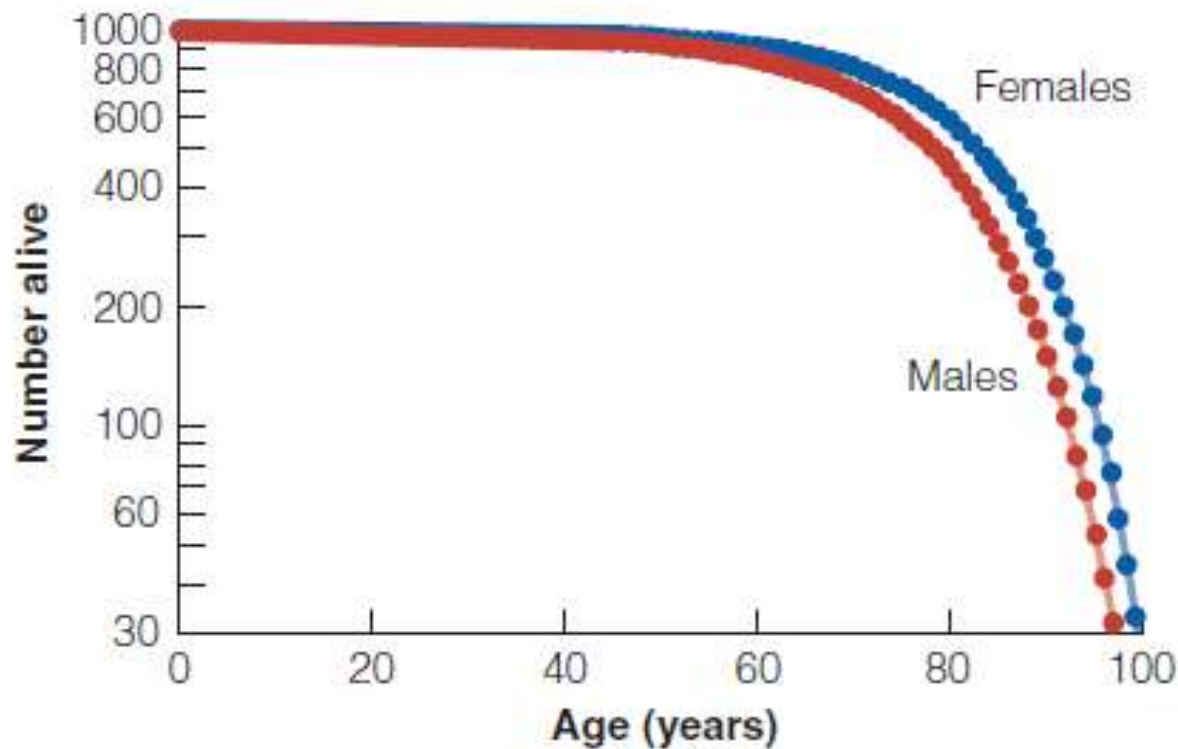


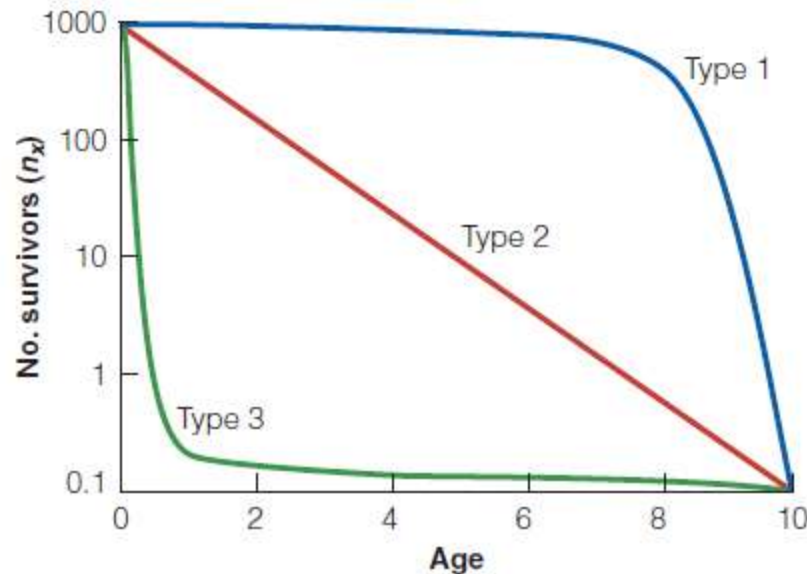
Figure 5 Survivorship curve for all males (red) and females (blue) in the United States in 2003 for a starting cohort of 1000 individuals. Life expectancy at birth was 75 years for males and 80 years for females. (Data from the U.S. National Center for Health Statistics, 2006.)

Survivorship curve

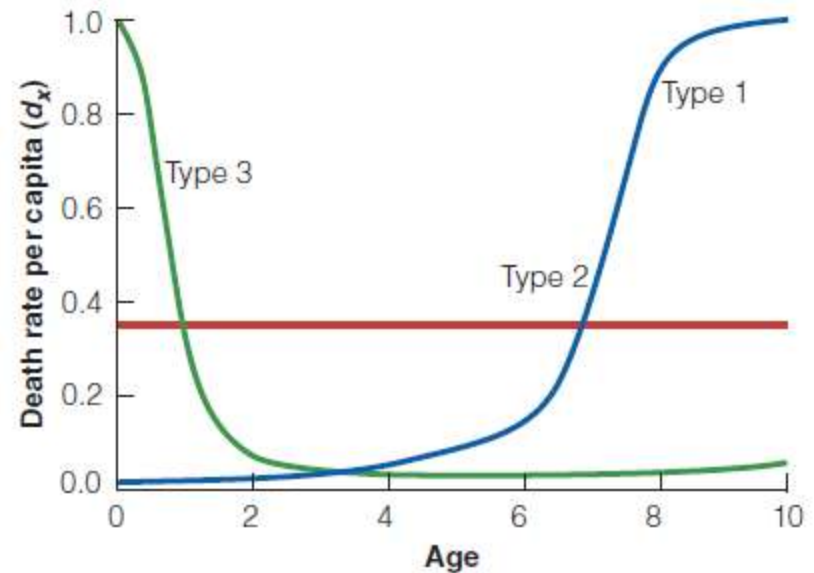
Type I- large mortality in the old age (e.g. humans)

Type II- similar mortality among different age groups (e.g. birds)

Type III- large mortality in the young age (e.g. insects)



(a)



(b)

Figure 6 Types of survivorship curves. (a) Hypothetical survivorship curves (n_x). (b) Mortality rate (d_x) curves corresponding to these hypothetical survivorship curves. Type 2 (red) curves show constant survival rate with respect to age. Type 1 (blue) curves show increasing mortality late in life, and Type 3 (green) curves show the highest mortality early in life. (After Pearl 1928.)

Fertility

l_x : proportion of the population surviving to age x .

a_x/a_0 (a_0 : # of young individuals, a_x : # of individuals surviving x . age)

b_x : number of offspring by females in their x age

Net reproductive rate (R_0): $\sum_{x=1}^{\text{max. age}} (l_x * b_x)$

If $R_0=1$, population size did not change

Table 5 Survivorship schedule (l_x) and fertility schedule (b_x) for women in the United States, 2007.

Age group	Midpoint or pivotal age x	Proportion surviving to pivotal age l_x	No. female offspring per female aged x per 5-year period (b_x)	Product of l_x and b_x
0-9	5.0	0.9945	0	0.0000
10-14	12.5	0.9939	0.0020	0.0020
15-19	17.5	0.9929	0.1432	0.1422
20-24	22.5	0.9913	0.2855	0.2830
25-29	27.5	0.9896	0.2863	0.2833
30-34	32.5	0.9878	0.2160	0.2134
35-39	37.5	0.9851	0.0918	0.0904
40-44	42.5	0.9809	0.0175	0.0172
45-49	47.5	0.9743	0.0075	0.0073
50 +	—	—	0.0	0.00

$$R_0 = \sum_{x=0}^{\infty} l_x b_x = 1.0388$$

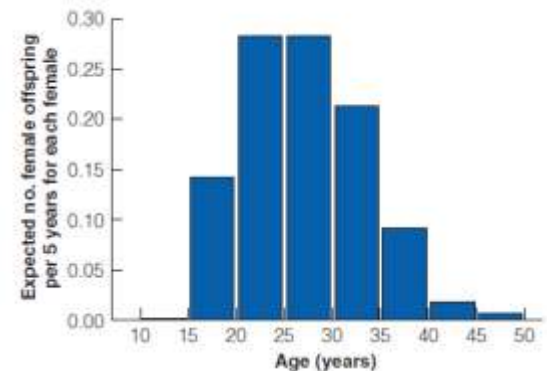


Figure 9 Expected number of female offspring per five-year period for each female in the United States in 2007. Data are from the final column in Table 5. The area under the histogram is the net reproductive rate R_0 . (Data from the Statistical Abstract of the United States 2007.)

Reproductive value

Reproductive value at age $x = (V_x)$: $\sum_{t=x}^{\text{max. age}} (l_t/l_x) * b_t$

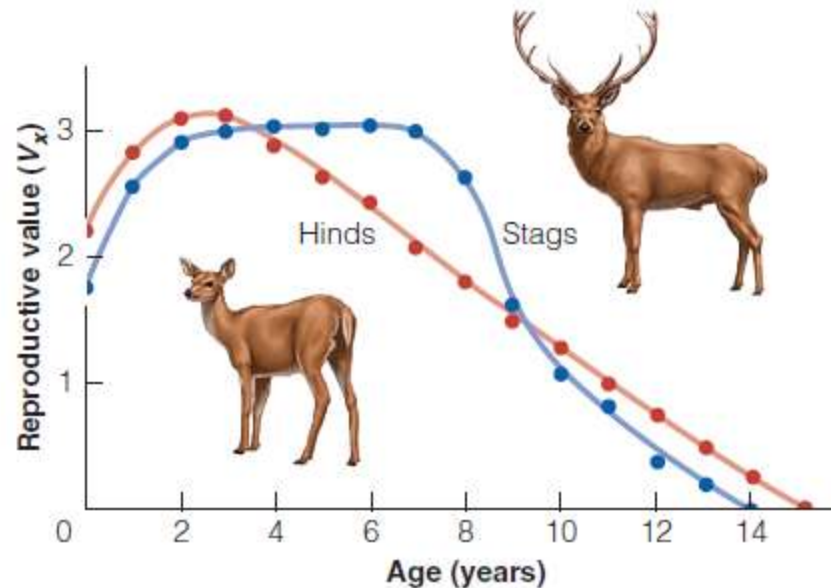


Figure 15 Reproductive value for red deer stags (males) of different ages, compared with that of hinds (females) on the island of Rhum, Scotland. Reproductive value is calculated in terms of the number of female offspring surviving to one year of age that parents of different ages can expect to produce in the future. (From Clutton-Brock et al. 1982.)

Age distribution

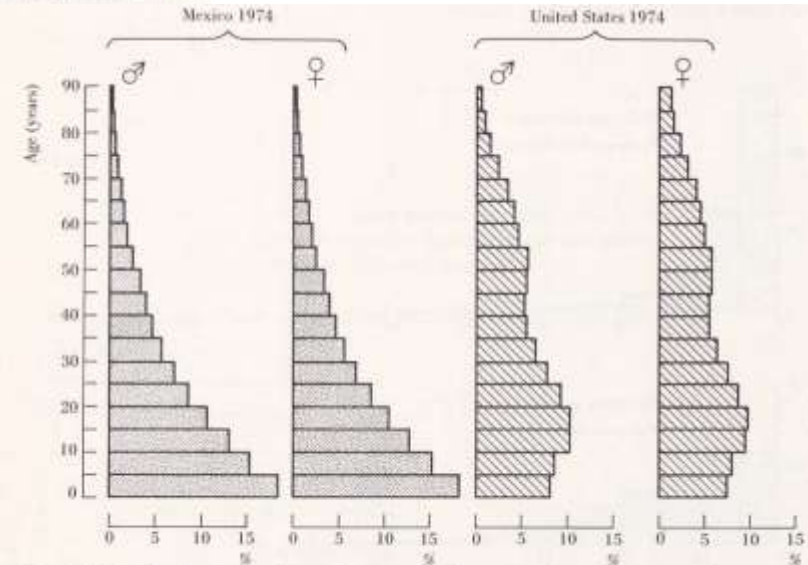
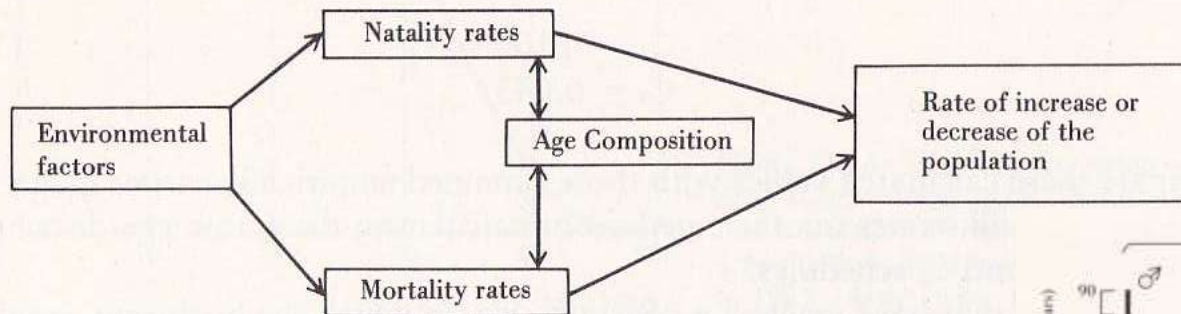
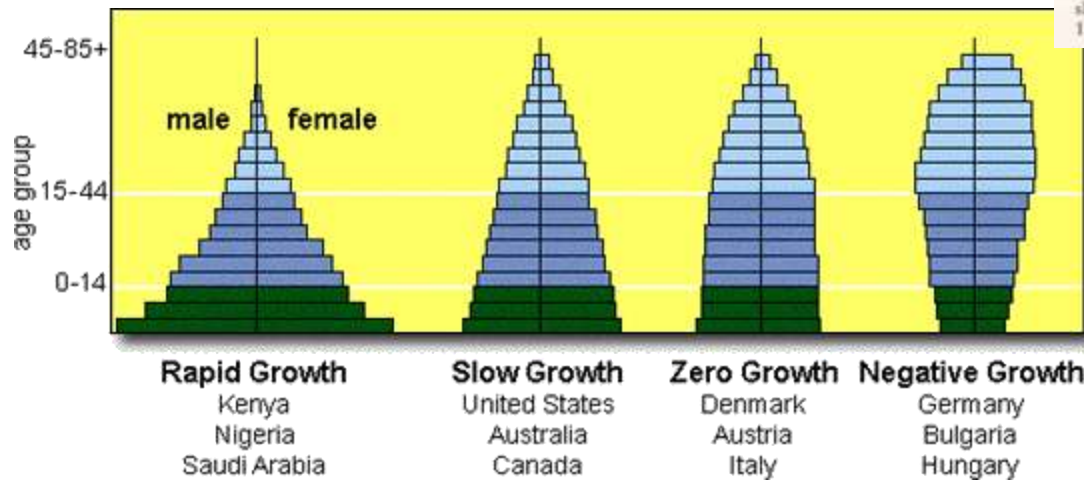


Figure 11.18 Age distributions for rapidly increasing human population in Mexico and slowly increasing population in the United States. (Data from Demographic Yearbook 1974.)



Modeling population size on the base of life table data

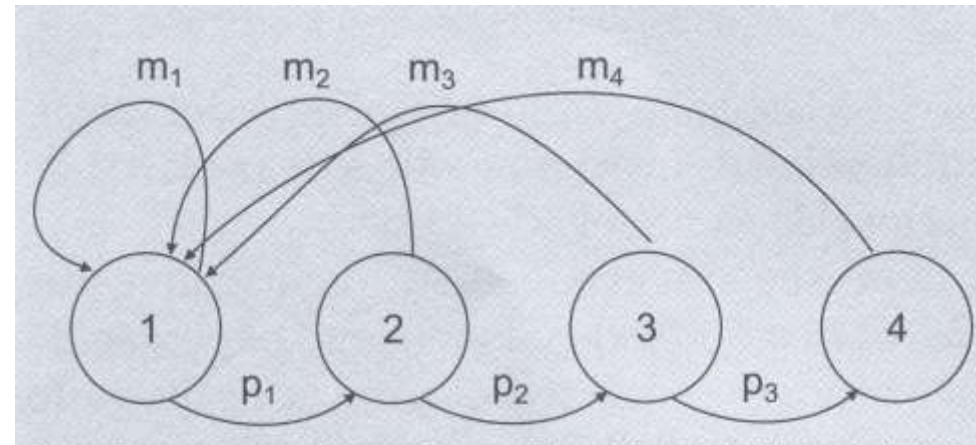
- Leslie model
 - If we know for each age group (a) the survival rate (p_a) and fertility (m_a)
 - Population size of each age groups (n_a), by which the entire population is estimatable for the next period (t)

Pl.

$$n_1(t+1) = n_1(t) * m_1 + n_2(t) * m_2 + \dots$$

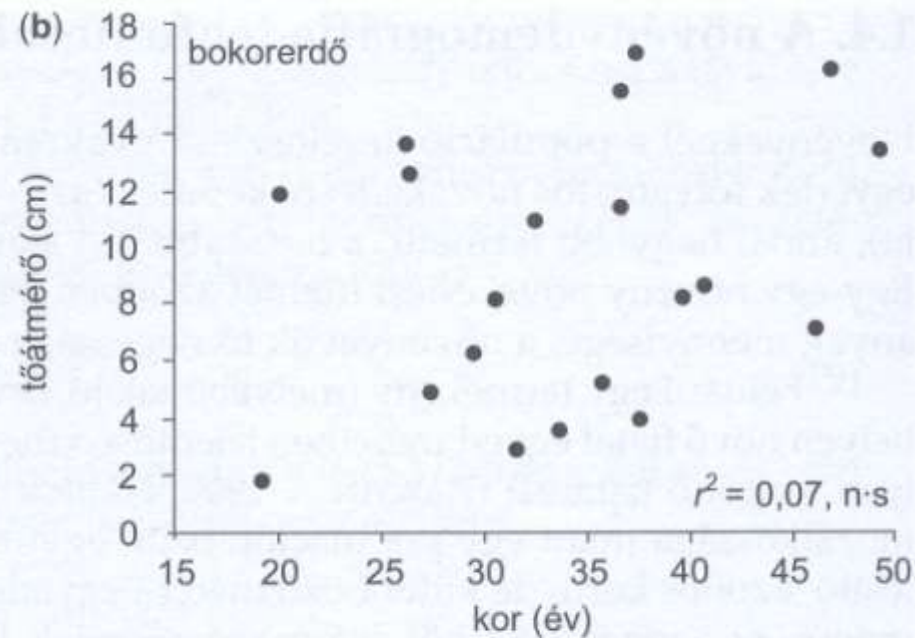
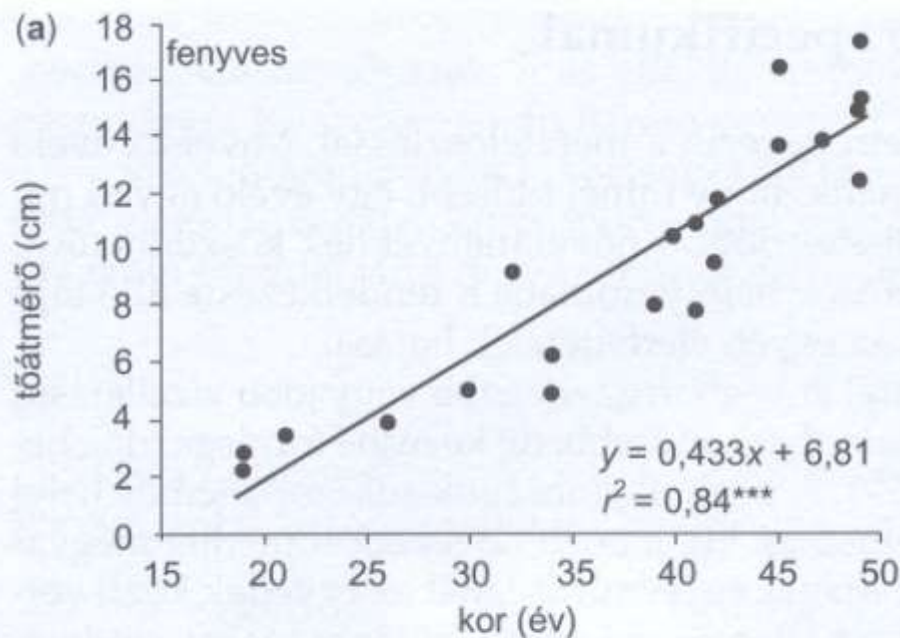
$$n_2(t+1) = n_1(t) * p_1$$

$$n_3(t+1) = n_2(t) * p_2$$



Speciality of plant demography

Age distribution could be different from size distribution – survival and fertility are size dependent for most plants



Manna tree (*Fraxinus ornus*) age (kor év) and size (diameter of stump, tőátmérő cm) at two different habitats:

- fenyves- soil with similar depth
- bokorerdő- soil with very varying depth

Population Growth

Exponential (Geometrical) growth

- If there is no death, one bacterium which cell able to proliferate every 20th minutes could cover the entire surface of the Earth within a day!

1. Multiplication rate constant. Let R_0 be a constant. If $R_0 > 1$, the population increases geometrically without limit; if $R_0 < 1$, the population decreases to extinction. For example, let $R_0 = 1.5$ and $N_t = 10$ when $t = 0$:

Generation	Population size (N_t)
0	10
1	$15 = (1.5)(10)$
2	$22.5 = (1.5)(15)$
3	$33.75 = (1.5)(22.5)$

Growth in Populations with Discrete Generations

$$N_{t+1} = R_0 * N_t$$

where:

- N_t abundance in the t^{th} period
- N_{t+1} abundance in the $t+1^{\text{th}}$ period
- R_0 net reproductive rate (λ , growth factor)

$$R_0 = N_{t+1} / N_t$$

The speed of the growth is depend on the # of birth and death within a period

In the case of plants the growth measured by growth of the biomass

Exponential growth

Discrete generations:

Species with a single annual breeding season (e.g. colorado beetle)

$$N_{t+1} = R_0 * N_t$$

Exponential growth when the net reproductive rate (R_0) constant

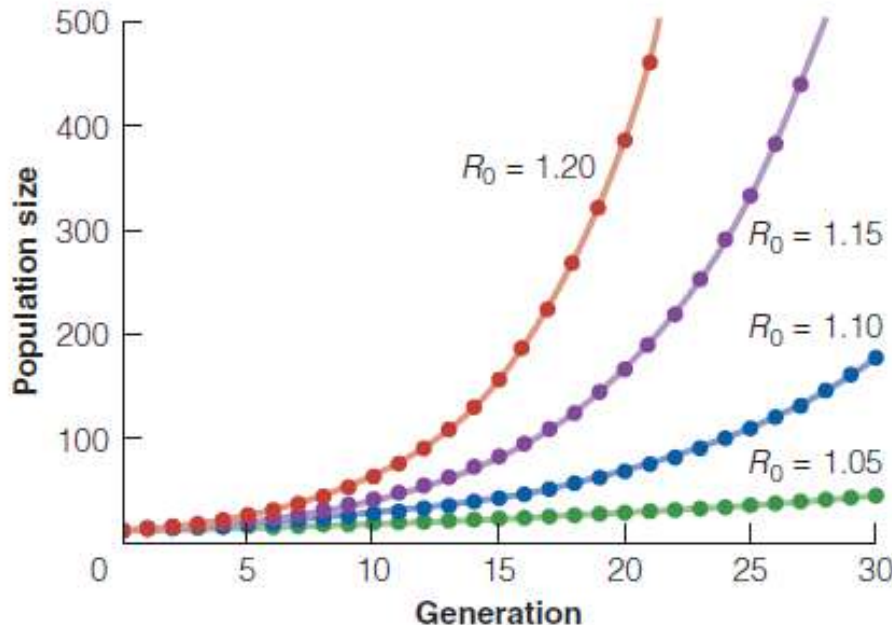


Figure 1 Geometric or exponential population growth, discrete generations, population growth rate (R_0) constant. Starting population is 10. Equation (1).

$R_0 > 1$: Population exponentially increasing

$R_0 = 1$: Population size is not changing

$R_0 < 1$: Population exponentially decreasing

$$N_t = N_0 * R_0^t$$

N_0 : Population size in the starting period (0th)

Exponential growth

Overlapping generation:

Species with prolonged or continuous breeding season (e.g. human)

change of population size within dt time interval:

dN

$$= r * N$$

dt

r : per-capita rate of population growth within dt time interval

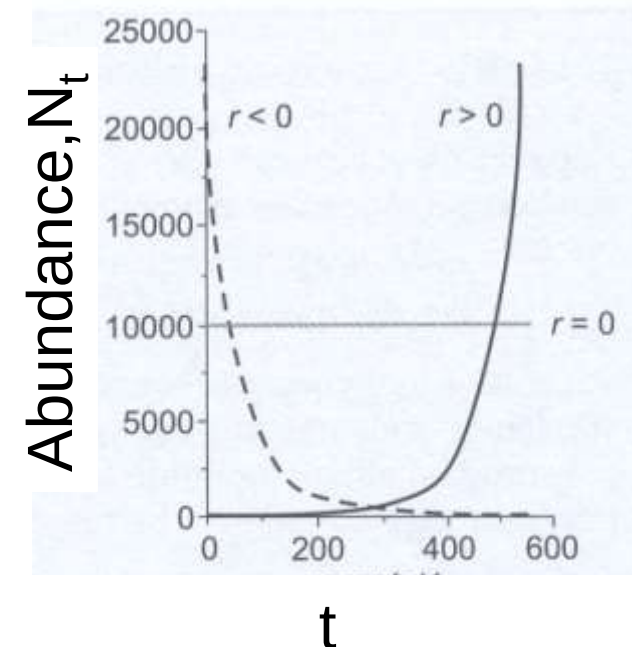
$$r = b - d$$

Where:

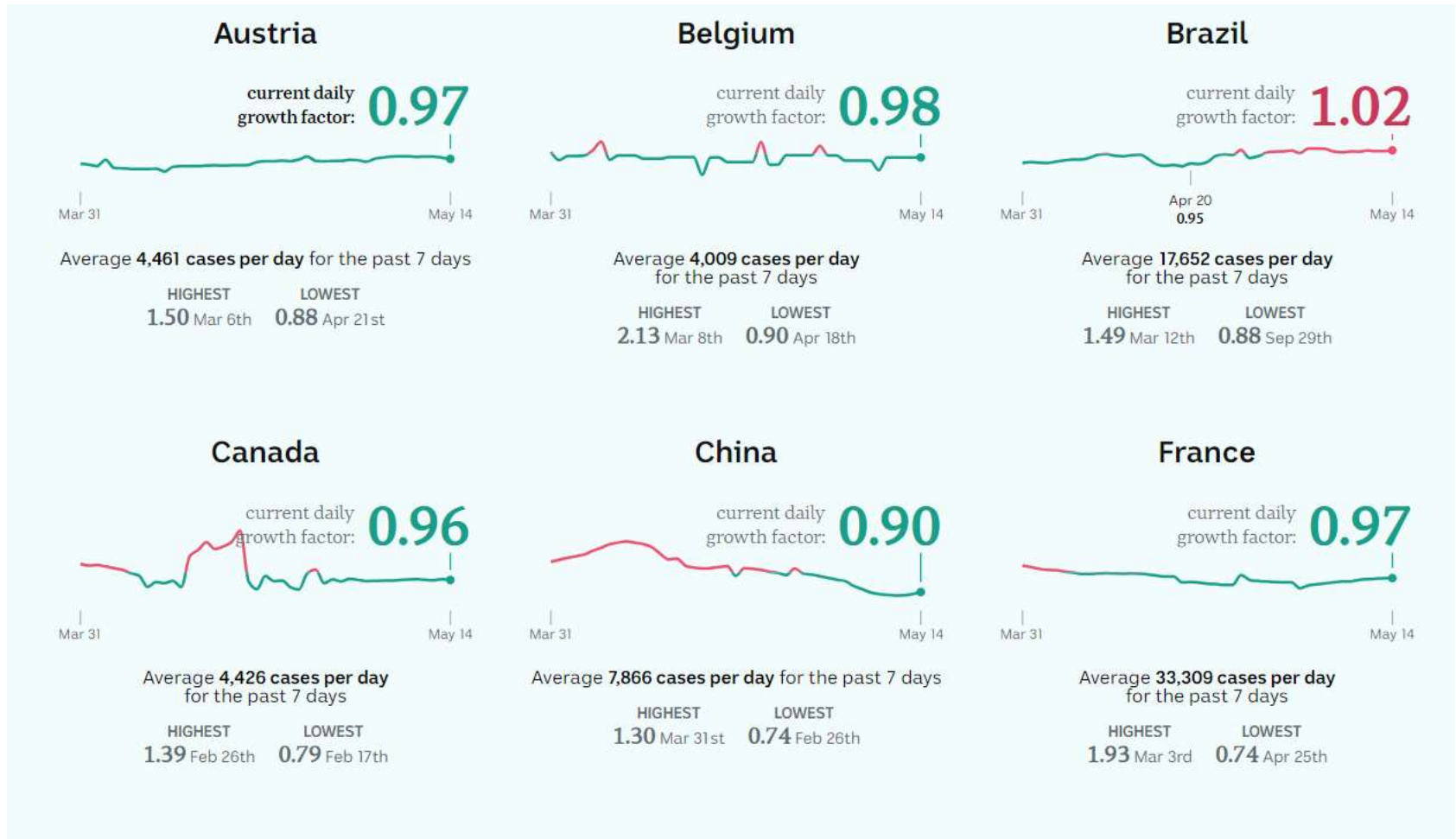
b : instantaneous birth rate

d : instantaneous death rate

Exponential increase/decrease when r independent from the N



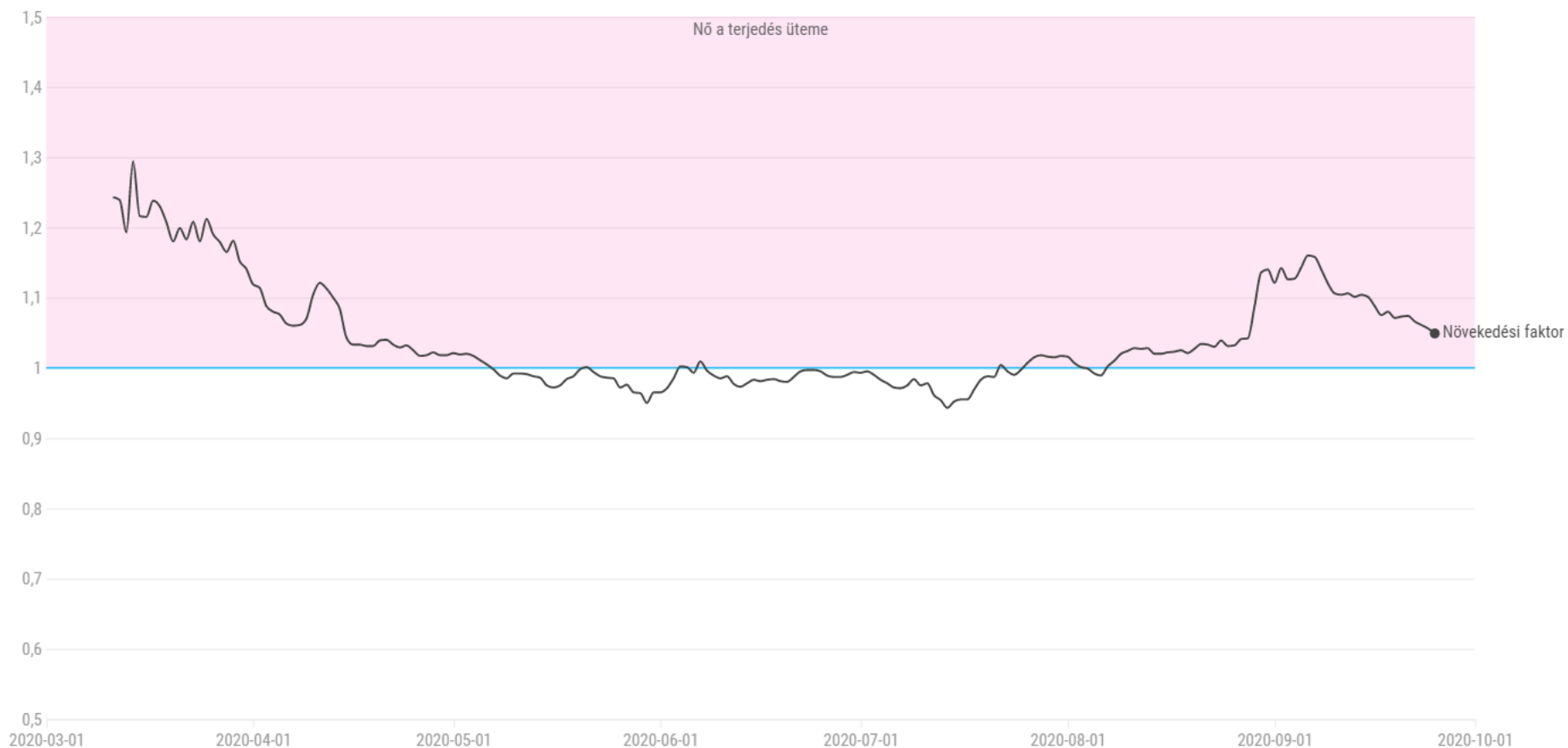
COVID-19



R_0 : Covid-19 reproductive rate (growth factor) in some countries

Az aktív fertőzöttek növekedési faktora (anf) Magyarországon

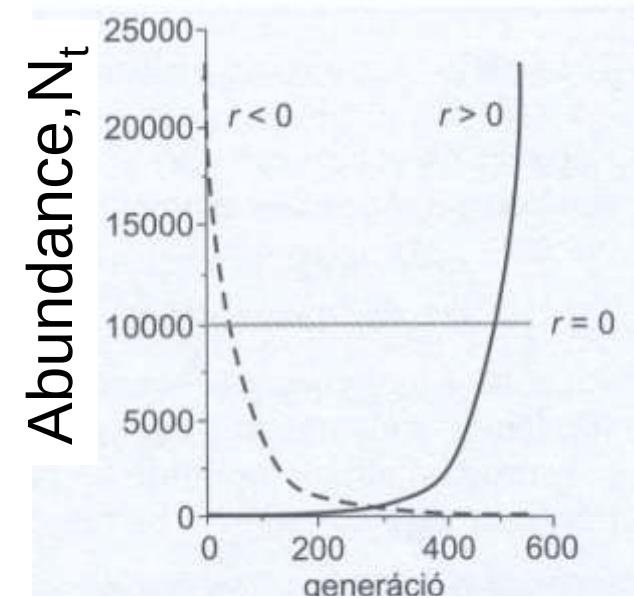
A növekedési faktor azt mutatja, hogy az aktív esetek száma milyen ütemben változik. A növekedési faktort úgy kapjuk meg, hogy az elmúlt öt nap átlagát elosztjuk az azt megelőző öt nap átlagával. Amennyiben a hányados 1 felett van, úgy még növekedés tapasztalható, ha egy alá esik, akkor elkezdhetünk bizakodni.



