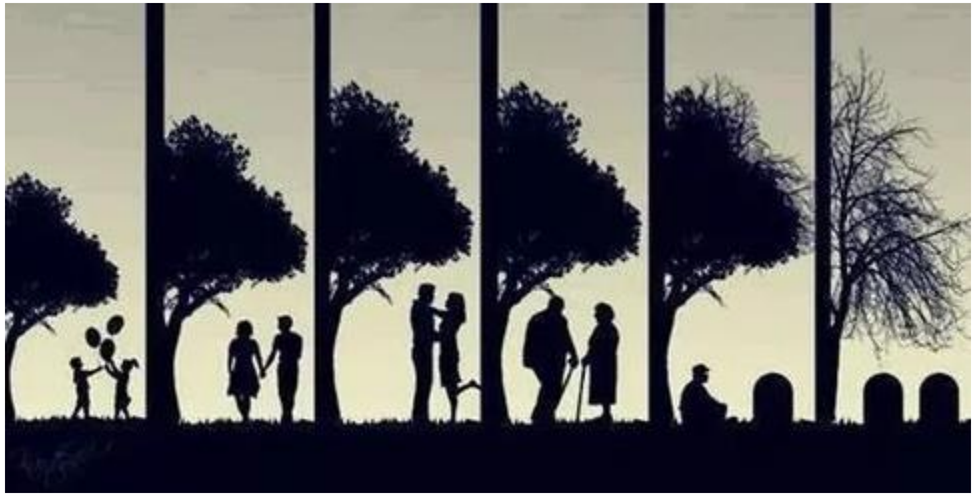
Wildtierkundekurs II

Theory 3: Survival



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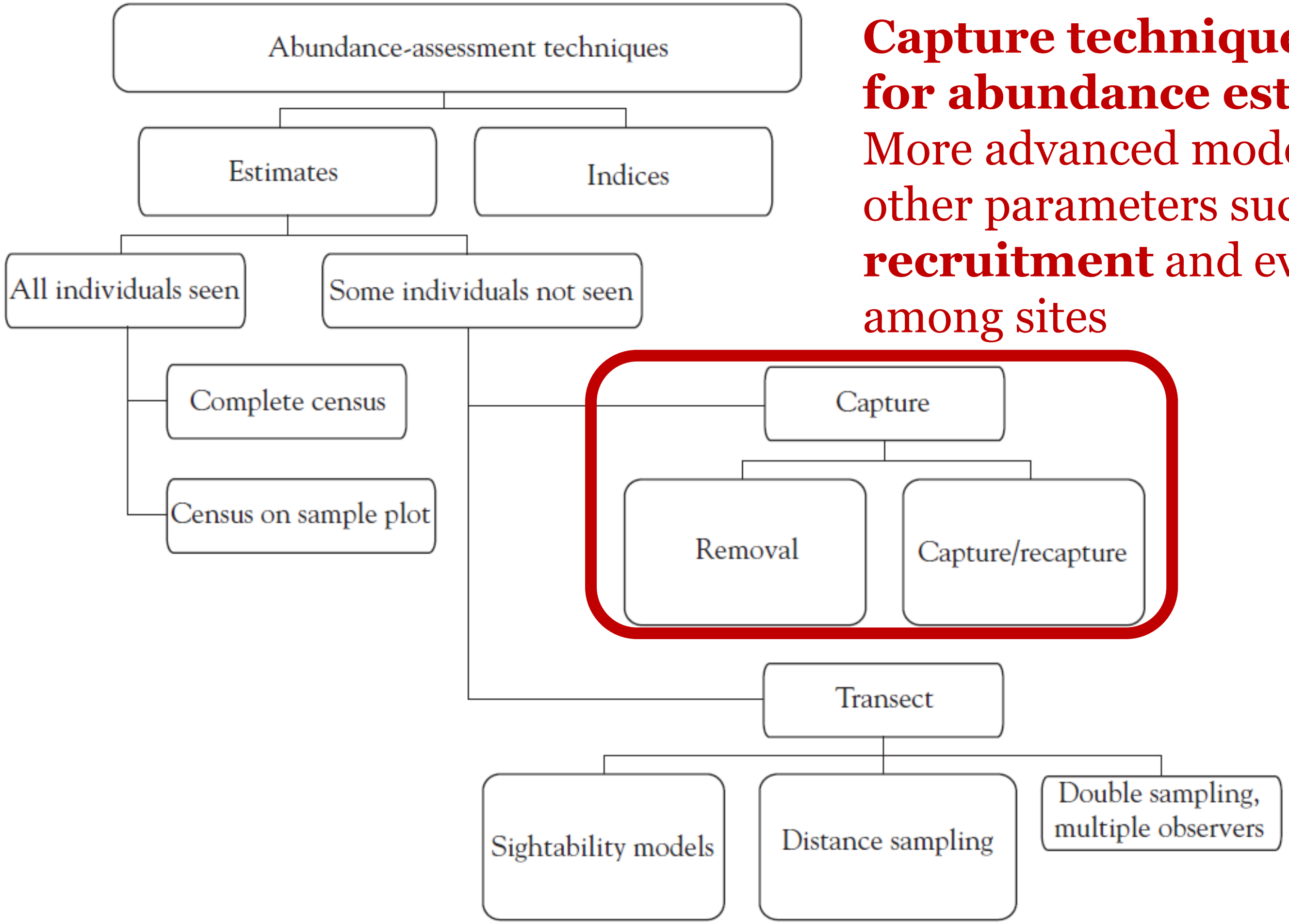
Capture related methods: survival & reproduction



Capture technique not only used for abundance estimation!
More advanced models can estimate other parameters such as **survival**, **recruitment** and even movement among sites

Estimating Population parameters

Abundance and Density

Survival

capture recapture models (e.g. Cormack-Jolly-Seber)

band recovery models (e.g. multi-state models)

known fate models (e.g. Kaplan-Meier)

Recruitment

reproduction

sex ratio

age structure

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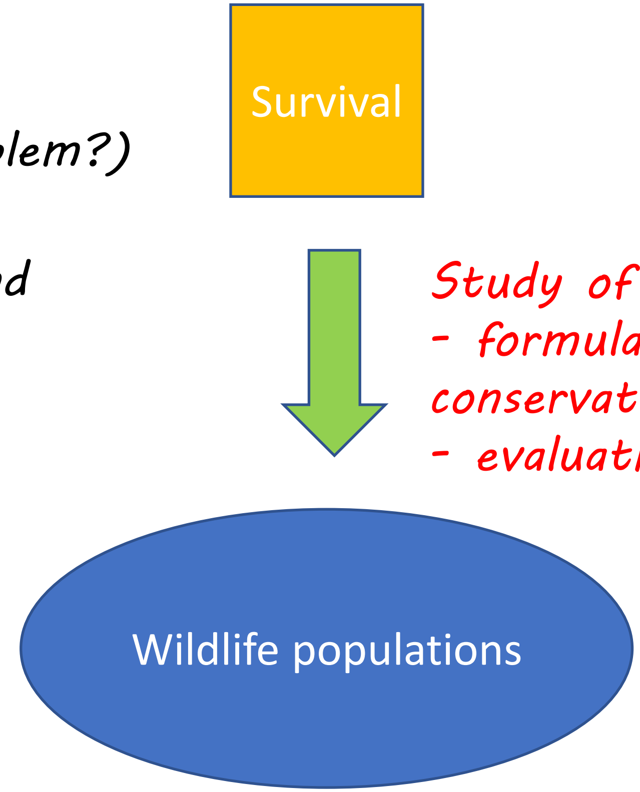
Survival in wildlife management and conservation

- *environmental influences on survival*
- *evaluation of population "health" (low survival=problem?)*
- *population viability analyses (e.g. estimation of growth and extinction parameters)*



Study of survival informs management and conservation
- *formulating and implementing management of conservation plans*
- *evaluating the efficacy of management strategies*

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Estimation of animal survival

3 main classes of survival estimators:

- **CMR → survivors are recorded**
- Band recovery models → deaths are recorded
- Known fate models → animals can be relocated

