Lecture: Ecology and evolution of life histories

Labs: Life tables and optimal life histories

Vladimír Remeš

OUTLINE

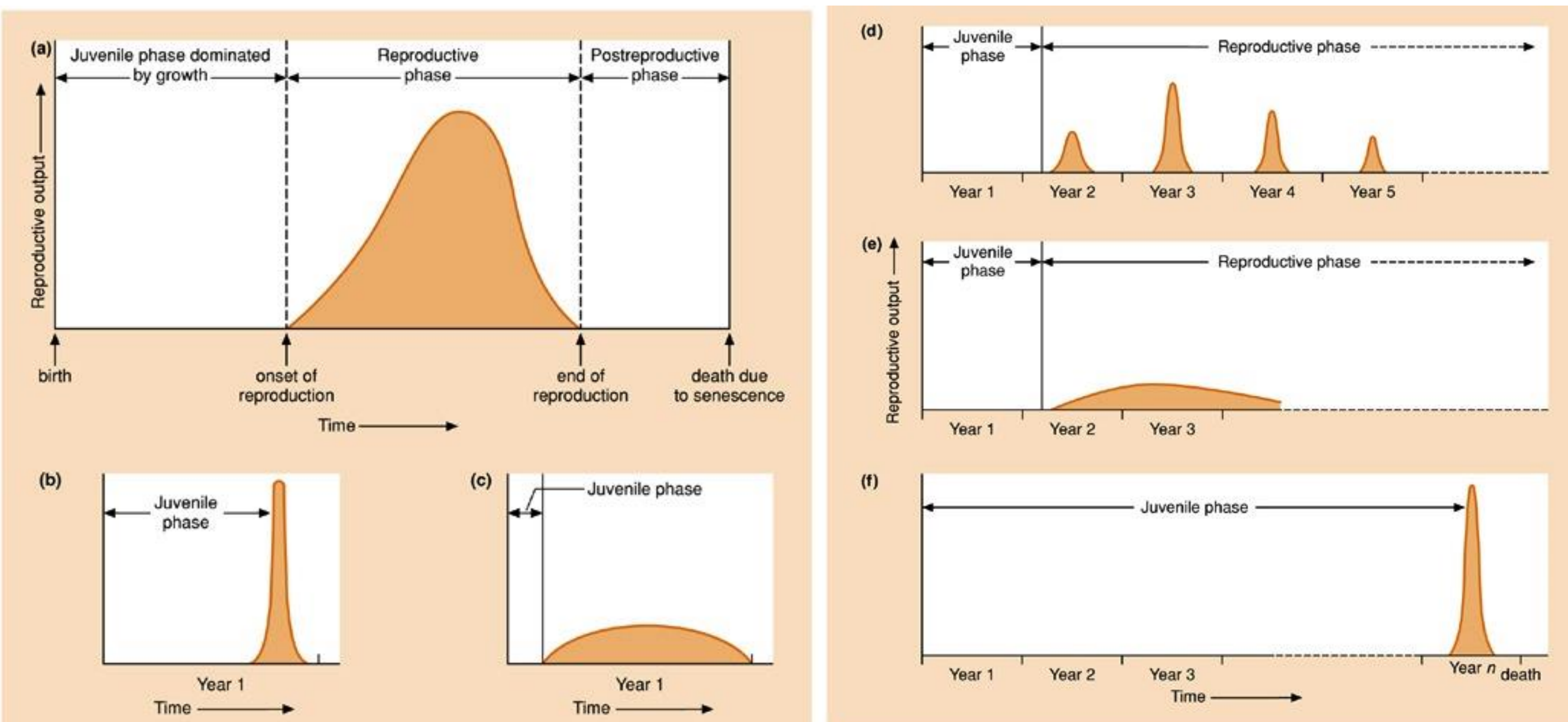
- What is life history?
- Life tables
- Fitness measures
- Optimizing life history
- Trade-offs
- Variation in life histories
- Methods to study life histories
- Main traits and trade-offs
- Life histories and the environment
- Applications

What is life history?

-- Life cycle and its quantitative analysis

-- *Empirical* question: What are the trade-offs and constraints under which evolution operates?

