An introduction to age-structured population models and some dolphin ageing!

Victor Ronget
vronget@uni-mainz.de

JOHANNES GUTENBERG UNIVERSITÄT MAINZ

Heterogeneity in vital rates

- Individuals are not **homogeneous** within a population:

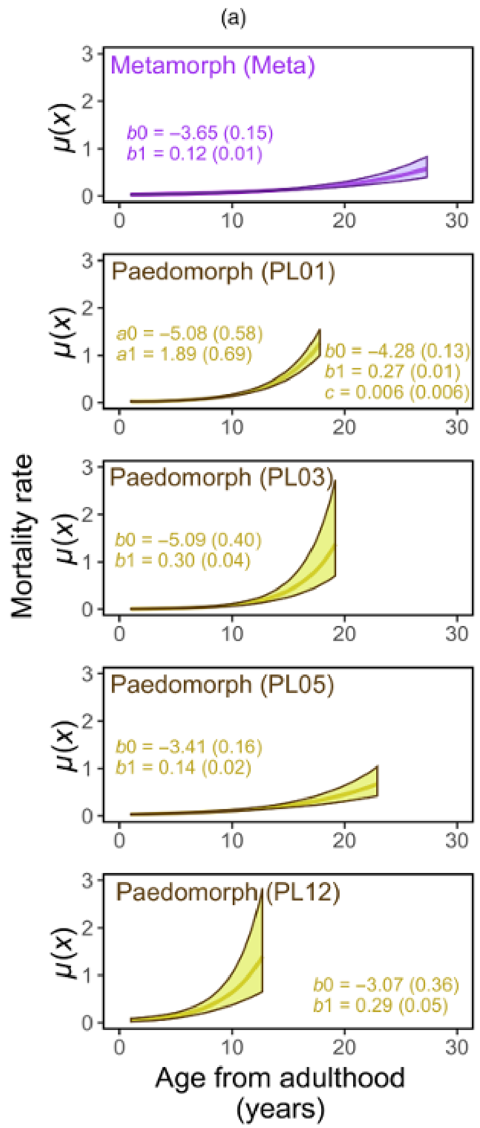
- Intrinsic variations: morphology, age…

- Extrinsic variations: temporal/spatial variations…

➔ **Can result in vital rates variations**

➔ How does it affect the dynamic of a population?

➔ Should we account for this heterogeneity?



Cayuela et al., 2024 JAE

Age-dependency of vital rates

- One of the **main axes of heterogeneity is age**

- For instance:

- **Juvenile** might not reproduce and/or are more likely to die
- **Older individuals** might suffer from senescence in survival and/or reproduction

Age can only increase with time:

-> Limited number of transitions

Packer et al.,
1998 Nature

The paradox of ageing evolution

- Ageing define as **physiological decline associated with age leading to reduced survival and/or reproduction**

- Ageing is **pervasive** across species

- But selection should purge deleterious mutations affecting older ages???

Packer et al.,
1998 Nature

➔The fundamental equation of population dynamics

$$\Delta N = B - D + \cancel{I - E}$$

ΔN : change of population size ($N_{t+1} - N_t$)

B : number of births

D : number of deaths

I : ~~number of immigrants~~

E : ~~number of emigrants~~

Only closed populations today

The exponential growth model

- Continuous time model with a **constant per capita growth rate**

(i.e. an individual is always producting the same number of new individuals)

- $$\frac{dN(T)}{dT} = rN(T)$$

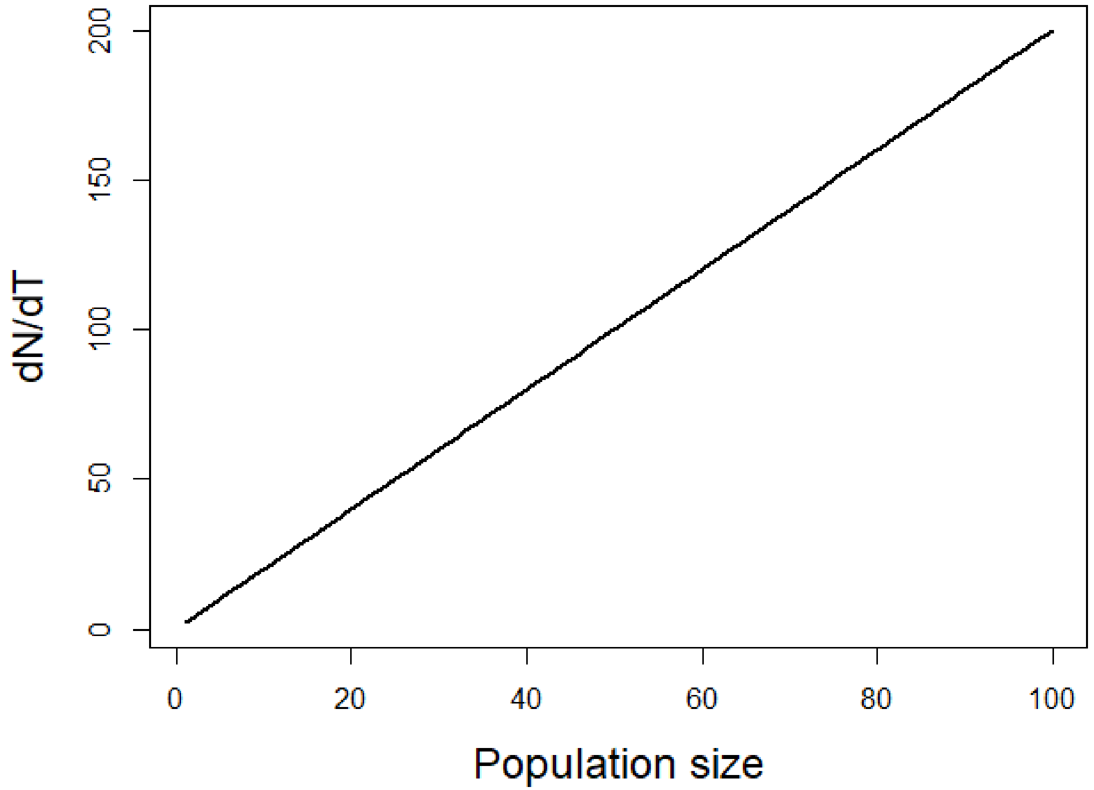
N(t) : population size (ind)

r : per capita growth rate ($time^{-1}$)

r includes both deaths and births

r > 0 increasing population

r < 0 decresing population



The exponential growth model

- Solving the differential equation:

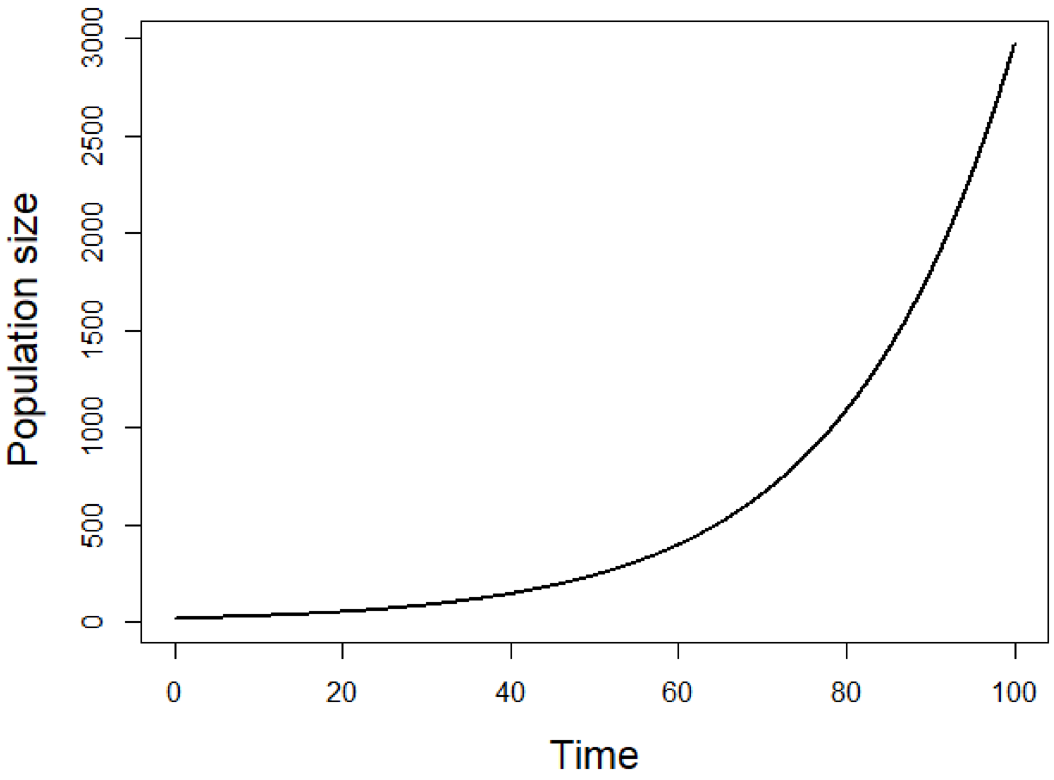
$$N(T) = N_0 e^{rT}$$

N0 : initial population size

- Exponential shaped curve

Population size is always increasing (density independant model)

- **We will apply that model for heterogenous populations (age-specific)**



Aim of this course

- Describe changes in vital rates with age **(Life table analyses)**
- Build a population projection model **(Leslie matrices)**
- Assess the key vital rates for the population **(Sensivity/Elasticity analyses)**
- A brief overview of the **evolutionary theories of aging**

(example with baboon life table then practice on the dolphin longitudinal data)

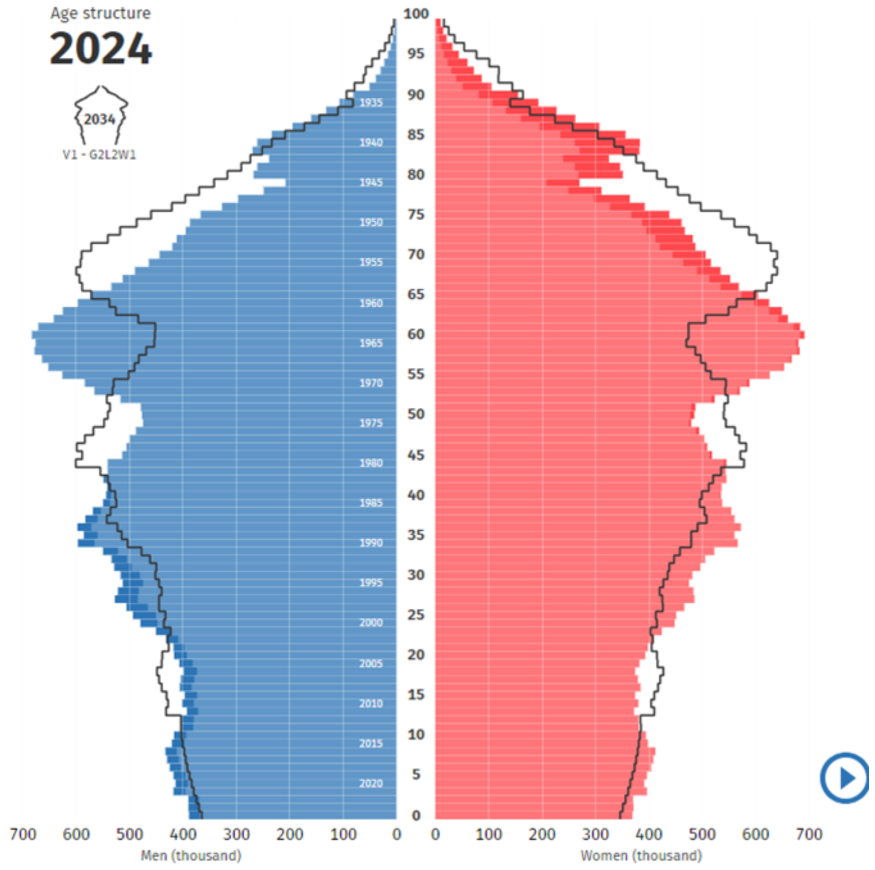
Age structure projection

- Follow the age composition of the population over time (age structure)

$$N_t \longrightarrow N_{t+1}$$

$$N_t = \begin{matrix} N_{1,t} \\ N_{2,t} \\ \dots \\ N_{k-1,t} \\ N_{k,t} \end{matrix} \qquad N_{t+1} = \begin{matrix} N_{1,t+1} \\ N_{2,t+1} \\ \dots \\ N_{k-1,t+1} \\ N_{k,t+1} \end{matrix}$$