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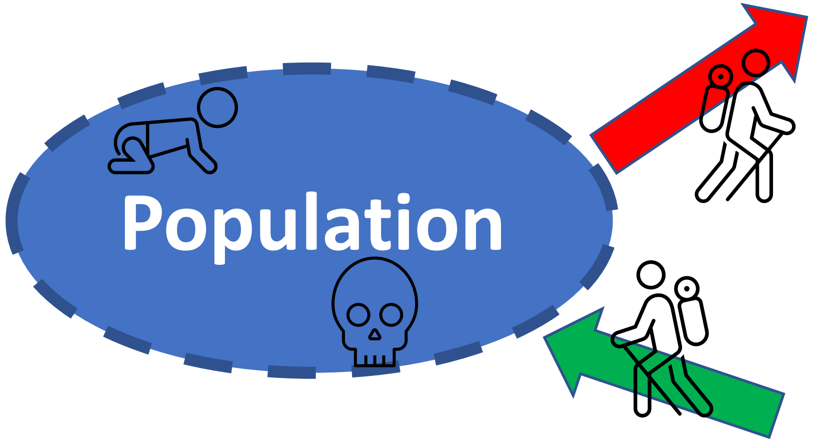
Open population CMR models

Assumption of closed population is difficult to fulfill for many studies

→ capturing continues over extended time periods

Open population models deal with the problem that after some time, animals might have been born, immigrated, emmigrated or died (i.e. detection probability would be biased!)



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Open population CMR models

Survival → difference between number of animals marked alive just before i+1 and number alive immediately after time i

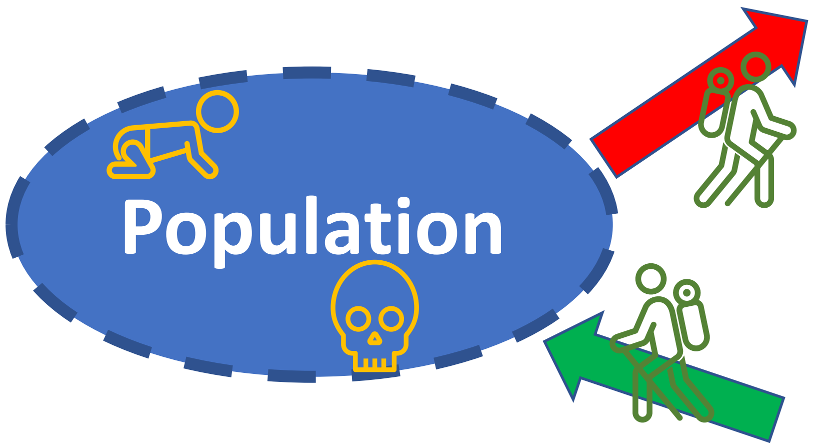
Recruitment → difference between estimated population size at time i+1 and expected number of survivors at time i+1 of the population size at time i

Note: only so called «apparent» survival and «apparent» recruitment can be estimated, as we can't distinguish animals dying from animals emigrating or animals being born from animals immigrating → but see robust design next.

Open population CMR models

Jolly-Seber (JS) open CMR models and its variants
estimate abundance, survival and recruitment

Cormack-Jolly-Seber (CJS) open CMR models and its variants
estimate survival of population

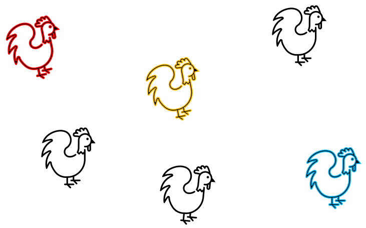


Mills 2006

Open population CMR models

k-sampling occasions (where k>2)

The **capture history** of each animal has to be recorded.



Because of possible deaths or emmigration the number of **marked animals alive before each capture session** must be estimated.

To estimate this number, we use information from animals captured BEFORE and AFTER but not during sampling occasion i.

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Revisiting capture histories for open populations

Capture histories contain information on survival as well

H1 [1,1,0,0,0,1,0,0,1,0,1,0] → $p_1 \phi_1 x\ p_2 \phi_2 x\ (1-p_1)\ \phi_{1...}$

H130 [0,1,1,1,0,0,0,0,0,0,0,0] → ... probably dead or emmigrated

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Open population CMR models

Assumptions:

- Equal catchability
- No effect of marking
- Animals do not lose marks
- All marks are seen and recorded
- Equal survival: Every marked animal has same chance of survival from time of capture i to occasion i+1

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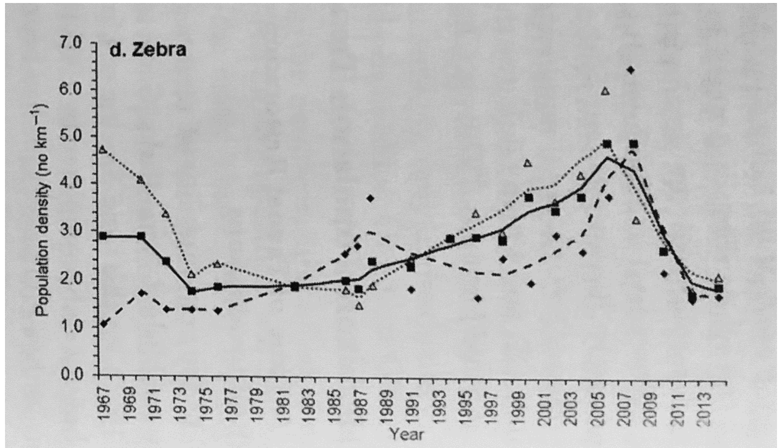
Example of Cormack-Jolly-Seber model



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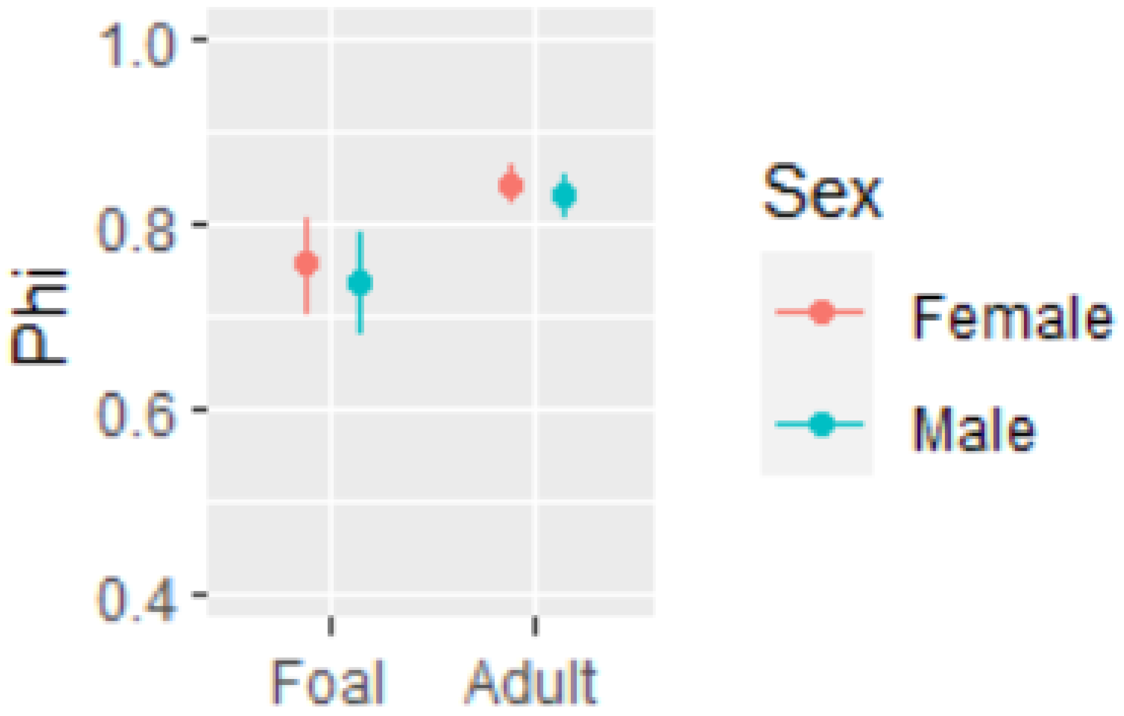