R_0 : Covid-19 reproductive rate (growth factor) in Hungary

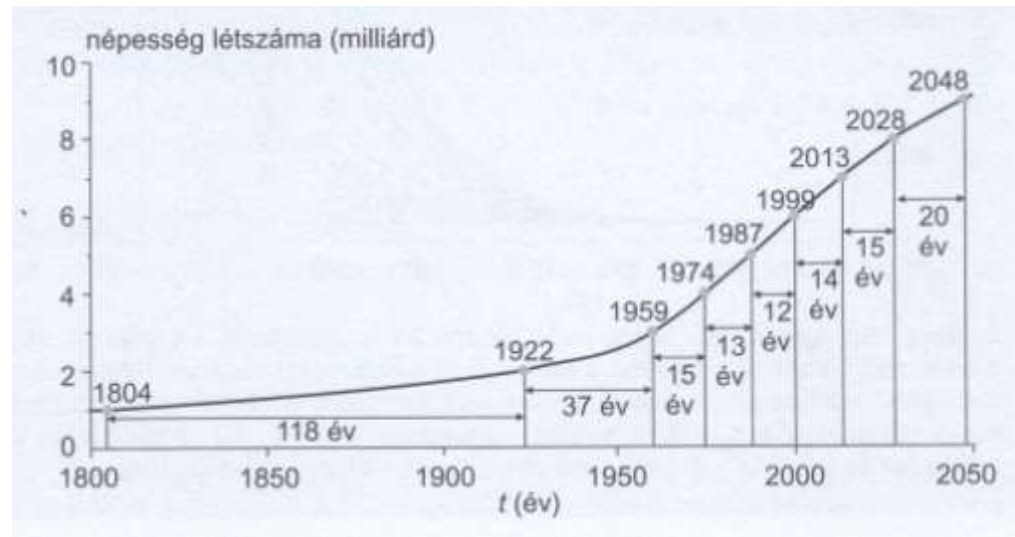
Exponential growth

Human population



t

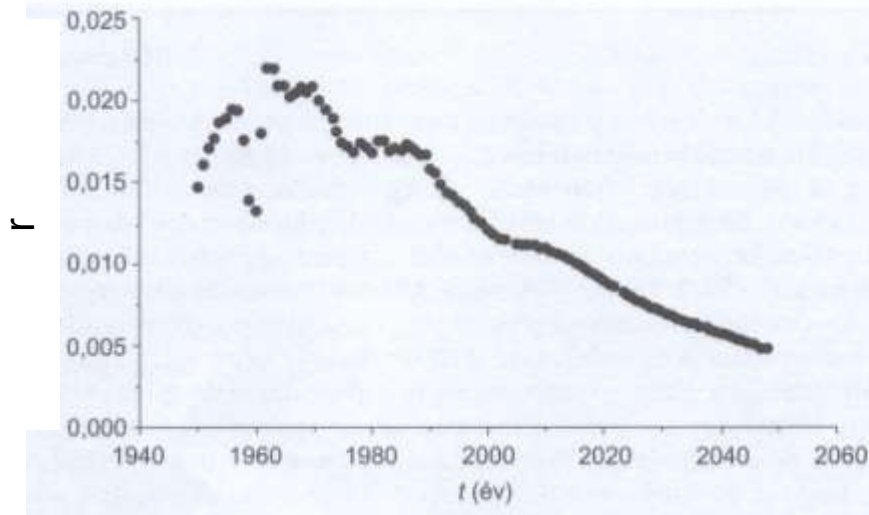
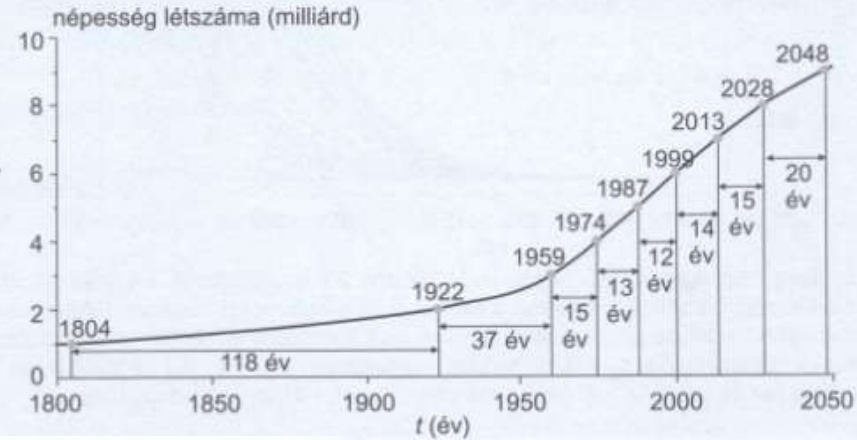
Population size
(billion people)



Population Growth

Human population size

4. ábra A világ népességének növekedése. A nyílak alatti számok az 1 milliárdos növekményhez szükséges időtartam hosszát adják meg. (Global Population Profile, 2002 nyomán).



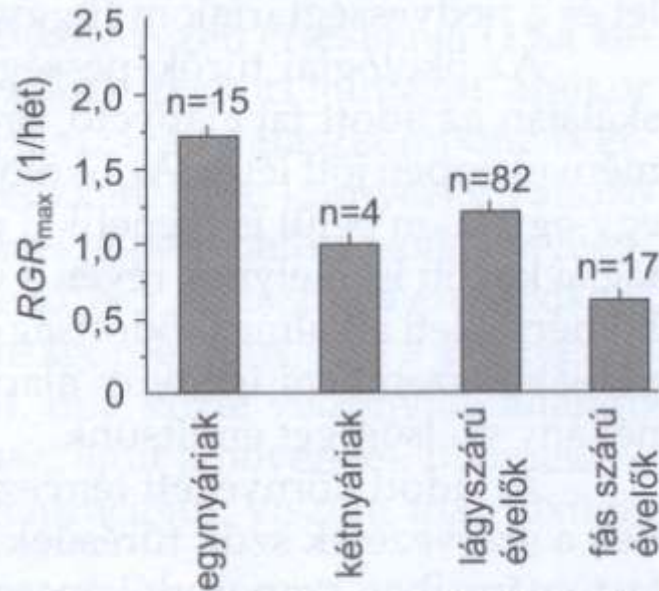
7. ábra A teljes emberi népesség növekedési üteme. A kiugróan alacsony értékeket 1960 körül egy kínai éhínség magyarázza (US CENSUS BUREAU adatai alapján).

év: year

In the case of the human population near stable r (population growth) was typical until ~1990, since then there is a decreasing tendency

r_0 (R_0): maximum reproductive rate (e.g. following catastrophe, epidemic, settling new area)

Population growth - plants



9. ábra Maximális vegetatív növekedési ráta (RGR_{max}) különböző növénycsoportokban. n — az egyes csoportok fajszáma (GRIME és HUNT 1975 és TILMAN 1988 nyomán).

Maximal RGR
of different
Plants
(herbaceous,
biennial,
perennial,
woody plants)

Relative growth rate (RGR)

$$RGR = \frac{1}{B} \cdot \frac{dB}{dt}$$

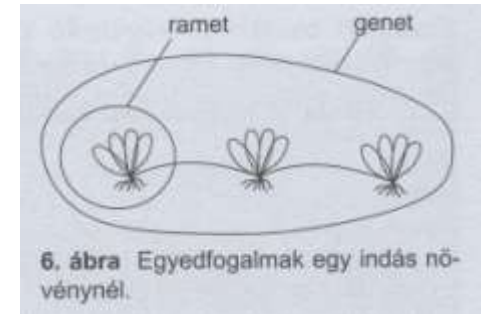
where:

B: biomass of the individuals

dB: change of the biomass with dt time interval

Algae (hydrological): RGR= 1.4/day

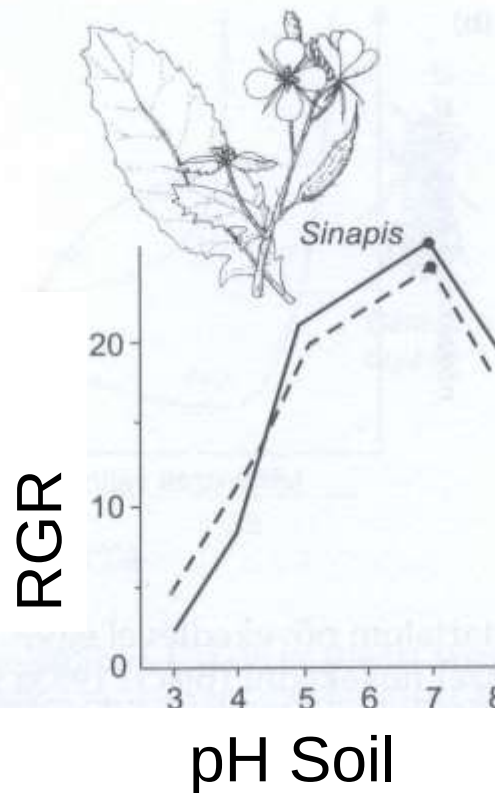
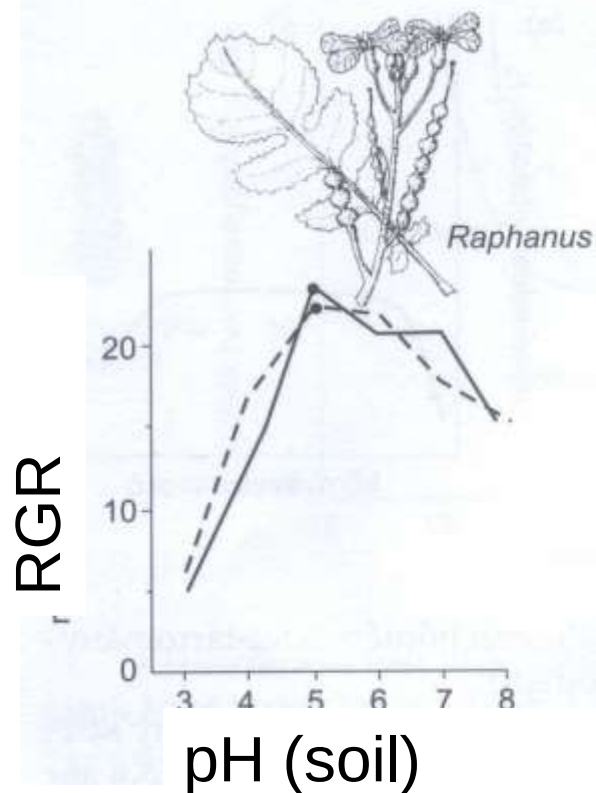
Weeds (terrestrial): RGR= 0.38/day



Population growth

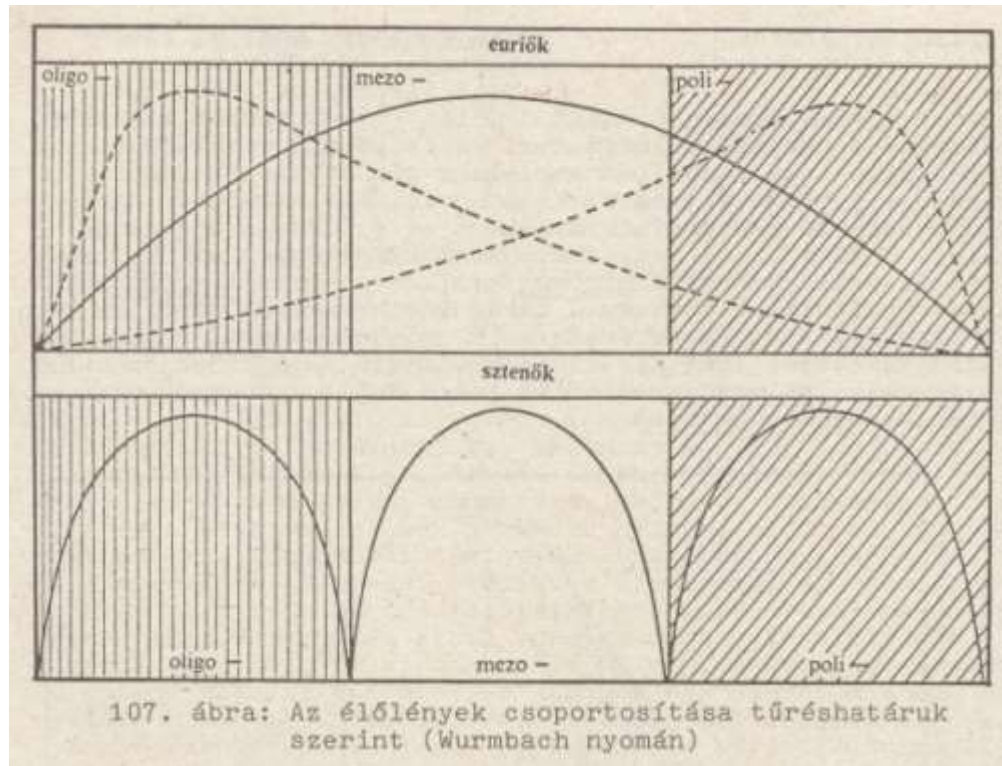
The role of ecological limiting factors

Ecological tolerance interval, where the $r_0 > 0$, $R_0 > 1 \implies$ population able to grow



14. ábra A mézskerülő repcsény retek (*Raphanus raphanistrum*) és a vadrepce (*Sinapis arvensis*) válaszgörbéi egyfajú veteményekben (monokulturában). Egy-egy vonal egy-egy kísérlet eredménye (MULLER-DOMBOIS, ELLENBERG 1974).

Ecological tolerance



Euriök - generalist

Sztenők - specialist

Population growth

Ecological tolerance interval, where the $r_0 > 0$, $R_0 > 1 \implies$ population able to grow

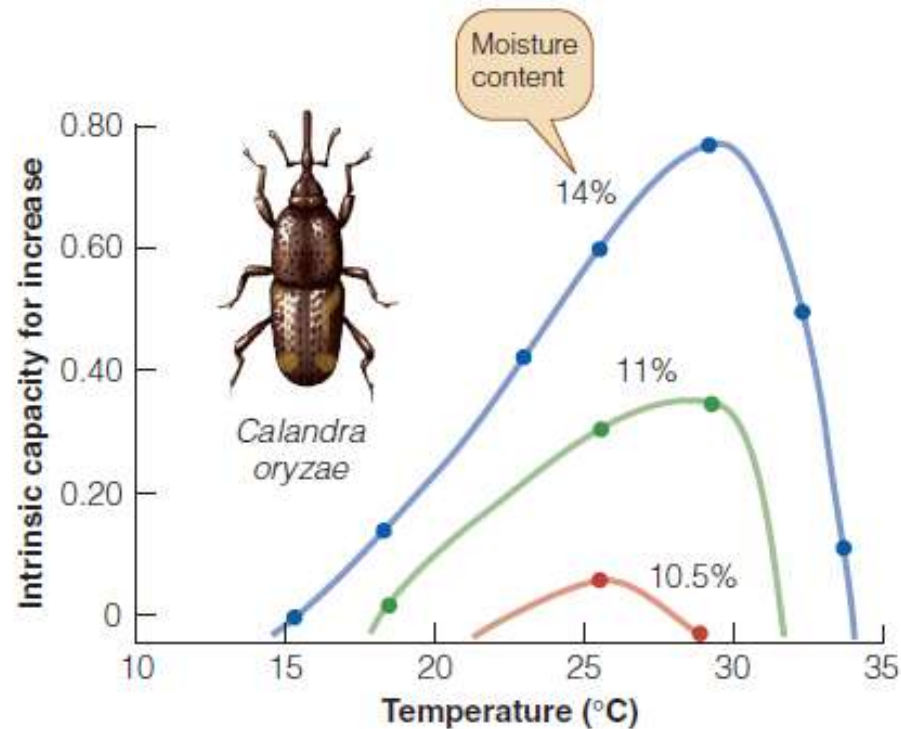
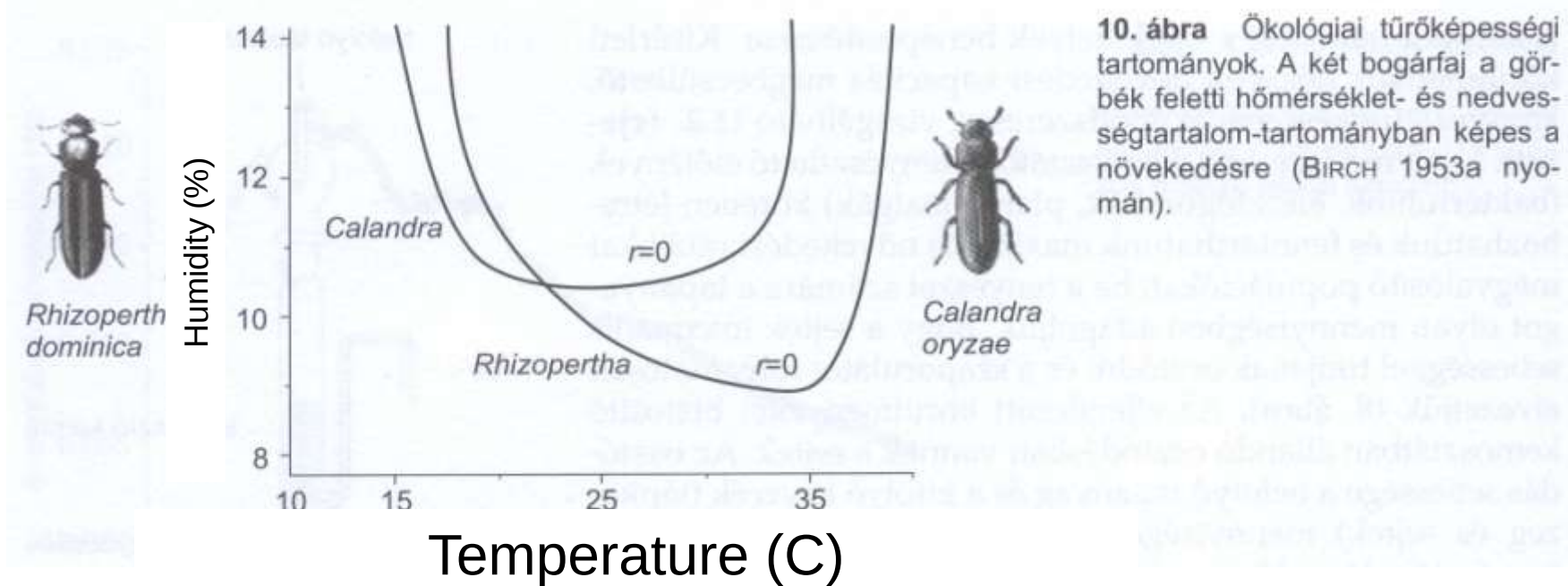


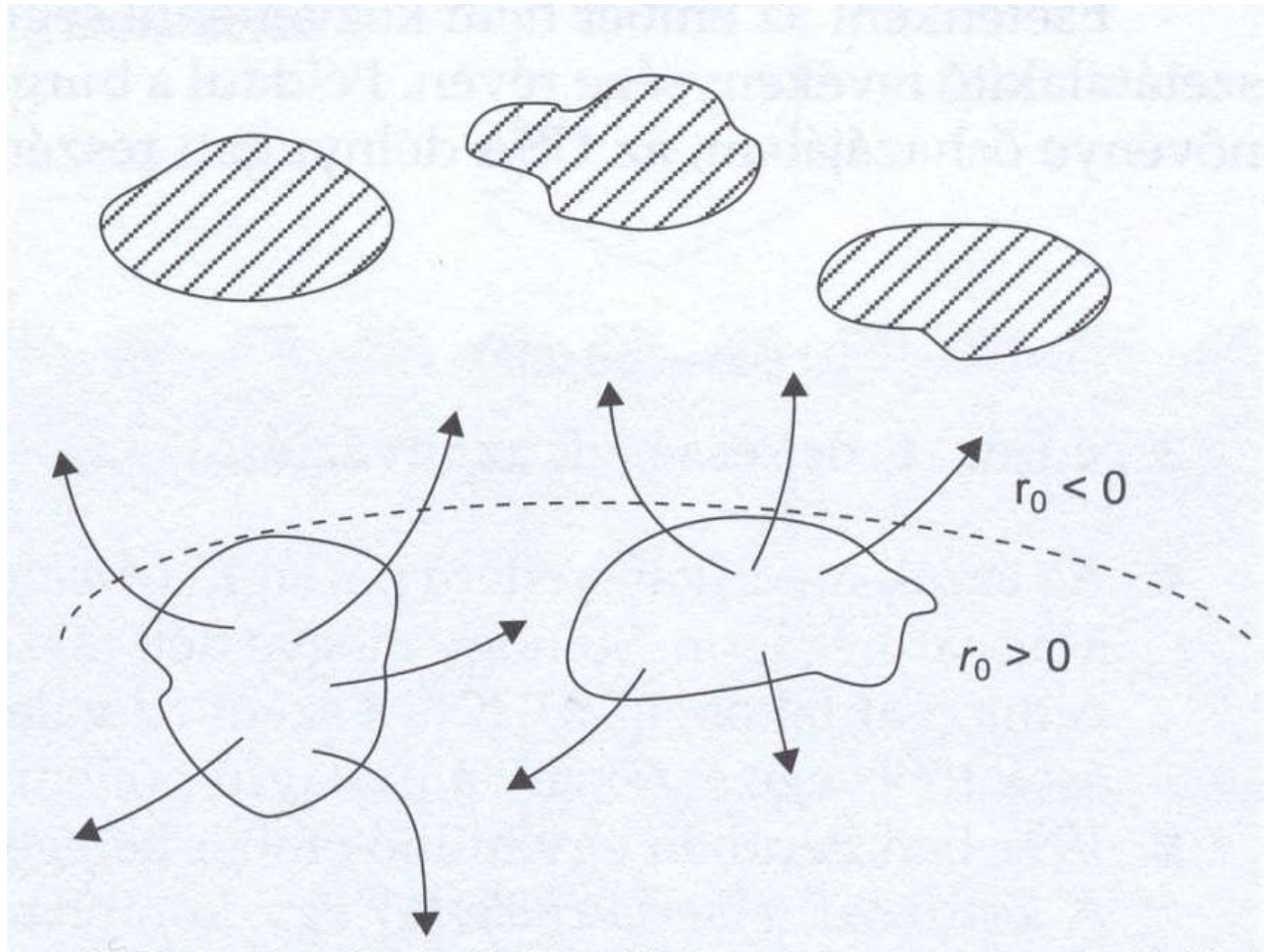
Figure 13 Intrinsic capacity for increase (r) of the grain beetle *Calandra oryzae* living in wheat of different moisture contents and at different temperatures. The higher the moisture content of the wheat, the more rapidly these beetles can increase in numbers. (After Birch 1953a.)

Population growth

Ecological tolerance interval, where the $r_0 > 0$, $R_0 > 1 \implies$ population able to growth



Population growth and dispersal

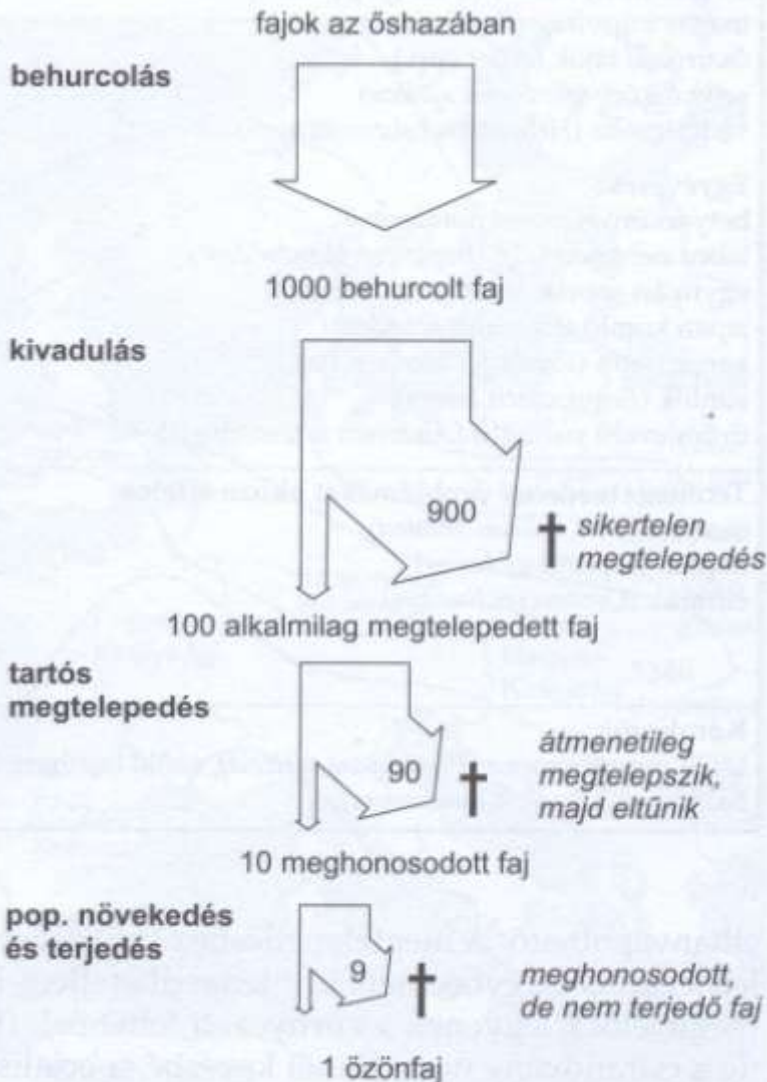


Population which $r > 0$ is source population
which $r < 0$ is sink population

Exponential growth

Typical for species with high dispersal

- Invasive species
- Speed of the dispersal depend on maximum growth rate (r_0)



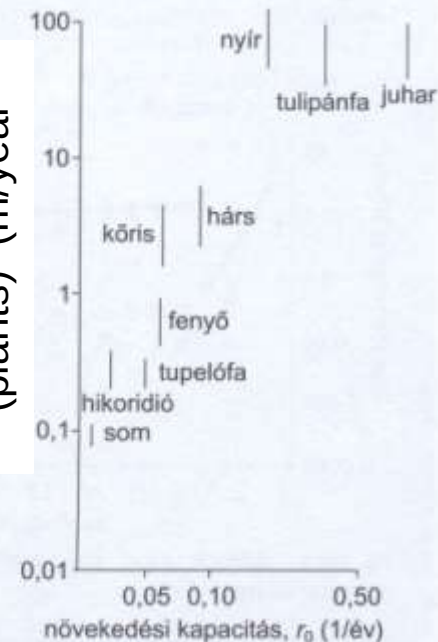
„10% role”
An average 10% of an introduced alien species survive in the new area

↑ An average 10% of these species could live longer in the new area

↑ An average 10% of these species could reproduce extremely-> invasive species

13. ábra Az őzönfajjá válás 10-es szabálya (WILLIAMSON és FITTER 1996 nyomán).

Speed of dispersal (plants) (m/year)



17. ábra Az Appalache-hegység déli részén honos fa nemzetségek terjedési sebességének függése a populációk növekedési kapacitásától. A függőleges vonalak a nemzetségbe tartozó fajok terjedési sebességeinek terjedelmét jelzik. Az adatok a szétszóródás és az életmenet jellemzők szabványosított vizsgálatából származó becslések (CLARK és mtsai 2001).

Density dependent population growth

Population growth could be regulated by environmental factors which influence and depend on the population size

– E.g.