$N_{k,t}$ is the number of individuals of age k at time t



Sex-specific age structure in Germany (Federal Statistical Office of Germany)

Age structure projection

- Projection over one time step:

Survival transitions

(if the individual survive, age increases of one year)

$$\begin{array}{ccc}
N_t & \longrightarrow & N_{t+1} \\
\| & & \| \\
N_{1,t} & & N_{1,t+1} \\
N_{2,t} & & N_{2,t+1} \\
\dots & & \dots \\
N_{k-1,t} & & N_{k-1,t+1} \\
N_{k,t} & & N_{k,t+1}
\end{array}$$

- Projection over one time step:

Reproduction transitions

(if an individual reproduces, young are produced)

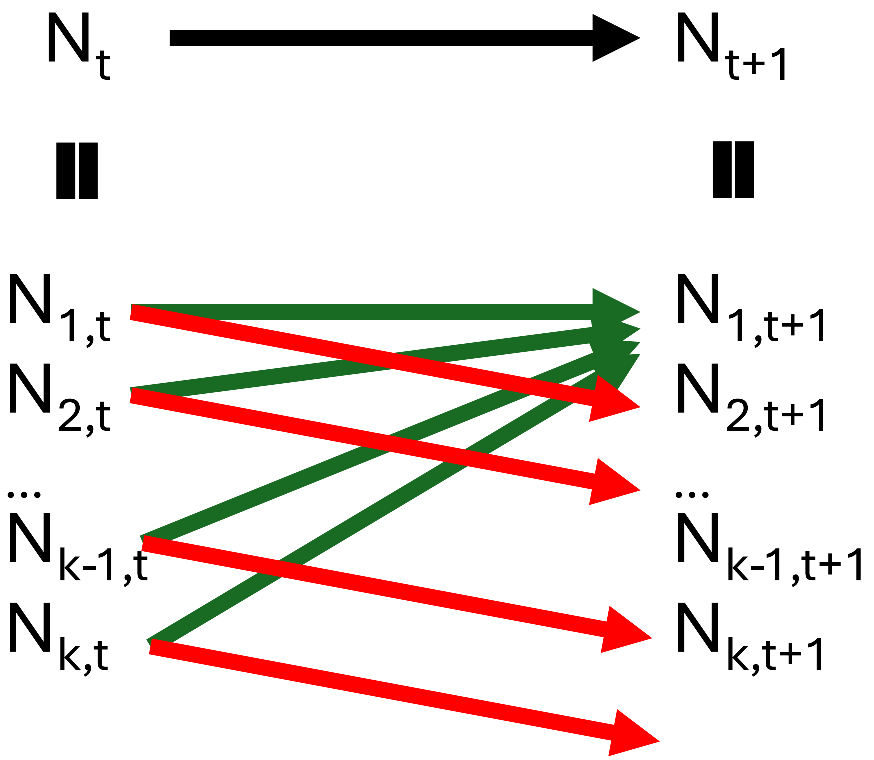
$$N_t \longrightarrow N_{t+1}$$

$$\begin{array}{ccc} N_{1,t} & & N_{1,t+1} \\ N_{2,t} & & N_{2,t+1} \\ \ldots & & \ldots \\ N_{k-1,t} & & N_{k-1,t+1} \\ N_{k,t} & & N_{k,t+1} \end{array}$$

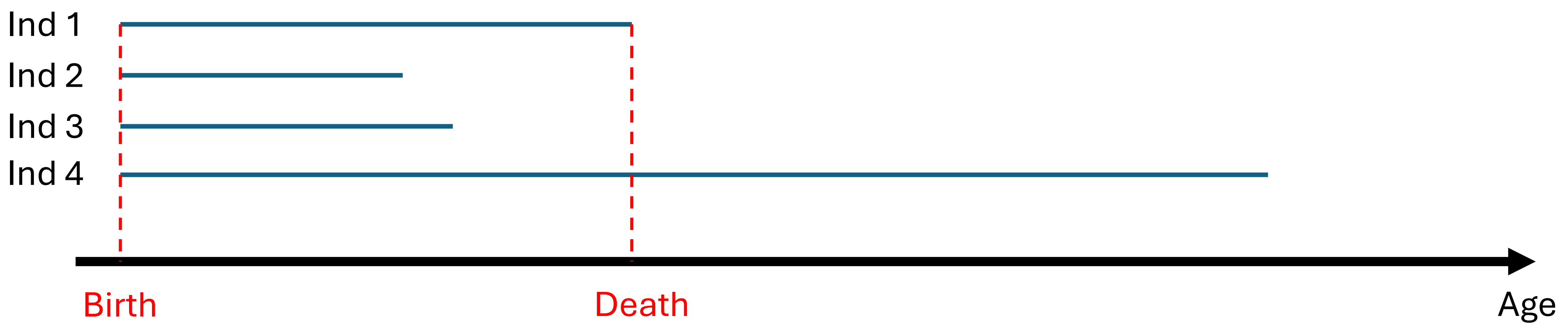
Age structure projection

- Projection over one time step:

Both survival and reproduction happen for each projection



Mortality probability

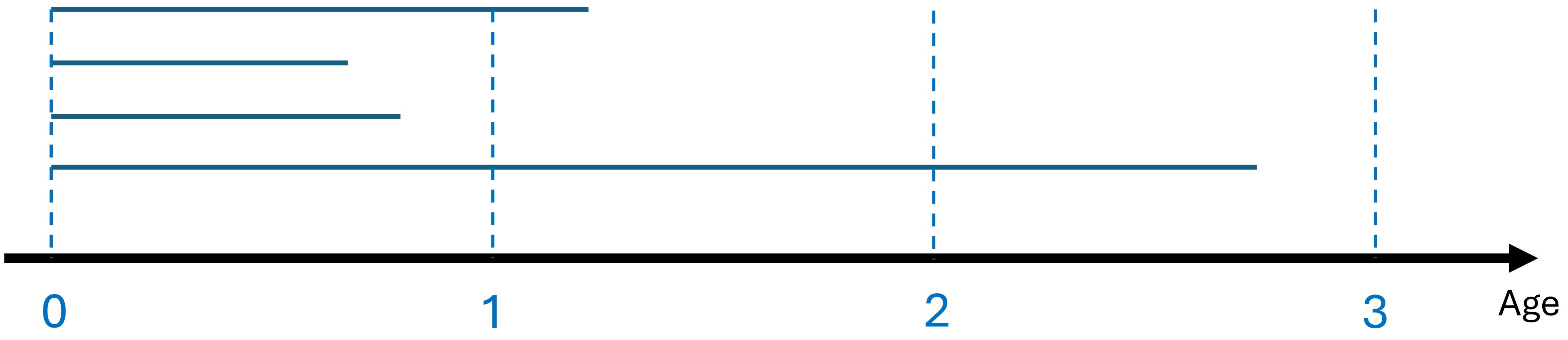


- Mortality probability is the proportion of individuals at risk dying during a specific interval

We need to know :

- The specific **censoring interval**
- The **number of individuals at risk of dying**
- The **number of death events** during the interval

Mortality probability



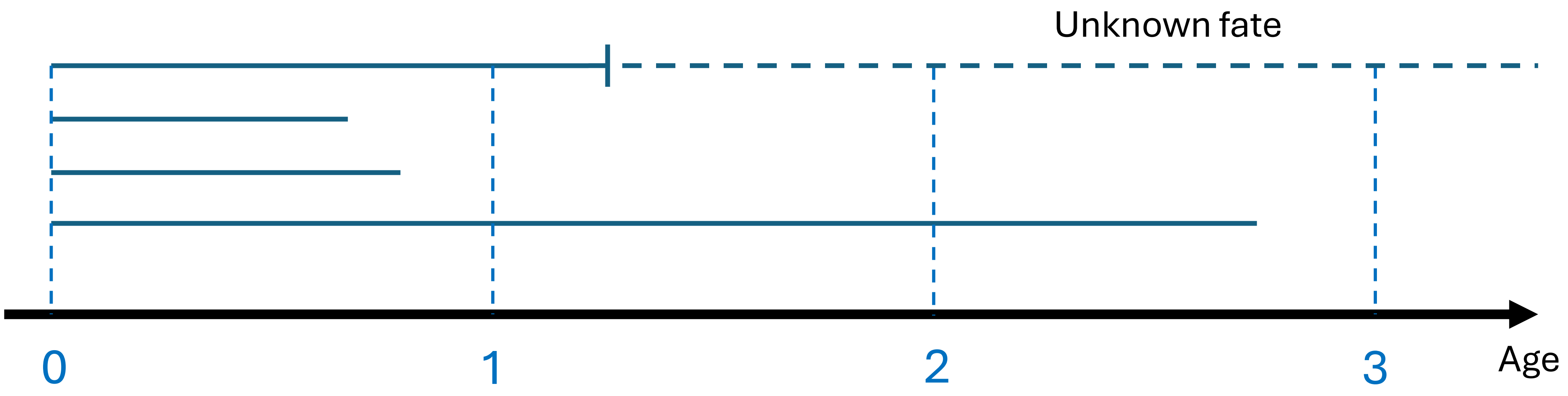
Let's compute the **mortality probability between 0 and 1**

- The specific censoring interval **= 0-1**
- The number of individuals at risk of dying **Nx = 4**
- The number of death event during the interval **Dx = 2**

qx = Dx/Nx = 0.5

-> To build a mortality table, **we calculate mortality probabilities for all age classes over regular time intervals**

The case of censored data



Individuals can be right censored (unknown fate).

To be at risk of dying the individuals must be not censored during the time interval

q0 = 2/4

q1 = 0/1

➔ Not in this course but it possible to account for unknown fate individuals and incomplete censoring **using capture mark recapture approaches.**

Mortality life table

- Describe the age-specific mortality rate **for each age class**

- **Yellow baboon female life table** (from Bronikowski et al., 2016 Scientific data)
- 618 females monitored in Kenya over 43 years
- See script

Age	Nx	Dx	qx	sx	lx	dx	Nfx	Nox	mx
0	580	131	0.22586207	0.7741379	1.0000000	0.22586207	92.91	0.00	0.000
1	428	56	0.13084112	0.8691589	0.7741379	0.10128908	00.44	0.00	0.000
2	355	27	0.07605634	0.9239437	0.6728489	0.05117442	36.17	0.00	0.000
3	314	16	0.05095541	0.9490446	0.6216744	0.03167768	03.46	0.00	0.000
4	288	11	0.03819444	0.9618056	0.5899968	0.02253460	81.84	3.00	0.005
5	264	13	0.04924242	0.9507576	0.5674622	0.02794321	53.53	107.23	0.211

Mortality

Reproduction

Mortality life table

The different columns of the mortality table :