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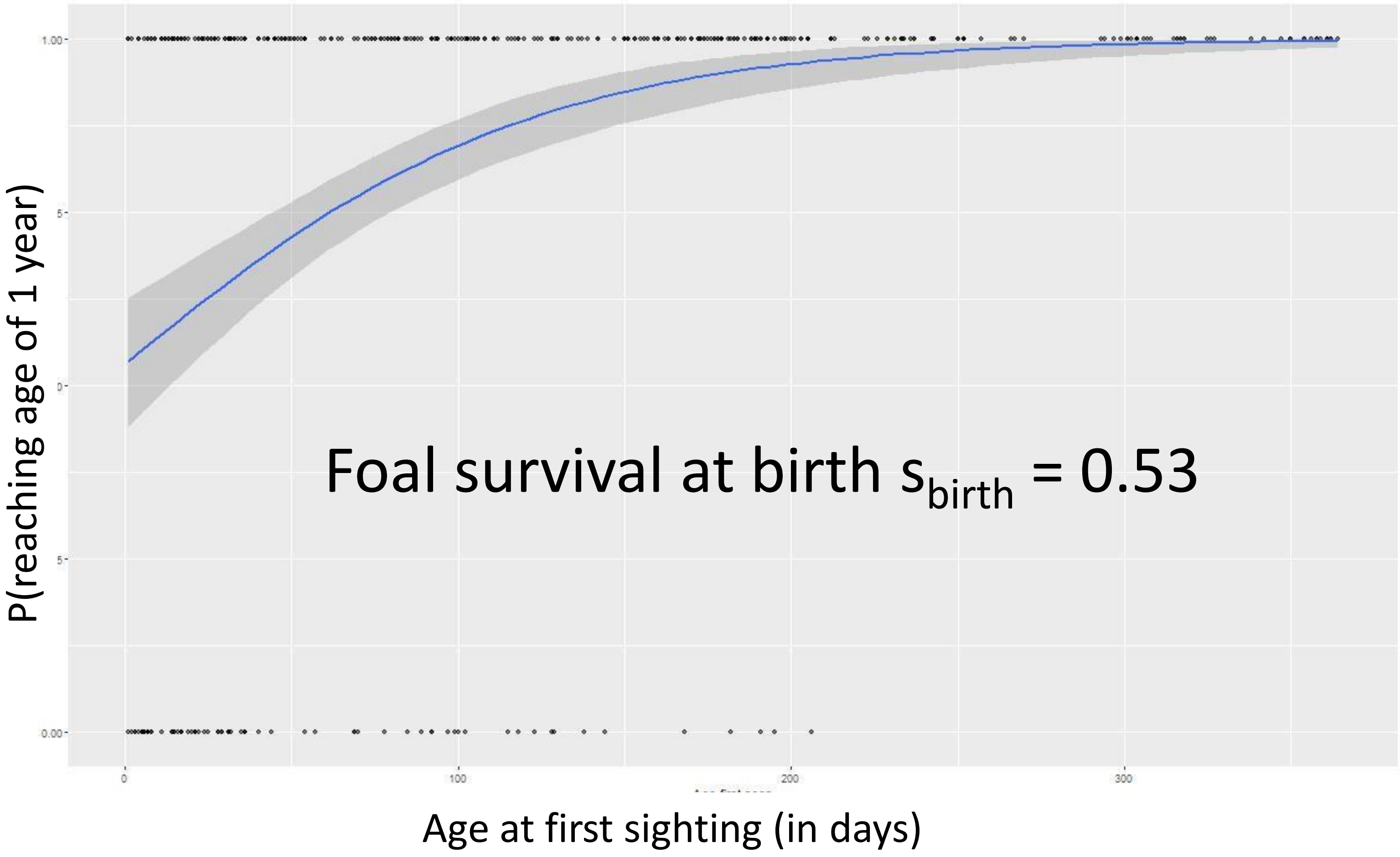
Zebra foal survival in HiP



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Estimation of animal survival

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Band recovery models

- Band recovery models are closely related to CMR models but instead of recapturing animals alive, marked animals found dead are recovered.
- Not all dead animals will be found → instead of detection probability of animals alive, the dead-recovery probability has to be modelled.
- Unknown parameters are recovery probability and survival.
- These models are best known from ringing schemes for birds.

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Example of band recovery model

Long-term roe deer fawn marking study orchestrated by Wildtier Schweiz

50 years of fawn marking, 20'000 fawns marked, over 4'000 animals recovered with reported death cause

Possible to estimate survival and cause-specific mortality

→ *information can be used for modelling population dynamics*

Mowing related deaths

Thousands of fawns are killed every year…

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The fawn marking project

Hunters and farmers work together to find and rescue fawns…

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The fawn marking project

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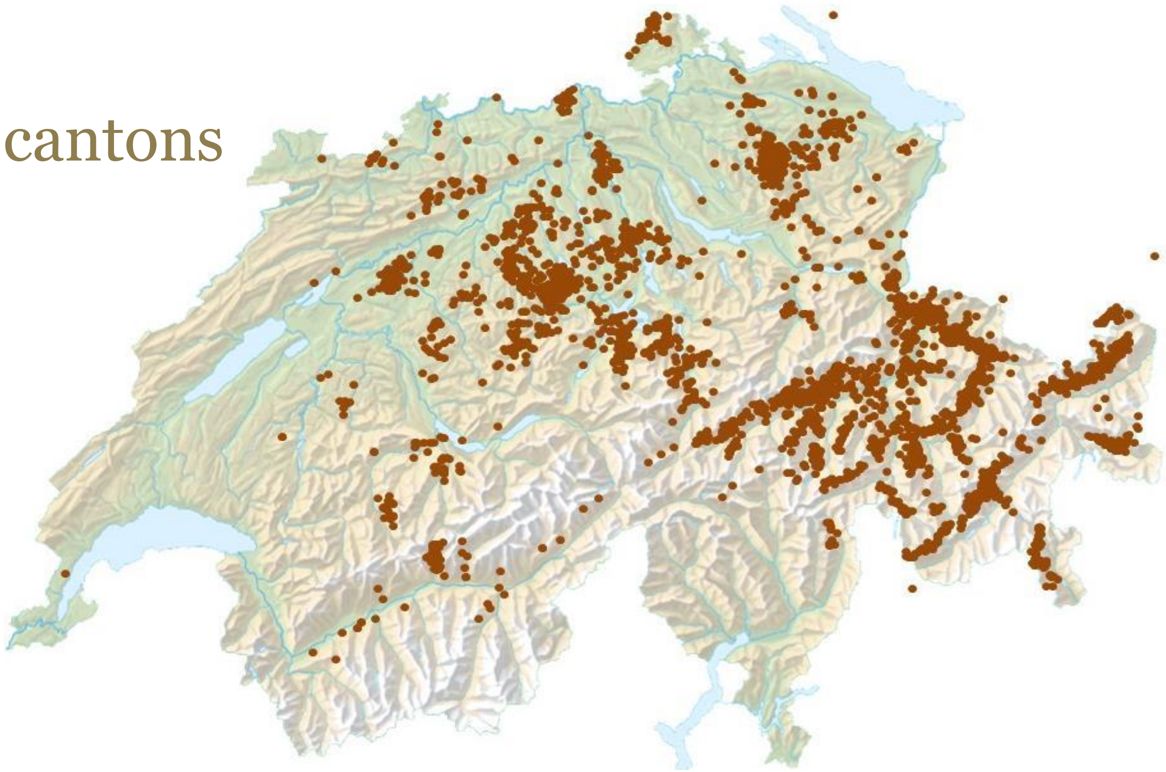
Wildtier Schweiz

The fawn marking project

Since 1971
With the participation of 22 cantons
18’294 were marked,
Of which 3901 recaptured
(21%)