- food
- site
- predators
- parasites

Regulation of the population growth is needed for the long existence of the populations

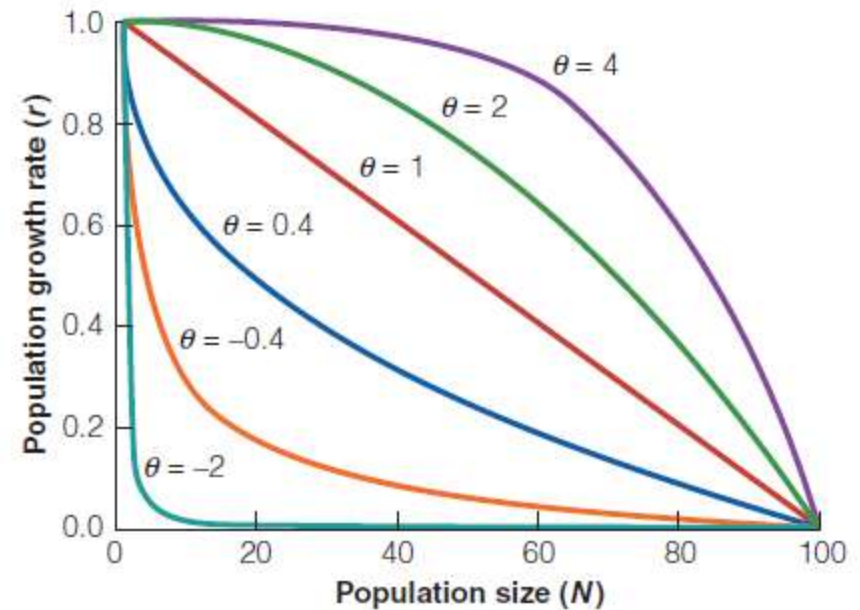
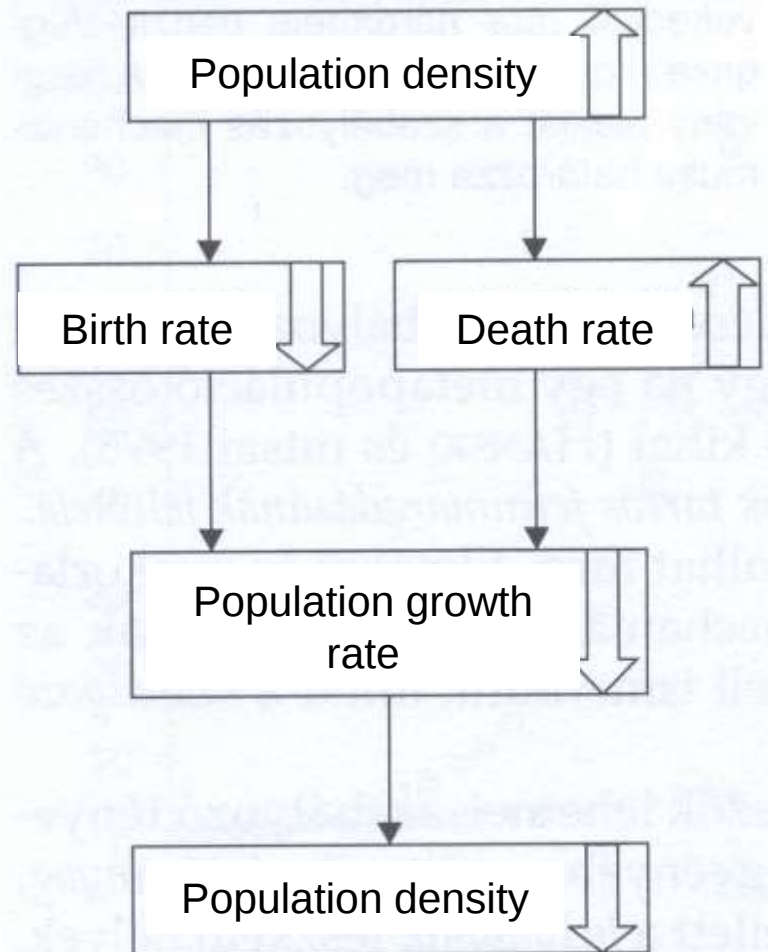
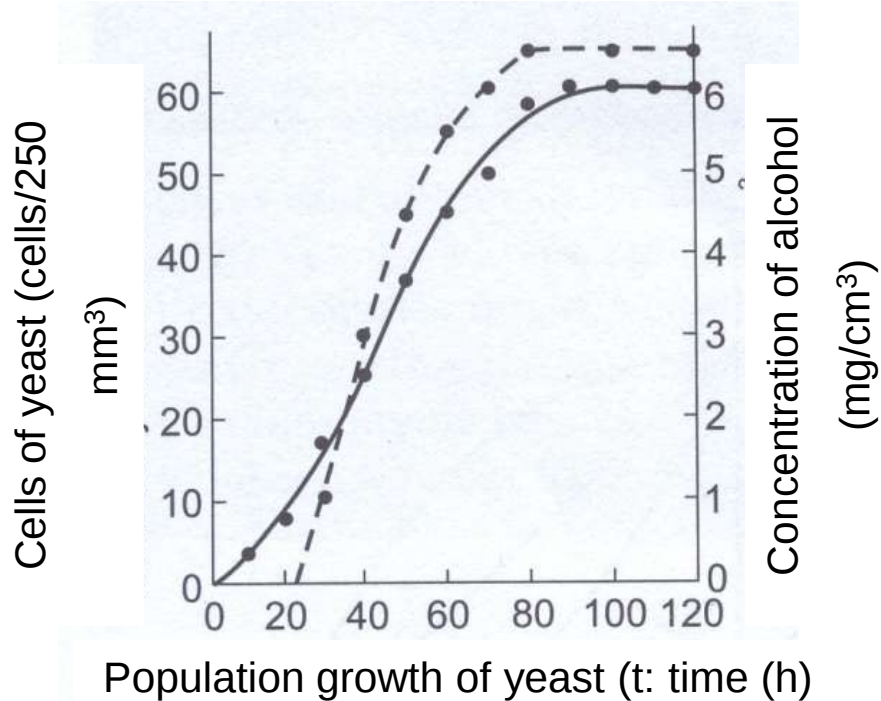


Figure 12 Population growth described by the theta (θ) logistic equation [Equation (12)]. For all of these curves, $K = 100$ and $r = 1.0$. The red line is identical to that shown in Figure 2 and represents the normal logistic equation assumption of a linear decline of population growth rate with increasing population size.

Density dependent population growth

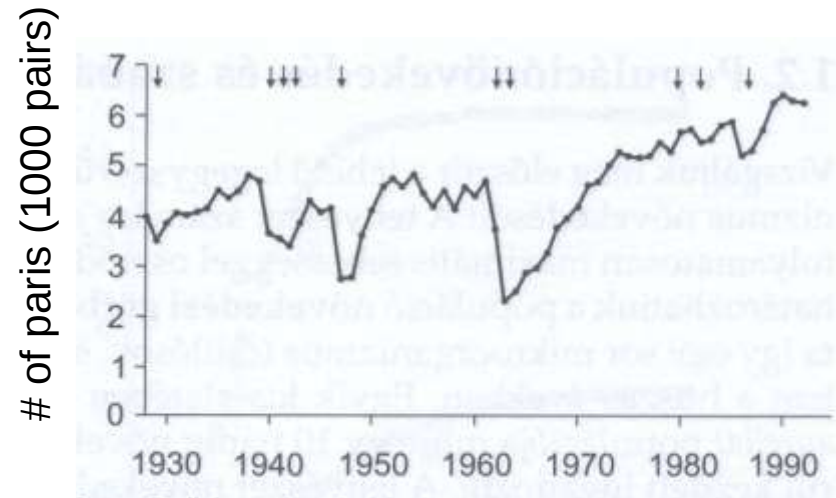
- Density dependent growth



Population growth

Ecological limiting factors:

- Corrective factors (Only modify the population size)
- Regulatory factors (population density influence the growth rate)



In the case of grey heron the cold winters (arrows) increase the death and decrease the population size but we can regard as corrective factors

Logistic model

$$\frac{dN}{dt} = r_0 * N * \left(1 - \frac{N}{K}\right)$$

where K: Carrying capacity

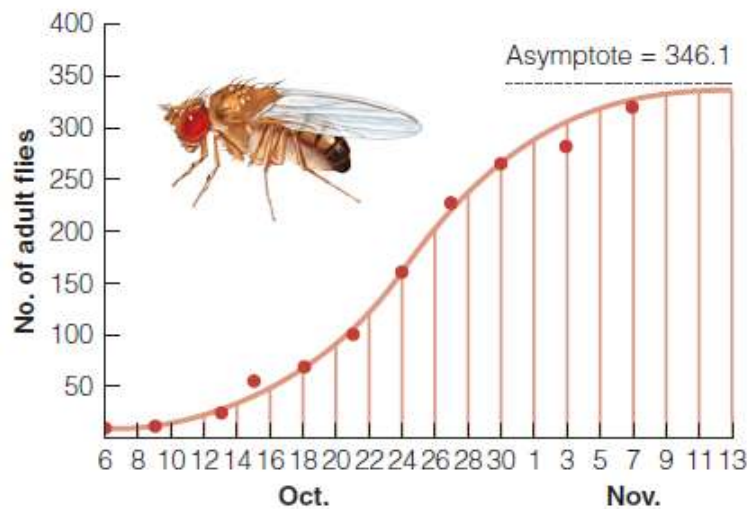


Figure 6 Growth of an experimental laboratory population of the fruit fly *Drosophila melanogaster*. The circles are observed census counts of adult flies, and the smooth curve is the fitted logistic equation. (After Pearl 1927.)

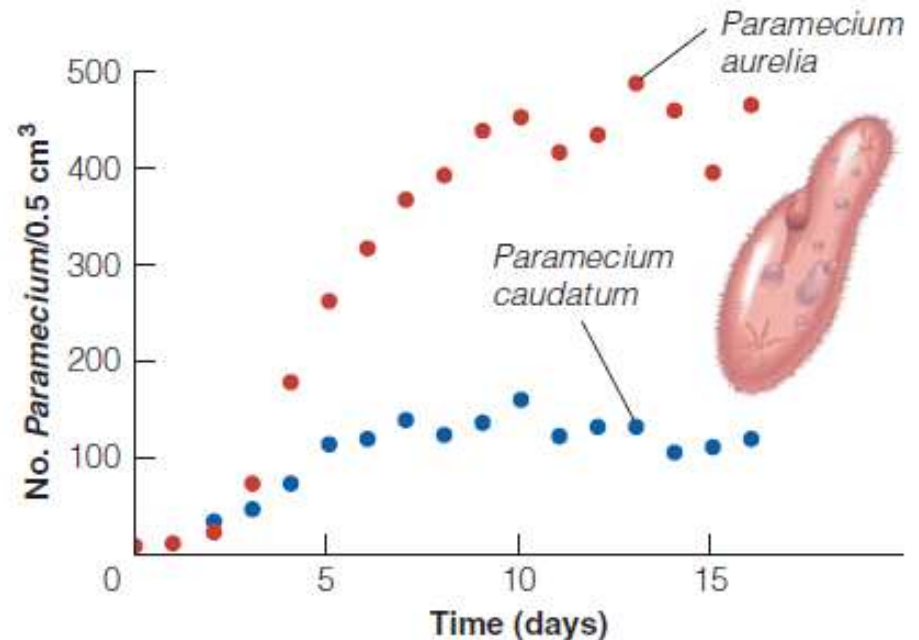


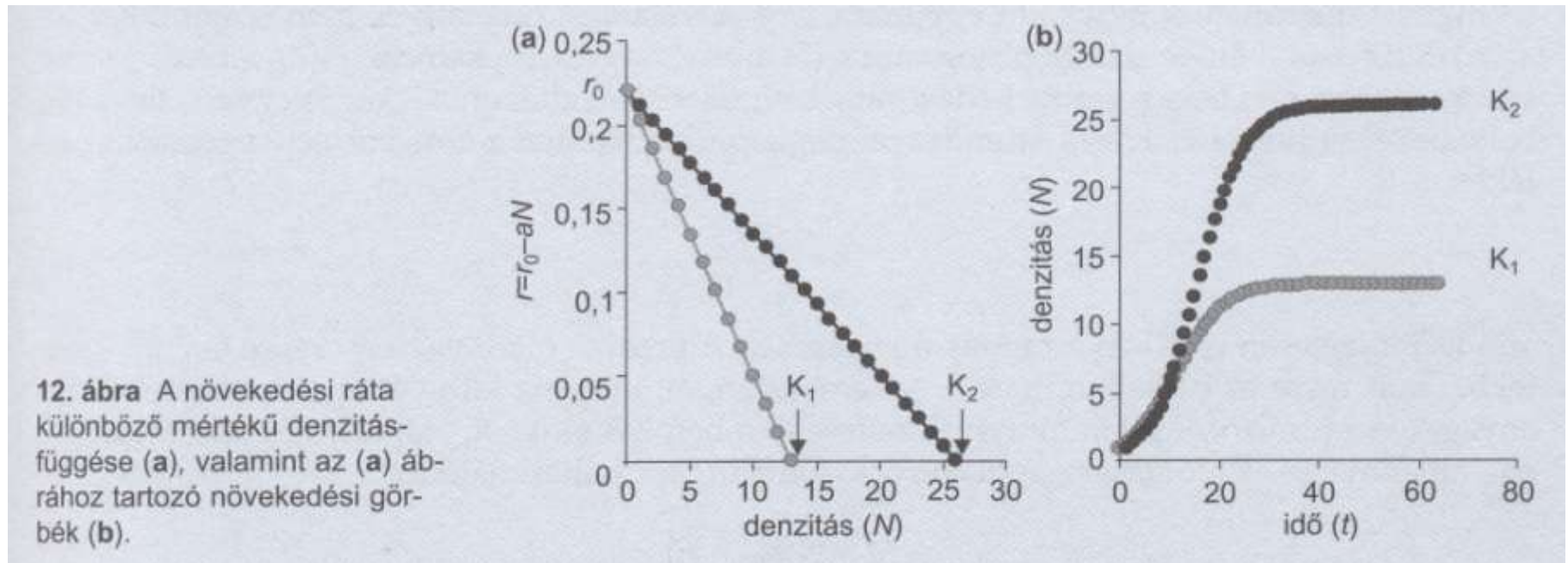
Figure 5 Population growth in the protozoans *Paramecium aurelia* and *P. caudatum* at 26°C in buffered Osterhout's medium, pH 8.0, with "one loop" of bacteria added as food. (Data from Gause 1934.)

Logistic model

$$\frac{dN}{dt} = r_0 \cdot N \cdot \frac{K-N}{K}$$

$$K = r_0 / a$$

Carrying capacity (K) is lower when density dependence of the growth rate is higher



density

time

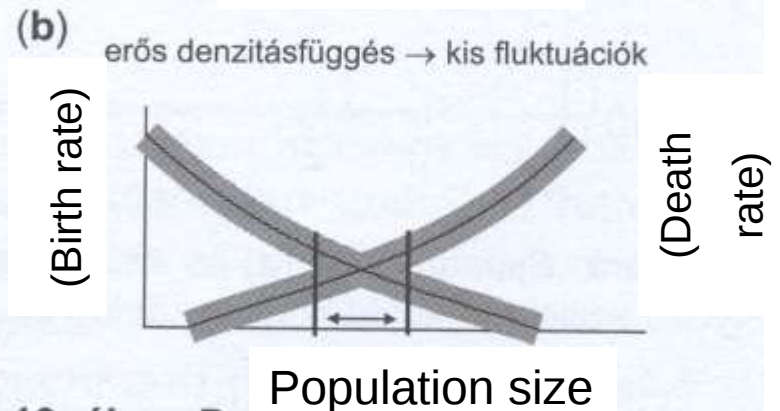
Logistic model

Fluctuation of the population size at K level is depend on the strenght of the density dependence

a- high fluctuation

b- small fluctuation

$$\frac{dN}{dt} = r_0 * N * \frac{K-N}{K}$$



10. ábra Denzitásfüggő születési és halálozási ráták logisztikus növekedés esetén. (a) Gyenge denzitásfüggés, (b) erős denzitásfüggés (CASE 2000 nyomán).

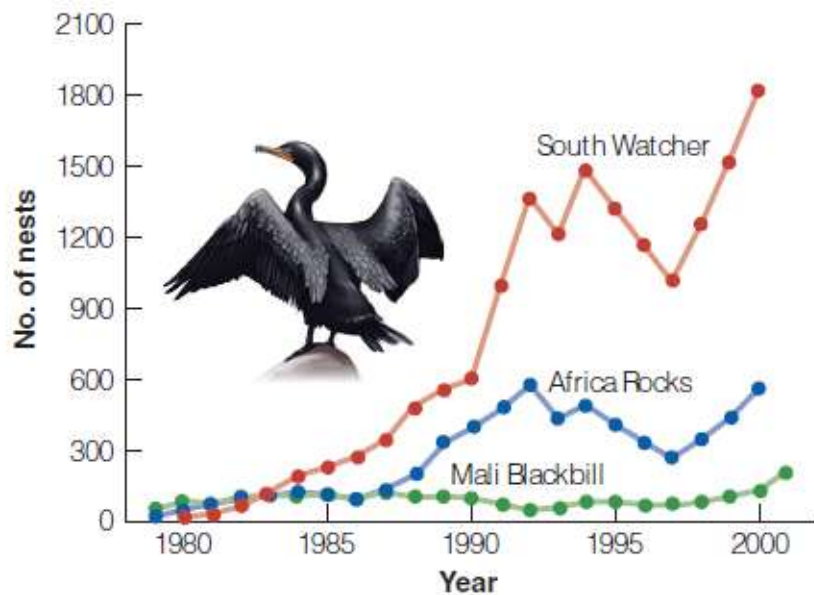
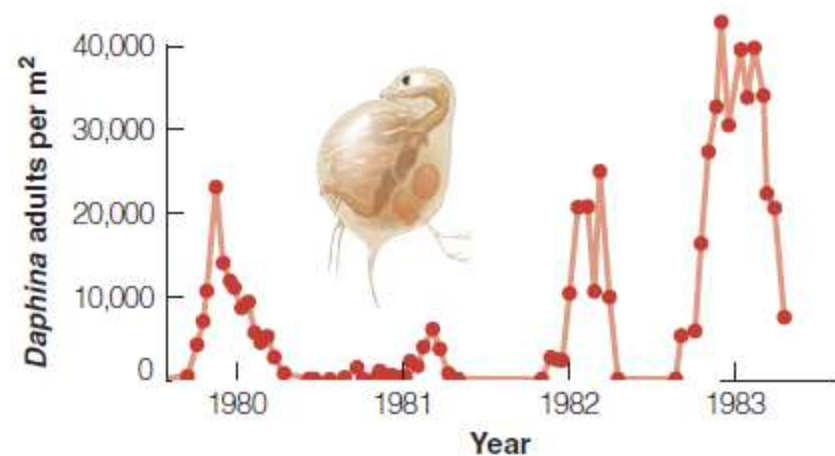
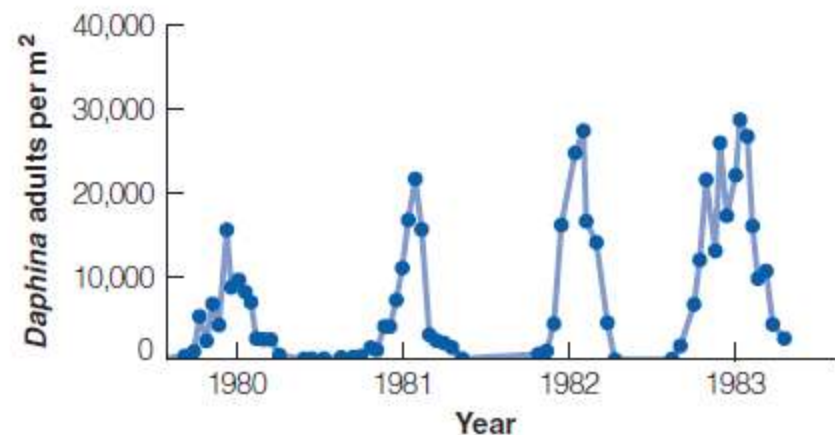


Figure 8 Growth of three colonies of the double-crested cormorant (*Phalacrocorax auritus*) on Lake Huron in the Great Lakes, 1978–2003. The drop in active nests during the mid-1990s was possibly due to climatic events, with some birds not nesting. Colony size differs, partly because of competition for nest sites and some colonies have stopped growing. (Data from Ridgway et al. 2006.)



(a) Eunice Lake



(b) Katherine Lake

Figure 11 Density of the cladoceran *Daphnia rosea* in Eunice Lake and Katherine Lake, British Columbia, from 1980 to 1983. Because these temperate lakes—(a) Eunice Lake and (b) Katherine Lake—show strong seasonal dynamics that vary from year to year, the population growth curve cannot be described by a simple equation like the logistic equation. (Data from Walters et al. 1990.)

For many years, the demographic approach was represented by a technique called key factor analysis, though in fact it identifies key phases (rather than factors) in the life of the organism concerned.

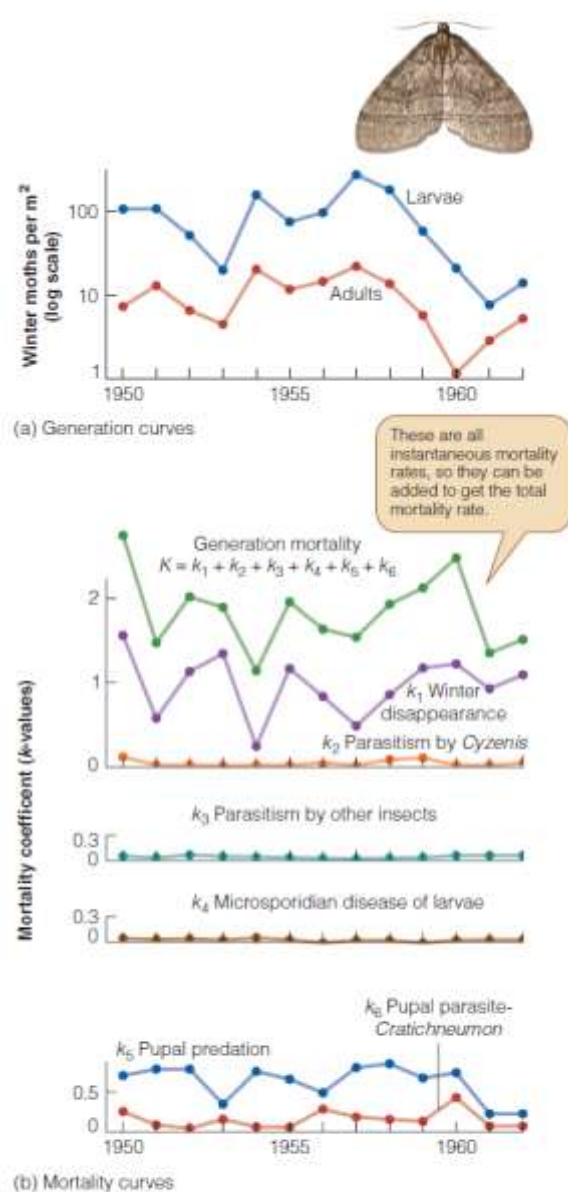


Figure 14 Key factor analysis of the winter moth in Wytham Woods near Oxford, 1950–1962. (a) Winter moth population fluctuations for larvae and adults. (b) Changes in mortality, expressed as k values, for the six mortality factors listed in Table 1. The biggest contribution to change in the generation mortality K comes from changes in k_1 , winter disappearance, which is the key factor for this population. (After Varley et al. 1973.)

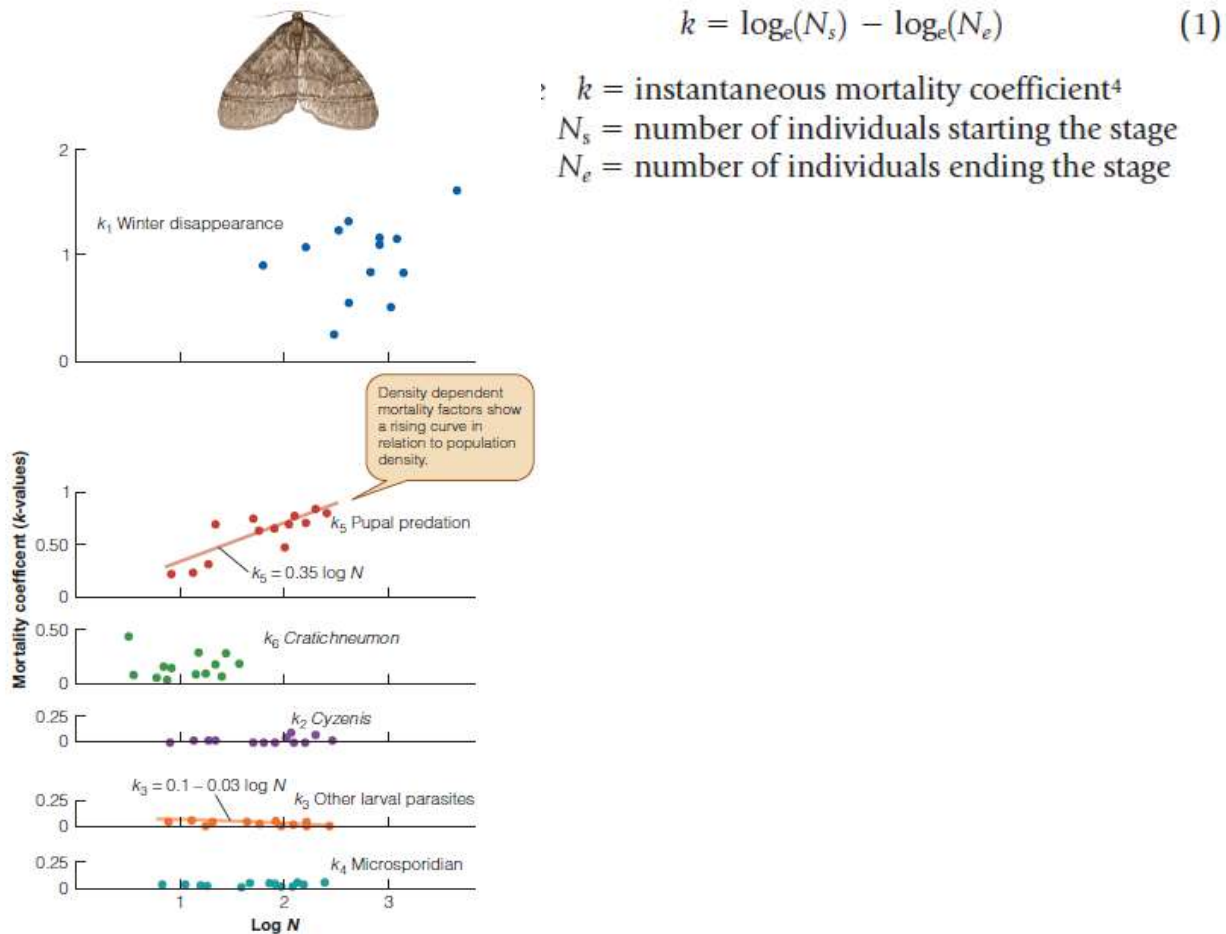
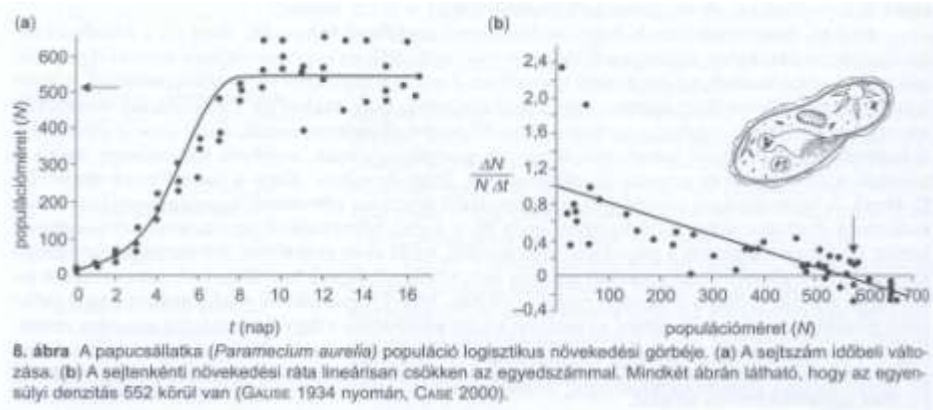


Figure 15 Relationship of winter moth mortality coefficients to population density. The k values for the different mortalities are plotted against the population densities of the stage on which they acted. k_1 and k_6 are density independent and quite variable, k_2 and k_4 are density independent but constant, k_3 is inversely density dependent, and k_5 is strongly density dependent. Compare these data with the idealized curves in Figure 16. (After Varley et al. 1973.)

Logistic model

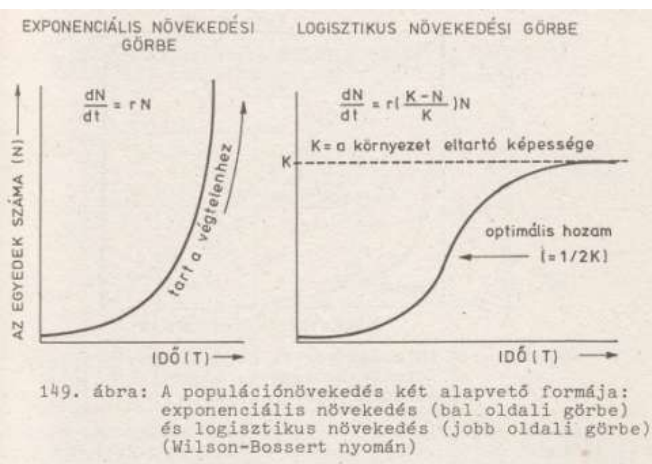


Implicit model: it is not contains the regulatory factors

$$\frac{dN}{dt} = r_0 * N * \frac{K-N}{K}$$

Optimal „harvesting/fishing”

For sustainable harvesting/fishing the population size need to keep at the $K/2$ level when the population able to produce the highest population growth



Optimal growth:

- $\frac{1}{2} K$
- $r_0/2a$

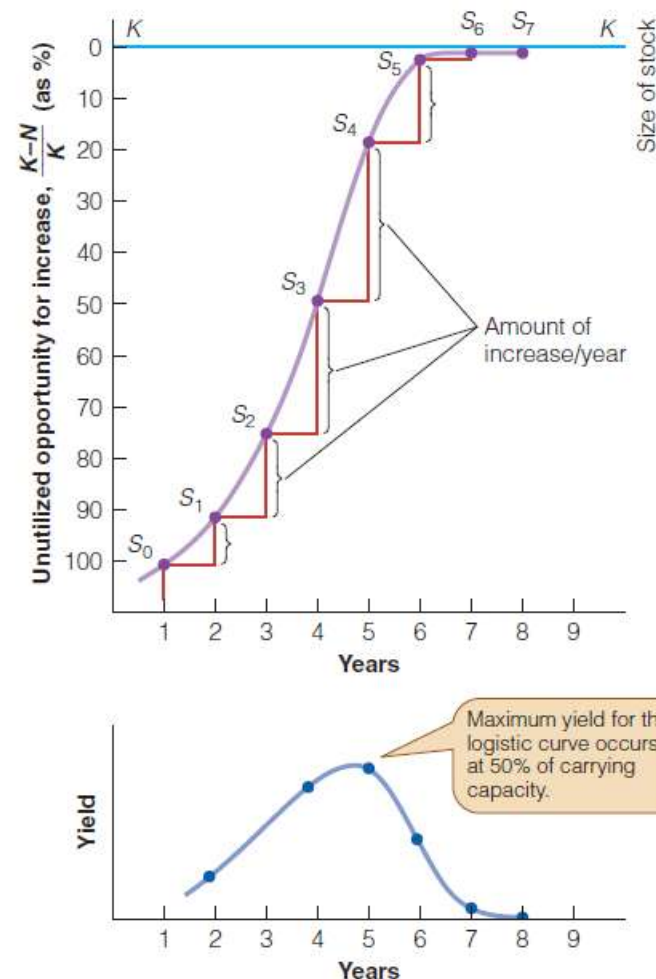
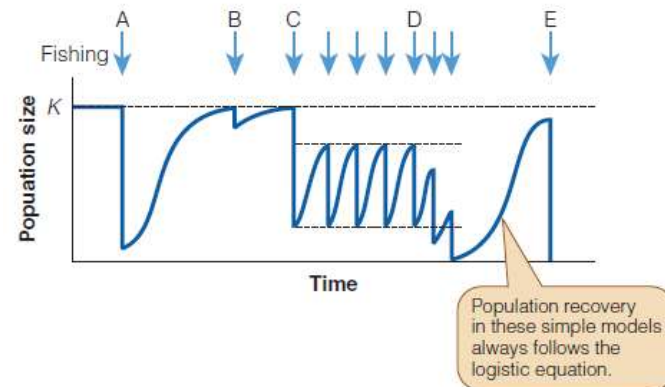


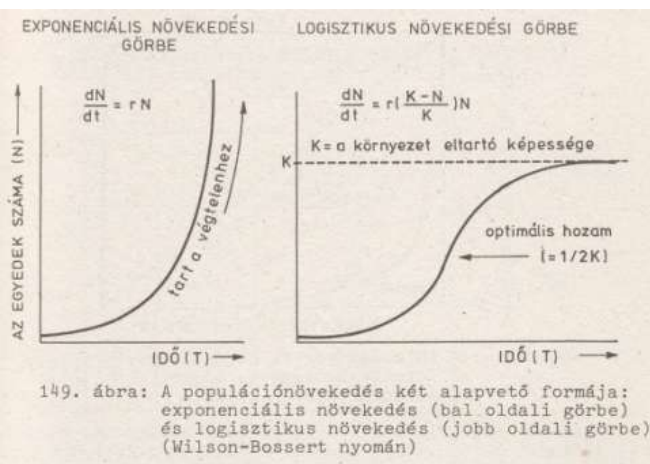
Figure 1 Use of sigmoid curve theory to describe the growth of a population that could be exploited. The amount of increase per year is the maximum yield that could be taken sustainably by the fishery. According to this model maximum yield is obtained by keeping the population at one-half of carrying capacity. (After Graham 1939.)