-- *Theoretical* question: Given these trade-offs and constraints, what is the optimal strategy to adopt?



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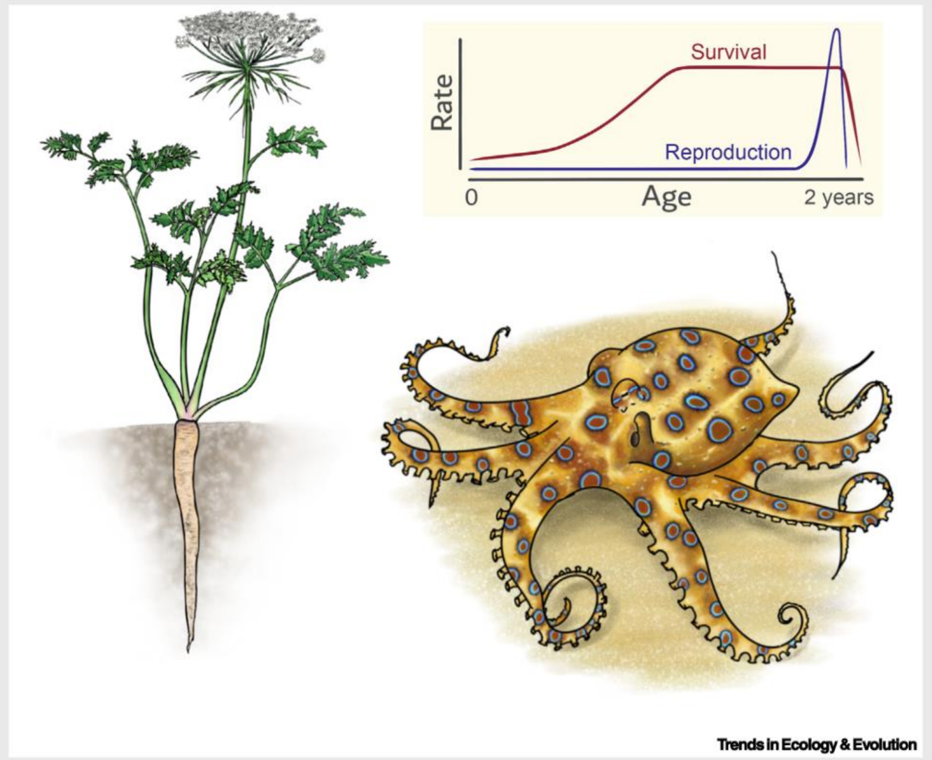

Figure I. Carrots (*Daucus carota*) and blue-ringed octopuses (*Hapalochlaena lunulata*) are distantly related organisms with very different forms and functions. Yet, these organisms have very similar life history strategies: As illustrated on the inset graph, relative rates of survival (red) start low but increase with size into adulthood, and, at around 2 years of age, both organisms die following a single reproductive event.

What is life history?

-- Characteristics derived from an (age-structured) life table (l_x, m_x)

-- Further traits linked to individual fitness

- Body size, growth rate, offspring size, sex ratio, physiology, morphology ….

-- Often used vaguely in the literature

A simplified cohort life table for female yellow-bellied marmots, *Marmota flaviventris*, in Colorado. The columns are ex

AGE CLASS (YEARS) x	NUMBER ALIVE AT THE START OF EACH AGE CLASS a_x	PROPORTION OF ORIGINAL COHORT SURVIVING TO THE START OF EACH AGE CLASS l_x	NUMBER OF FEMALE YOUNG PRODUCED BY EACH AGE CLASS F_x	NUMBER OF FEMALE YOUNG PRODUCED PER SURVIVING INDIVIDUAL IN EACH AGE CLASS m_x
0	773	1.000	0	0.000
1	420	0.543	0	0.000
2	208	0.269	95	0.457
3	139	0.180	102	0.734
4	106	0.137	106	1.000
5	67	0.087	75	1.122
6	44	0.057	45	1.020
7	31	0.040	34	1.093
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9	12	0.016	16	1.336
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11	3	0.004	0	0.000
12	2	0.003	0	0.000
13	2	0.003	0	0.000
14	2	0.003	0	0.000
15	1	0.001	0	0.000
Total			519	