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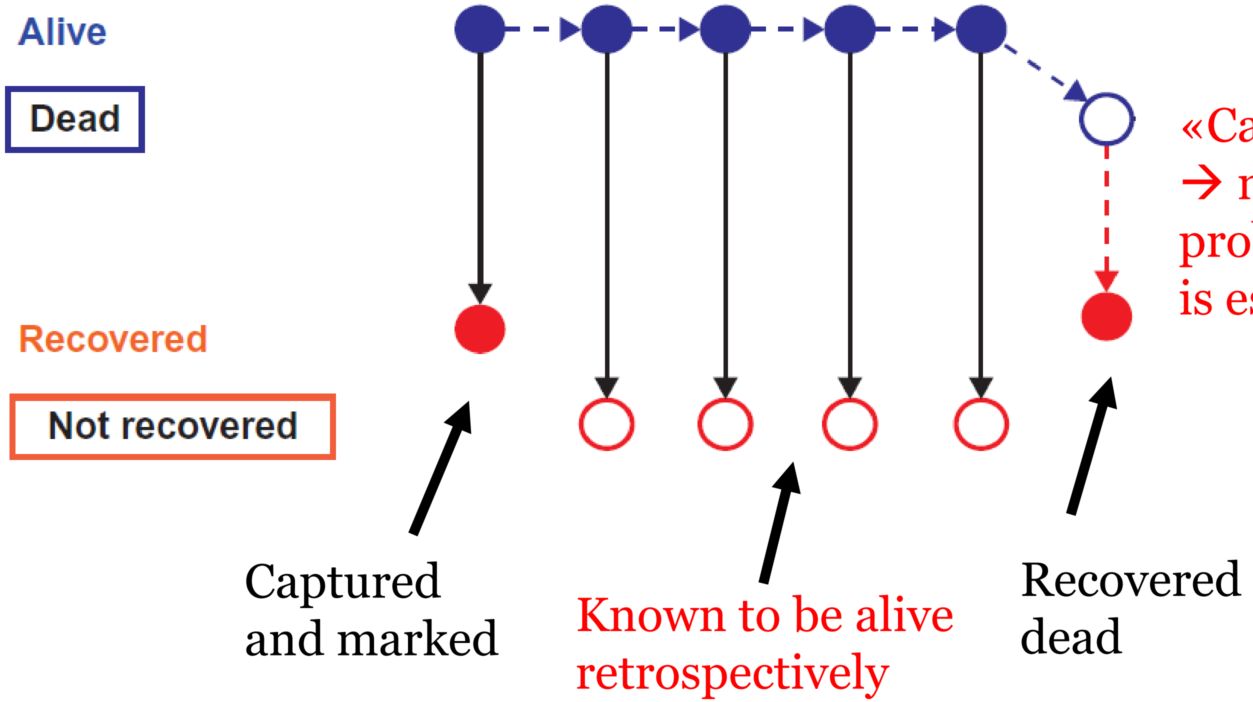
Band recovery models

Adapted from Kery & Schaub BPA 2011



«Capture history» is [1,0,0,0,0,1,0,...] → most likely survival and recovery probability given the capture histories is estimated

Results in a «capture history» similar to CMR models → holds information on surival and recovery probability

Example of band recovery model

Capture histories allow modelling **unbiased** cause-specific mortality

Example: Estimate unbiased mortality using long-term fawn mark-recovery data:

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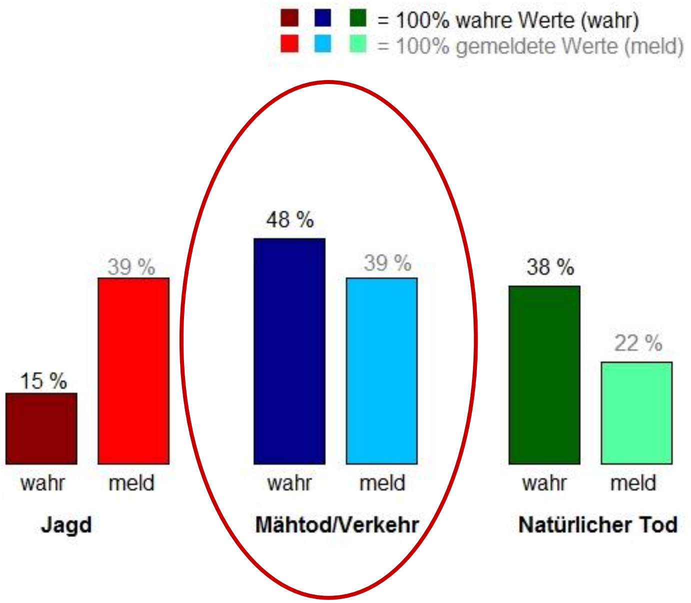
Example of band recovery model



estimated 13% of all marked fawns are killed in mowing accidents

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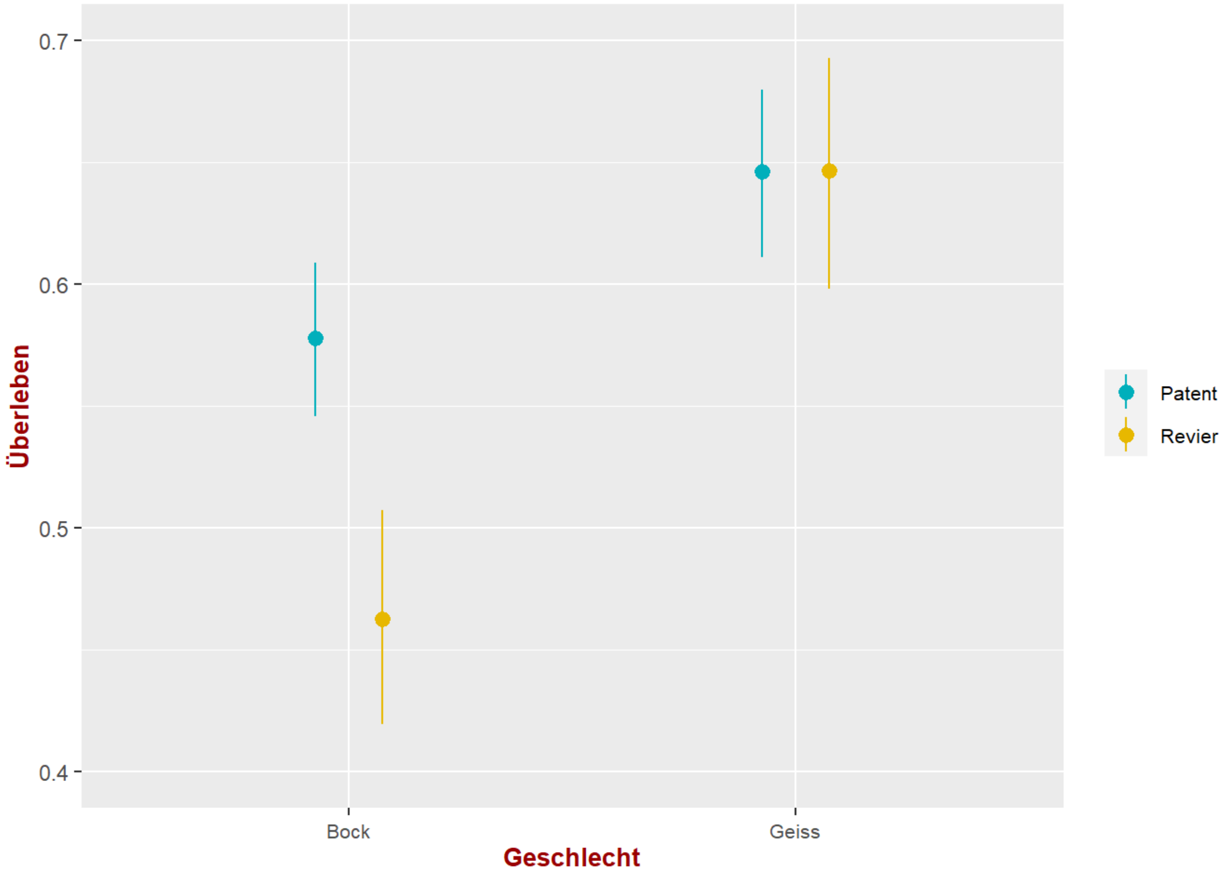
Example of band recovery model

Compare Revier & Patent Cantons

- *Male survival differs among the two systems*
- *Femae survival is similar among systems*



Estimation of animal survival

3 main classes of survival estimators:

- CMR → survivors are recorded
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- **Known fate models → animals can be relocated**

Known fate survival models

Principle: you mark a cohort of animals and follow their fate.