Optimal „harvesting/fishing”



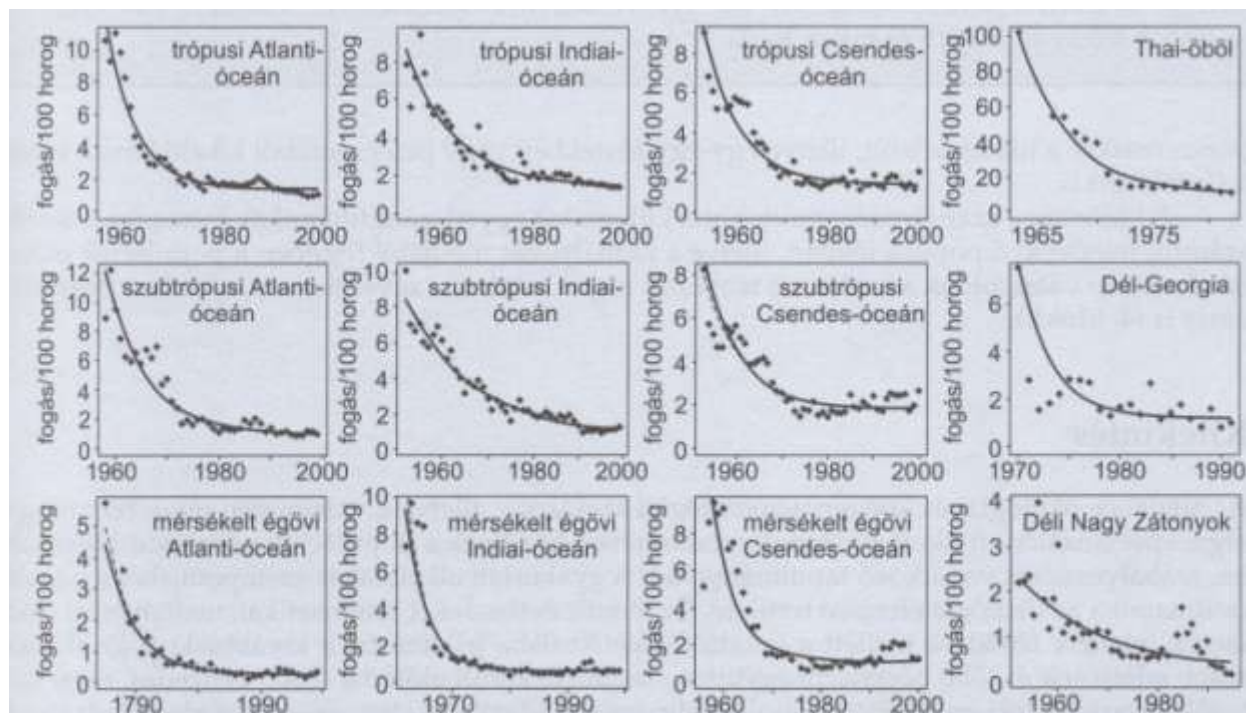
For sustainable harvesting/fishing the population size need to keep at the $K/2$ level when the population able to produce the highest population growth

For it need to know correctly the N , r_0 and K values
– Unfortunately, there are several bad examples (God fishing) by human habit



Optimal growth:

- $\frac{1}{2} K$
- $r_0/2a$



33. ábra: Az ábrákon az Észak-atlanti tőkehal (*Gadus morhua*) populációiban egységesen bekövetkezett gyors fogáscsökkenés követhető nyomon az 50-es évektől napjainkig, különböző oceáni régiókban (OLSEN és mtsai megjelenés alatt).

Monod model

Explicit model: contain the dynamics of regulatory factors

$$r(b) = r_0 \cdot \frac{c}{c+k}$$

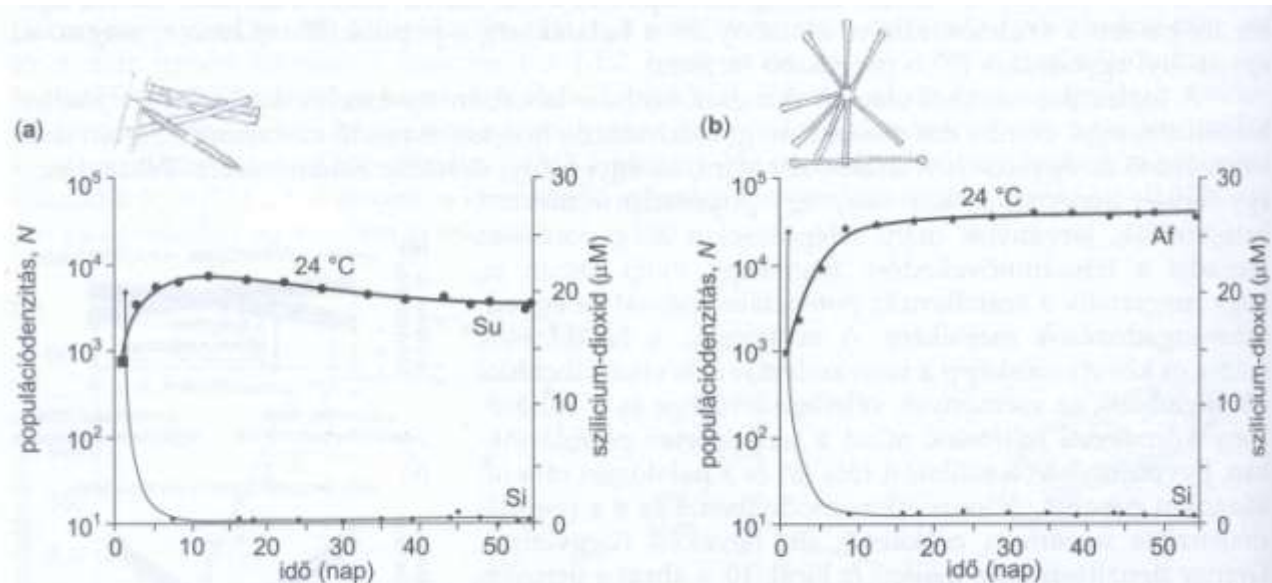
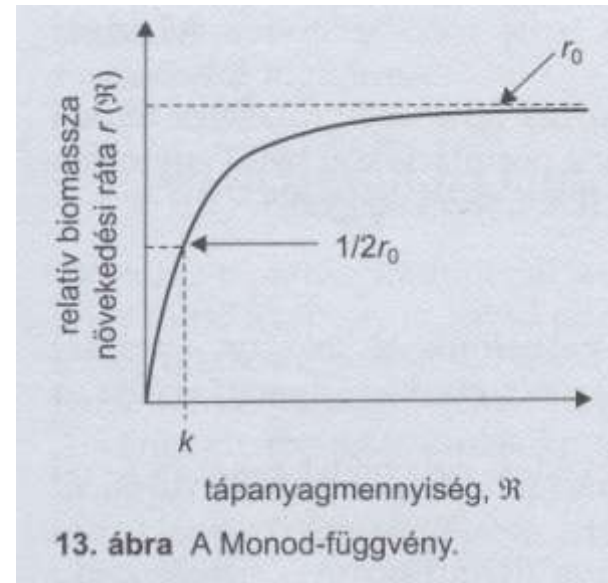
Ahol

$r(b)$: relative growth of biomass

r_0 : a maximum growth rate

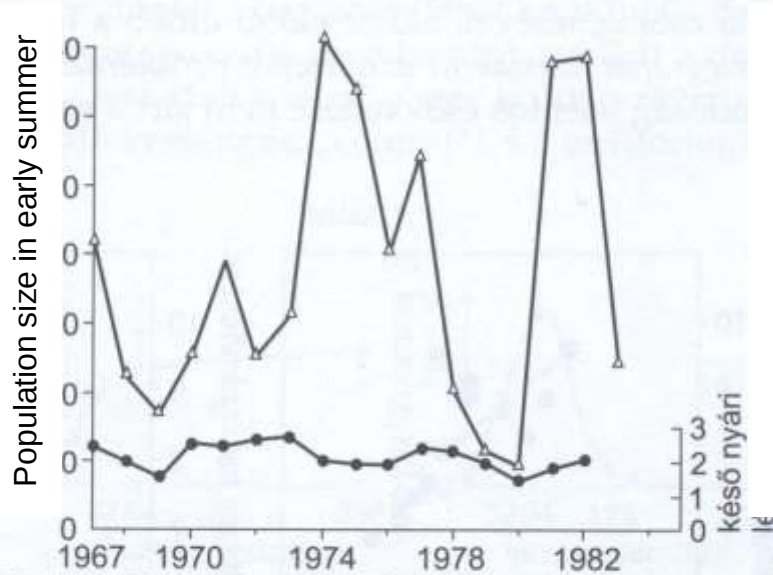
c : concentration of limiting source ($\mathcal{R}$)

k : half-saturation constants,



11. ábra *Synedra ulna* (a) és *Asterionella formosa* (b) kovamoszatok tiszta tenyészeinek növekedése és a szabályozó szilícium-dioxid-koncentráció változása az időben, 24 °C-on (TILMAN 1981 nyomán).

Regulation of population growth



25. ábra Sebes pisztráng (*Salmo trutta*) populáció kora nyári (Δ) és késő nyári (●) létszáma (ELLIOTT 1984, BEGON és mtsai 1986 nyomán).

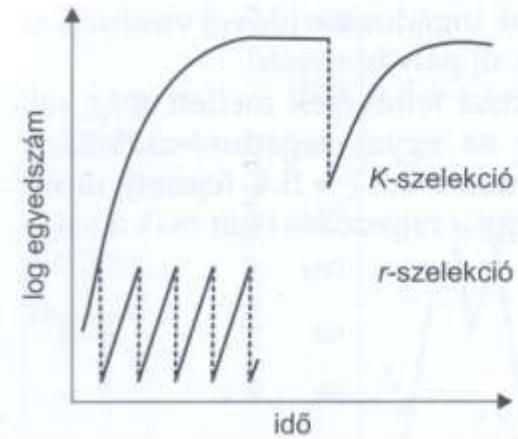
Population size in late summer

Regulatory factors

- Which season they act
- Which stadium/age groups are sensitive to the density change
- Which stadium/age groups are critical to the density change

In the case of salmon the late summer death rate is density dependent

Regulation of population growth

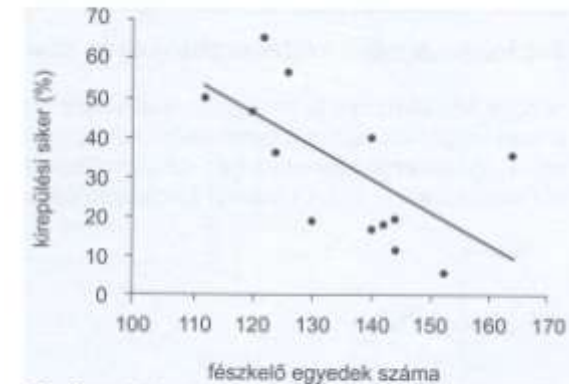


26. ábra Tenyésztési sémák. A szaggatott vonalak a tenyészet kis denzitásra csökkentését jelölik. Az *r*-szelekciós séma átlagosan alacsony denzitáson, a *K*-szelekciós séma átlagosan magas denzitáson tartja a tenyészetet. (Az *y* tengely a denzitás logaritmusát mutatja!)

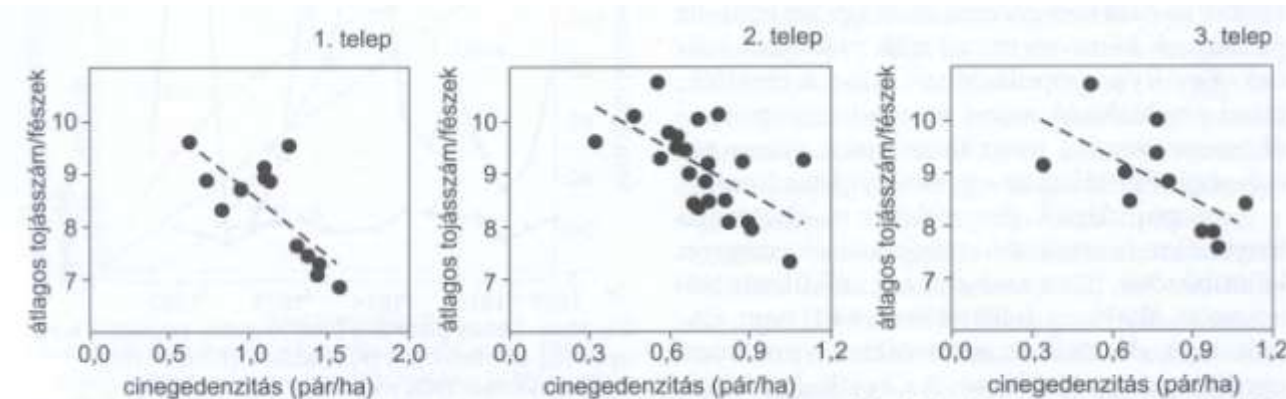
Regulation:

- Outside the breeding season (r-selection)
- During the breeding season (K-selection)

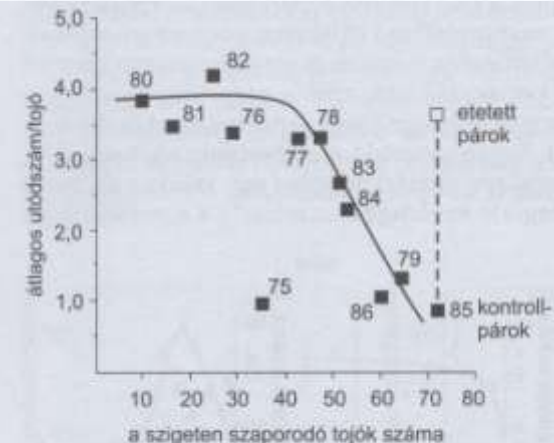
II.1. Szabályozott populációnövekedés



28. ábra A fészkelés sikeressége (tojások hányad részéből származik kirepülő fióká egy-egy fészkekben) különböző méretű bütykös ásólud (*Tadorna tadorna*) populációkban (PATTERSON és mtsai 1983).



27. ábra Széncinege (*Parus major*) párok átlagos tojásszámának függése a fészkelő párok denzitásától (pár/hektár), 3 különböző odutelepen. Egy-egy pont egy-egy év adata (Вотн 2000 nyomán).



31. ábra Egy táplálékhozzáadási kísérlet egy kanadai énekes verébsármány (*Melospiza melodia*) populációban 1985-ben. A számok a pontok mellett az adatfelvétel évét jelölik (ARCESE és SMITH 1988, BEGON és mtsai 1986 nyomán).

Population growth regulation and demography

Critical stadiums/age groups: their density influence the birth/death in the population

Sensitive stadiums/age groups: these groups sensitive to the density

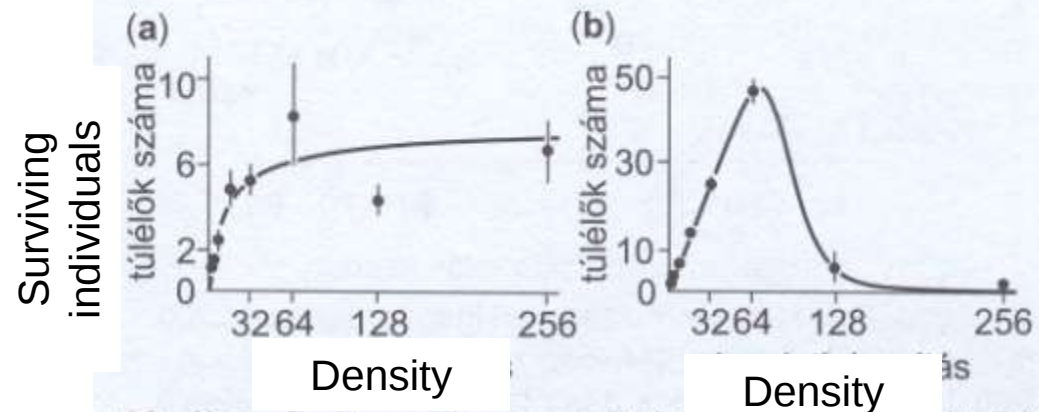
e.g.. Flue in the population of Papua-New Guinena

Sensitivity: new born and elderly people, higher death rate because of the flue

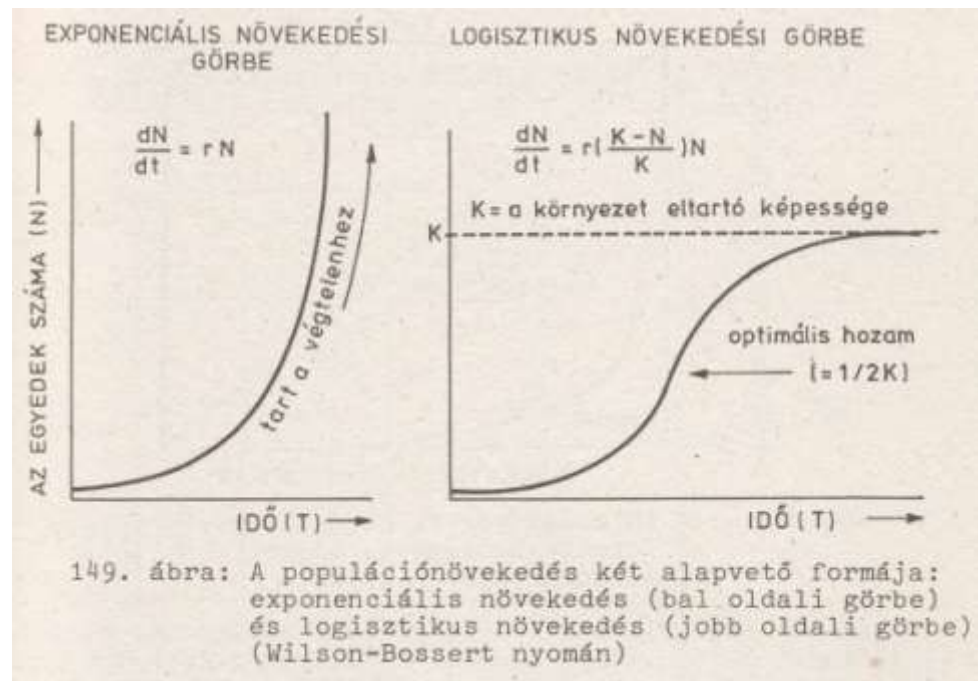
Critical: teenager and young adults, the most responsible groups of dispersal of the flue

When competition among individual vary with population density, growth will depend on density:

- Contest competition (a)
- Scramble competition (b)



29. ábra Pontosan kompenzált (a) és túlkompenzált (b) denzitásfüggés bogaraknál. A pontok az átlagot, a bajuszok a szórást jelölik. (a) *Stegobium paneceum*, (b) *Lasioderma serricorne* (BELLOWS 1981).



High r value

- Living in extreme habitats
- Dominantly limited by abiotic factors, living transient habitats

Importance of fast finding of habitats

Importance of fast invasion of habitats

Surviving large changes (abiotic)

Life history strategies

R-K strategists, R-K continuum

Characteristics of r- and K-selected organisms

r-organisms	K-organisms
Exponential growth	Logistic growth
Type III survivorship curve	Type I survivorship curve
short-lived	long-lived
small	large
weak	strong or well-protected
waste a lot of energy	energy efficient
less intelligent	more intelligent
have large litters	have small litters
reproduce at an early age	reproduce at a late age
fast maturation	slow maturation
little care for offspring	much care for offspring
strong sex drive	weak sex drive
small size at birth	large size at birth
High dispersal speed	Low dispersal speed

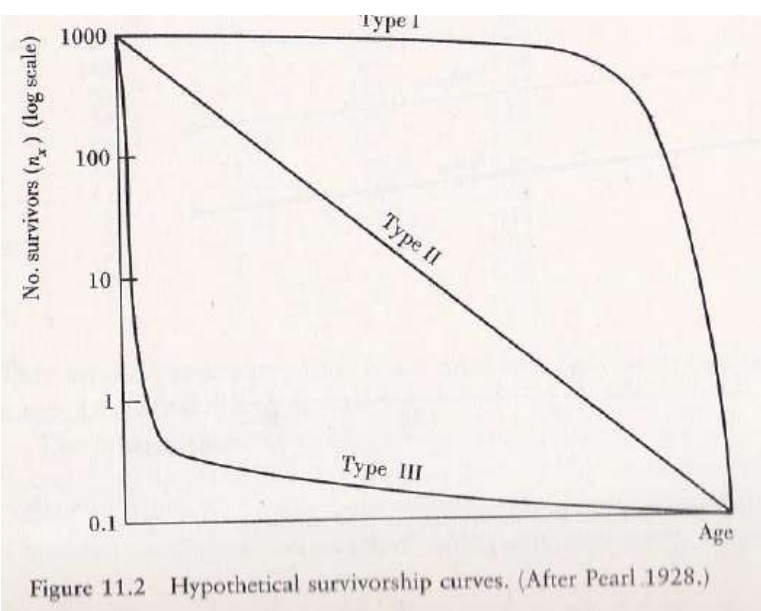
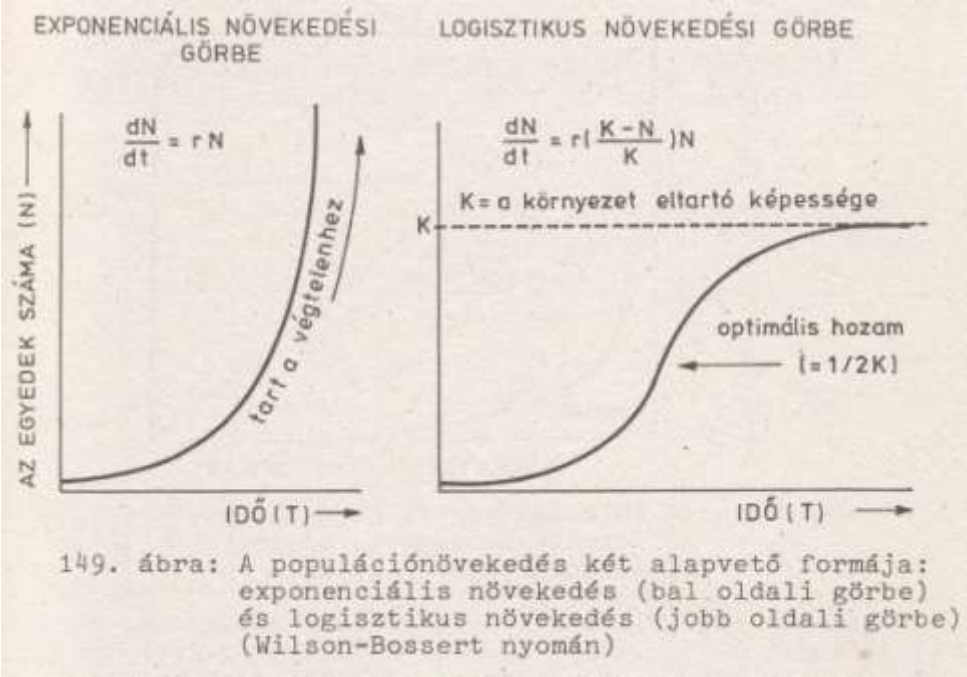


Table 2 Characteristics of *r*-selected species and *K*-selected species. Many species will have characteristics intermediate between these two extreme life history strategies.

<i>r</i> -selected life history	<i>K</i> -selected life history
Small-sized organisms	Large-sized organisms
Many small reproductive units (seeds, spores, offspring)	Few larger reproductive units
Little energy used per reproductive unit	Much energy used to produce one reproductive unit
Early maturity	Late maturity and often parental care
Short expectation of life	Long life expectancy
Single reproductive episode (semelparous)	Many reproductive episodes (iteroparous)
Type 3 survival curve (Figure 6)	Type 1 or 2 survival curve

Common dandelion, *Taraxacum officinale*, plants were either left for five years in crowded, multispecies communities (*K*-selecting), or were ‘weeded out’ twice per year, early in their adult lives, such that they had to regrow again from root stumps or re-establish from newly deposited seed (*r*-selecting). They were then grown side by side, in a common garden, either from seeds or as cuttings from established plants

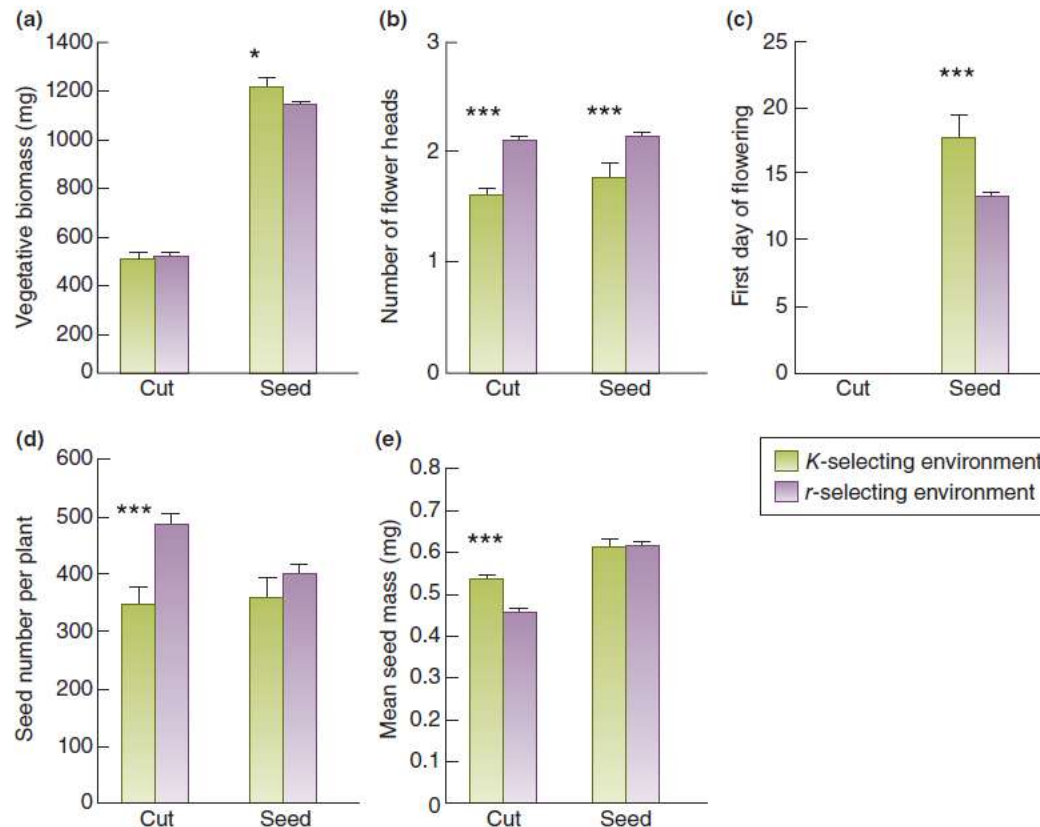


Figure 7.20 Evidence for *r*- and *K*-selection in dandelions. Results of an experiment in which dandelions, *Taraxacum officinale*, were subjected for five years to either a *K*-selecting environment (grown crowded with several other species) or an *r*-selecting environment (repeatedly weeded out and hence subjected to persistent density-independent mortality). They were then grown in a common garden either as cuttings from established plants (‘cut’) or from seed. Bars are ± 1 SE; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. (a) Vegetative biomass, (b) number of flower heads per plant, (c) period to first flowering, (d) seed number per plant, (e) mean seed mass. Source: After Lipowsky *et al.* (2012).

10.07

Evolution and Ecology

Darwin and Wallace (1958) Natural Selection – operates through the following steps:

1. Variation occurs in every group of plants and animals, Individuals are not identical in any population
2. Every population of organisms produce an excess of offsprings
3. Competition will occur among these offspring for the resources they need to live
4. The most fit offspring will survive. Among all the offspring competing for limited resources, only those individuals best able to obtain and use these resources will survive
5. If the characteristics of the most fit organisms are inherited, these favored traits will be passed on the next generation

The environments that organisms inhabit shape the evolution that occurs.

Traits favored by natural selection are the products of one or more individual genes – alleles of a locus change in frequency over time

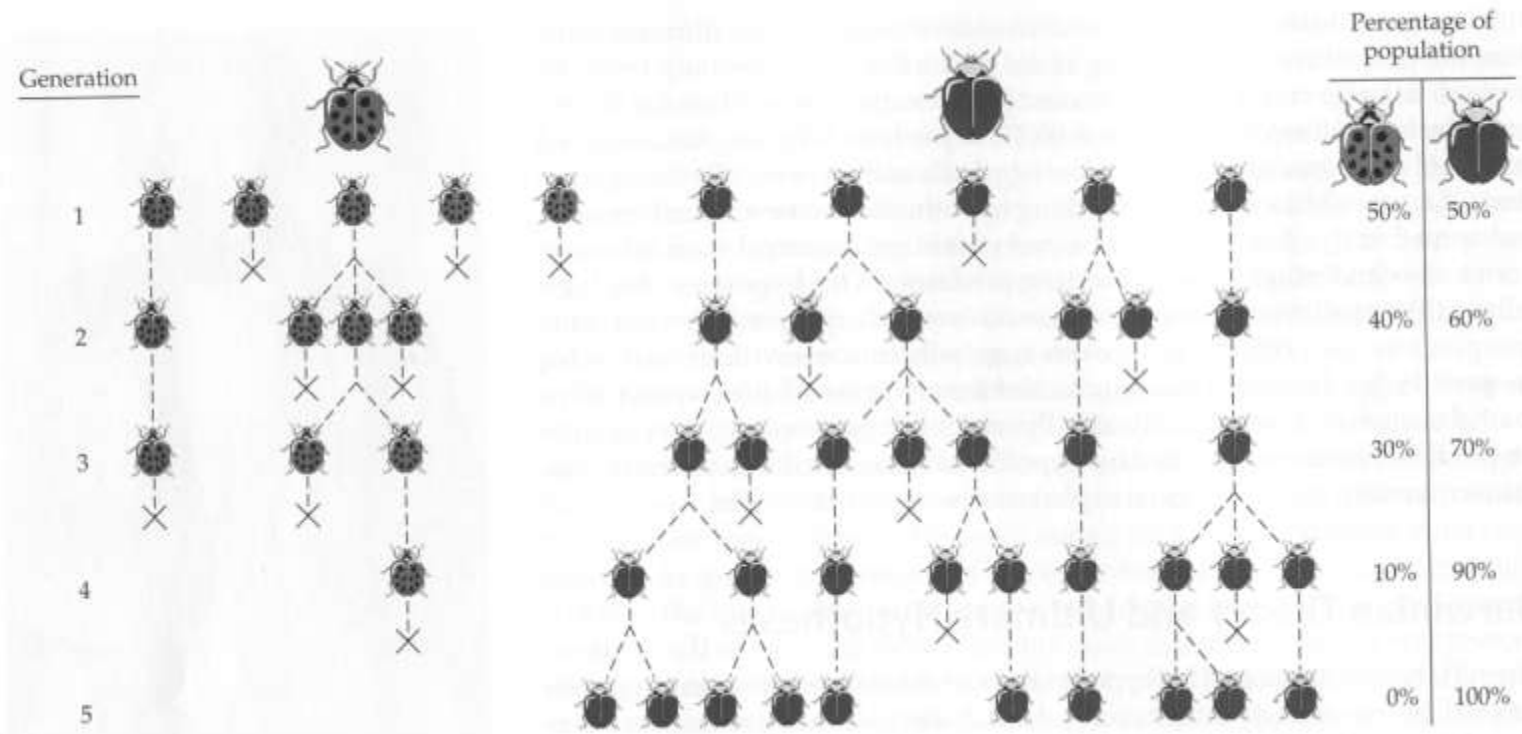
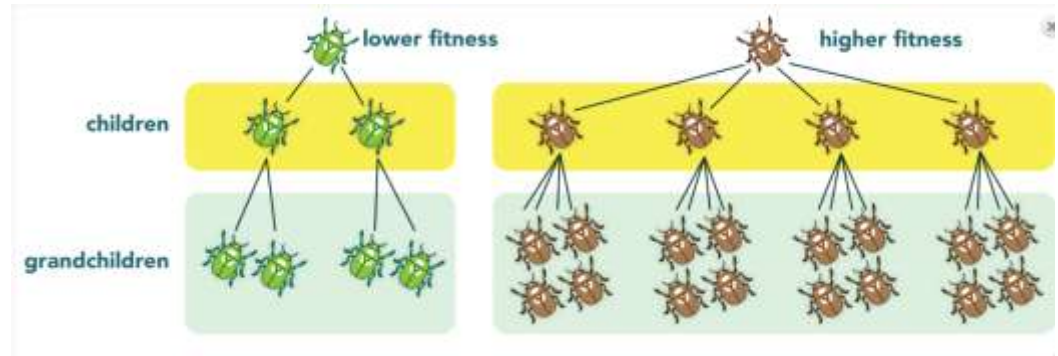
Evolution through natural selection results in **adaptation** and under appropriate conditions produce new species (**speciation**)

Evolution and Ecology

Darwinian fitness: Survival of the form (phenotypic or genotypic) that will leave the most copies of itself in successive generations

Two basic components:

- survival
- Reproductive success



Evolution and Ecology

Adaptation

Natural selection acts on phenotypes

Changes in gene frequencies occur only when there is a correlation between genotype and phenotype

Three types of selection operate on phenotypic characters

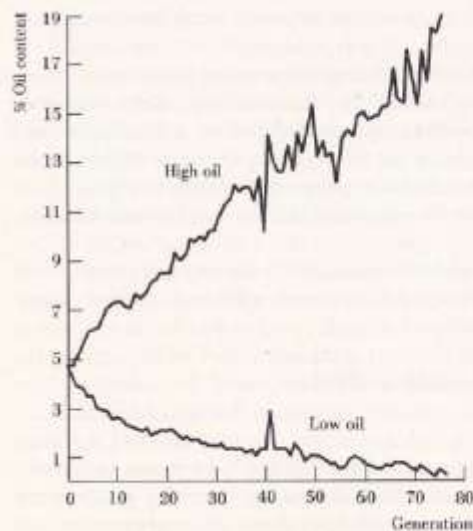


Figure 2.2 Directional selection in corn (maize), *Zea mays*, for high and low oil content over 76 generations. (After Dudley 1977.)