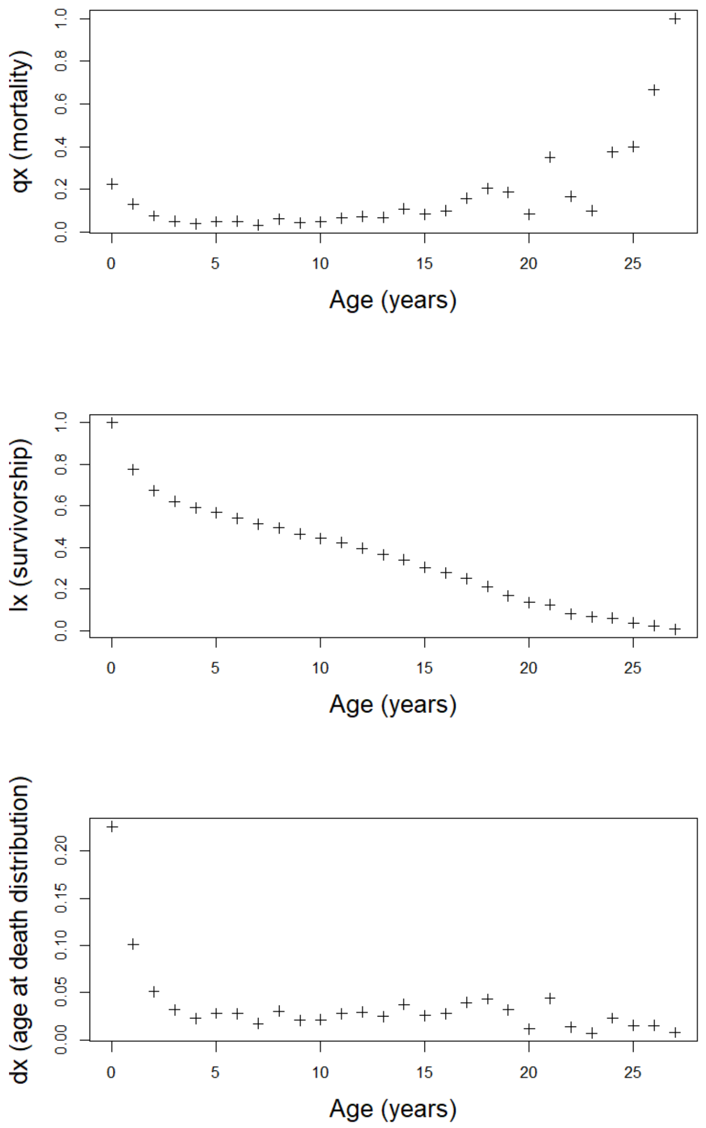
- **Age (x)**: age at the start of the age class
- **Nx**: number of individuals at risks of dying
- **Dx**: number of individuals dying during the age interval
- **qx**: mortality probability during the age interval (mortality probability)
- **sx**: survival probability during the age interval (survival probability)
- **lx**: proportion of individuals remaining at a specific age (survivorship)
- **dx**: proportion of individuals dying during a specific age interval

Mortality life table

- Age, Nx and Dx are only needed to compute everything here.

-> Try to recompute every column from Age, Nx and Dx

- qx, sx, lx and dx are **different presentations of the same data.**



Outputs from mortality tables

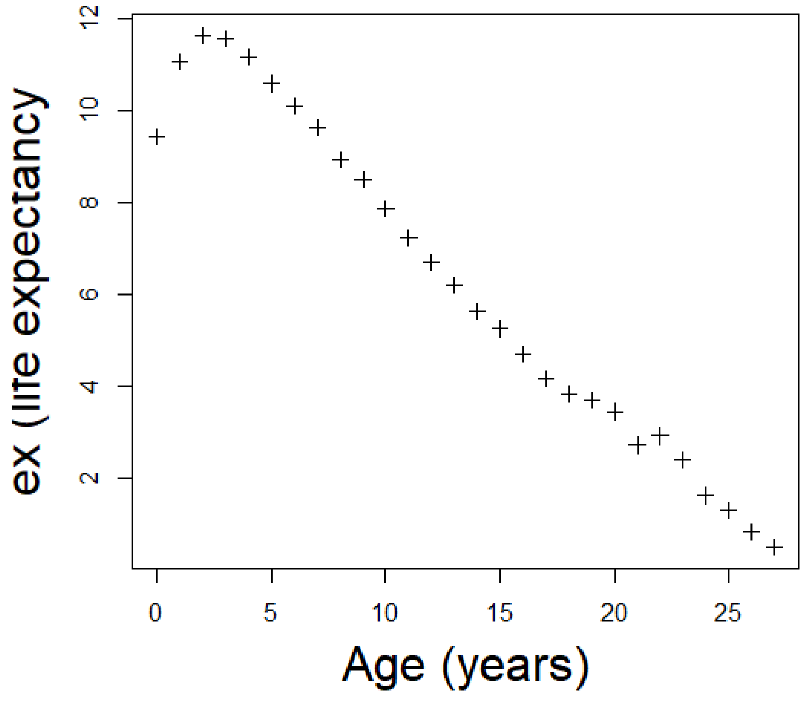
- Longevity measures

- ex: **life expectancy at age x**

Average age at death from a specific age

- $ex = \frac{\sum_{x}^{+\infty} lx}{lx}$ - 0.5

We need to specify when the individuals die inside the censoring interval (half of the interval here)

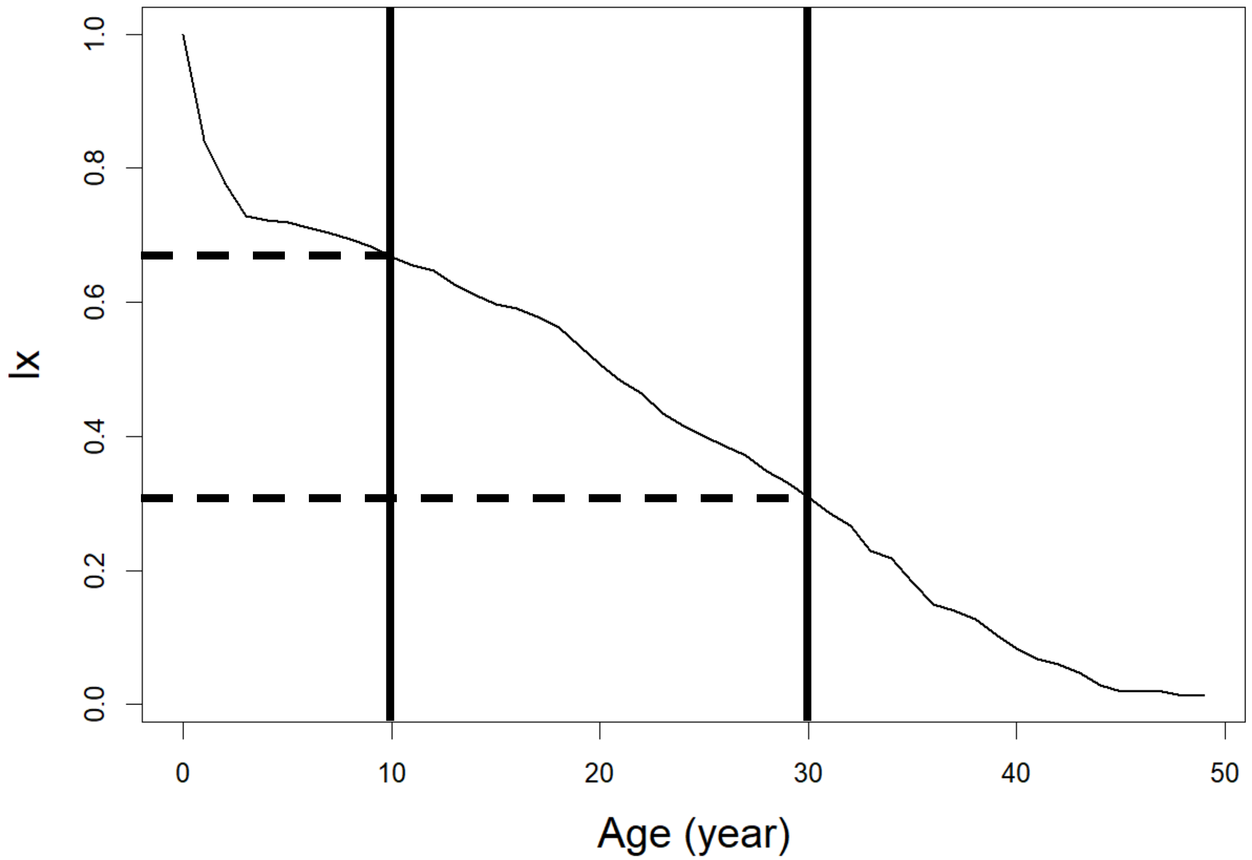


- **Maximum longevity**

- **Median longevity**

Outputs from mortality tables

- Fitting mortality models
- **μ(t): mortality rate or force of mortality or mortality hazard**



$$q(10;30) = 1 - \frac{l(30)}{l(10)} = 0{,}54$$

Probability to die between 10 and 30 years

We can calculate this probability for smaller and smaller intervals ([10;20], [10,11],[10,10.1] …)

$$\mu(x) = \lim_{\Delta x \to 0} \frac{F_X(x+\Delta x) - F_X(x)}{\Delta x(1 - F_X(x))}$$

With $F_X(x)$ the cumulative age at death distribution

$F_X(x) = 1 - \mathrm{S(x)}$

Outputs from mortality tables

Mortality is decreasing with age for young and increasing for older individuals

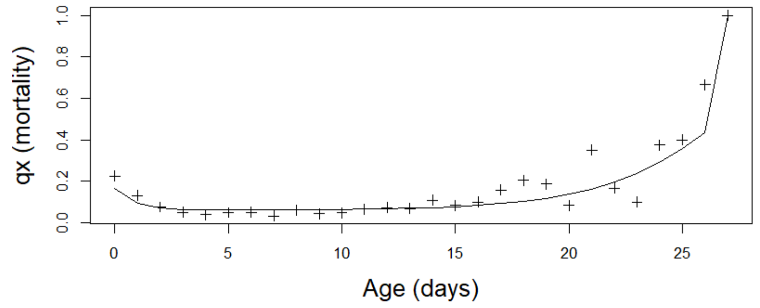
➔ Bathtub Siler model

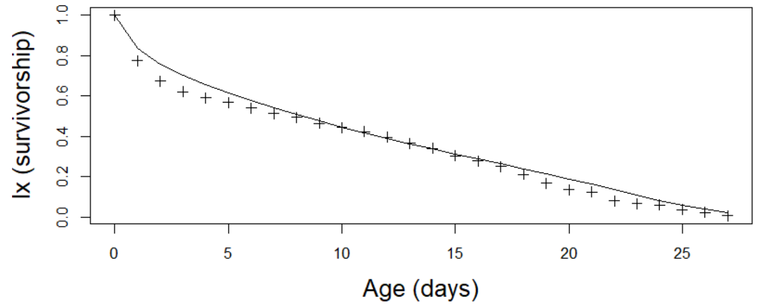
➔ $\mu(t) = a_1 e^{-b_1 t} + a_2 + a_3 e^{b_3 t}$

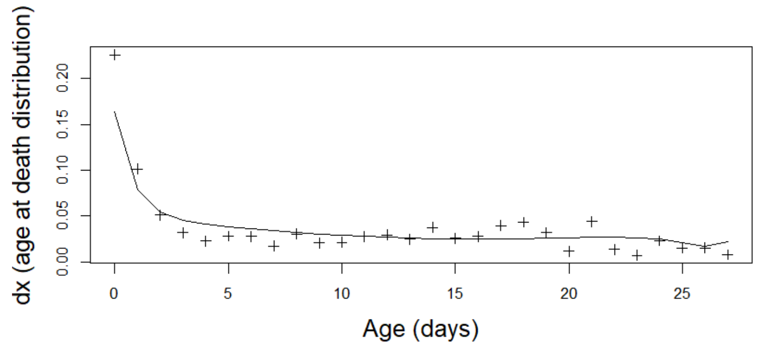
Continuous age modelling

Smooth age-specific mortality when sample size is low

b_3 exponential rate of increase of mortality (**actuarial ageing rate**)







Dolphin mortality data

- Bottlenose dolphin mortality dataset (McEntee et al., 2023 PROCB)
- 35 years of monitoring with 1005 individuals
- Individuals can be recognized based on their morphology
- **Date of birth and of supposed death available** for well monitored individuals

Dolphin mortality data

- **Let’s build the mortality table for that population!**

- Different mortality table for females and males

- Some assumptions:

➢ Hard to sex individuals before 3 years of age

➢ **Combined life table from 0 to 3 years of age then sex-specific**

- Column « Time » : age at death or censoring
- Column « Event » : 1 if dead, 0 if censored
- Column « Sex » : unknown, males or females

Dolphin mortality data

- You should end up with that result:

Females

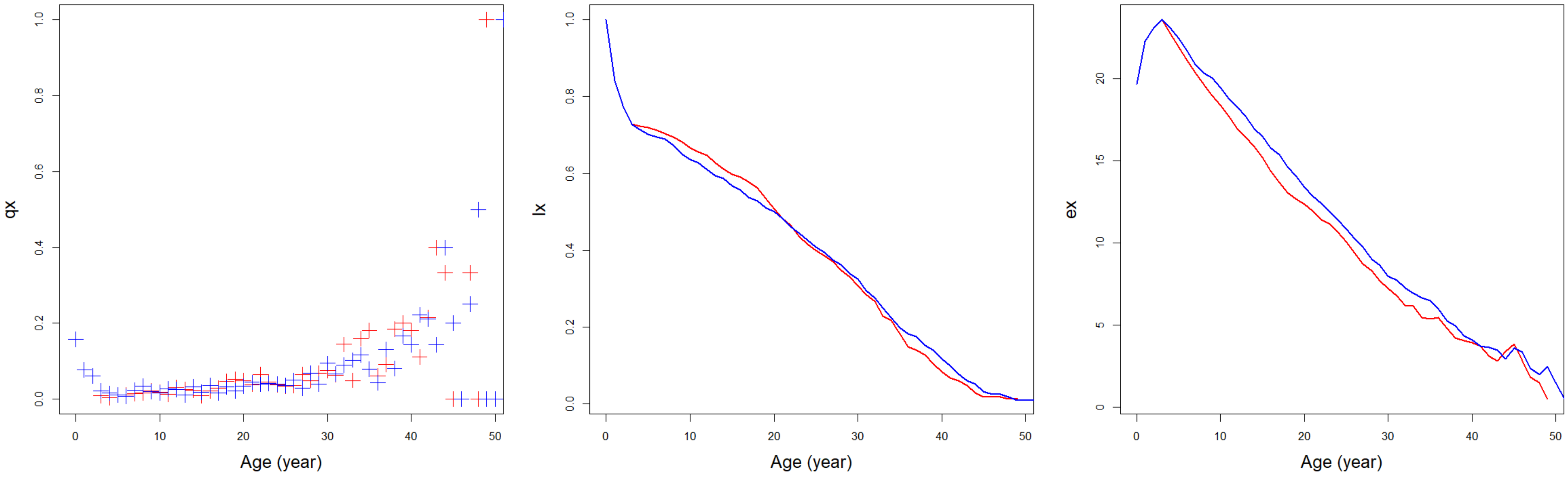
Age	Nx	Dx	qx	sx	dx	lx	ex
0	992	157	0.158266129	0.8417339	0.158266129	1.0000000	19.67878
1	839	65	0.077473182	0.9225268	0.065211802	0.8417339	22.28485
2	771	47	0.060959792	0.9390402	0.047336624	0.7765221	23.11433
3	462	4	0.008658009	0.9913420	0.006313294	0.7291854	23.58238
4	457	2	0.004376368	0.9956236	0.003163554	0.7228722	22.78398
5	453	5	0.011037528	0.9889625	0.007943803	0.7197086	21.88193

Males

Age	Nx	Dx	qx	sx	dx	lx	ex
0	992	157	0.15826613	0.8417339	0.15826613	1.0000000	19.68204
1	839	65	0.07747318	0.9225268	0.06521180	0.8417339	22.28872
2	771	47	0.06095979	0.9390402	0.04733662	0.7765221	23.11852
3	464	10	0.02155172	0.9784483	0.01571520	0.7291854	23.58685
4	451	7	0.01552106	0.9844789	0.01107382	0.7134702	23.09537
5	444	5	0.01126126	0.9887387	0.00790987	0.7023964	22.45161

Dolphin mortality data

- Comparing females and males age-specific mortality



- **No consistent differences between males and females**

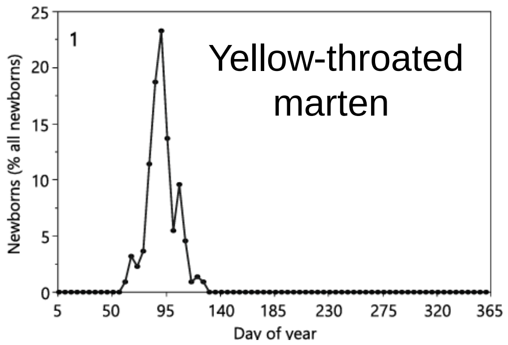
Fertility transitions

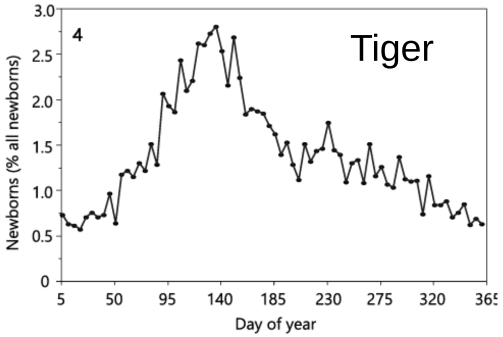
- **We have to compute the fertility transitions now**

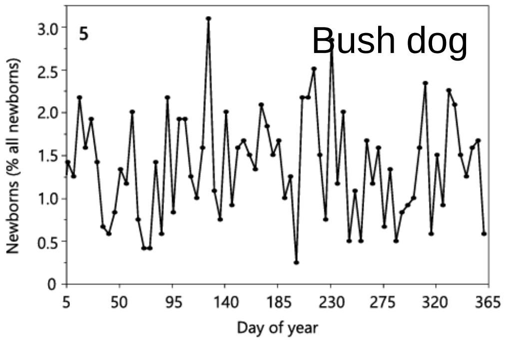
-> Few assumptions to consider:

- **Only females are tracked** (assumption that males are not limiting for the reproduction of females but also male demographic data are lacking)

- **Birth pulse model**, births are happening at a specific regular interval (works for seasonal species and long-lived species with high monitoring effort)







Heldstab et al., 2018 J BIOL RHY

Fertility transitions

- **mx: average number of daughter produced per female of age x**

Total number of offspring

- $$mx = \frac{Nox}{Nfx} \times BSR$$

Birth sex-ratio
0.5 if no info

Number of female at risk

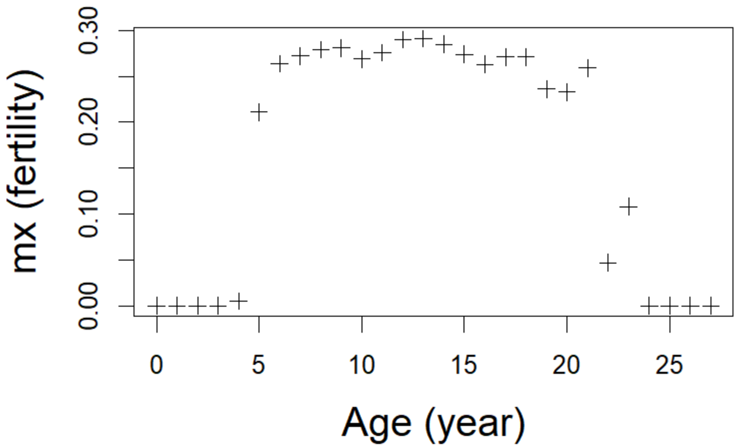
- Coming back to the baboon life table!

Full life table

- The **age interval should be the same** for mortality and fertility parameters.

For baboons reproduction is continuous!

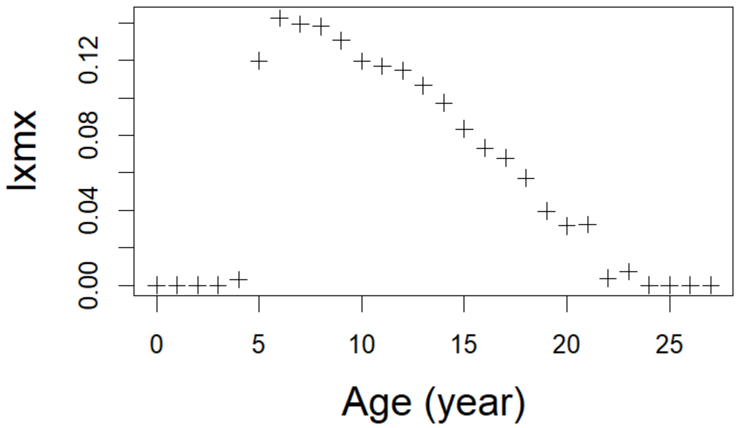
but long-lived species (high number of time intervals)



➢ Outputs of the full life table

- **Lifetime reproductive success**

$$R0 = \sum lx\ mx$$



- **Generation time**

$$G = \frac{\sum xlxmx}{\sum lxmx}$$

Dolphin fertility data

- Let’s build the fertility table! (data from Karninski et al., 2018 Proc B)

- For each birth in the population:

➢ **Age of the mother reported** (maternal.age.at birth)

➢ **Id of the mother reported** (maternal.id)

- Few assumptions to help you:

sharkbay.org

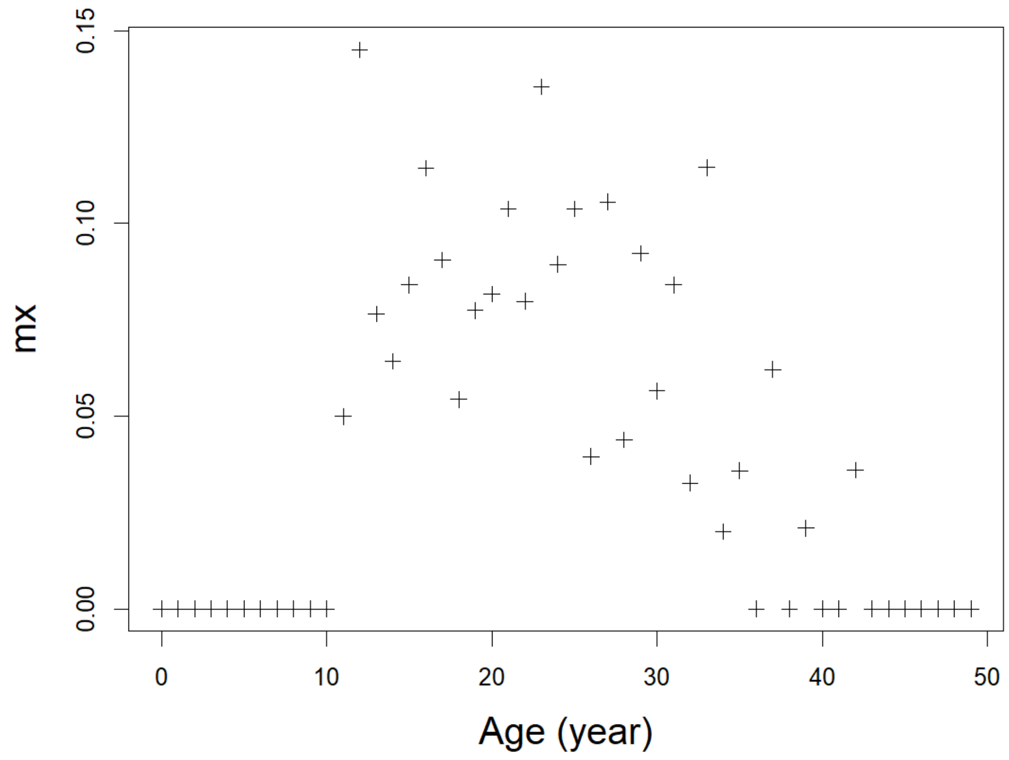
➢ All females reaching maturity will **reproduce at least once**

➢ The age distribution of mother in that sample is the **same as the age distribution of all females** in the population

Dolphin fertility data

- You should end up with that result:

Age	Nx	Dx	qx	sx	dx	lx	ex	mx
0	1003	157	0.156530409	0.8434696	0.156530409	1.000000000	17.416374	0.00000000
1	846	65	0.076832151	0.9231678	0.064805583	0.843469591	19.555701	0.00000000
2	781	47	0.060179257	0.9398207	0.046859422	0.778664008	20.141643	0.00000000
3	308	4	0.012987013	0.9870130	0.009503956	0.731804586	20.399351	0.00000000
4	304	2	0.006578947	0.9934211	0.004751978	0.722300631	19.661184	0.00000000
5	302	5	0.016556291	0.9834437	0.011879945	0.717548653	18.788079	0.00000000
6	297	5	0.016835017	0.9831650	0.011879945	0.705668708	18.095960	0.00000000
7	292	6	0.020547945	0.9794521	0.014255933	0.693788764	17.397260	0.00000000
8	286	7	0.024475524	0.9755245	0.016631922	0.679532830	16.751748	0.00000000
9	279	9	0.032258065	0.9677419	0.021383900	0.662900908	16.159498	0.00000000
10	270	7	0.025925926	0.9740741	0.016631922	0.641517007	15.681481	0.00000000
11	263	5	0.019011407	0.9809886	0.011879945	0.624885085	15.085551	0.05032431
12	258	11	0.042635659	0.9573643	0.026135878	0.613005140	14.368217	0.14705882
13	247	9	0.036437247	0.9635628	0.021383900	0.586869262	13.985830	0.07859014
14	238	8	0.033613445	0.9663866	0.019007911	0.565485362	13.495798	0.06673258
15	230	3	0.013043478	0.9869565	0.007127967	0.546477451	12.947826	0.08823529
16	227	7	0.030837004	0.9691630	0.016631922	0.539349484	12.112335	0.12049754

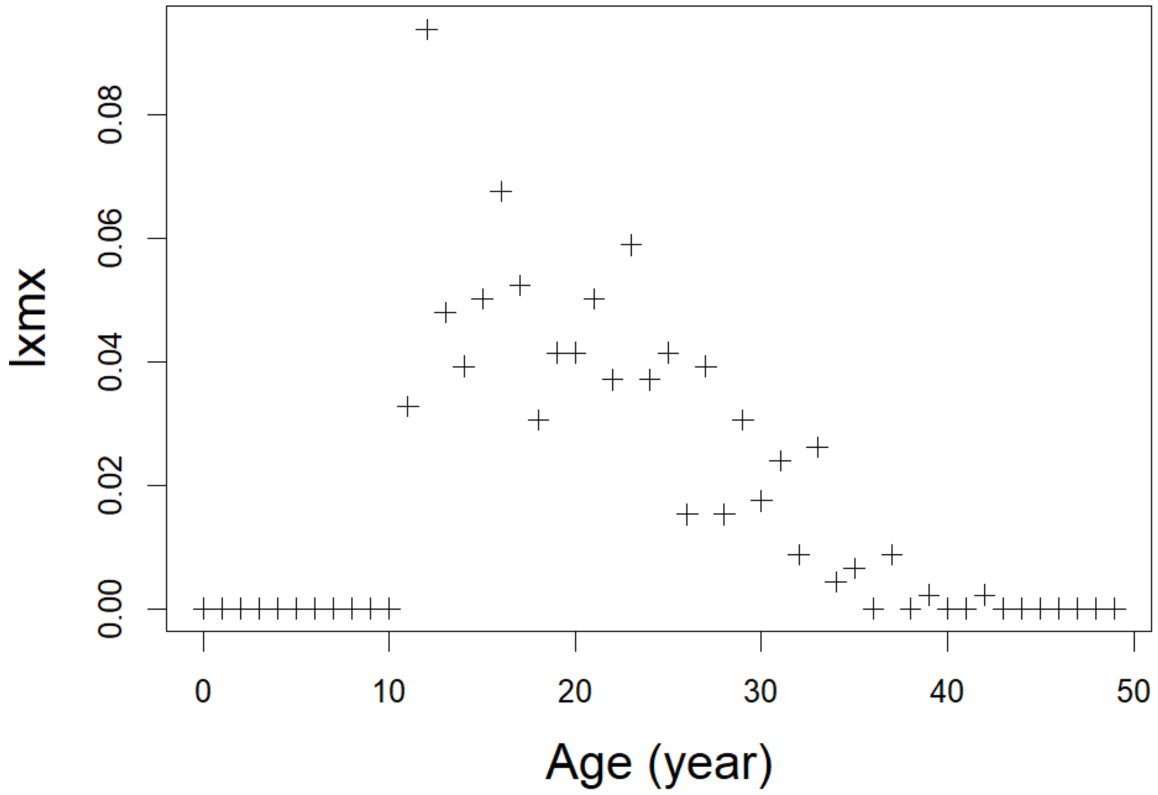


Dolphin life table

- Outputs from the life table:

- R0 = 0.9225393

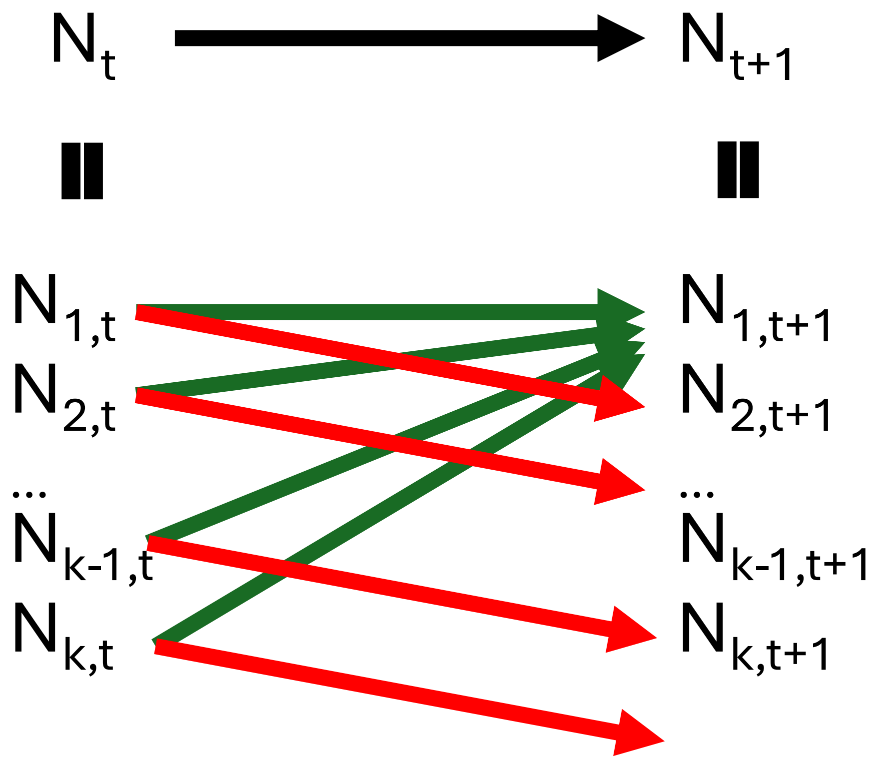
- G = 20.32861



Age structure projection

- Projection over one time step:

Both survival and reproduction happen during the projection



Matrix population models

- First introduced by Leslie (1945), *“On the use of matrices in certain population mathematics.”* Later called **Leslie matrices.**

- But developped a lot since then (Caswell 2001 book for an overview and popbio R package for the analysis)

- **Discrete time model** projecting the population composition at a regular time span and **accounting for demographic differences between classes.**

Matrix population models

- Build the projection matrix M so that :

  $$\mathbf{N_{t+1} = M \times N_t}$$

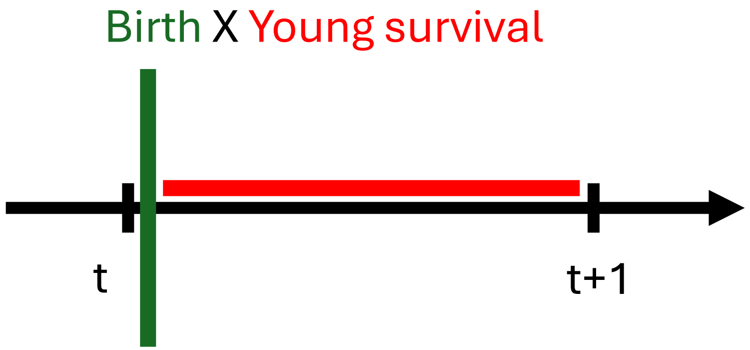
- The value a_{ij} inside the projection matrix M is **the transition rates** (or vital rates) from one class to the next one.

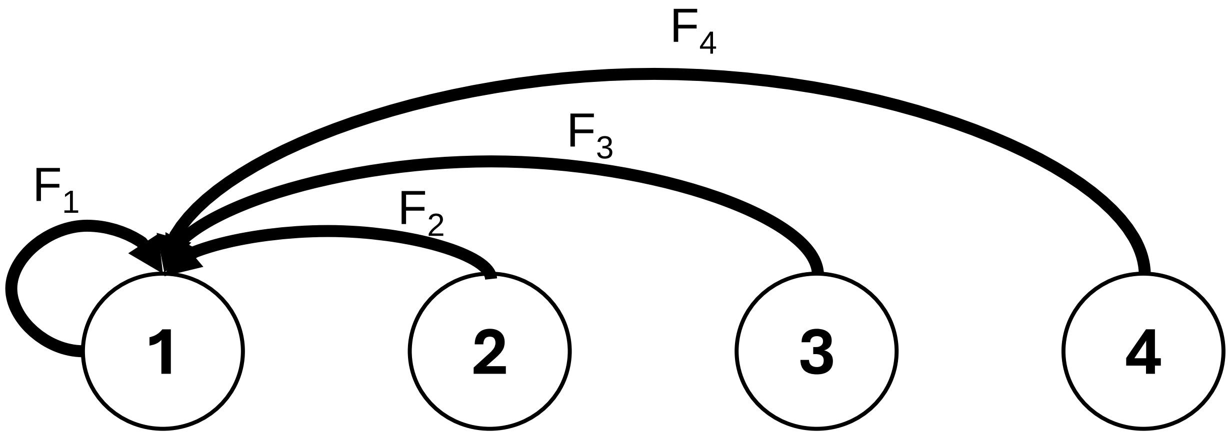
- Let’s build the life cycle diagram

Fertility transition F

- **Prebreeding census**

Birth pulse just after the censoring event then survival of the young



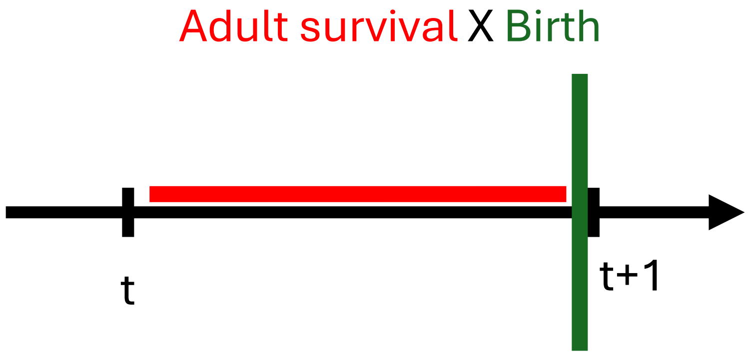


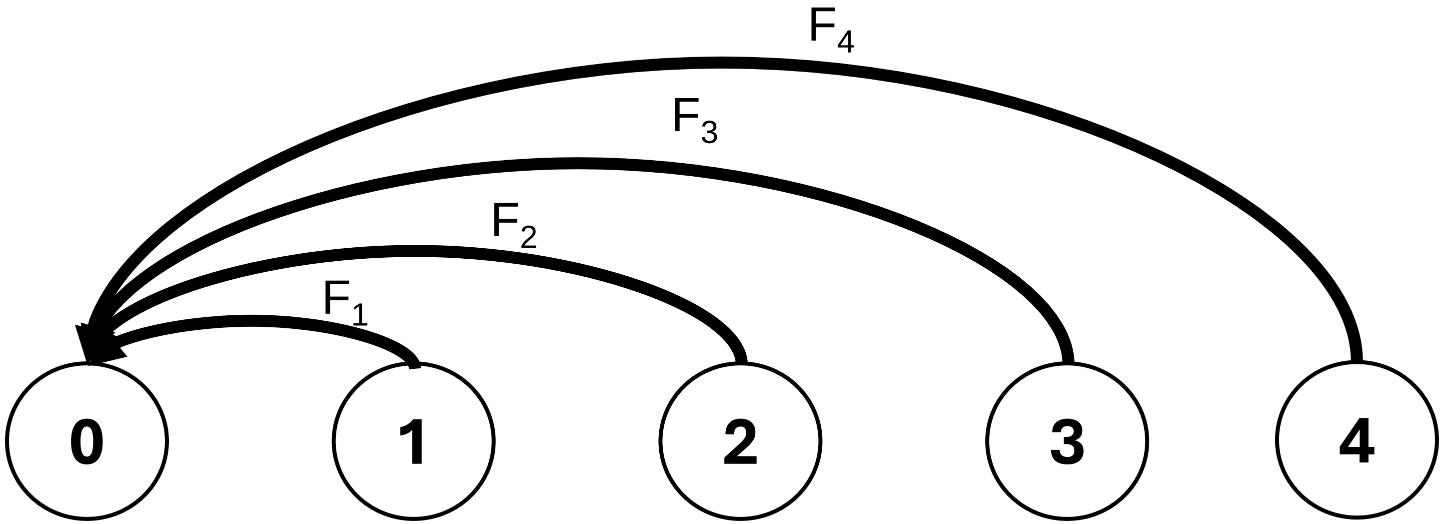
- **Age class 0 is not tracked**, just included implicitly in the model