Assumptions:

- **no animals** are **lost** during the study or **added** after the study start
- Possible to follow animals closely using telemetry or similar techniques
- All animals have same survival probability and are monitored for the same period of time
- Fates of animals are independent

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Known fate survival models

Then survival for a given time interval is simply a binomial model (tossing a coin with death on one side and survival on the other):

Survival = x surviving animals relative to total number n

$$\hat{S} = \frac{x}{n}$$

binomial variance $$\hat{\mathrm{var}}\left(\hat{S}\right) = \frac{\hat{S}\left(1-\hat{S}\right)}{n}$$

Adjusted finite survival rates

Often one is interested in **standardized survival times** such as annual survival, or monthly survival. These times may not coincide with estimated study survival (S_O). Estimated survival times can be easily converted:

Adjusted finite survival rate = $(S_O)^{t_s / t_o}$

where t_s = standardized time interval (e.g., 28 days)

t_o = observed time interval (e.g., 35 days)

Example of adjusted finite survival rates

We observe a finite survival rate (S_o) for hare leverets of 0.067 for 35 days. (S_o = 0.067; t_o = 35 days)

Monthly survival rate (t_s = 28 days) is:

$$(S_0)^{\frac{t_s}{t_o}} = 0.067^{\frac{28}{35}} = 0.115/month$$

Daily survival rate (t_s = 1 day) is:

$$(S_0)^{\frac{t_s}{t_o}} = 0.067^{\frac{1}{35}} = 0.926/day$$

From Karp & Gehr 2020

Known fate survival models

In reality, animals are often captured over extended time periods (staggered entry) and some fates may be unknown due to losses (censoring)

→ Failure time models can deal with this

→ Most popular failure time model is the Kaplan-Meier method

Kaplan-Meier method

- Non-parametric survival estimator
  → no assumption on underlying distribution of deaths events
- allows for staggered (i.e. continuous) entry and censoring (i.e. loss) of animals
- For each time period compare number of deaths to number of animals at risk of dying → survivorship curve (proportion of animals alive at time t)

Survival

$$\hat{S}(t) = \prod_{i=1}^{t} \left[1 - \left(\frac{\text{Number of deaths at time } i = d_i}{\text{Number at risk at time } i = r_i} \right) \right]$$

Variance

$$\mathrm{var}\left[\hat{S}(t)\right] = \frac{\left[\hat{S}(t)\right]^2 \left[1 - \hat{S}(t)\right]}{r_t}$$

Example of Kaplan-Meier method

Study on northern bowhite quail radio-tagged in North Carolina (Pollock et al. 1989)

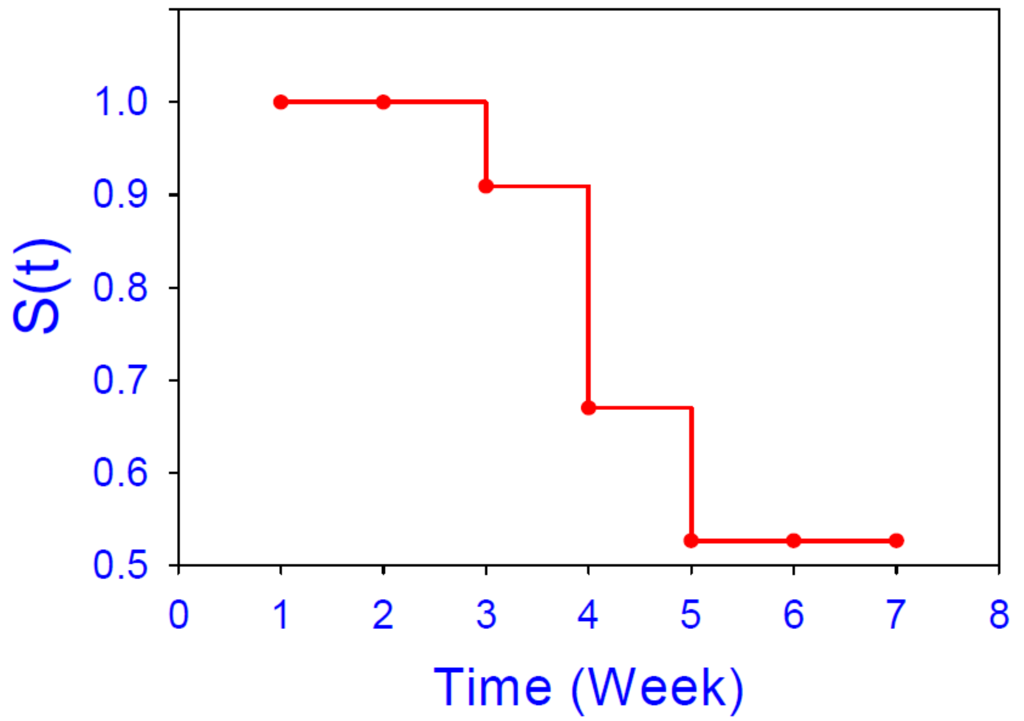
Survival

week	N at risk	N deaths	No censored	No added	$1-\frac{d_j}{r_j}$	$S_t = \prod_{j=1}^{t}\left(1-\frac{d_j}{r_j}\right)$
1	20	0	0	1	1-0/20=1	1.00

7 week survival = 0·526 - can be converted to standardized survival times as discussed before

Example of Kaplan-Meier method

Visualization of the Kaplan-Meier survival time results in a step function



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Kaplan-Meier method: assumptions

- Marked animals are representative for the population (age, sex, etc.)
- Marks do not affect survival
- Reason for censoring is not related to fate
  (e.g. marks of poached animals removed will bias survival estimator)
- Fates of animals are independent
  (e.g. fates of litter mates may not be independent
  → predator removing entire litters)

Kaplan-Meier method: additional notes

- Precision is a function of nr of animals at risk
  → large sample size is better

- Survival will be biased if animals of higher death risk will die first
  → Staggered entry can account for this – ideally number of animals at risk should remain as constant as possible
  → One can restrict survival estimation to period where number of animals at risk is large (exclude beginning of study and end of study where only very few animals remain – potentially non-random sample in the end)

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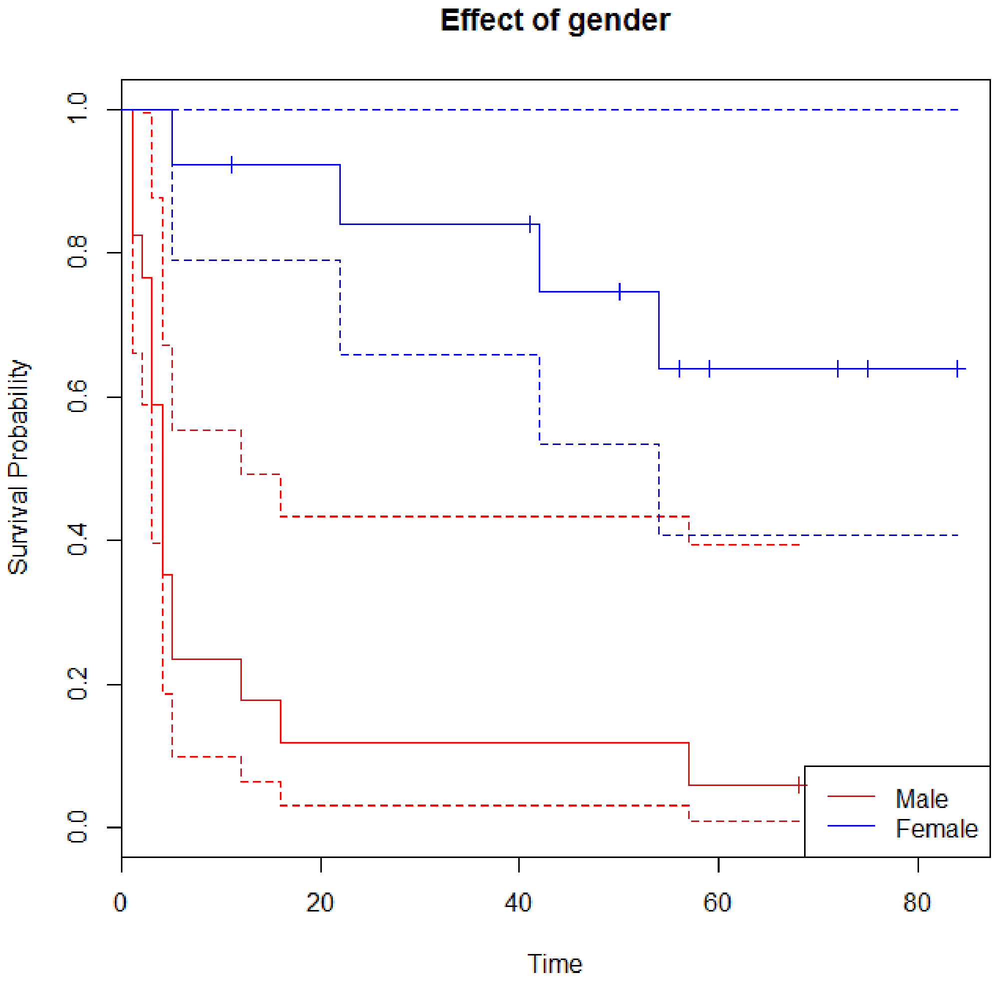
Kaplan-Meier method: additional notes