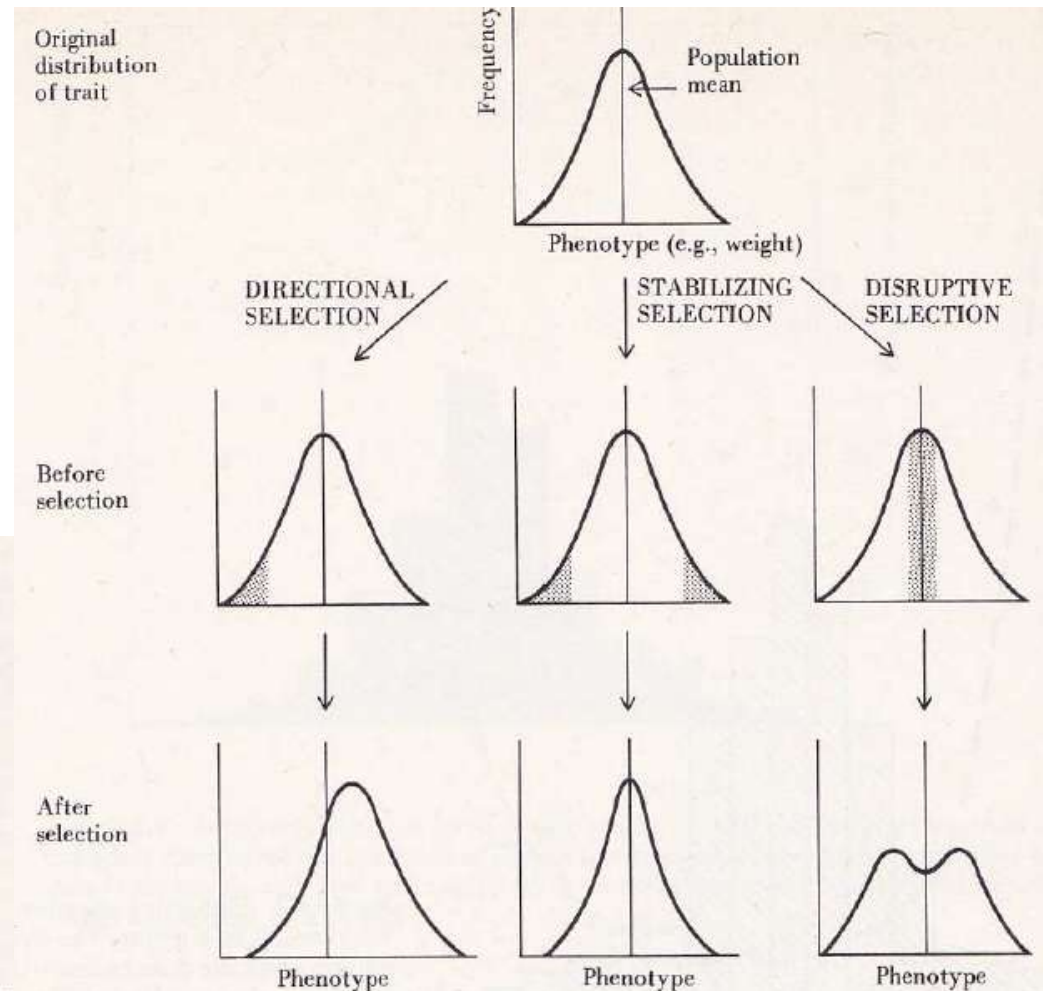


Figure 2.1 Three types of selection on phenotypic characters. Individuals in the shaded areas are selected against.

Evolution and Ecology

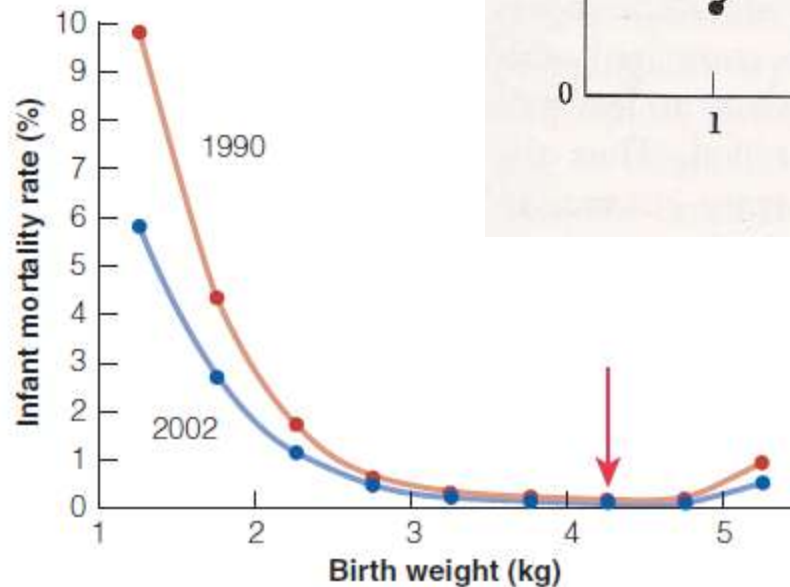


Figure 4 Stabilizing selection for birth weight in humans. Data from United States for infants, 1990 and 2002. The optimal birth weight (red arrow) is 4.25 kg, with a broad range of minimal mortality between 3.2 kg and 4.8 kg. Because of medical advances, infant mortality has been falling steadily, so the 1990 curve is higher than the 2002 curve. (Data from National Center for Health Statistics 2006).

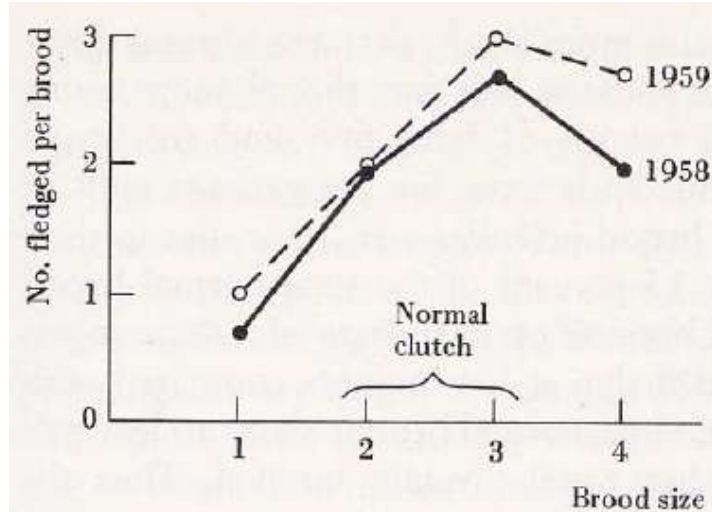
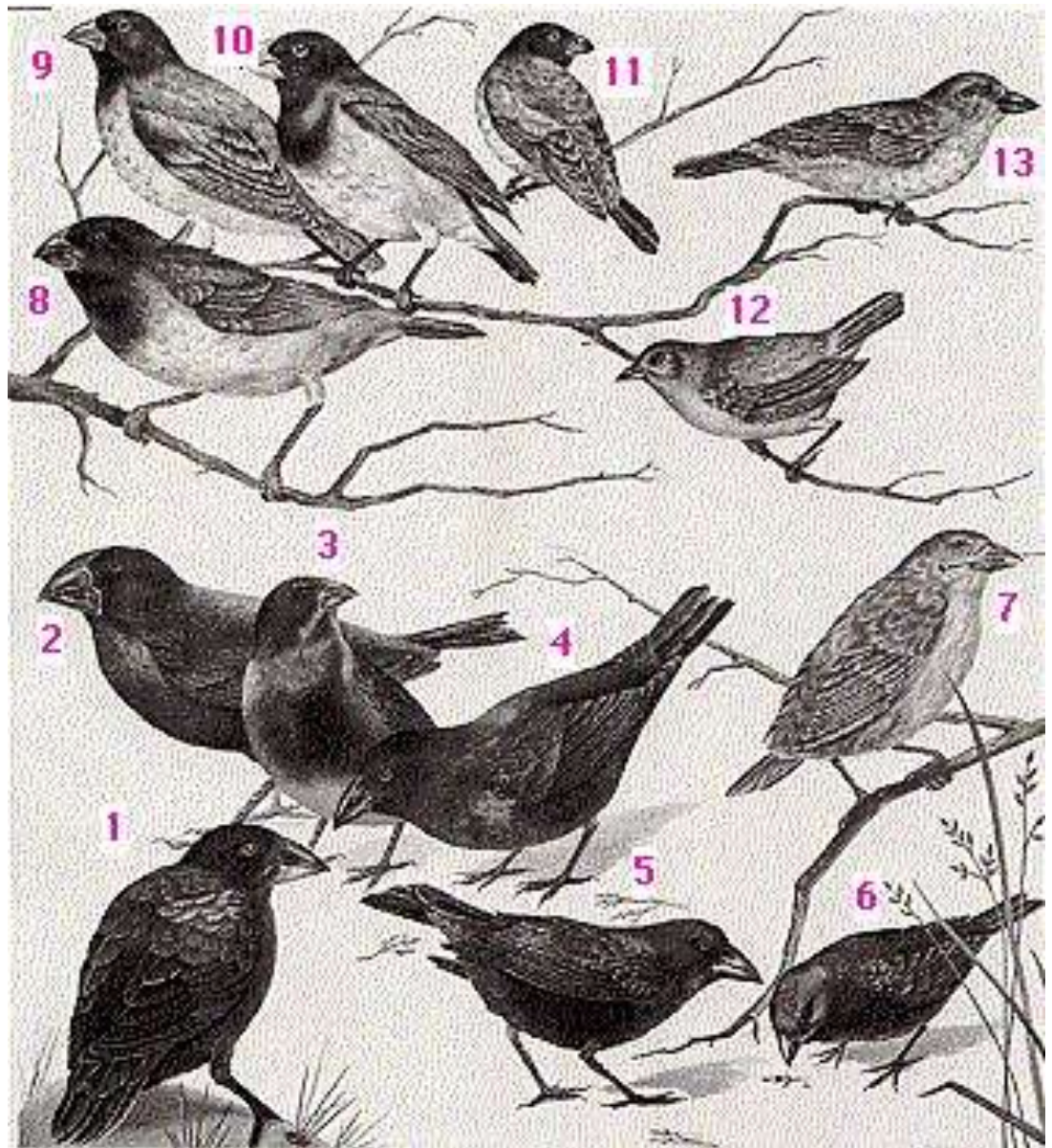


Figure 2.5 Production of young swifts (*Apus apus*) in relation to clutch size in England. The normal clutch is two to three; broods were increased to four artificially. Larger broods do not produce more young, and natural selection is stabilizing. (After Perrins 1964.)

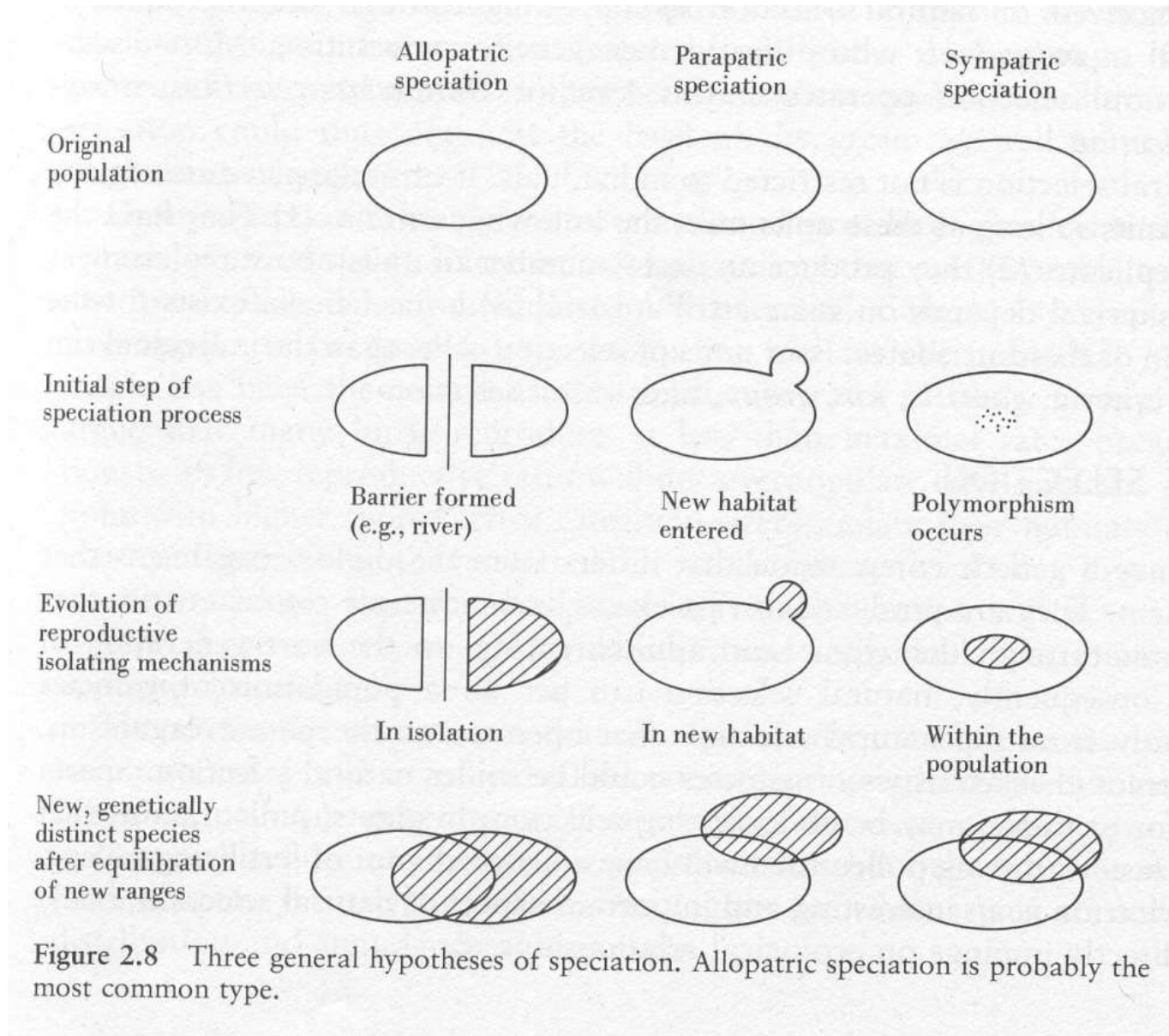
Darwin finch, Galapagos islands
Adaptive radiation – disruptive
selection

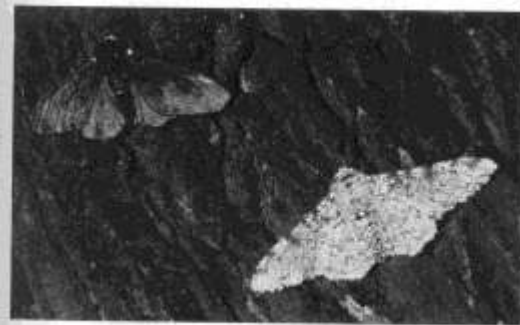
1. Large cactus finch (*Geospiza conirostris*)
2. Large ground finch ([*Geospiza magnirostris*](#))
3. Medium ground finch ([*Geospiza fortis*](#))
4. Cactus finch (*Geospiza scandens*)
5. Sharp-beaked ground finch (*Geospiza difficilis*)
6. Small ground finch (*Geospiza fuliginosa*)
7. Woodpecker finch (*Cactospiza pallida*)
8. Vegetarian tree finch (*Platyspiza crassirostris*)
9. Medium tree finch ([*Camarhynchus pauper*](#))
10. Large tree finch ([*Camarhynchus psittacula*](#))
11. Small tree finch (*Camarhynchus parvulus*)
12. Warbler finch (*Certhidia olivacea*)
13. Mangrove finch (*Cactospiza heliobates*)



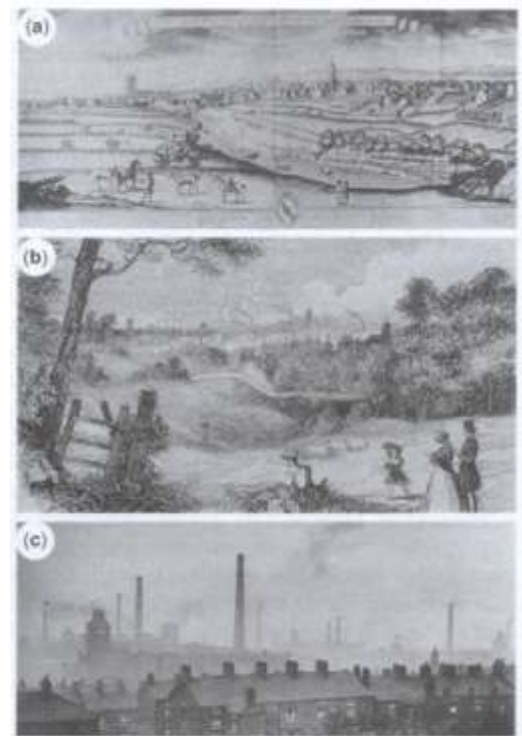
film

Speciation





10 The salt and pepper moth *Biston betularia*. One typical (light coloration) individual and one melanic (black) individual are shown in each photograph. Photographs (left) by Michael Tweedie; (right) photograph by Bruce Grant.



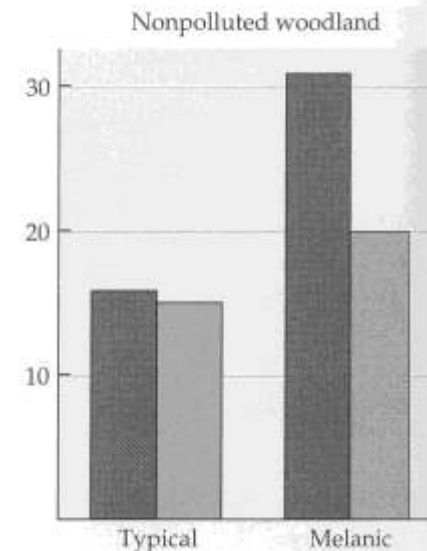
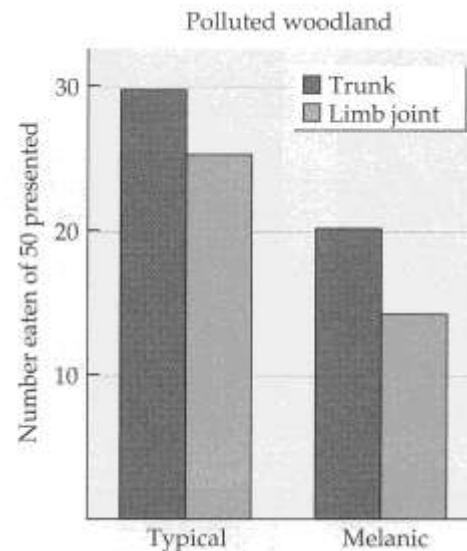
13. ábra Manchester környékének lát képe (a) 1730, (b) 1860 és (c) 1954-ben. Az a és b képet ugyanazon a helyen állva készítették, míg a c ugyanannak a területnek a képe máshonnan fényképezve (Russey 2006 nyomán).

Natural selection of peppered moth species during XIX-XX century in UK.

Ratio of dark types increased in polluted habitats against white types – industrial melanism

Evolutionary processes can be fast

In polluted woodland are more dark types comparing to not polluted woodland



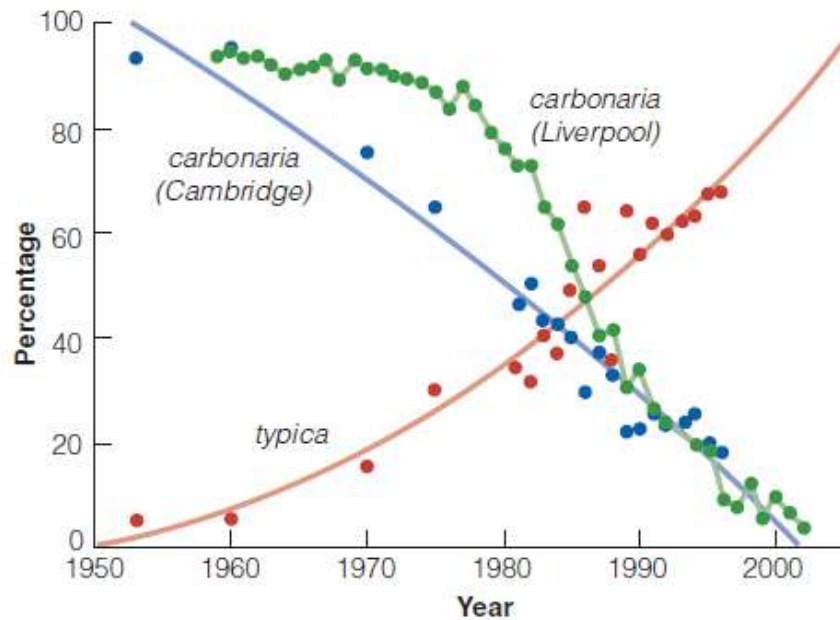
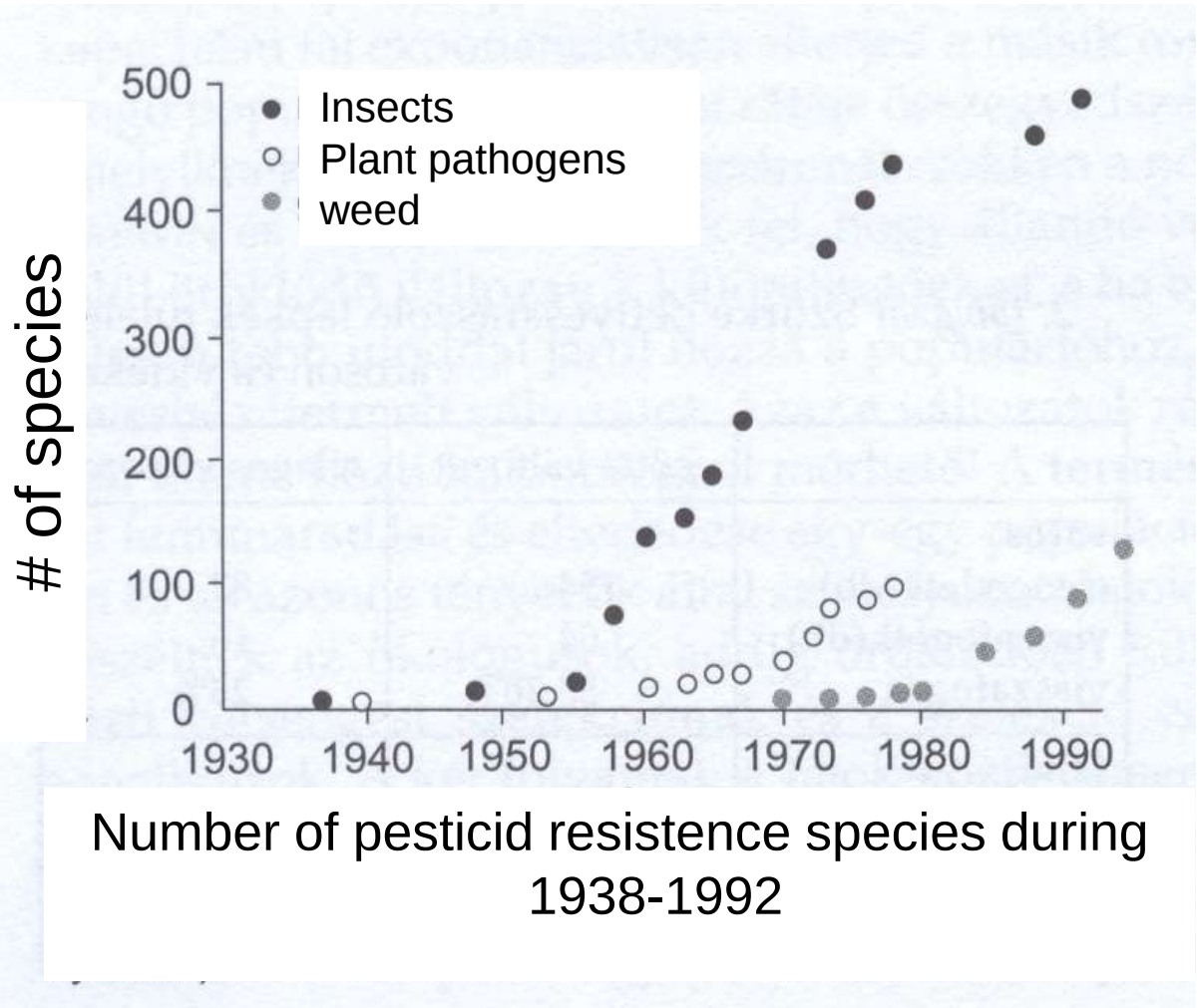


Figure 1 Evolution in the peppered moth *B. betularia* in England and North America. The photo shows both phenotypes of the peppered moth. The black form, *carbonaria*, has been declining in abundance since 1950 with the decline in industrial pollution in central England. The same change has occurred in eastern North America. Differential bird predation is believed to be the major mechanism of selection. (Photo: H. B. D. Kettlewell; data from Majerus 1998.)

Evolutionary processes can be fast



Unit of selection

Species ?

Group ?

Individual?

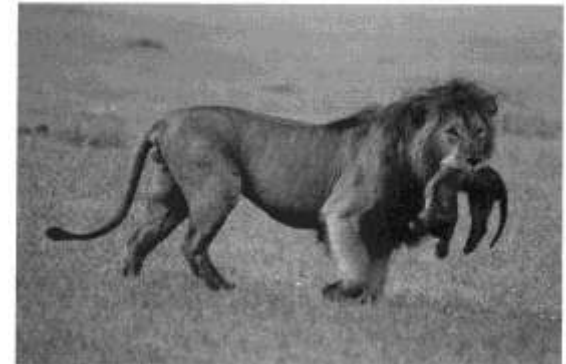
Gene ?!

(„Selfish gene” DAWKINS 1976)

<https://ia601602.us.archive.org/6/items/pdfy-RHEZa8riPwBuUyrV/The%20Selfish%20Gene.pdf>

- Individual – gene machine of genes
- Individual not, but gene forming individual could be immortal
- Recent genes had higher fitness than not existing one
 - Higher fitness even against fitness of others (e.g. lions)
- Selfish Genes vs. Altruistic behaviour
 - Level of altruism is higher among individuals with high genetic similarity,

Behaviour Ecology



Lion behaviour

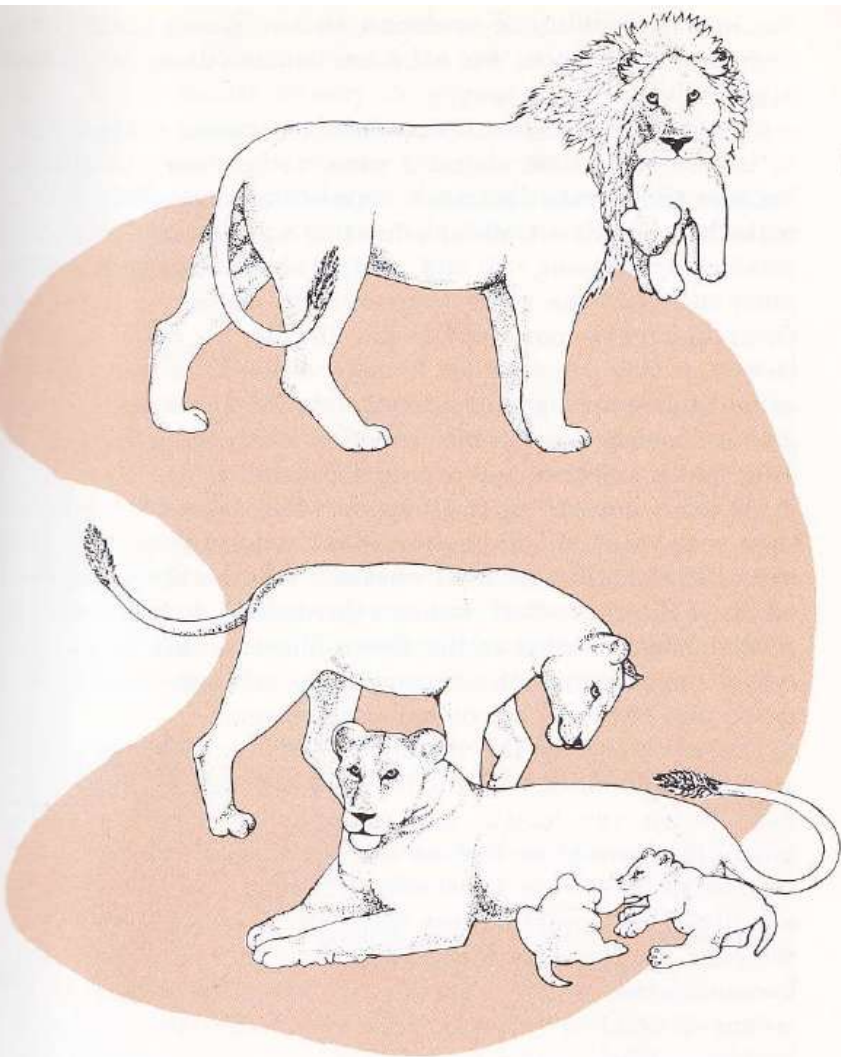
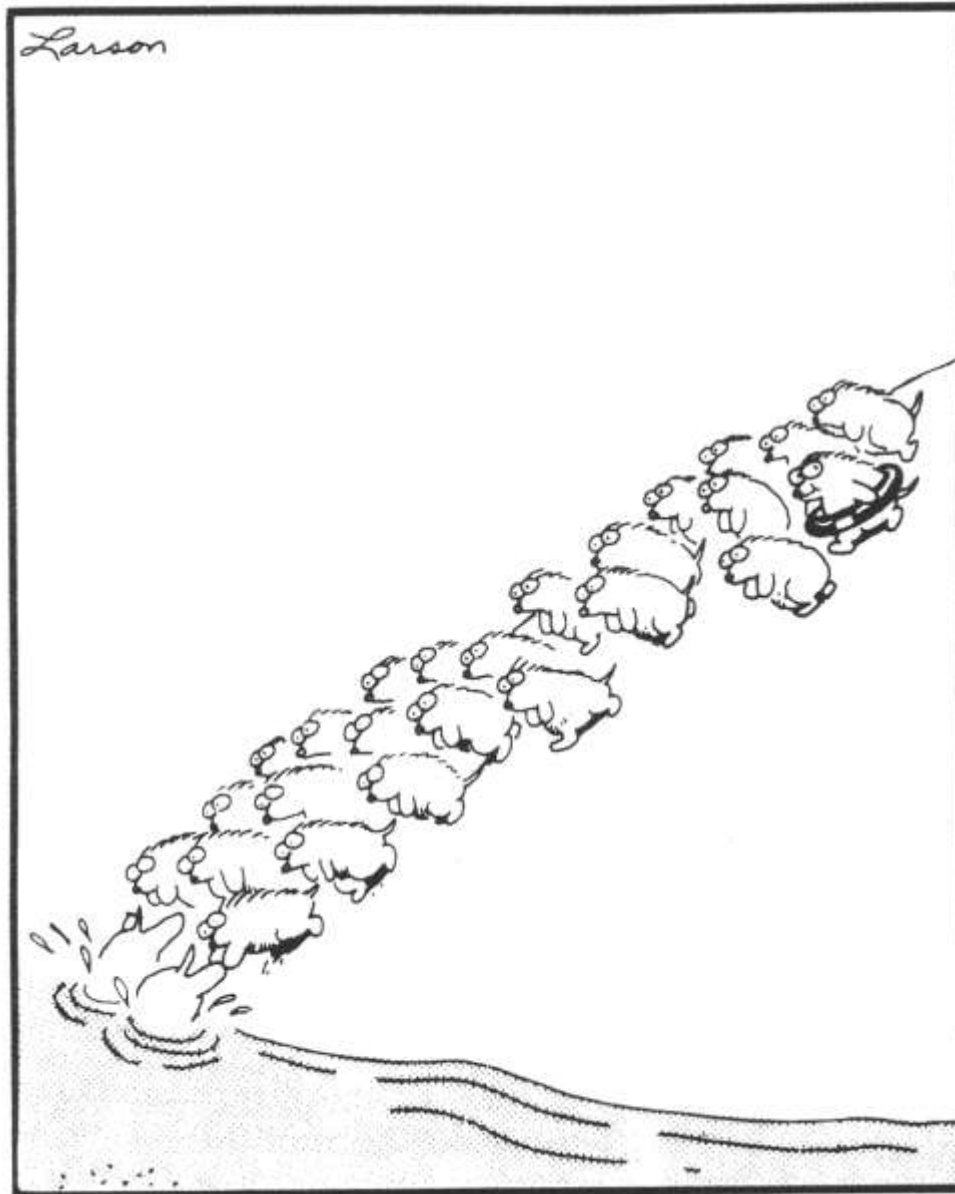


Fig. 1.1. Top: when a new male takes over a lion pride, he kills the young cubs fathered by the previous males. Bottom: a female suckles her sister's cub alongside her own.