Fertility transition F

- **Postbreeding census**

Adult survival then birth pulse just before the censoring event



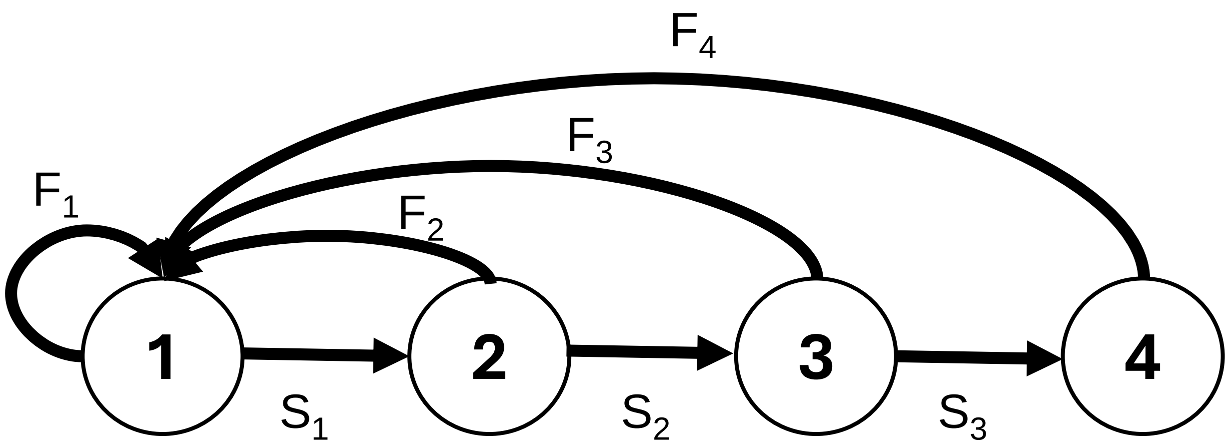


- **Age class 0 is included in that model**

Survival transition transition S

- Prebreeding census

Only survival to consider (prebreeding example here)

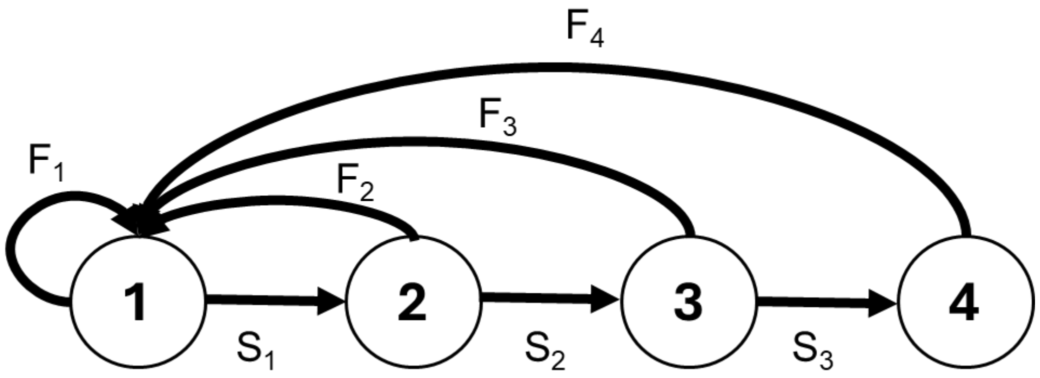


Matrix population models

- The value $\color{blue}{\mathbf{a_{ij}}}$ inside projection matrix correspond to **the transition rates** (or vital rates) from one age class to the next one.

Starting class at t (columns)

Ending class at t+1 (rows)	F1	F2	F3	F4
	S1	0	0	0
	0	S2	0	0
	0	0	S3	0



Matrix population models

- Now that we have the **projection matrix M**, let's try to **project the population** to the next time step :

$$\begin{pmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{pmatrix} \mathbf{N_t}$$

$$\mathbf{M} \begin{pmatrix} F1 & F2 & F3 & F4 \\ S1 & 0 & 0 & 0 \\ 0 & S2 & 0 & 0 \\ 0 & 0 & S3 & 0 \end{pmatrix} \quad \begin{pmatrix} F1N_{1,t}+F2N_{2,t}+F3N_{3,t}+F4N_{4,t} \\ S1N_{1,t} \\ S2N_{2,t} \\ S3N_{3,t} \end{pmatrix} \mathbf{N_{t+1}}$$

- Most of outputs can be easily computed from M with the R package popbio

Important output of MPMs

- **For leslie matrices, the age distribution will reach an equilibrium**
- **Baboon postbreeding matrix example**

0.00	0.00	0.00	0.00	0.01	0.21	0.26	0.27	0.28	0.28	0.27	0.28	0.29	0.29	0.28	0.27	0.26	0.
0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
[illegible]	0.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	[illegible]	0.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	[illegible]	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	[illegible]	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	[illegible]	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.97	[illegible]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	[illegible]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.96	[illegible]	0.00	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	[illegible]	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	[illegible]	0.93	0.00	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	[illegible]	0.89	0.00	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	[illegible]	0.92	0.00	0.
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	[illegible]	0.90	0.

Important output of MPMs

- **λ (lambda) : asymptotic population growth rate**

Dominant eigen value of matrix M

$N_{t+1} = \lambda N_t$ (at equilibrium)

λ >1 increasing population

λ =1 stationnary population

λ <1 decreasing population

r = log(λ)

(remember $N(T) = N_0 e^{rT}$)

Important output of MPMs

- **Stable stage distribution**

Right eigen vector (scaled so the sum is 1)

➢ Percentage of individuals belonging to each age class at equilibrium.

- **Reproductive value**

Left eigen vector (scaled so first value is 1)

➢ Number of offspring that an individual of a specific age class is expected to produce over his remaining lifetime

Important output of MPMs

- **Sensitivies S**

$$S_{ij} = \frac{d\lambda}{da_{ij}}$$

Sensitivity of λ to an additive change of a specific transition rate a_{ij}

➔ Understand **which transition is important** for the population growth rate of the specific population

➔ But not easily comparable between transitions with different scales

Survival vs fertility

Important output of MPMs

- **Elasticities E**

$$E_{ij} = S_{ij}\frac{a_{ij}}{\lambda} = \frac{dlog(\lambda)}{dlog(a_{ij})}$$

Sensitivity of λ to an proportional change of the transition rate aij **scaled**

Elasticities are more comparable between the different transitions

→ Understand what transition is important for the population growth rate of the specific population

→ **The intensity of selection should be stronger on vital rates with higher elasticities**

Dolphin MPM

- **Let's build the population projection model based on the dolphin life table!**

- Prebreeding model first

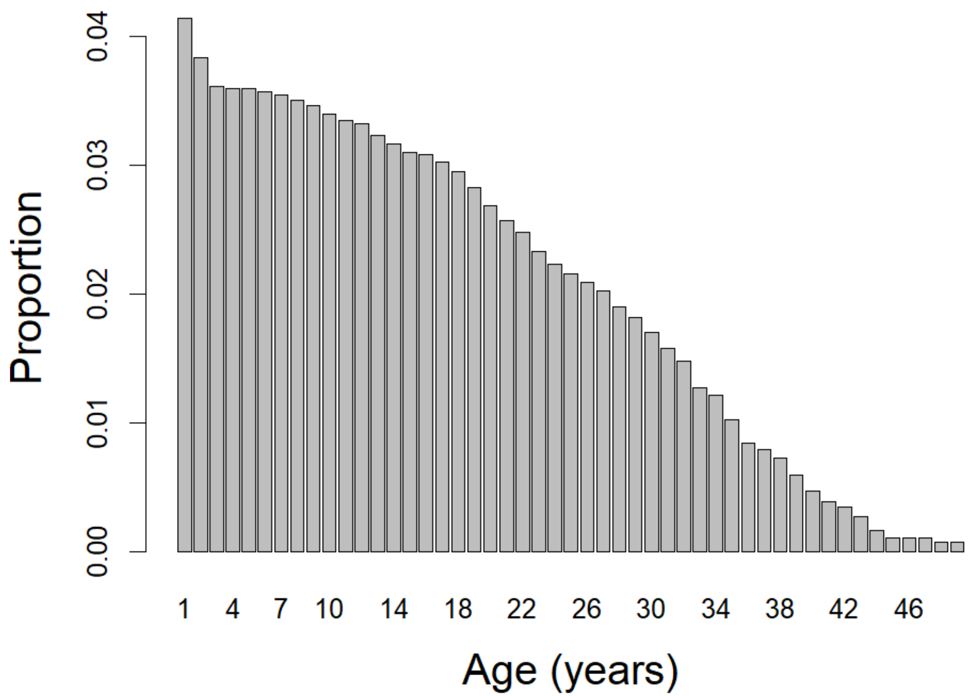
- Extract all outputs (lambda, stable distribution, reproductive value and elasticities) and interpret them