- Kaplan-Meier method can be extended to test for differences in survival of different groups (e.g. sex, age, etc.)



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Kaplan-Meier method: additional notes

- In depth survival modelling with multiple predictors requires more sophisticated models

→ Cox-proportional hazard models (CPH)

CPH-models are the most widely used survival analysis for known fate data sets → multi-variate regression approach

Time independent covariates

$$h_i(t) = h_0(t) \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_p x_{ip})$$

Hazard → instantaneous risk of dying due to covariates

Time dependent baseline hazard → form of baseline hazard unspecified

Proportional hazard: $\frac{h_i(t)}{h_j(t)}$ is constant over time

Estimating Population parameters

Abundance and Density

Survival

capture recapture models (e.g. Cormack-Jolly-Seber)

band recovery models

known fate models (e.g. Kaplan-Meier)

Recruitment

reproduction

sex ratio

age structure

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Estimating reproduction

Reproduction is an important vital rate.

It determines population growth together with survival and movement.

→ remember BIDE equation:

$$N_{t+1} = N_t + \text{Births} + \text{Immigration} - \text{Deaths} - \text{Emigration}$$

There are different ways of accounting for reproductive output, e.g. offspring per adult female, or female offspring per adult female, or offspring per adults, etc.

→ Important to clearly define what one is talking about

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Estimating reproduction

Handling/sampling methods e.g. ultrasound or from dead animals (e.g. harvested) :

- Counting corpora lutea, uterine scars (mammals) or postovvulatory folicles (birds)
- Counting embryos (mammals)
- Females, e.g. pregnancy rates from pregnancy hormones in feces or blood samples
- Males, e.g. testis size, sperm counts, etc.

Reproductive output must be scaled by in utero survival. e.g. an ovum must be fertilized and implanted to become a fetus and fetus must survive to birth, etc.

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Estimating reproduction

In the field

- Proportion of population breeding
- Number of young observed per female

→ Again requires scaling, not all animals breeding will conceive, many juveniles die shortly after birth!

In models (focus on net contribution to population growth)

- e.g. CMR models to estimate recruitment

*Paternity and Maternity can be established from observations in the field or more reliably with **genetic markers***

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Sex ratio and age structure

Not all animals in a population are equal!

- Individuals contribute differently to population growth depending on sex and age.
- Sex- and age structure of a population have important consequences for long term population dynamics

→ Think about growth of human population consisting of
  → all 50 year old people
  → all children

→ Think about growth of red deer population consisting of
  → 10 males and 100 females
  → 100 males and 10 females

Sex ratio

Sex-ratio is defined as: males per female or vice versa, or proportion of males in the population

Sex-ratio (SR) changes with life stages (due to unequal survival of males and females):

- Primary SR → at conception
- Secondary SR → at birth
- Tertiary SR → later date, e.g. end of parental care
- Quaternary SR → breeding adult population

Breeding sex ratio** may be very different from **population sex ratio
→ breeding sex ratio in elephant seals may be 1:20!

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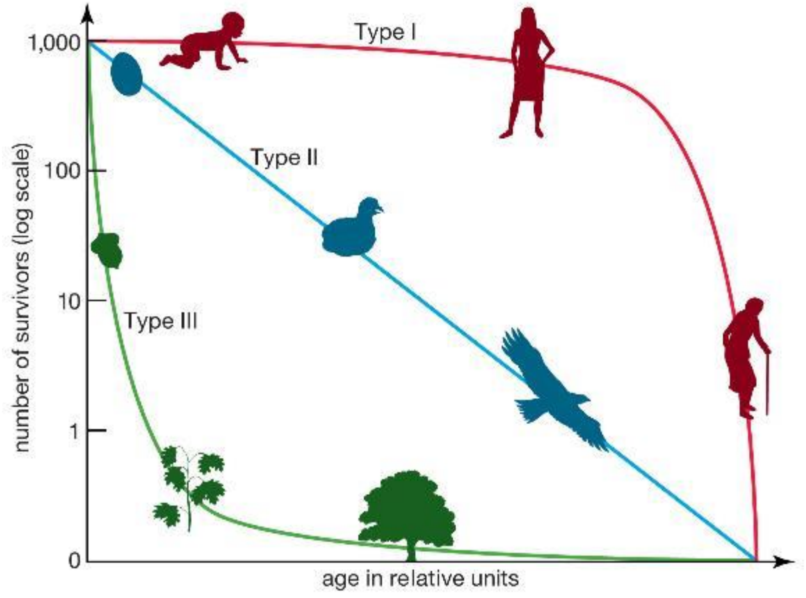
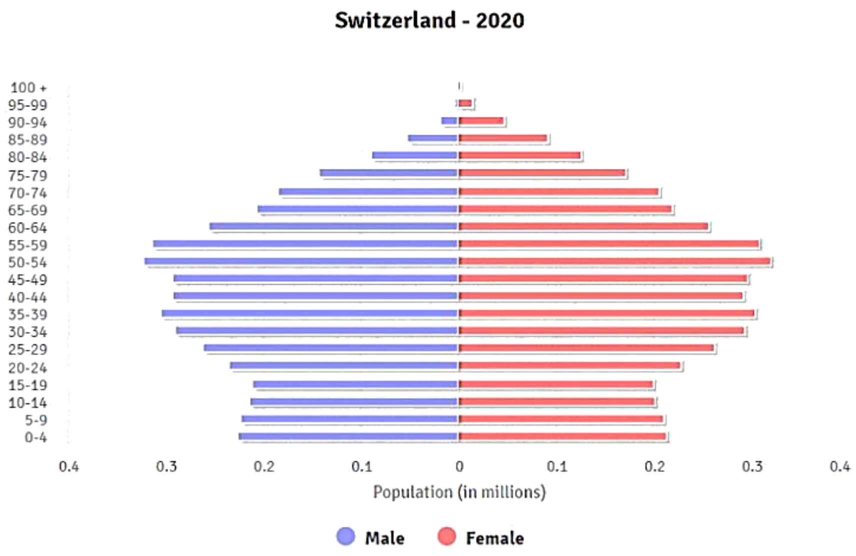
Age structure

- Composition of different ages or stages in population
- Result of animals dying over time
- General form of age structure will depend on form of the survival curve





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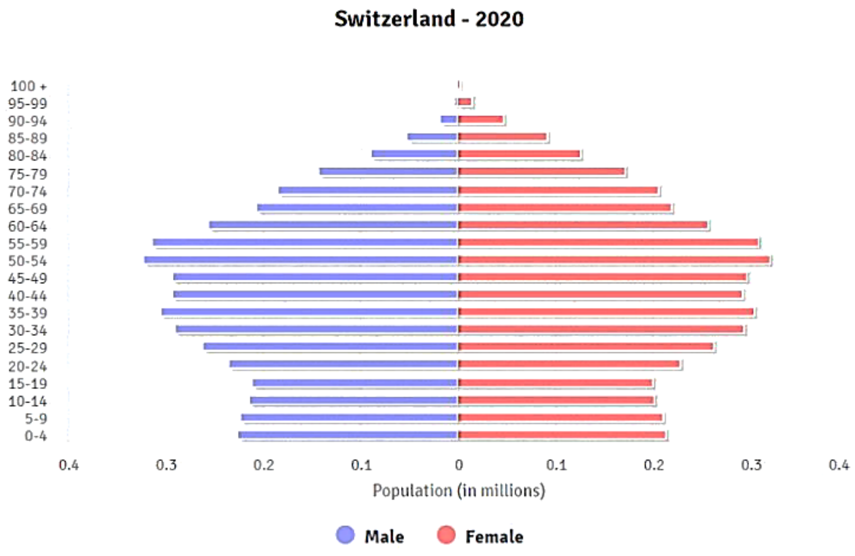
Population age structure

A stable age distribution exists for a constant survival and population growth rate

The stable age distribution will only be reached after some time

The relationship between *age distribution*, *survival* and *population growth* is the basis for **life table analyis**

→ **by knowing two the third can be deduced**, e.g. age structure and population growth rate allow calculation of survival



Males and females have different age distributions!