Observation	Causal explanations	Functional explanations
1. Females are synchronous in oestrus	Chemical cues? Take-overs by males	Better cub survival Young males survive better and have greater reproductive success when they leave pride if in a group
2. High rate of copulation	Female infertility Time of ovulation concealed	Each copulation of less value to a male Increased paternity uncertainty may protect cubs from males Elicits competition between male coalitions, so females get best protectors taking over pride
3. Young die when new males take over pride	Abortion (?chemical) Take-over males kill or evict young	Females come into oestrus quicker Male removes older cubs which would compete with his young

Group – individual interest ?



Evolutionarily Stable Strategy (ESS)

Individual <-> Group

Optimal <-> Stable behaviour

Hawk and Dove model



Table 7.1. The game between Hawk and Dove. After Maynard Smith (1976b)

(a) Pay-offs: Winner + 50 Injury -100
 Loser 0 Display -10

(b) Pay-off Matrix: average pay-offs in a fight to the attacker.

Attacker	Opponent	
	Hawk	Dove
Hawk	(a) $\frac{1}{2}(50) + \frac{1}{2}(-100)$ $= -25$	(b) +50
Dove	(c) 0	(d) $\frac{1}{2}(50 - 10) + \frac{1}{2}(-10)$ $= +15$

Notes:

(a) When a Hawk meets a Hawk we assume that on half of the occasions it wins and on half the occasions it suffers injury.

(b) Hawks always beat Doves.

(c) Doves always immediately retreat against Hawks.

(d) When a Dove meets a Dove we assume that there is always a display and it wins on half of the occasions.

-stable ratio of strategies when an average hawk and an average doves has similar benefit

h – ratio of hawks

$1-h$ – ratio of doves

Cost-benefit:

hawk $H = -25h + 50(1-h)$

doves $G = 0h + 15(1-h)$

ESS : $H = G$

$$h_{\text{hawk}} = 7/12$$

$$h_{\text{doves}} = 5/12$$

(ESS) if:

1. 7/12 of individuals behave as hawk, 5/12 of individuals behave as doves

or

2. Each individuals behave 7/12 as hawk and 5/12 behave as doves (mixed strategy)

- Net benefit at ESS : **6,25!**

- hawk: $(-25 \times 7/12) + 50 (5/12) = 6,25$

- doves: $(0 \times 7/12) + 15 (5/12) = 6,25$

- Net benefit - **only doves: 15! – optimal, but not stable!!!**

- **ESS: 6,25 – not optimal, but stable!!!**

- The best strategy depend on behaviours of others.
- There is no “absolut best strategy” only ESS, which depend on existing strategies in the population and cost/benefit of it.

The cost/benefit of behaviour strategies could depend on various factor in the nature and could change in space and time.

Example in the nature:

Serious fights (high ratio of “hawk” strategy) – benefit >>> cost

Fights for breeding

- Reed deer
- Narval
- Sea lion



Only ritual behaviours (high ratio of “dove” strategy) – benefit <<< cost

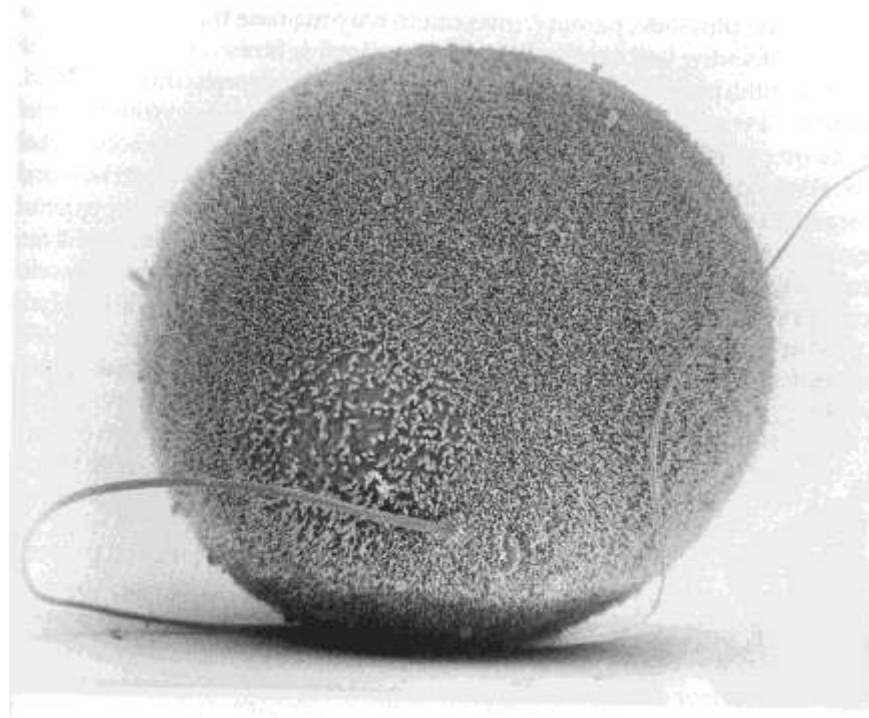
- Ratle snake



Evolution

Conflicts:

- Between sexes (One sex (female) give more to the offspring – potentially it could have less maximum offspring than the other sex (male))
- Between parents and offsprings (Care of offsprings reduce the chance to produce more offsprings)

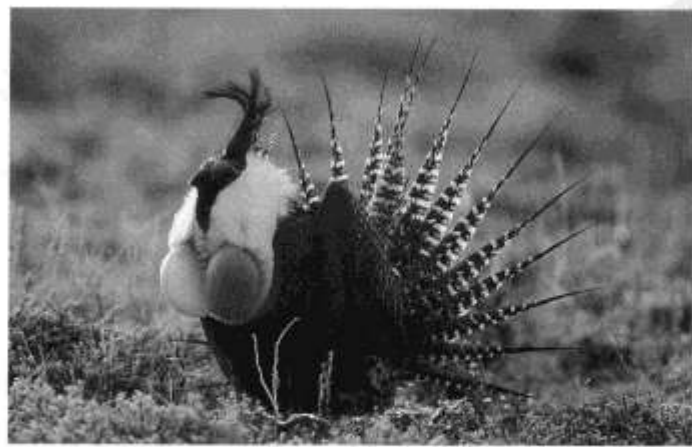


For sex which could have potentially less offsprings (females) – very important to find the partners (males) with the best quality. -> They choose

Sexual selection:

Selection for traits which increase mating/pairing of sex (males) which could have potentially more offsprings

Sexual selection between and within sexes



12 Sexually selected "ornaments" of males. Darwin believed that sexual selection via female choice was responsible for the evolution of elaborate plumage and remarkable displays in male birds such as the quetzal (left) and the sage grouse (top right). Darwin argued that the strange horns and snouts of certain beetles (bottom right) also arose via female choice, although males actually use these structures primarily as weapons when fighting for mates. Photographs by Bruce Lyon; Marc Dantzker; and the author.

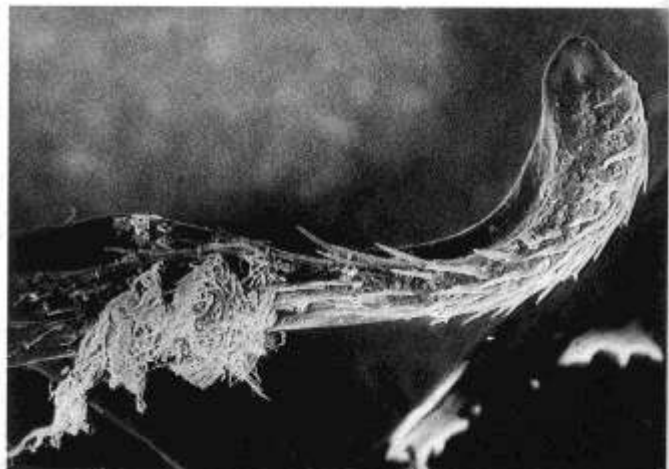
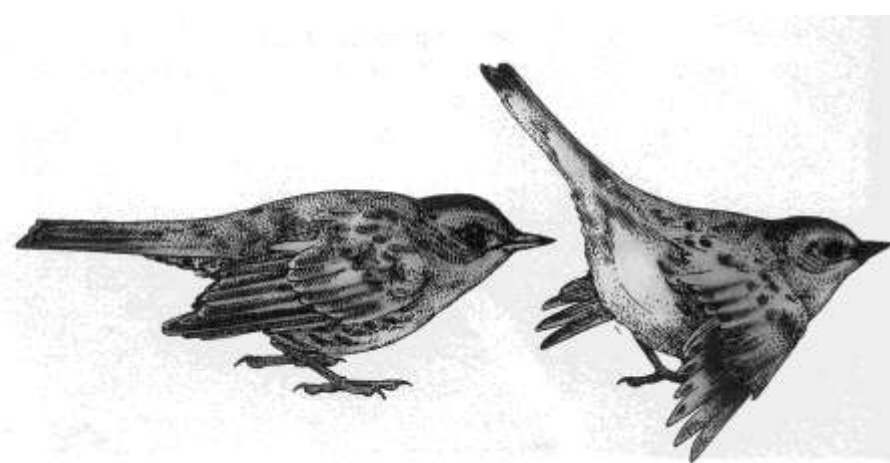
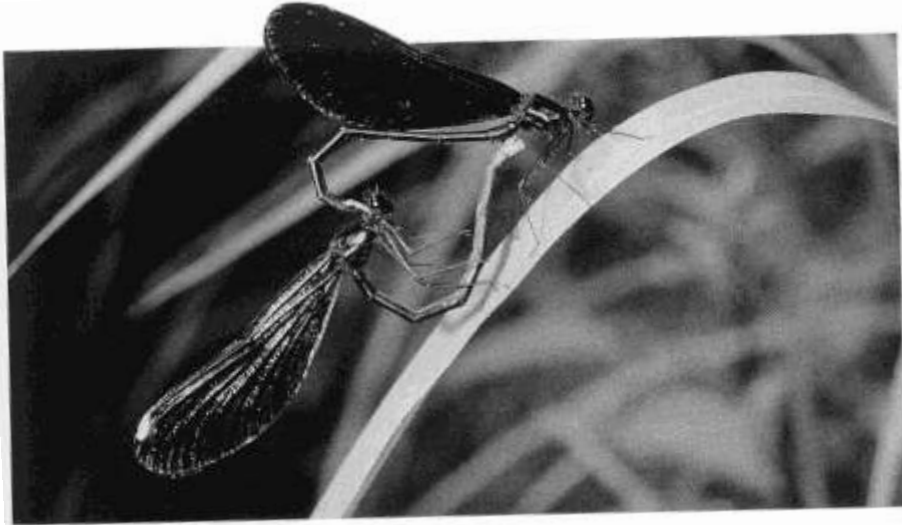
Sexual selection

Intrasexual competition - within sex



Sperm competition

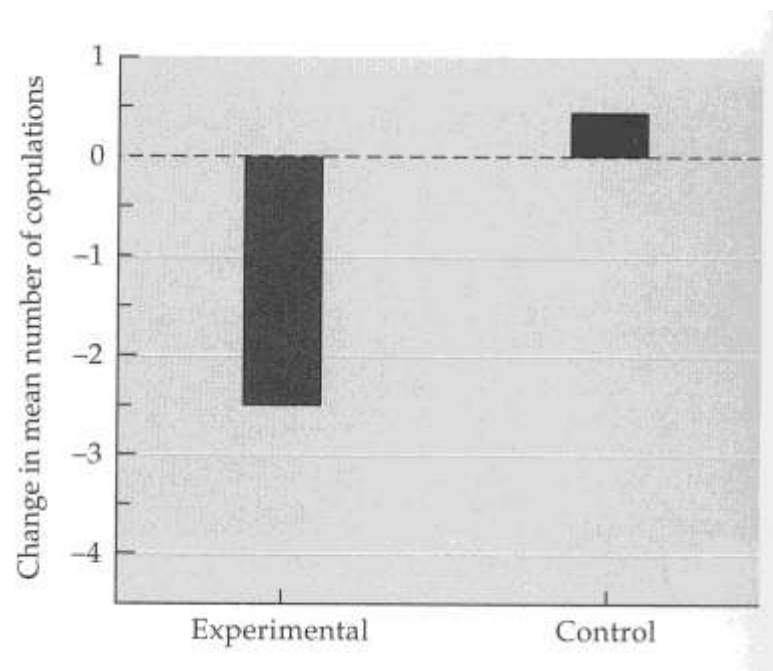
Intrasexual competition – competition after mating among males (whose sperm will fertilise the eggs)



Sexual selection

Intrasexual competition, between sexes- Mate choice of females

38 Removal of eyespots from a peacock's tail reduces his attractiveness to females. After 20 eyespots had been cut from their tails, males averaged two fewer mates in the following breeding season compared with their performance in the previous year. After Petrie and Halliday [906].



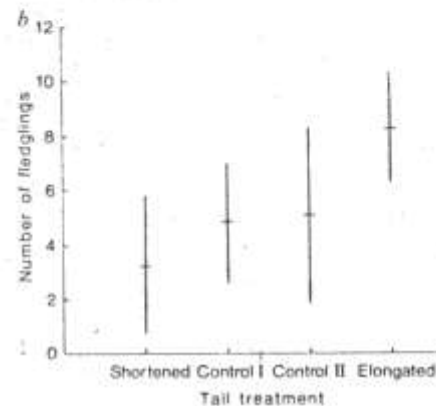
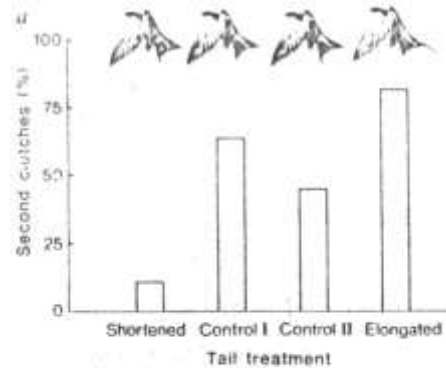
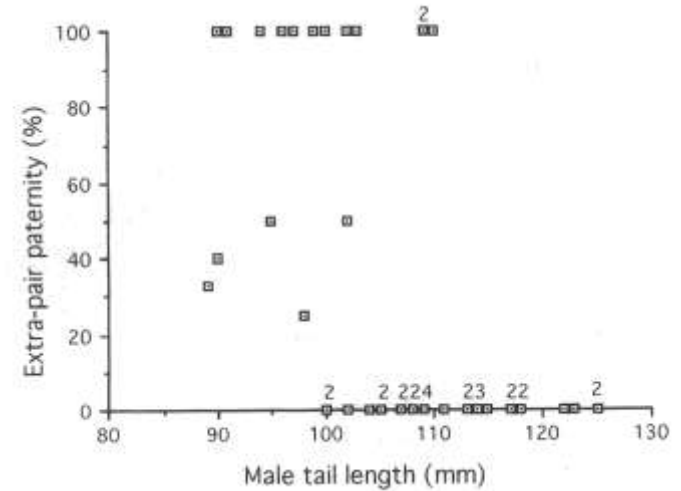
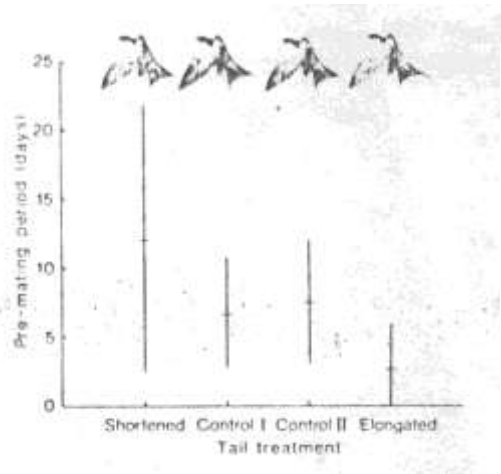
Intrasexual competition

Barn swallow

- Females prefer males with longer tail feathers
- Females prefer males with symmetric tail feathers

Mate choice by female

Handicap principle



Why the tail is not long for every males?

Males with experimentally elongated tail feathers was able to rear the offspring but new feathers moult in Africa were shorter with more fault bars than control – less survival probability

Only males with good condition could have long tail

Nemcsak a toll hossza, hanem a tollak szimmetriája is fontos

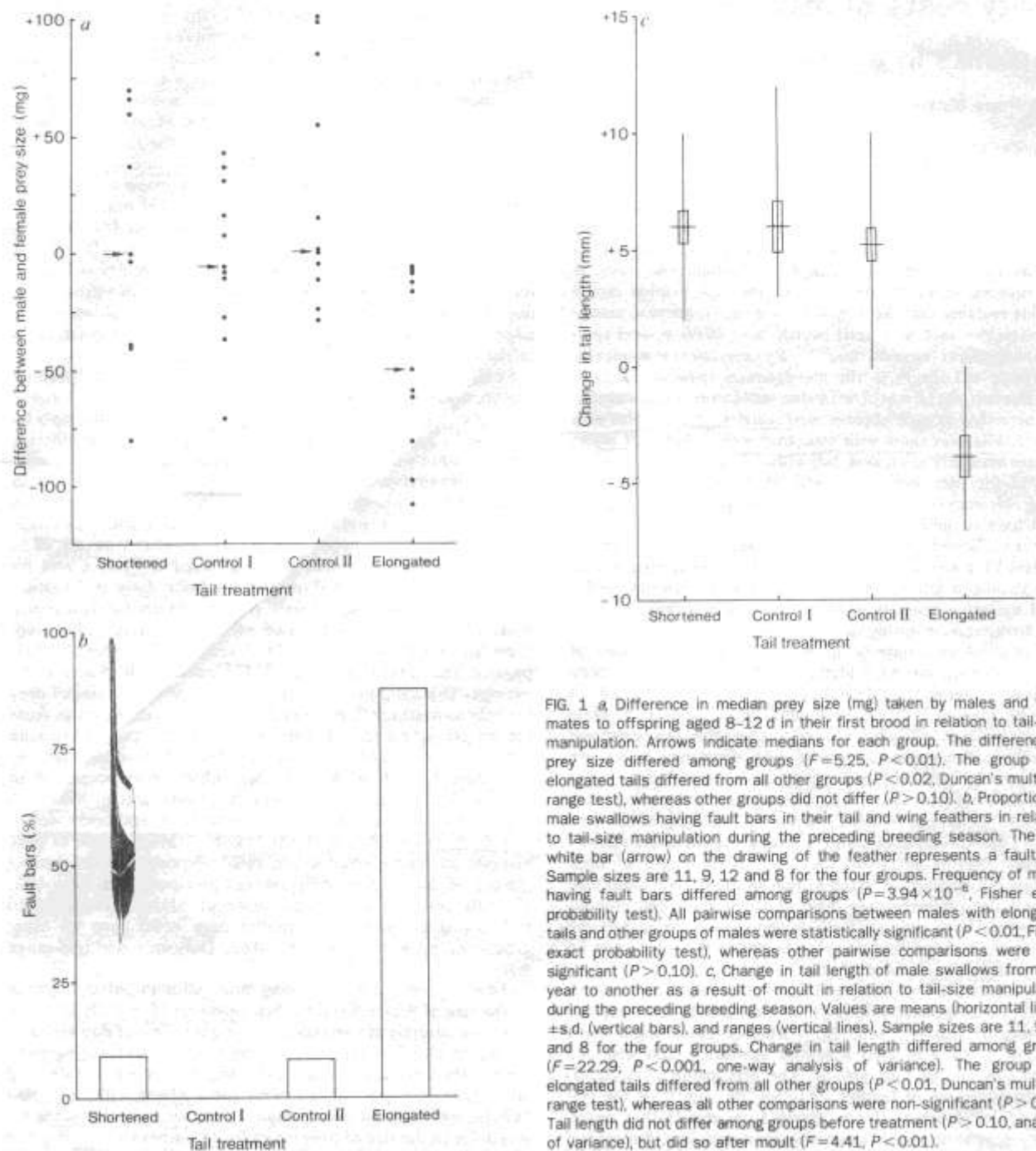


FIG. 1 *a*, Difference in median prey size (mg) taken by males and their mates to offspring aged 8–12 d in their first brood in relation to tail-size manipulation. Arrows indicate medians for each group. The difference in prey size differed among groups ($F=5.25$, $P<0.01$). The group with elongated tails differed from all other groups ($P<0.02$, Duncan's multiple-range test), whereas other groups did not differ ($P>0.10$). *b*, Proportion of male swallows having fault bars in their tail and wing feathers in relation to tail-size manipulation during the preceding breeding season. The thin white bar (arrow) on the drawing of the feather represents a fault bar. Sample sizes are 11, 9, 12 and 8 for the four groups. Frequency of males having fault bars differed among groups ($P=3.94 \times 10^{-8}$, Fisher exact probability test). All pairwise comparisons between males with elongated tails and other groups of males were statistically significant ($P<0.01$, Fisher exact probability test), whereas other pairwise comparisons were non-significant ($P>0.10$). *c*, Change in tail length of male swallows from one year to another as a result of moult in relation to tail-size manipulation during the preceding breeding season. Values are means (horizontal lines), $\pm$ s.d. (vertical bars), and ranges (vertical lines). Sample sizes are 11, 9, 12 and 8 for the four groups. Change in tail length differed among groups ($F=22.29$; $P<0.001$, one-way analysis of variance). The group with elongated tails differed from all other groups ($P<0.01$, Duncan's multiple-range test), whereas all other comparisons were non-significant ($P>0.10$). Tail length did not differ among groups before treatment ($P>0.10$, analysis of variance), but did so after moult ($F=4.41$, $P<0.01$).

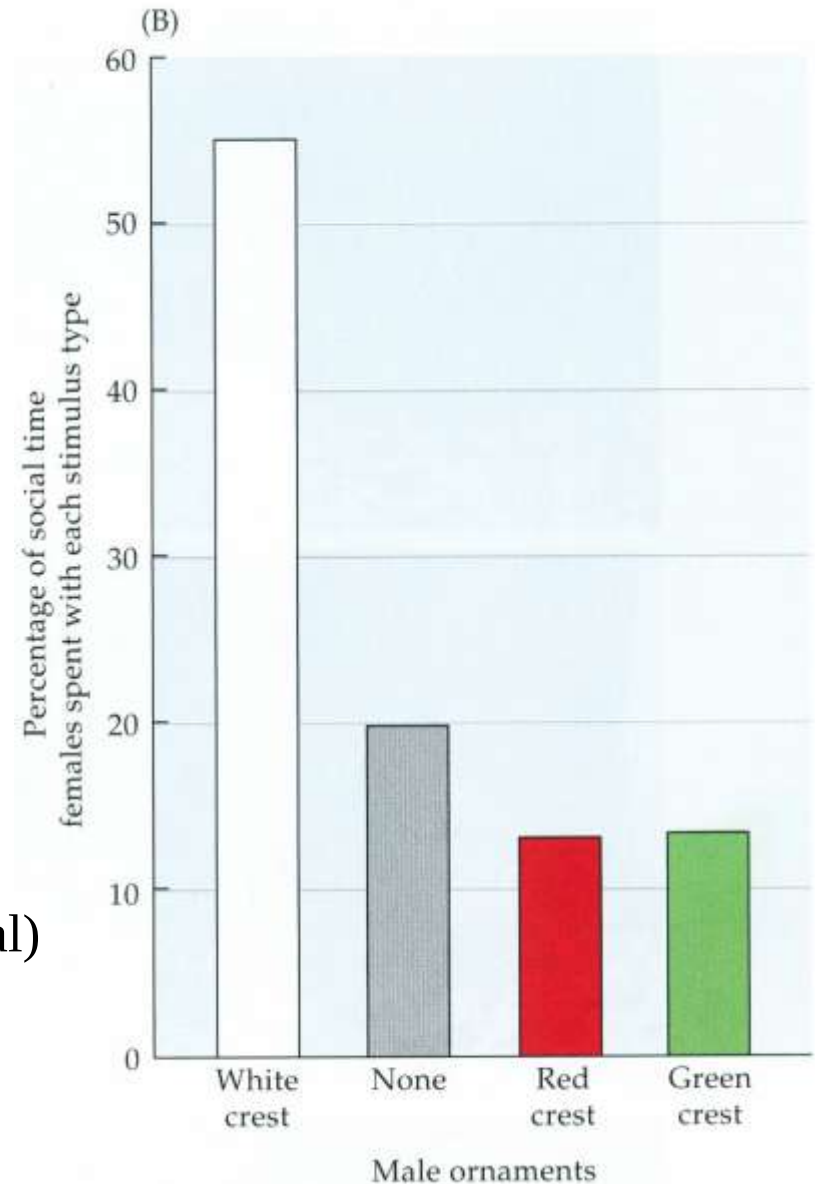
Sensory exploitation – new traits which could improve mating/paring of males

- Zebra finch experiment

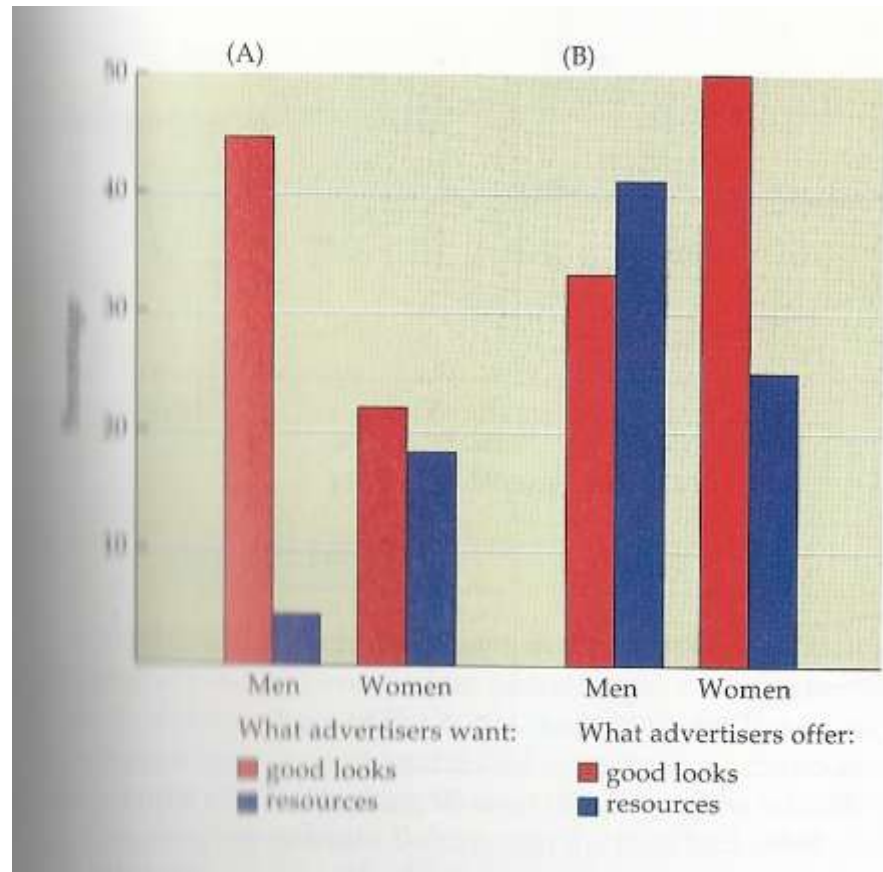


Glueing white feather on the head of finch increased the interest of females toward these males during pairing.

New kind of males trait (behaviour/morphological) can be successful if it is attractive for females.