Dolphin MPM

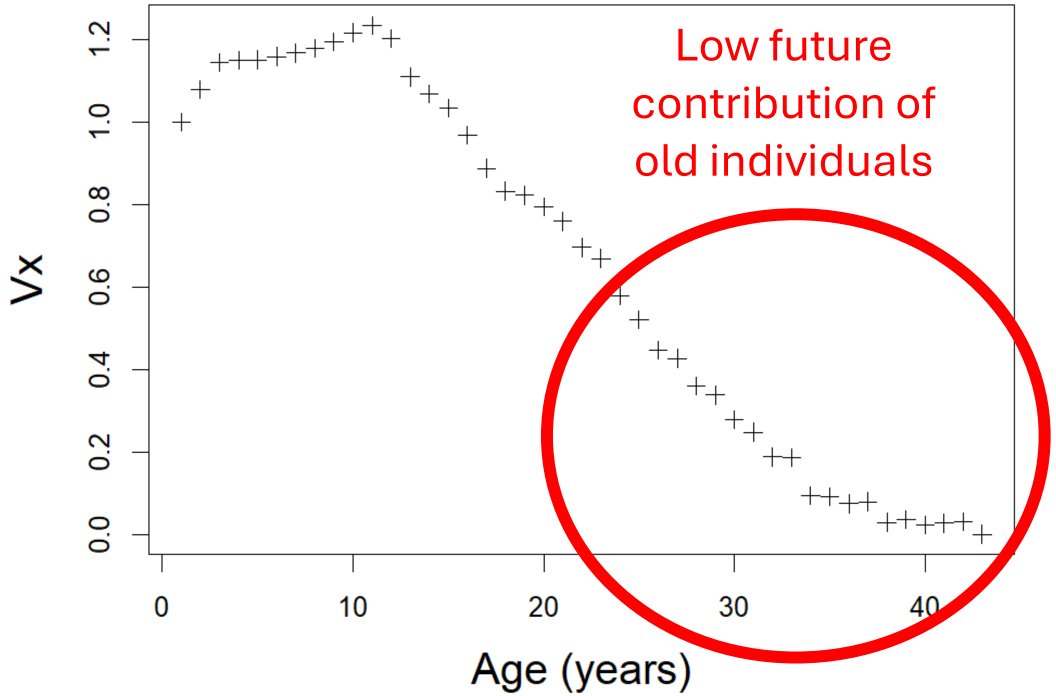
- **Outputs :**

λ = 0.9960586

Stable age distribution

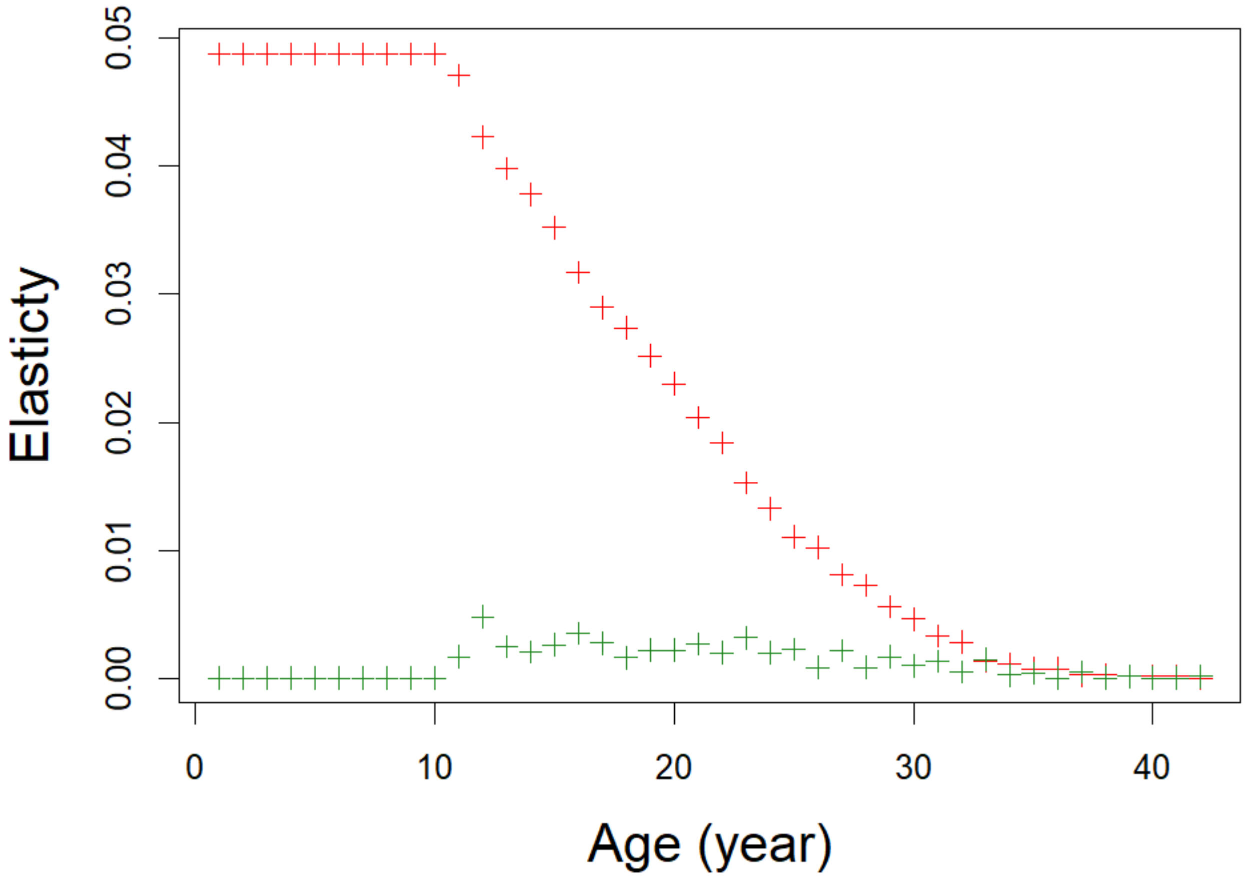


Reproductive values



Dolphin MPM

- **Elasticities of survival transitions = 0.951**
- **Elasticities of fertility transitions = 0.049**



- **Decline of the strength of selection on survival transitions with age**
- **Selection shadow**

Hamilton's forces of selection

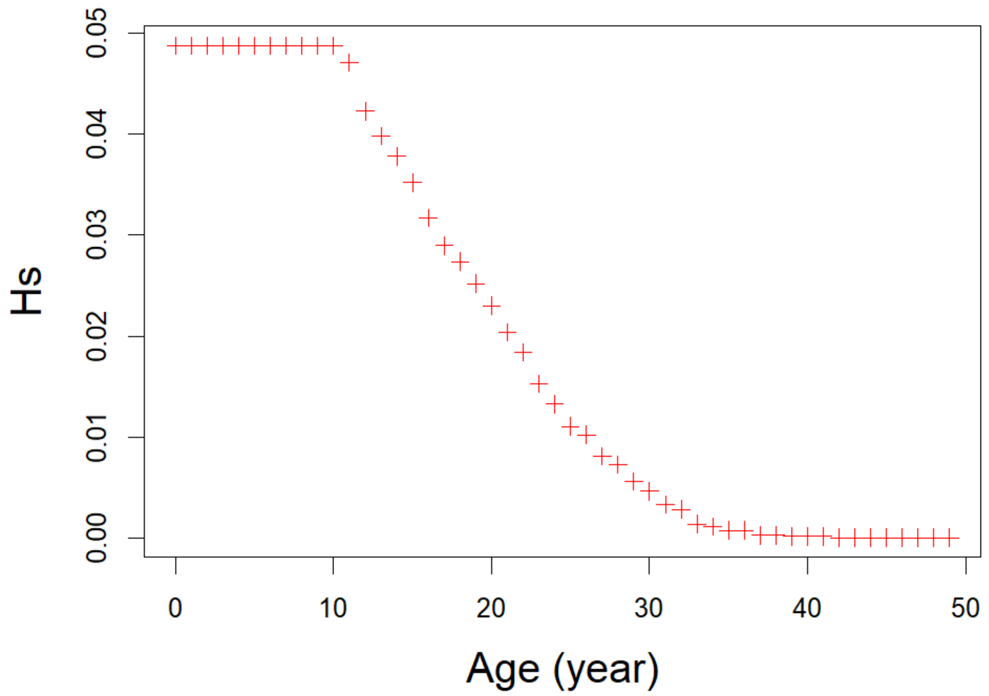
- Hamilton (1966) : **assess the effect of age-specific mutation on fitness**

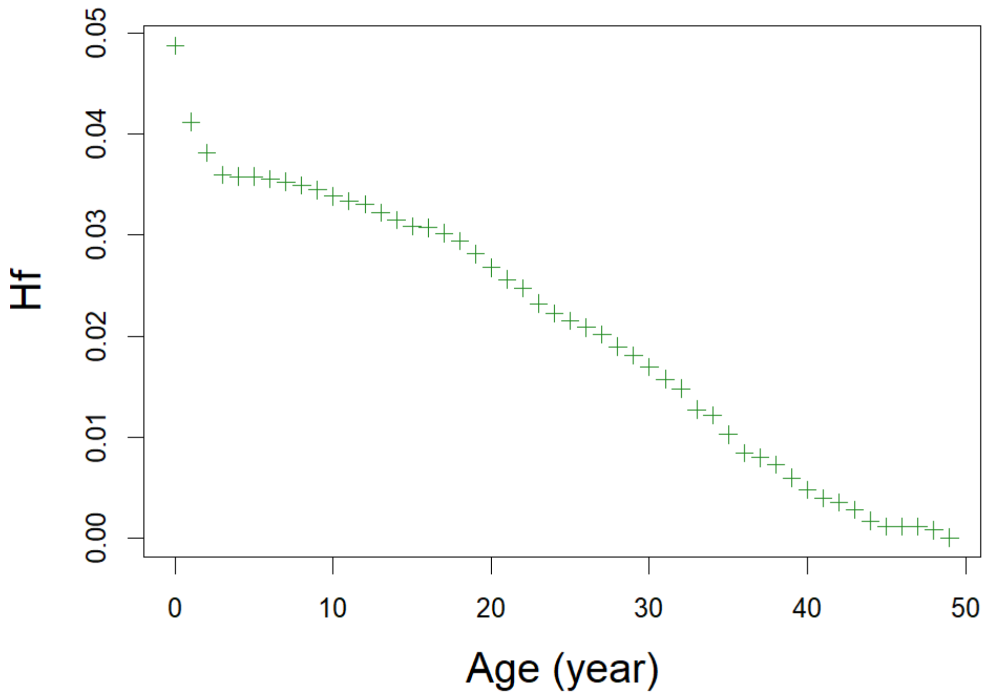
- $H^{+} = \frac{dr}{dlog(p_a)} = \frac{\sum_{a+1}^{\infty} e^{-rx} lxmx}{\sum_{0}^{\infty} xe^{-rx} lxmx}$ (additive effect of mutation **on log survival**)

- $H^{*} = \frac{dr}{dm_a} = \frac{e^{-ra} l_a}{\sum_{0}^{\infty} xe^{-rx} lxmx}$ (additive effect of mutation **on reproduction**)

- Let's compute both selection gradients!

Hamilton's forces of selection





$$H^{+} = \frac{dr}{dlog(p_a)} = \frac{dlog(\lambda)}{dlog(p_a)}$$

This is an elasticity measure!

$$H^{*} = \frac{dr}{dm_a}$$

This is not an elasticity measure!

Hamilton’s forces of selection

- The force of selection on survival and reproduction is declining with age
- **Selection shadow**, at old ages deleterious mutations are not selected against
- **Mutation accumulation** theory of ageing (Medawar, 1952)
- **Antagonistic pleotropy** (Williams 1957), genes that have beneficial effect early in life but deleterious later in life are selected

Age-dependant vs constant model

➢ **Do we really need to account for age-dependance precisely?**

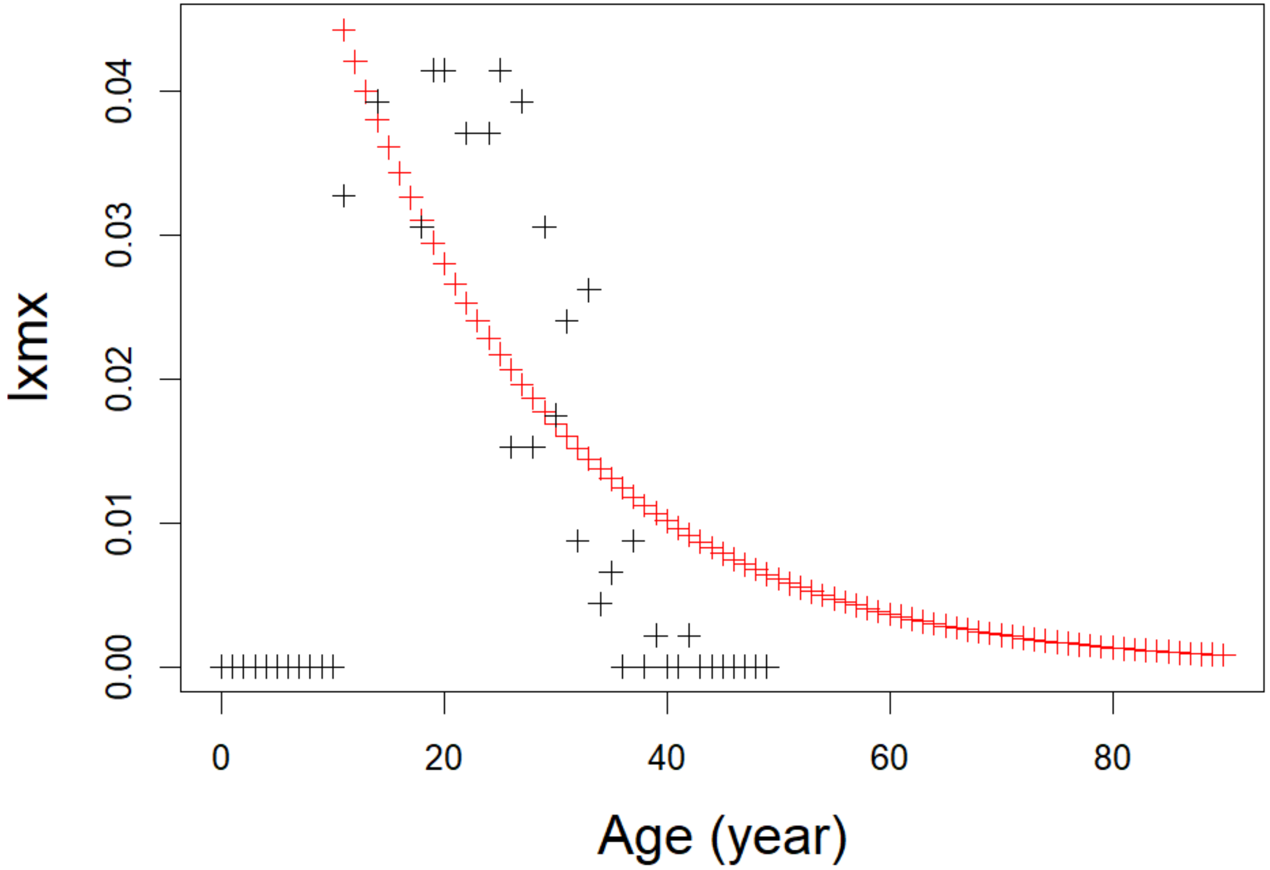
- Let's build a **simple model** to test that :