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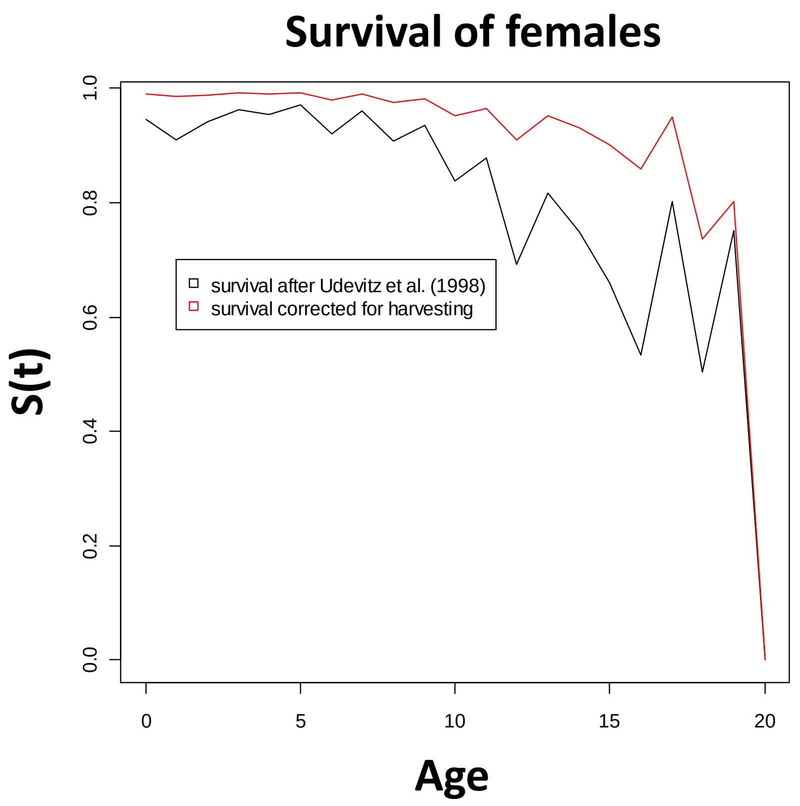
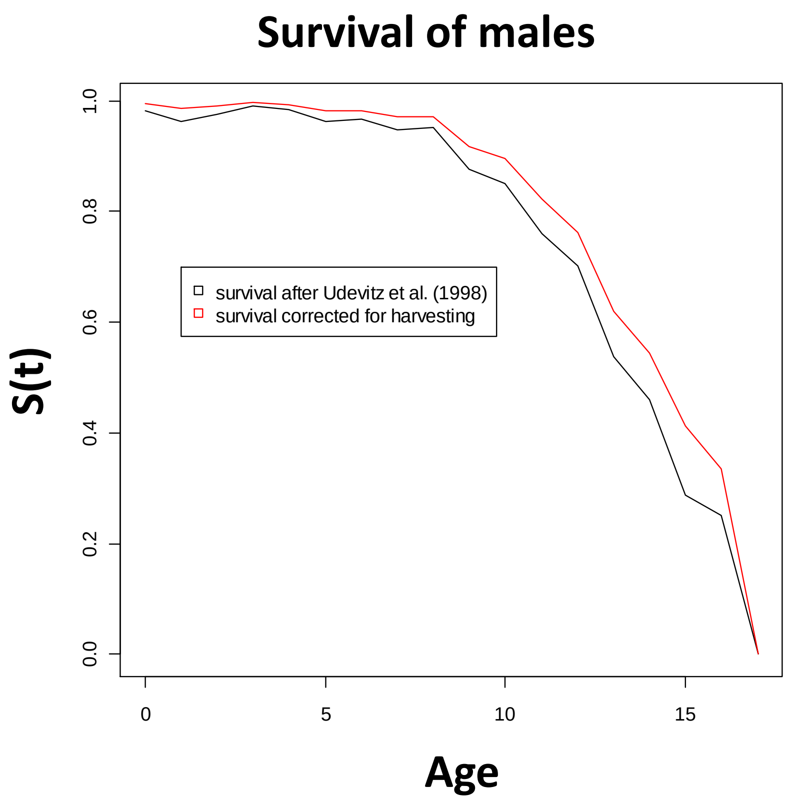
Life table analysis with ibex mortality data





- Interdependence of age structure, growth rate and survival was used to estimate survival corrected for harvesting

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Interpretation of age structure

The age structure ALONE does NOT tell you anything about population growth!

→ A decreasing and an increasing population can have the same age structure.

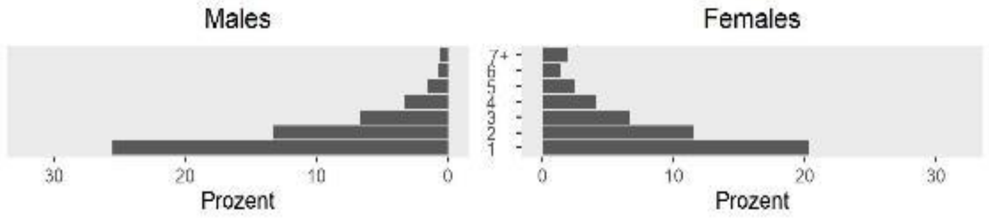
→ Populations with different age structures can have the same growth rate.

Even if age distribution is constant you need information about **general survival patterns** of a species to interprete age distributions

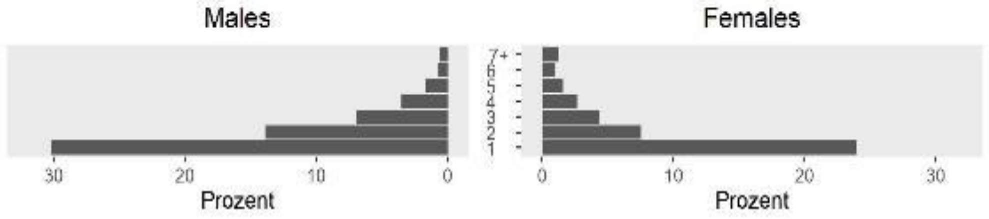
Age structures of animals dead and alive

Data from roe deer marking study 1971-2020

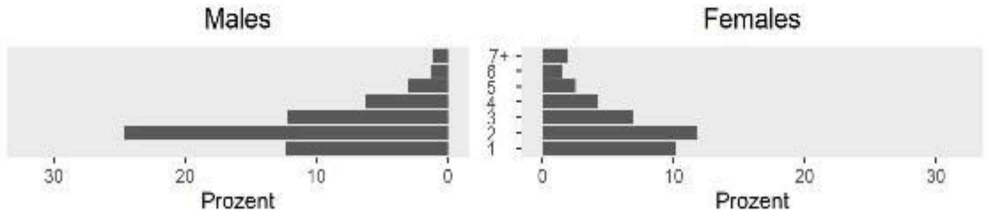
Standing population



Natural deaths



Harvest



Sexes and age classes are not hunted randomly

The age structure of the standing population and age-at-death distribution will only be the same if all stages have the same probability of dying!