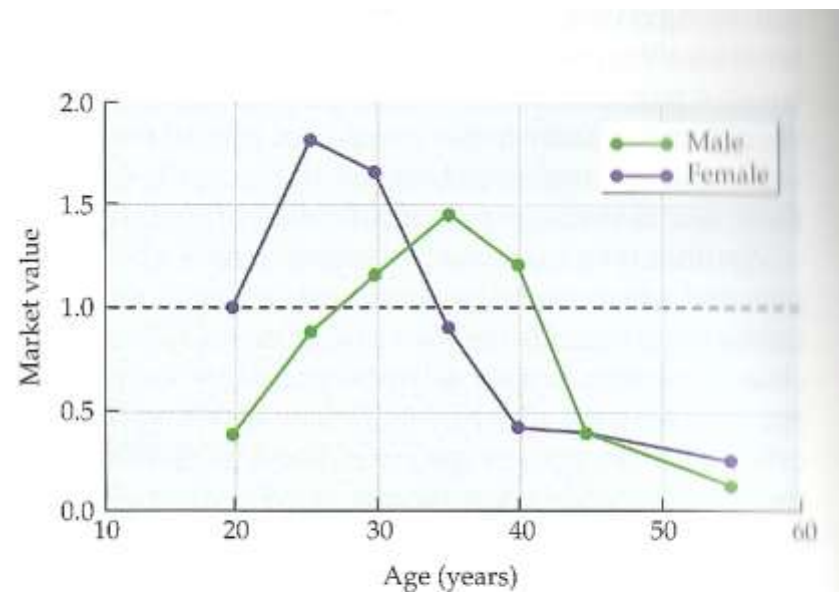
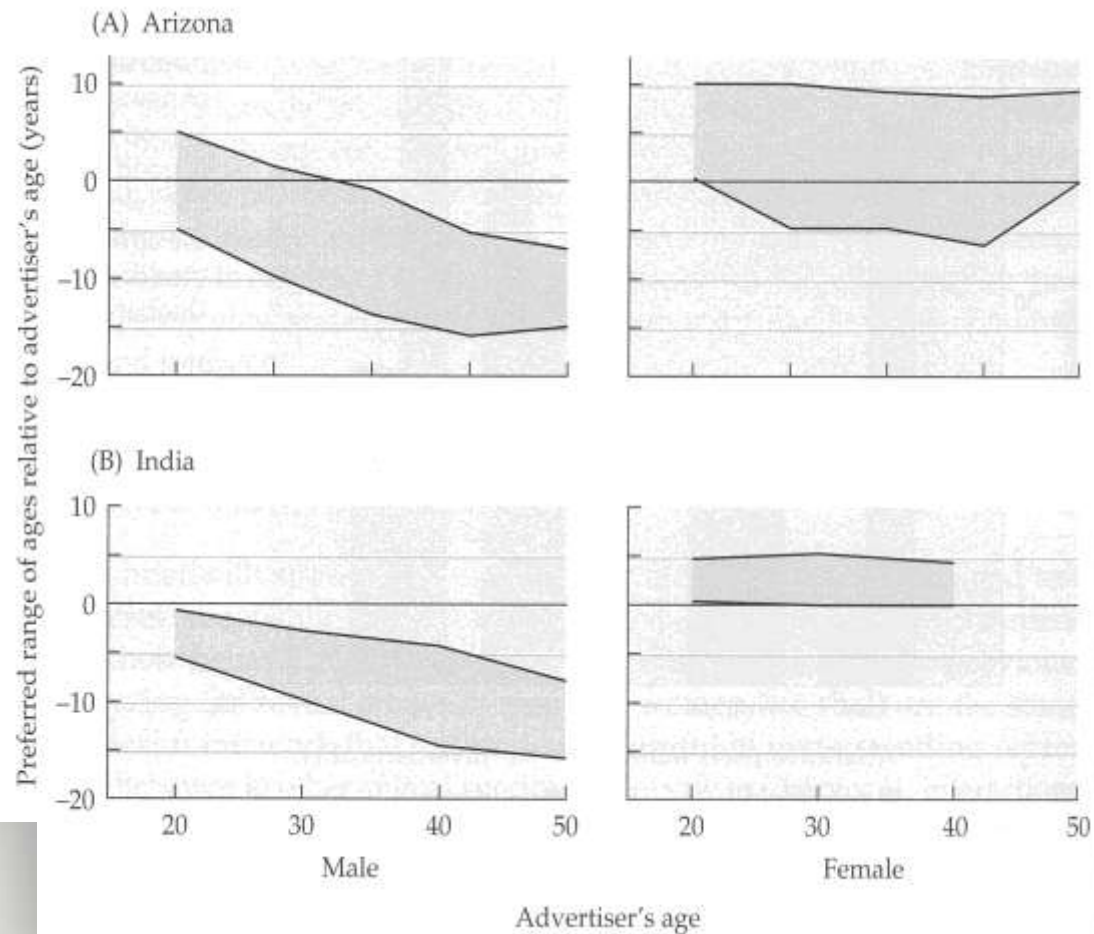


Human is totally different ???



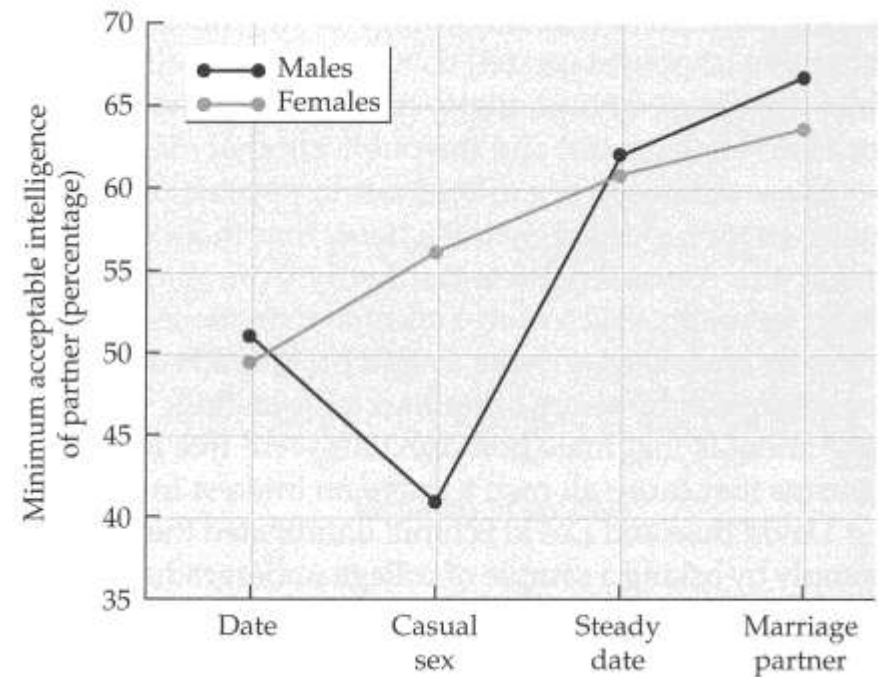
What want and offer men and women in the ordinary dating advertising

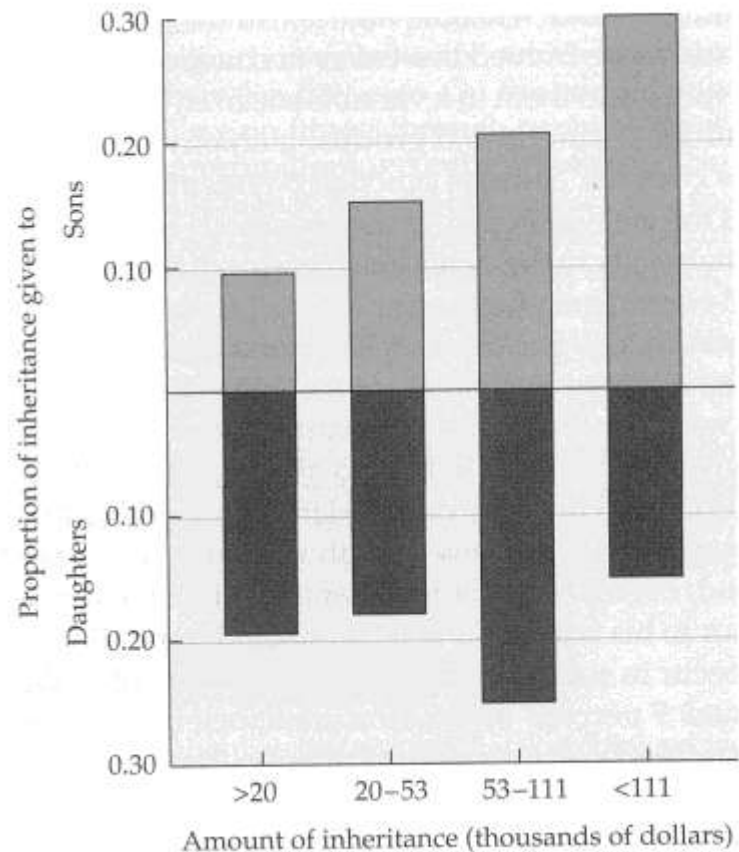
6 Different cultures show similar mate preferences. Men advertise for younger women and women advertise for older men in both (A) the *Arizona Solo* and (B) the *Times* of New Delhi, India. The advertisers indicated their own age and the maximum and minimum ages they would accept in potential partners. After Kenrick and Keefe [613].



- Males prefer the most fertile age group both in Arizona and in India
- In the case of females preference different from males, not the age alone

13 Sex differences in mate selectivity. College men differ from college women in the minimum intelligence that they say they would require in a casual sexual partner. However, men and women have similar standards with respect to the minimum intelligence they say they would require in a marriage partner. After Kenrick et al. [614].





24 Inheritance decisions. Wealthy Canadian parents bias their legacies toward their sons, who are more likely than daughters to convert exceptional wealth into exceptional reproductive success. After Smith et al. [1073].

Inheritance decision: division of the inheritance between daughters and sons depend on the amount of inheritance

Among animals, females produce more male offspring and/or provide more resources to male offspring when male partner is high quality

Parental care

„any investment by the parent in an individual offspring that increases that offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring” (Trivers)

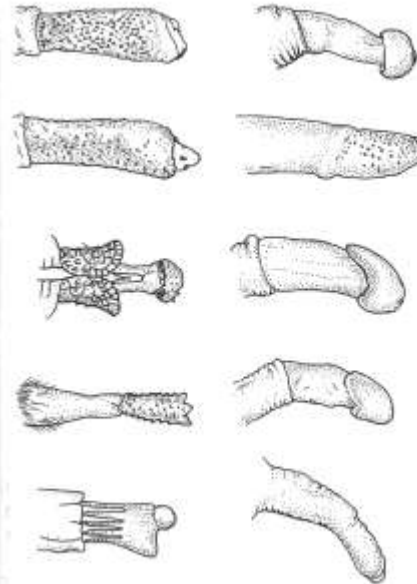
Monogamy – social monogamy -> both sex contribute in the parental care

Polygyny -> males mates with several females, females only with one male, usually the females provide parental care

Poliandry -> females mates with several males. males only with one females, usually the males provide parental care

Promiscuity -> both males and females either sex may care ofsprings

Human-> Social monogamy



36 Female choice for stimulating male genitalia? The more elaborate penises on the left, which might provide more copulatory stimulation, are from primate species in which females regularly mate with more than one male, and so might evaluate the copulatory performance of several males. The simpler (less stimulating?) penises on the right are from species in which a single male usually copulates with a female during one estrous cycle. After Dixson [329] and Eberhard [346].

10.14

Interspecific interactions, Niche theory, Competition model

Interaction among species

- Competition	- / -
- Predation	+/-
- Commensalism,	+/0
- Amensalism, allelopathy	0/-
- Mutualism	+/+
- Neutralism	0/0



Niche theory. Competition. Models of competition

- Living conditions and Resources influence the distribution and abundance
 - Living conditions , independent from the condition of the living organism: eg. temperature, humidity, soil composition, pH of the water, salinity, pollution
 - Resources: all things which quantity could modify by the living organism

Resources:

Solar radiation

Inorganic materials:

- CO₂
- minerals
- Oxygen
- N
- H₂O

Other organism

Burrows

Seeds

.....etc,

Classification of resources:

- essential
- perfectly substitutable
- complementary
- antagonistic
- inhibitor

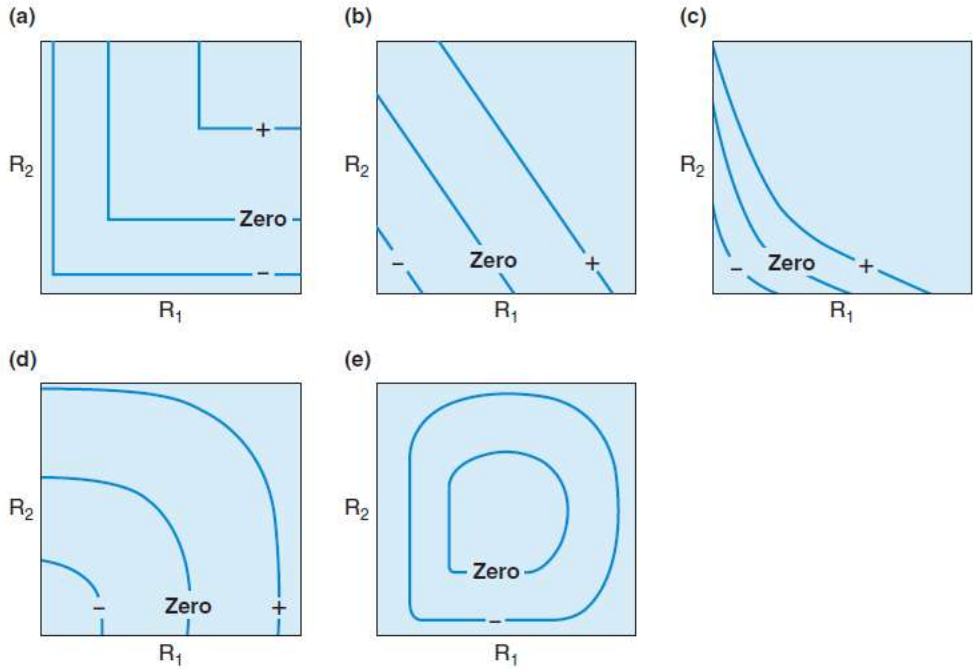


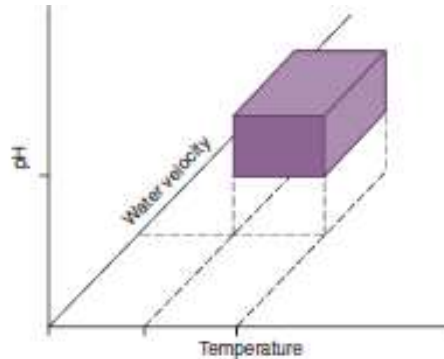
Figure 3.30 Resource-dependent growth isoclines. Each of the growth isoclines represents the amounts of two resources (R₁ and R₂) that would have to exist in a habitat for a population to have a given growth rate. Because this rate increases with resource availability, isoclines further from the origin represent higher population growth rates: isocline - has a negative growth rate, isocline zero a zero growth rate and isocline + a positive growth rate. In the respective figures, resources are (a) essential, (b) perfectly substitutable, (c) complementary, (d) antagonistic and (e) inhibitory. *Source:* After Tilman (1982).

Niche

Population/species needs large number (N) resources for living

Niche: niche is an „N-dimensional hypervolume“, where the dimensions are environmental conditions and resources, that define the requirements of an individual or a species to practice its way of life, more particularly, for its population to persist (Hutchinson)

- Fundamental niche, part of the N-dimensional hypervolume where the given population/species could occur



- Realised Niche, part of the N-dimensional hypervolume where the given population/species occurs

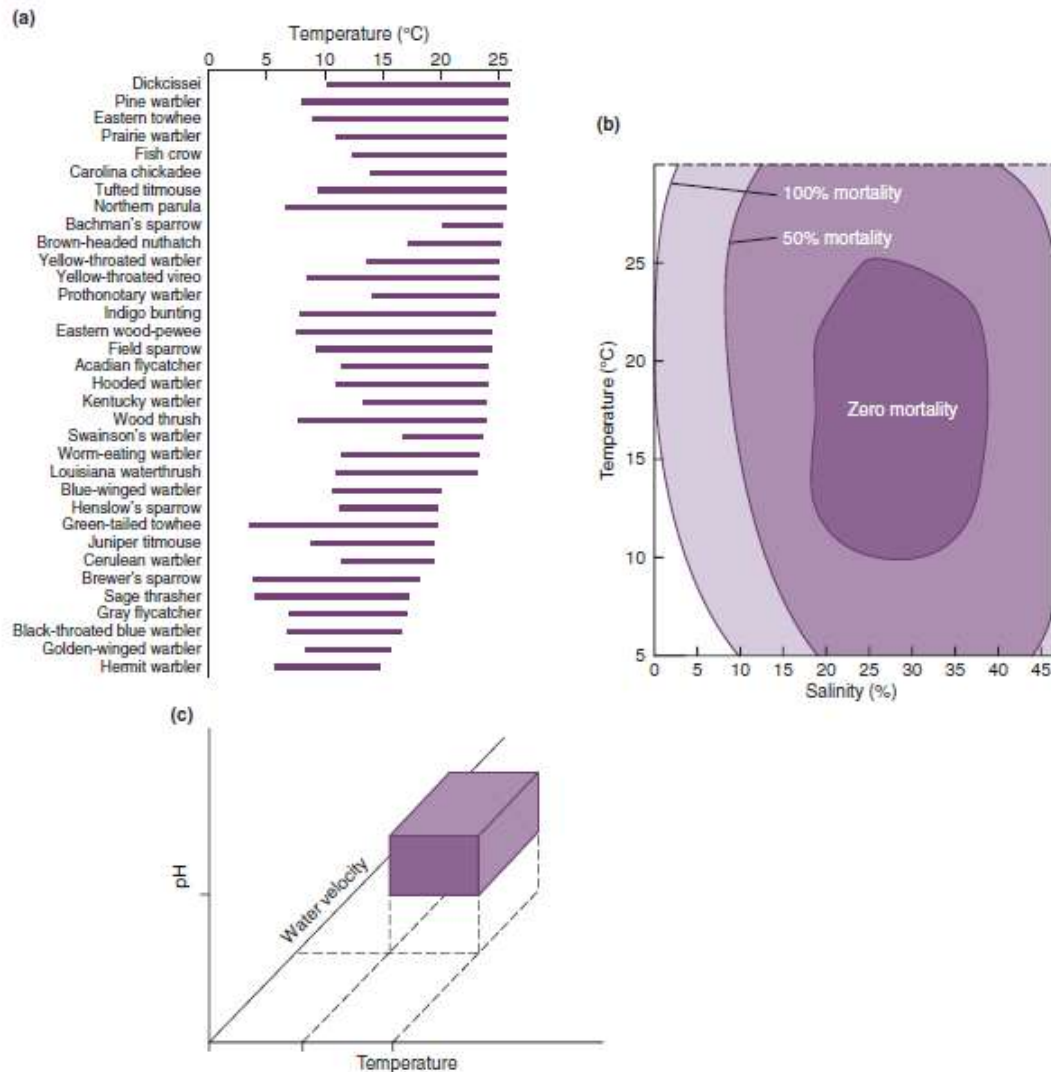
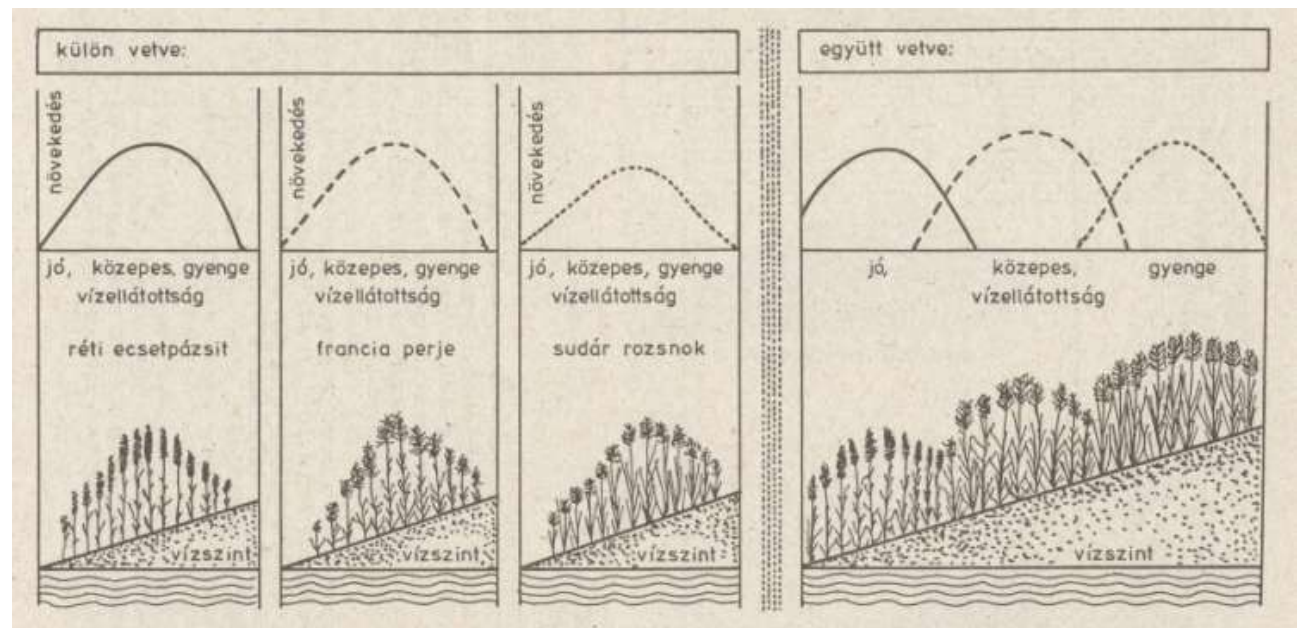


Figure 2.2 The ecological niche in one, two and three dimensions. (a) A niche in one dimension showing the thermal range of passerine birds in southern Canada and the contiguous USA recorded during the North American Breeding Bird Survey 2002–06 in relation to minimum and maximum thermal limits of an average of 10 occurrence locations for each species (measured in each case as mean springtime breeding season temperature). (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities. (c) A diagrammatic niche in three dimensions for a stream-dwelling alga showing a volume defined by temperature, pH and water velocity; in reality, the niche would not appear as a neat cuboid defined by the three tolerance ranges because, for example, temperature tolerance may be reduced when pH is low. *Source:* (a) Data from Coristine & Kerr (2015). (b) After Haefner (1970).

Niche

Niche: niche is an „N-dimensional hypervolume", where the dimensions are environmental conditions and resources, that define the requirements of an individual or a species to practice its way of life, more particularly, for its population to persist (Hutchinson)

- Fundamental niche, part of the N-dimensional hypervolume where the given population/species could occur



Growth of three grass species in relation to water availability when it was seeding separately (left part) and mixed way (right part).

- Realised Niche, part of the N-dimensional hypervolume where the given population/species occurs

Competition

- Intraspecific, density dependent growth

- Interspecific

Interference -> Contest

Exploitative -> Scramble

Competition Types – The Basics

Two types of interspecific competition (also saw for intraspecific):

Exploitative = indirect competition

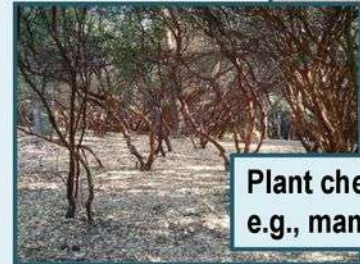
Competition through a common resource → scramble



Plant competition for nutrients

Interference = direct competition

Aggressive / physical encounters for resources → contest



Plant chemical warfare e.g., manzanita

Competition between species when their niche overlapping

The level of the niche overlap indicate the level of the competition

In the case of large niche overlap:
1- niche segregation or 2- the last competitive species will gone

When the niche overlap occur for resources which has no or minimal regulatory function of the species -> there is minimal competition

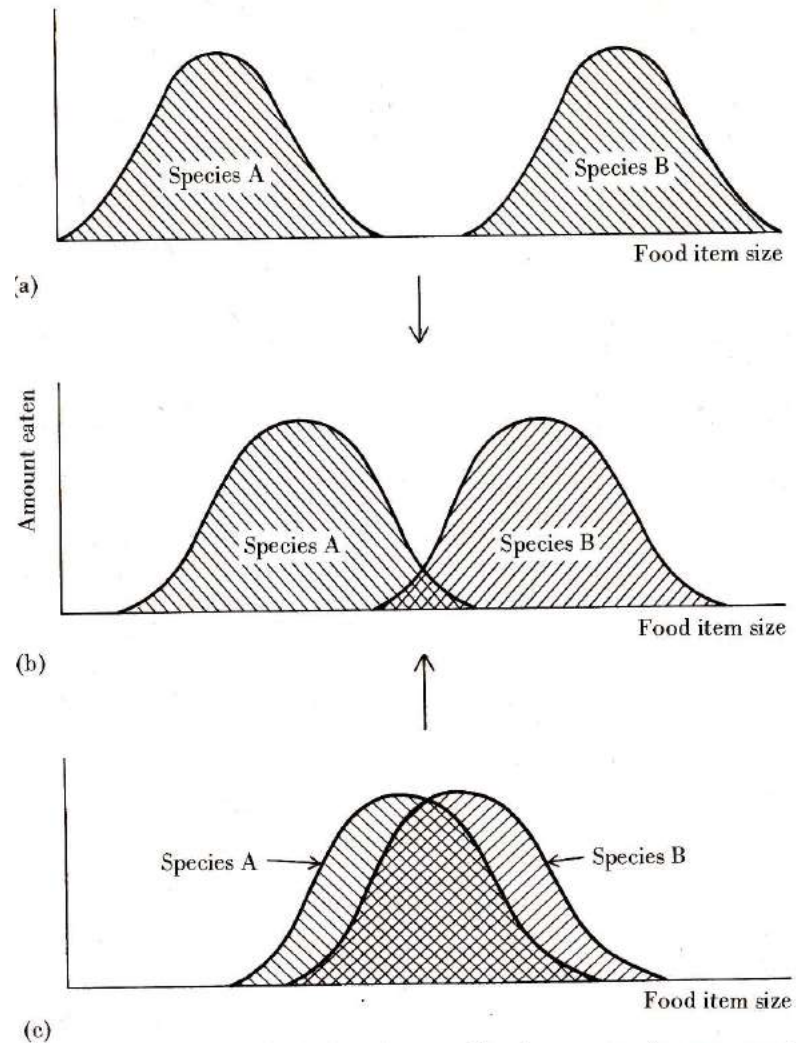


Figure 13.20 Hypothetical resource-utilization curves for two species. Food size is the resource for which competition may occur in this hypothetical situation. Arrows indicate direction of evolutionary pressures toward case (b).

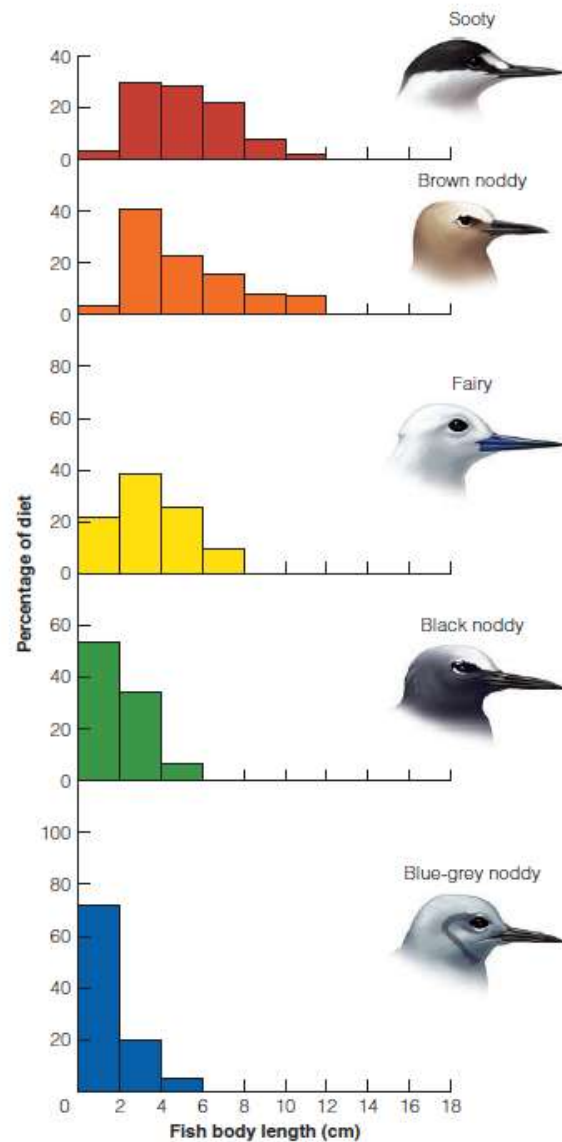
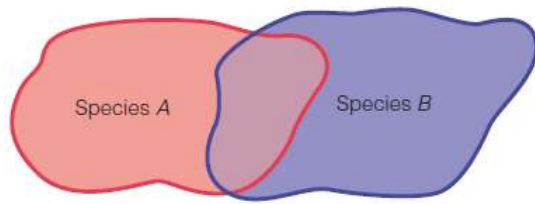
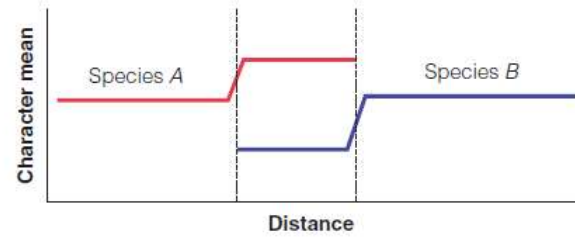


Figure 19 Resource partitioning in five species of terns on Christmas Island, Pacific Ocean, as seen in frequency distributions of prey size. Terns are arranged in order of size from the largest species at the top to the smallest at the bottom. The two largest terns are nearly the same size and eat very similar sizes of fish, but the sooty tern feeds at sea several hundred kilometers from land and the brown noddy tern feeds within 100 km of land. (From Ashmole 1968.)



(a) Geographic distribution



(b) Character changes

Figure 22 Schematic view of character displacement arising from interspecific competition in the zone of overlap of two species. The character measured must be one that is critical in competition between the species. This scheme is inferred as an explanation of the observations illustrated in Figure 23.