LIFE HISTORY – BIG PICTURE

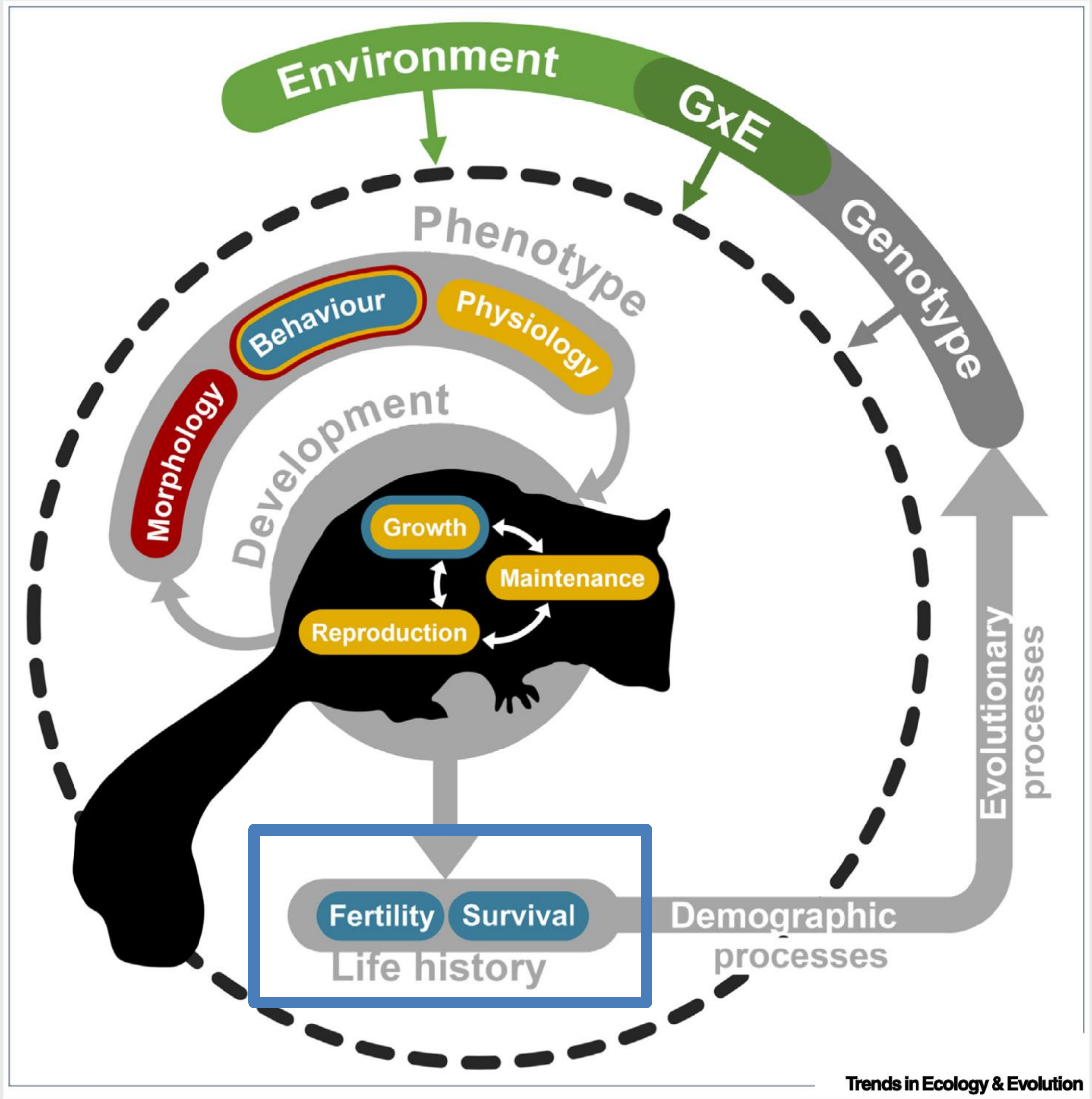

Figure I. A schematic view of a framework to examine and quantify life history strategies, showing the relationships between different trait types. Colors illustrate what currencies traits are measured in: energy (orange), space (red), and time (blue).