1) **Constant mortality** from birth (average qx weighted by lx)

2) **Constant fertility** from maturity (average mx weighted by lx after age 11)

- Compare that model with the previous one!

Age-dependant vs constant model

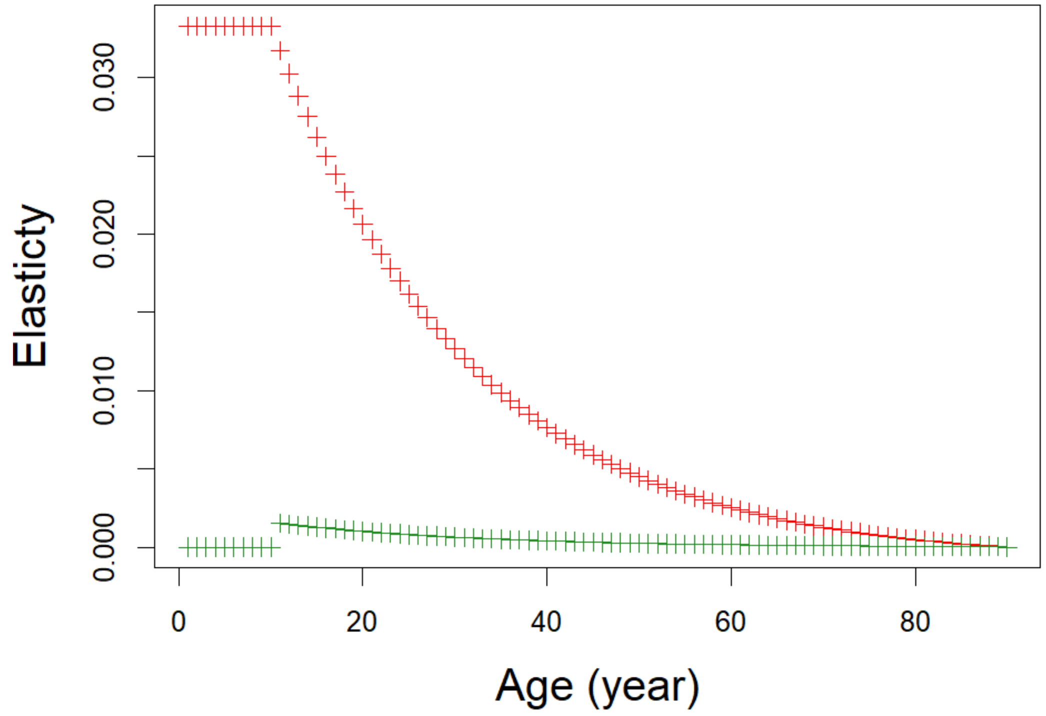


- **R0 = 0.877 (-0.046)**
- **G = 28.783 (8.455)**

- **Older individuals are living longer in that model**

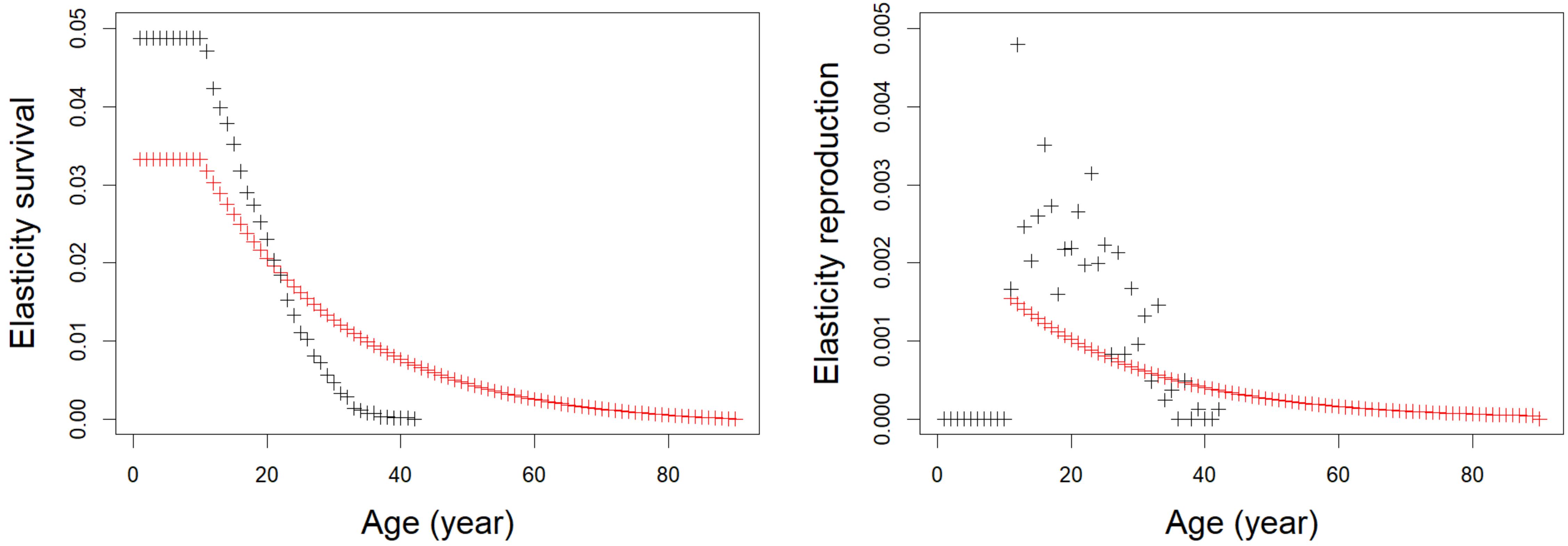
Age-dependant vs constant model

- λ = 0.996 (-0.001)
- **Elasticities of survival transitions = 0.967 (0.0155)**
- **Elasticities of fertility transitions = 0.033 (-0.0155)**



- **Age-dependance is not needed for the decline of the strength of selection!**

Age-dependant vs constant model

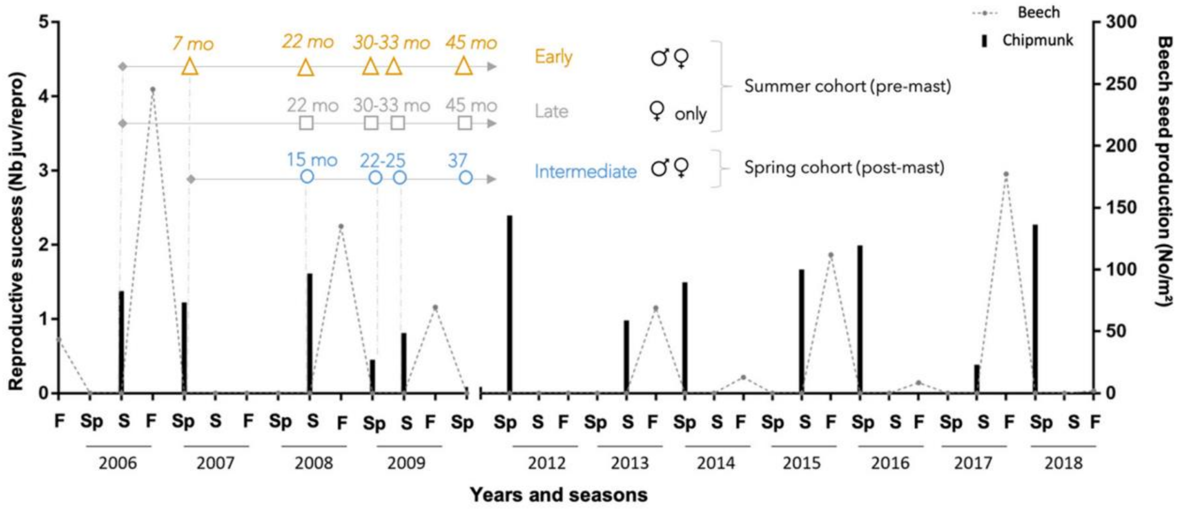


- **The contribution of old individuals is overestimated**
- **The contribution of young individuals is underestimated**

Some recommendations

- **Precise age-dependancy is not always needed**, for instance here 3 age classes (young, adult, old) would have captured well the dynamic of the dolphin population
- **You need to know well the life cycle of your species to model it!**
- Methodological developpement of those models is **heavily biased toowards long-lived and/or seasonal species**

Allain et al., 2023 Oikos



Some ideas to extend the model

➢ **Include maternal age effect in the model**

Juvenile survival decline with maternal age for the young

How the force of selection change with age for survival, fertility and maternal effect?

➢ **Include orphan mortality effect in the model**

Before weaning juveniles are very dependant on their mother (juveniles won’t survive if the mother died)

How does including orphan mortality affect the force of selection with age on vital rates?

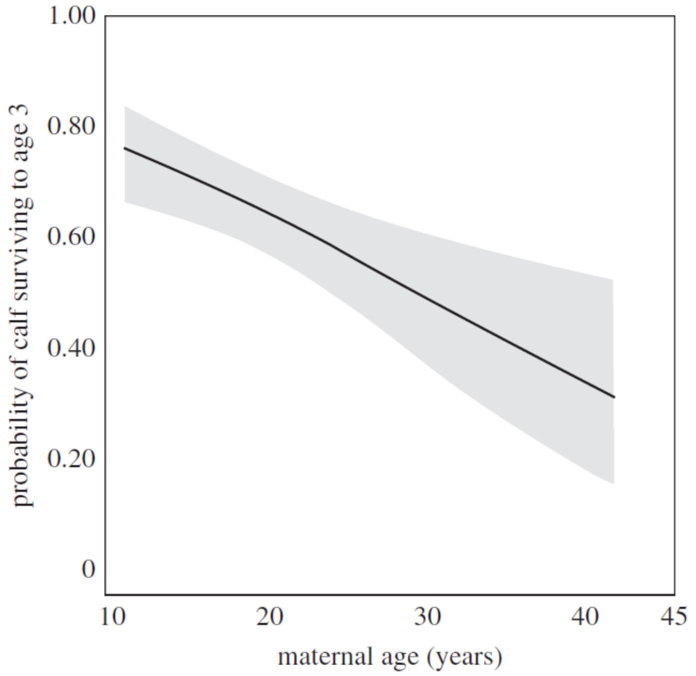


Figure 1. Partial effects of maternal age on calf survival. The probability of a calf surviving to age 3 decreased with maternal age (estimate $= -0.06325$, s.e. $= 0.02015$, $z = -3.140$, $p < 0.005$).