Species Interactions I: Competition

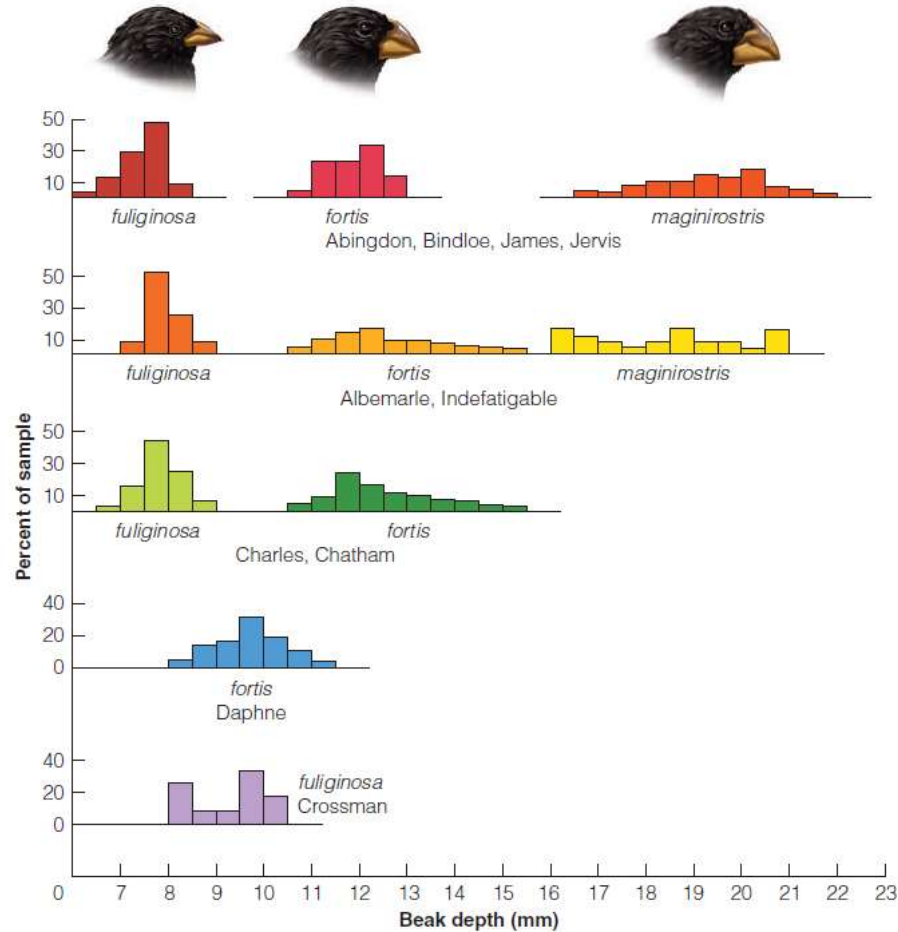
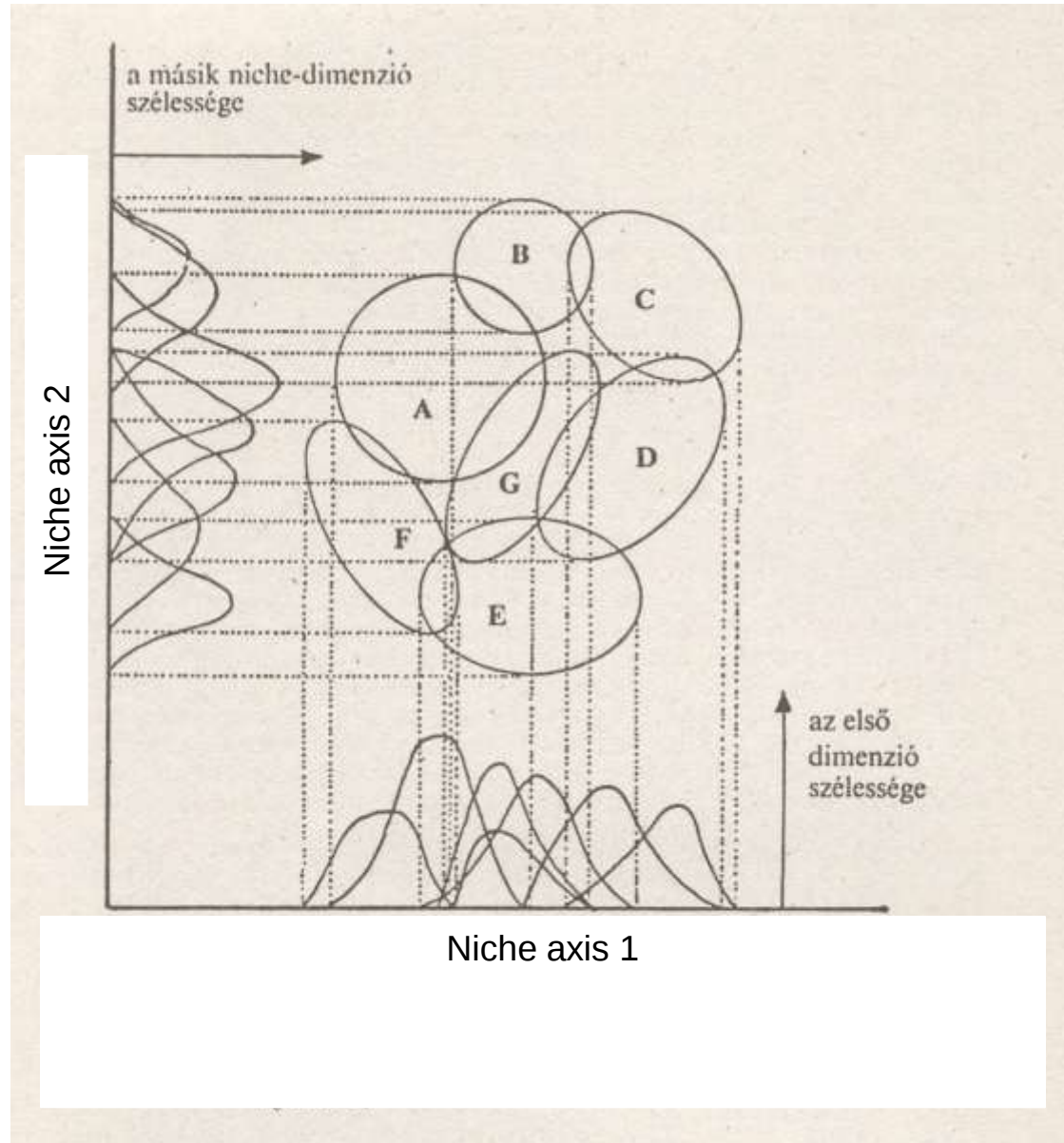


Figure 23 Character displacement in beak size in Darwin's finches from the Galápagos Islands. Beak depths are given for *Geospiza fortis* and *G. fuliginosa* on islands where these two species occur together (upper three sets of islands) and alone (lower two islands). *Geospiza magnirostris* is a large finch that occurs on some islands. (After Lack 1947.)

Permanent coexisting of species

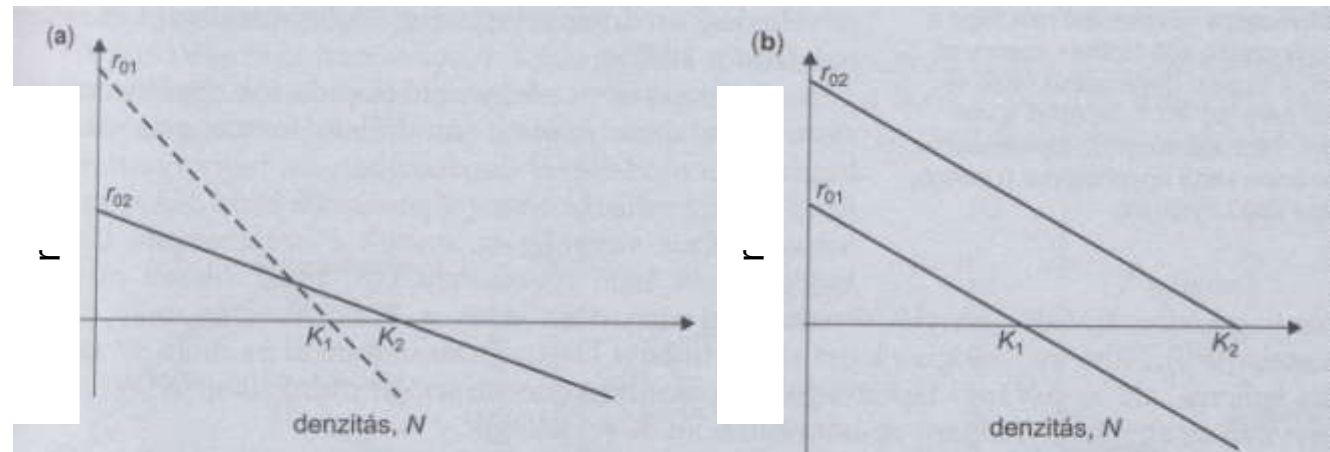


Competition among species when only one factor regulate the population growth

If two species compete and the same factor regulate both of them:

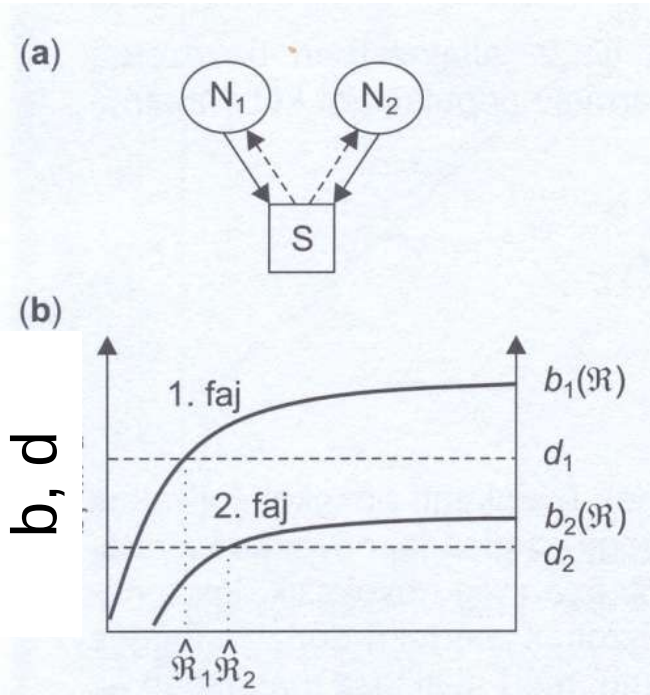
Species with the higher carrying capacity (K) will win and remains in the area

When only one factor regulate the growth of populations, only one population will exist



Density

The outcome of the competition depend on the efficiency of the usage of the resources



When only one resource regulate the growth of populations, only the population will exist which reach the equilibrium population size at the lowest concentration of the given resource

Concentration of resource

Faj -> species

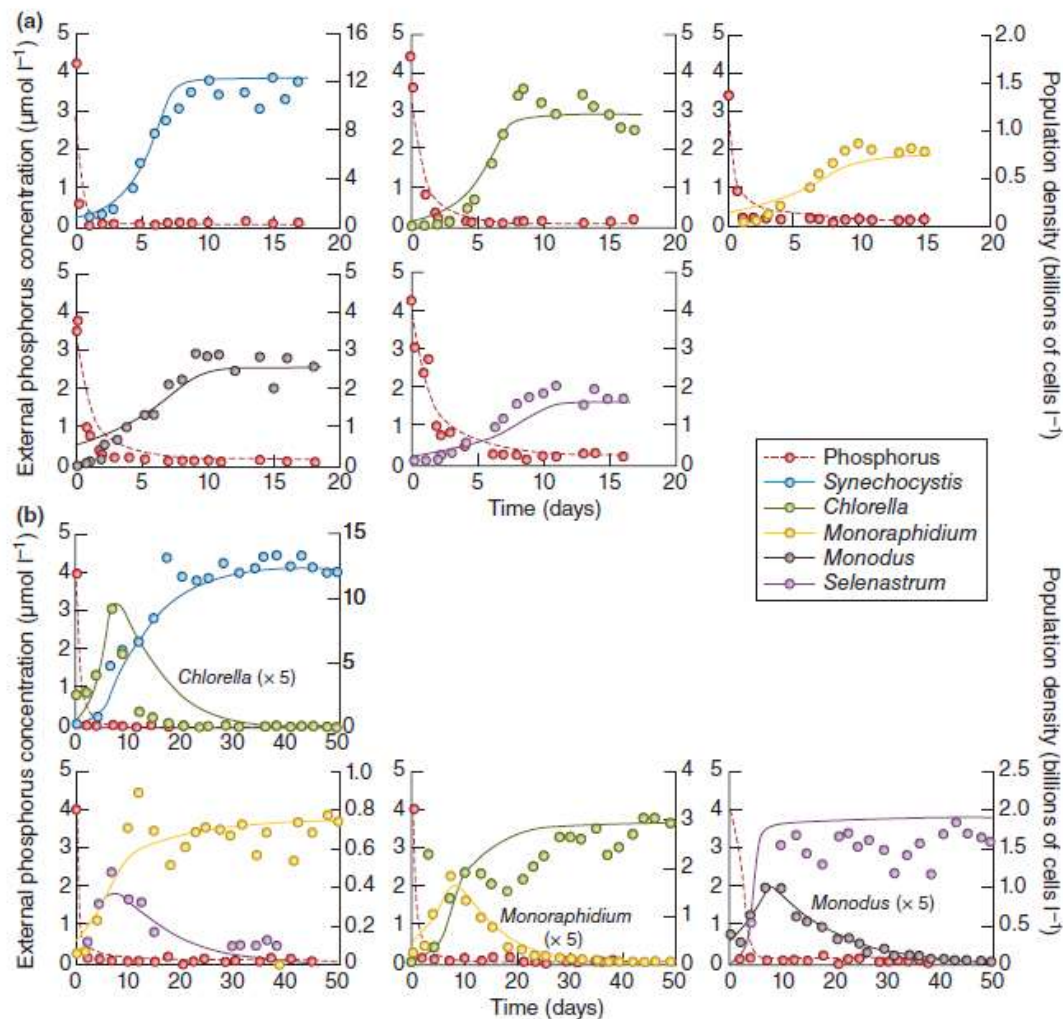
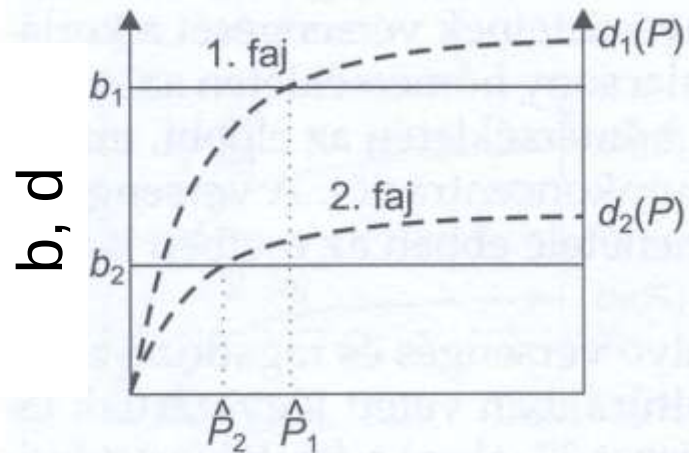
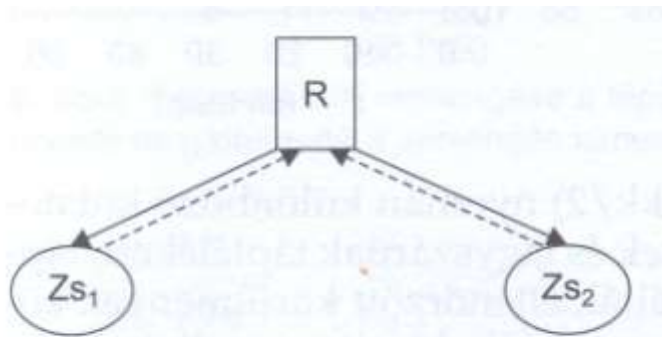


Figure 8.1 Competition between phytoplankton species for phosphorus: winners are those that reduce phosphorus concentrations to lower levels. (a) Each of five species (names and symbols shown in panel), when grown alone in a laboratory chemostat, establishes a stable population and maintains a resource, phosphorus (red dots), at a constant low level: *Synechocystis* ($0.030 \mu\text{mol l}^{-1}$) < *Chlorella* ($0.059 \mu\text{mol l}^{-1}$) < *Monoraphidium* ($0.117 \mu\text{mol l}^{-1}$) < *Selenastrum* ($0.160 \mu\text{mol l}^{-1}$) < *Monodus* ($0.182 \mu\text{mol l}^{-1}$). (b) With symbols retained from (a), it is apparent that when species are grown together in pairs, the only one to survive is the one that had previously reduced phosphorus to the lower level. (Densities have been multiplied by five in the cases indicated, so they can be visualised in the same figure. The lines are drawn simply to indicate general trends.) *Source:* After Passarge *et al.* 2006).

The outcome of the competition depend on the efficiency of avoiding predators/parasites



Density of predator/parasite



When the same predator/parasite regulate the growth of populations, only the population will exist which reach the equilibrium population size at the highest density of the given predator/parasite

Lotka-Volterra competition model when there are several mutual regulatory factors of two species

Growth of the two species depend on density of both own and both on density of the other species, when there are at least two regulatory factors

1. Growth of 1st species

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha_{12} N_2)}{K_1}$$

2. Growth of 2nd species

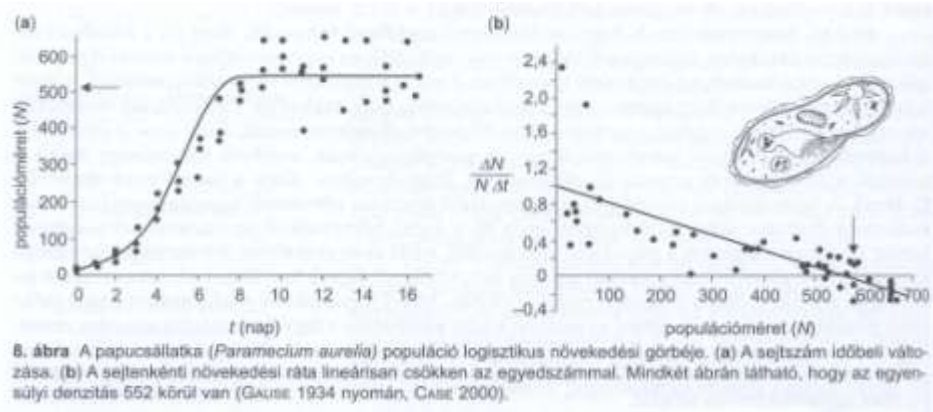
$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \alpha_{21} N_1)}{K_2}$$

α_{12} , α_{21} : conversion factor for expressing species x in units of species y

N_2 individuals of 2nd species == $\alpha_{12} \cdot N_2$ individuals of 1st species

N_1 individuals of 1st species == $\alpha_{21} \cdot N_1$ individuals of 2nd species

Logistic model



K: Carrying capacity

$$\frac{dN}{dt} = r_0 * N * \frac{K - N}{K}$$

Modelling coexistence of two species

$$N_1 \rightarrow \alpha_{12} N_2$$

$$N_2 \rightarrow \alpha_{21} N_1$$

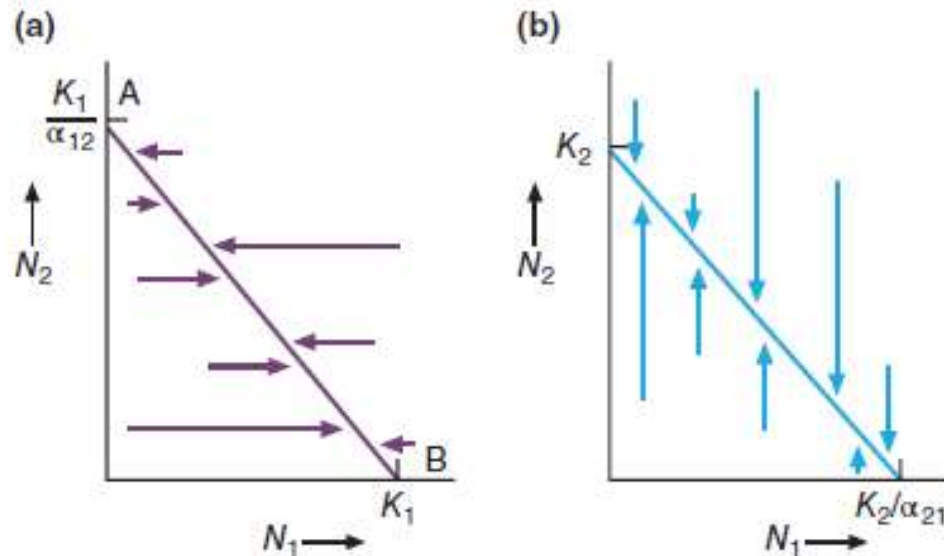


Figure 8.9 The zero isoclines generated by the Lotka–Volterra competition equations. (a) The N_1 zero isocline: species 1 increases below and to the left of it, and decreases above and to the right of it. (b) The equivalent N_2 zero isocline.

Modelling coexistence of two species

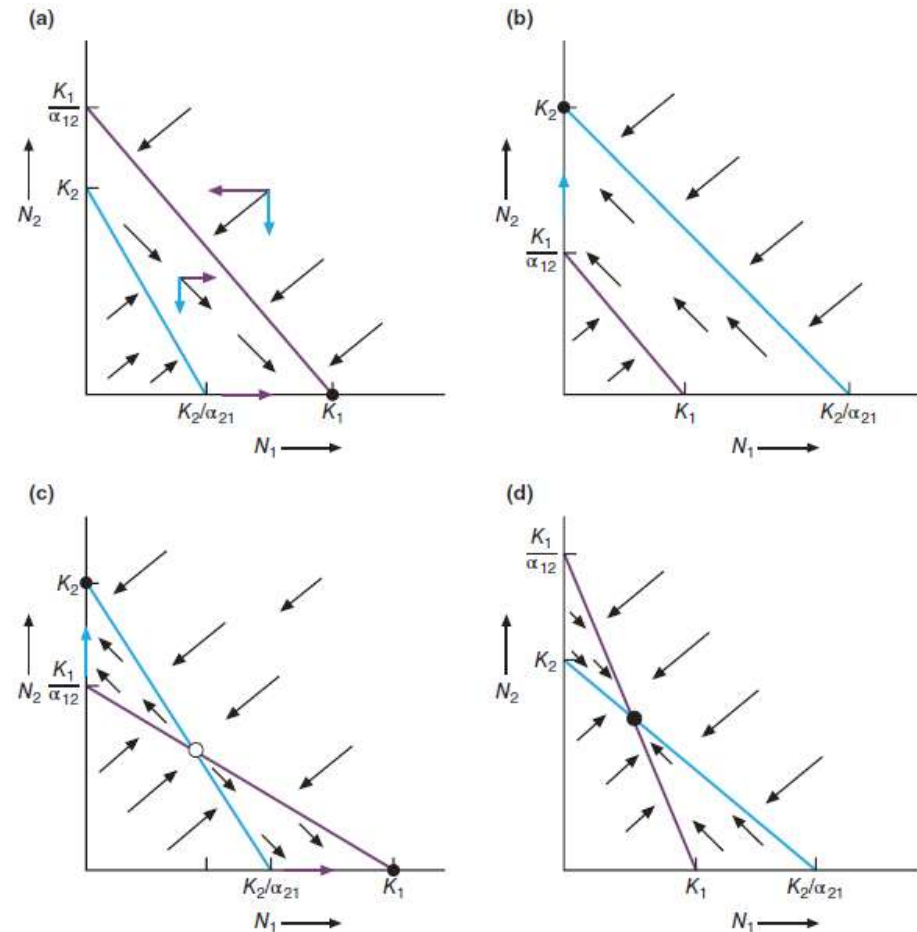
$$N_1 \rightarrow \alpha_{12} N_2$$

$$N_2 \rightarrow \alpha_{21} N_1$$

when interspecific competition is less important than intraspecific, the species coexist

$$\frac{K_1}{\alpha_{12}} > K_2 \quad \text{and} \quad \frac{K_2}{\alpha_{21}} > K_1$$

Figure 8.10 The outcomes of competition generated by the Lotka–Volterra competition equations for the four possible arrangements of the N_1 and N_2 zero isoclines. Vectors, generally, refer to joint populations, and are derived as indicated in (a). The solid circles show stable equilibrium points. The open circle in (c) is an unstable equilibrium point. For further discussion, see the text.



Opportunity of permanent coexistence

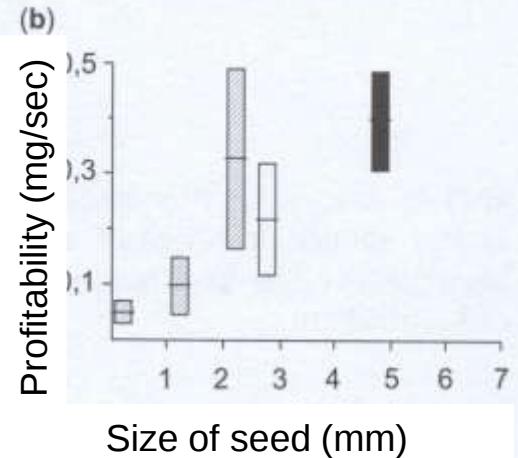
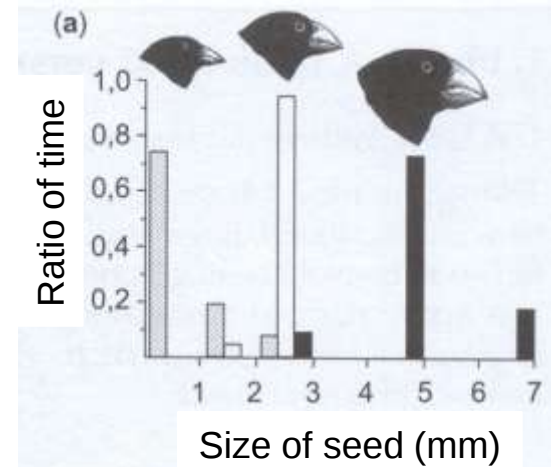
It is larger when difference between the type of resources is larger

When intraspecific competition is stronger than interspecific competition

$$\alpha_{12} < 1, \alpha_{21} < 1$$

Gause law, competitive exclusion principle:

Two species which compete for the same limited resource cannot coexist at constant population values



The outcome of the competition depend on the environment

In the case of grain beetles the moisture and temperature modify the outcome of the competition

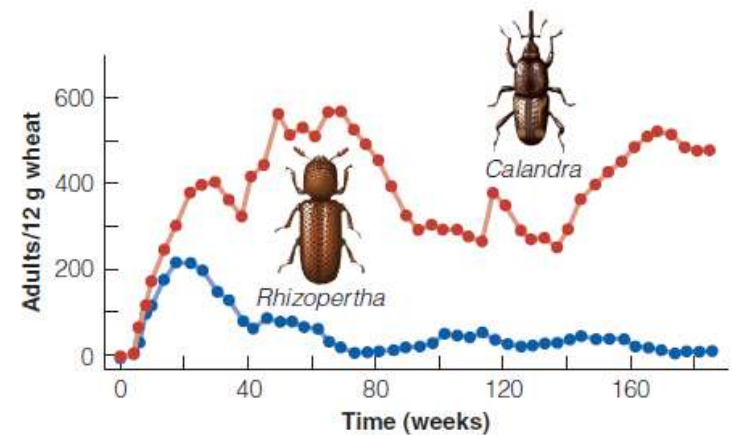


Figure 11 Population trends of adult grain beetles (*Calandra oryzae* and *Rhizopertha dominica*) living together in wheat of 14% moisture content at 29.1°C. *Calandra* eliminates *Rhizopertha* in competition at this temperature. (After Birch 1953b.)

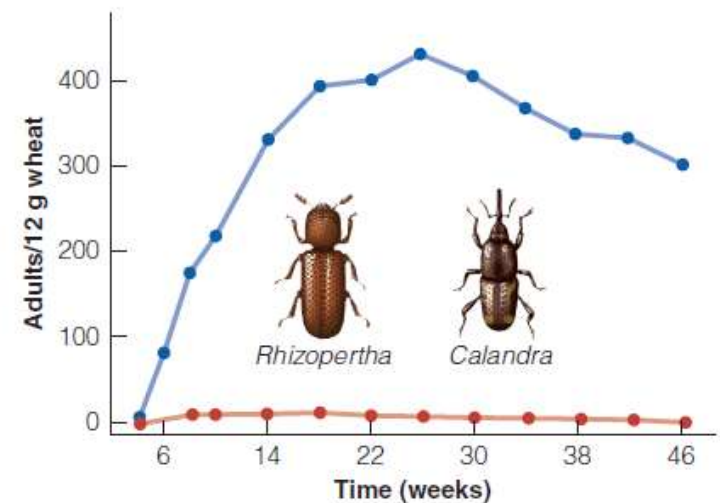


Figure 12 Population trends of adult grain beetles (*Calandra oryzae* and *Rhizopertha dominica*) living together in wheat of 14% moisture content at 32.3°C. *Calandra* goes extinct and *Rhizopertha* wins in competition at this temperature. (After Birch 1953b.)

Niche segregation

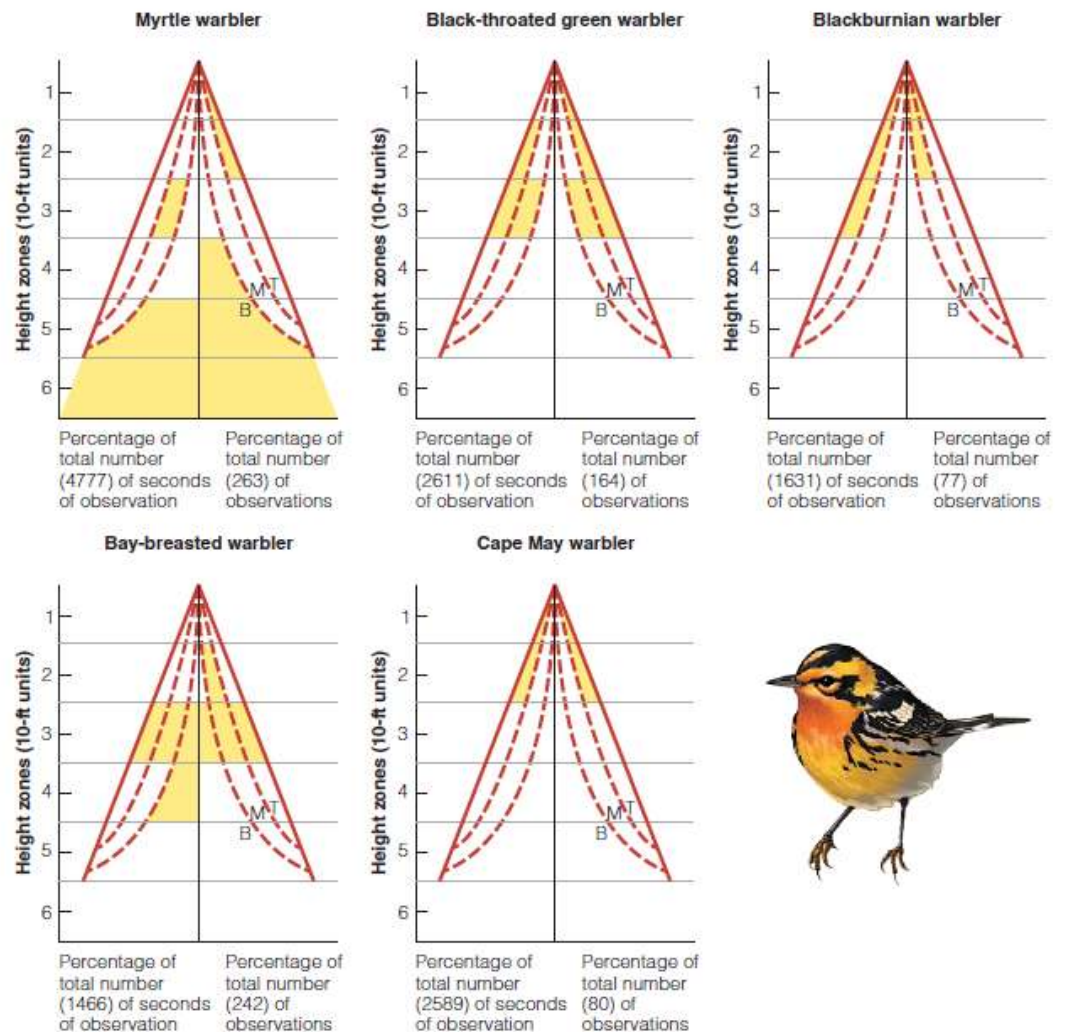
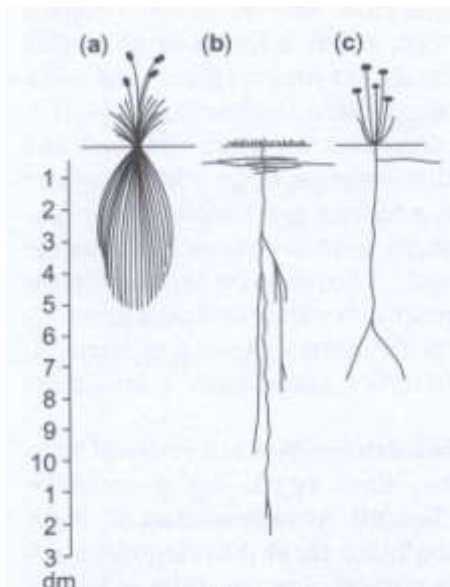


Figure 14 Feeding positions of five species of warblers in the coniferous forests of the northeastern United States. The zones of most concentrated feeding activity are shaded. B = base of branches, M = middle of branches, T = terminal portions of branches. The blackburnian warbler is illustrated. (After MacArthur 1958.)

Feeding positions of five species of warblers (*Dendroica* sp)

In heterogeneous (space and/or time) environment there is a chance for coexistence of species by niche segregation

- Environmental inhomogeneity

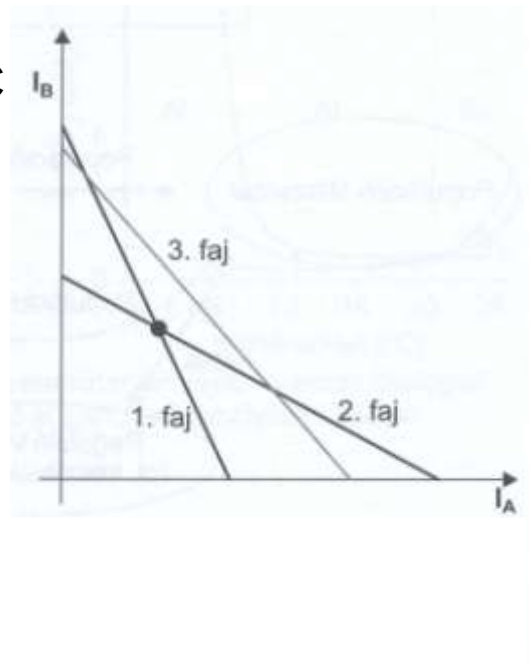


Roots of plants

How many species could live together permanently?

The number of permanently coexisting population of species could not be more than the number of regulatory factors

(In the case of C pieces of regulatory factors, maximum C species could live together)



Regulatory component of growth of competing population need to be enough different for permanent coexisting