LIFE HISTORY – BIG PICTURE

-- **Survivorship schedule (l_x)**
(Actuarial component)
+
-- **Fecundity schedule (m_x)**
(Reproductive component)

Modern life table

AGE CLASS (YEARS) x	NUMBER ALIVE AT THE START OF EACH AGE CLASS a_x	PROPORTION OF ORIGINAL COHORT SURVIVING TO THE START OF EACH AGE CLASS l_x	NUMBER OF FEMALE YOUNG PRODUCED BY EACH AGE CLASS F_x	NUMBER OF FEMALE YOUNG PRODUCED PER SURVIVING INDIVIDUAL IN EACH AGE CLASS m_x
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+

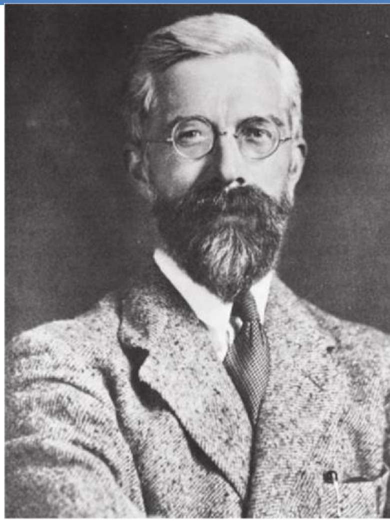
-- Body size
-- Growth rate
-- Offspring size
-- Sex ratio
-- Physiology
.....

Life history
(narrow sense) = ”vital rates”

Fitness

(Use a fitness measure to compare different life histories)

Life history
(broad sense)



R. A. Fisher (1930)

LIFE TABLES

<u>Components</u>

-- Source data

- Actuarial component: **number of individuals**

  l_x : *survivorship schedule, survivorship curve*

- Fecundity component: **number of offspring**

  m_x: *fecundity schedule, maternity function*

-- Other columns are calculated…

AGE CLASS (YEARS) x	NUMBER ALIVE AT THE START OF EACH AGE CLASS a_x	NUMBER OF FEMALE YOUNG PRODUCED BY EACH AGE CLASS F_x
0	773	0
1	420	0
2	208	95
3	139	102
4	106	106
5	67	75
6	44	45
7	31	34
8	22	37
9	12	16
10	7	9
11	3	0
12	2	0
13	2	0
14	2	0
15	1	0
Total		519