Other approaches to describe populations

- Population reconstruction using age-at-harvest data (abundance and age structure over time)

- Matrix projection models (projection of population dynamics under different scenarios)

- Integrated population models (combined estimation of vital rates movement and population growth using different data sets)

In the end we're interested how temporal changes in vital rates affect population structure and growth, i.e. long term development of wildlife populations!

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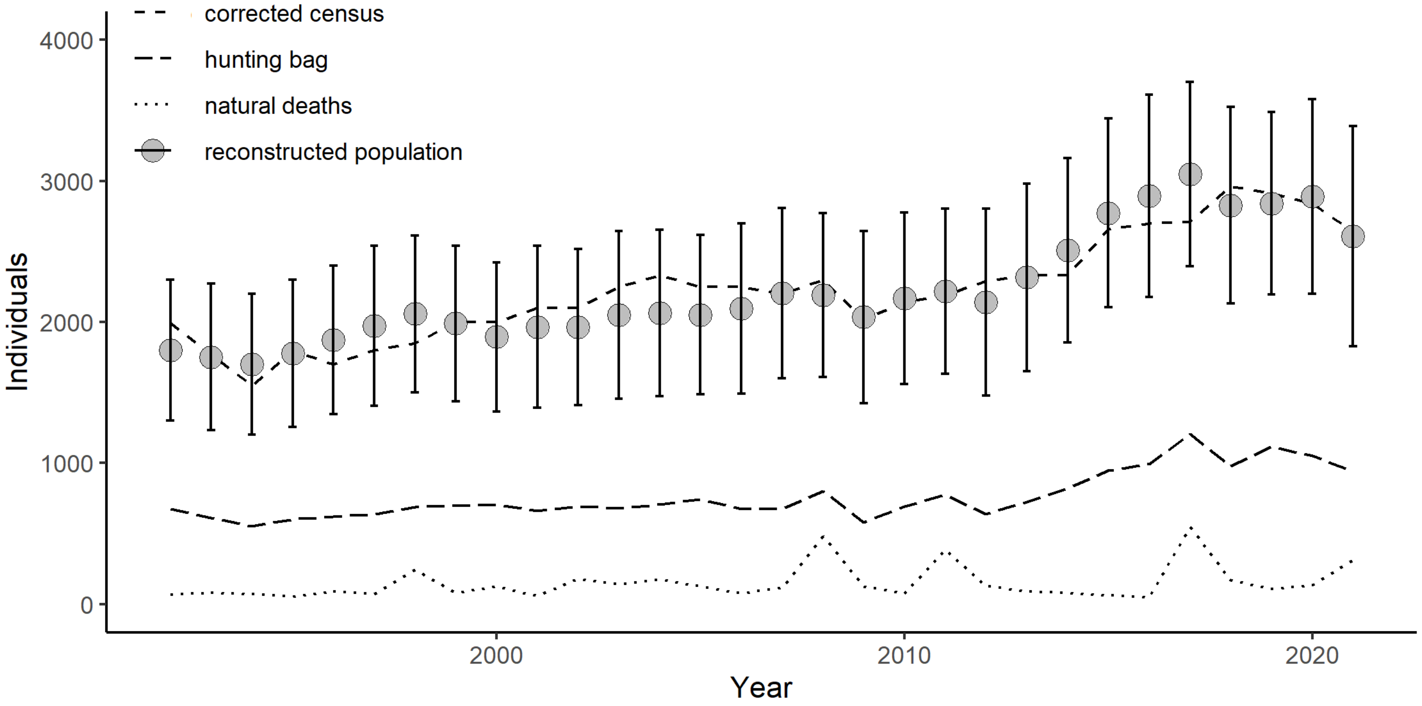
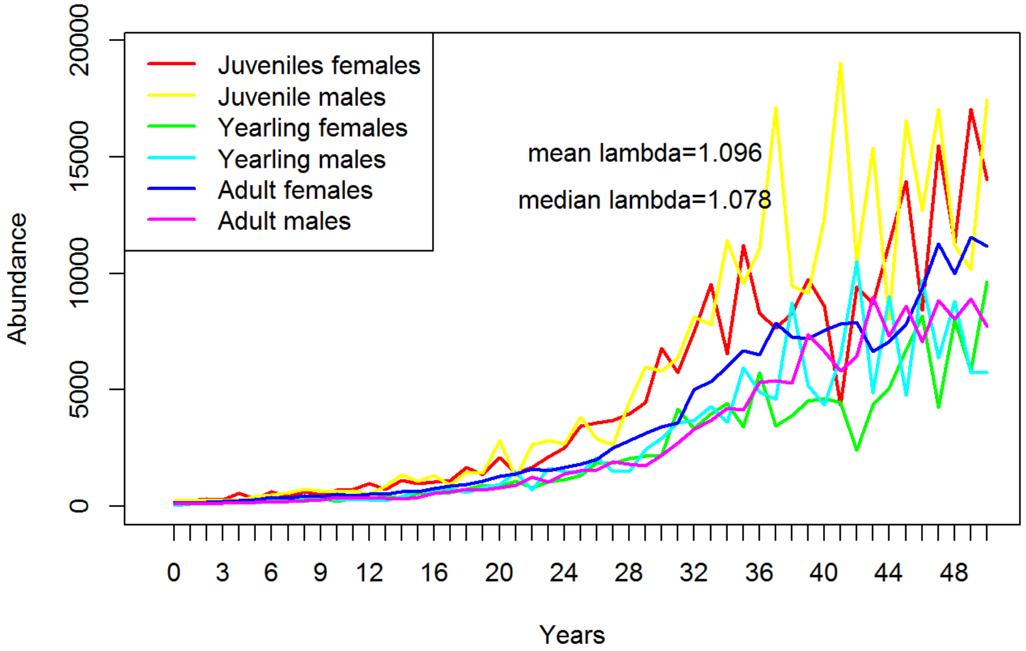
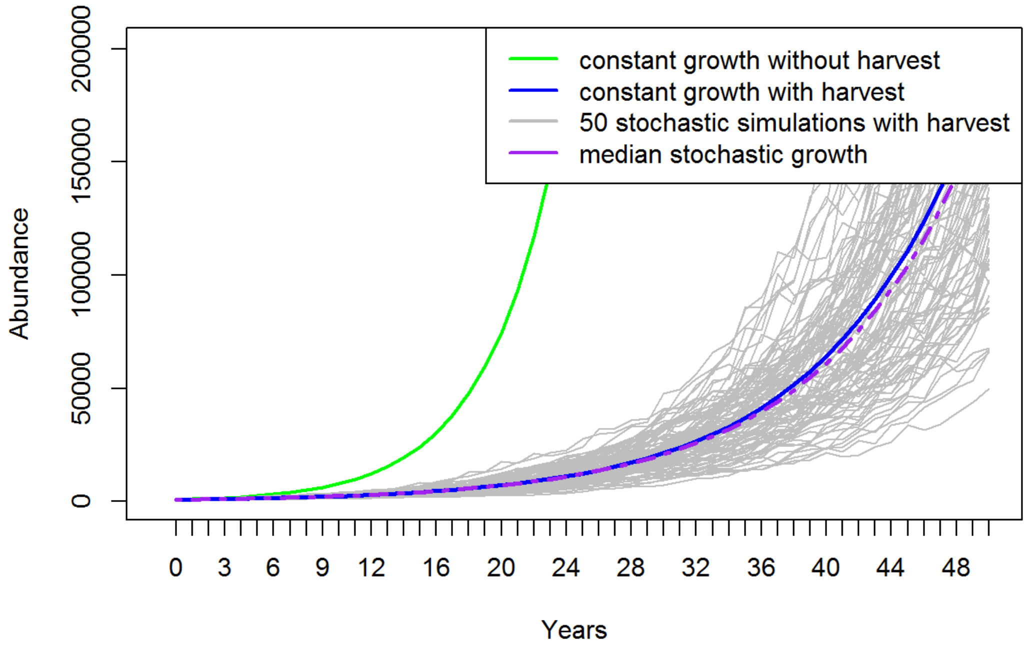
Applications for management



- Population reconstruction using age-at-harvest data (abundance and age structure over time) together with auxilary information (e.g. survival)

Applications for management





- Matrix projection models (projection of population dynamics under different scenarios using estimates of survival and reproduction)

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