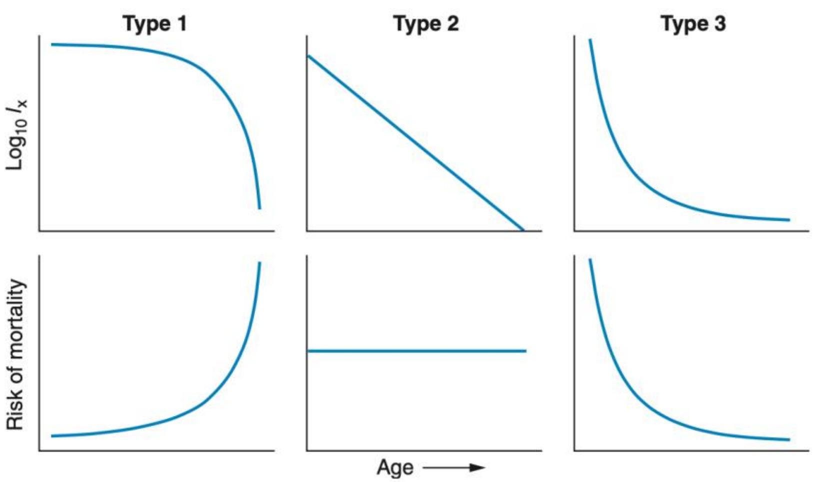
LIFE TABLES

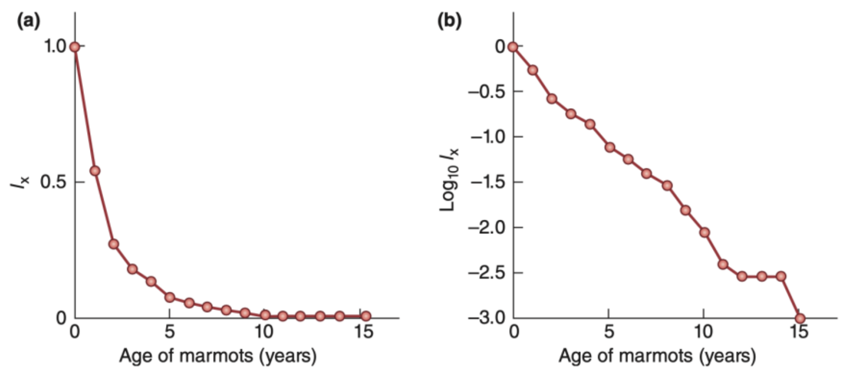
Survivorship curves: l_x

-- Per cohort: the *proportion* of the cohort that survives to age *x*

-- Per individual: the *probability* that an individual survives from birth to age *x*

-- $l_x = \frac{S_x}{S_0}$





-- Survival from x to x+1: $p_x = \frac{S_{x+1}}{S_x} = \frac{l_{x+1}}{l_x}$

Components

-- Fecundity schedule m_x

-- Net (or basic) reproductive rate $R_0 = \sum l_x m_x = \sum F_x / S_0$

A simplified cohort life table for female yellow-bellied marmots, *Marmota flaviventris*, in Colorado. The columns are explained in the text.

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1	420	0.543	0	0.000	0.000
2	208	0.269	95	0.457	0.123
3	139	0.180	102	0.734	0.132
4	106	0.137	106	1.000	0.137
5	67	0.087	75	1.122	0.098
6	44	0.057	45	1.020	0.058
7	31	0.040	34	1.093	0.044
8	22	0.029	37	1.680	0.049
9	12	0.016	16	1.336	0.021
10	7	0.009	9	1.286	0.012
11	3	0.004	0	0.000	0.000
12	2	0.003	0	0.000	0.000
13	2	0.003	0	0.000	0.000
14	2	0.003	0	0.000	0.000
15	1	0.001	0	0.000	0.000
Total			519		0.670

What is Darwinian fitness?

-- "The ability to leave descendants, in a long-term, taking into account the differential rate of increase of genotypes in a population"

-- Concept itself not controversial, but its operational definition (**fitness measure**) problematic

-- What is the "best" fitness measure depends on assumptions about populations

Fitness measure (examples)	Assumptions
r (R_0 = LRS)	Constant environment Density-independent (What does it mean?) Stable-age distribution (Stationary population)
Invasion exponent	Constant environment Density-dependence with a stable equilibrium
Geometric mean of r	Temporally stochastic environments
Inclusive fitness	Social environment
ESS	Frequency-dependence

Calculating fitness measures

-- ***R_0*: Net (or basic) reproductive rate**

- No. of offspring produced on average by an individual over its lifespan
- From life table, $\sum l_x m_x = \sum F_x / S_0$

-- ***r*: Instantaneous (or intrinsic) rate of increase**

- Per capita population growth rate [individuals / (individual x time)]

- Approximate: $\frac{\ln(R_0)}{T_c}$, where T_c is the cohort generation time, $T_c = \frac{\sum x l_x m_x}{\sum l_x m_x} = \frac{\sum x l_x m_x}{R_0}$ (mean age of the parents of all the offspring produced by a single cohort)

- Exact: from implicit Euler-Lotka equation $1 = \sum \lambda^{-x} l_x m_x = \sum e^{-rx} l_x m_x$

How to increase fitness?

-- Higher survival and fecundity at all ages

-- Earlier onset of reproduction; reproducing longer

"Darwinian daemon" (perfect organism)

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-- Which components to increase?

- Reproductive value (age classes)

- Sensitivity & elasticity (individual components)

-- Convenient to use:

- Projection matrices

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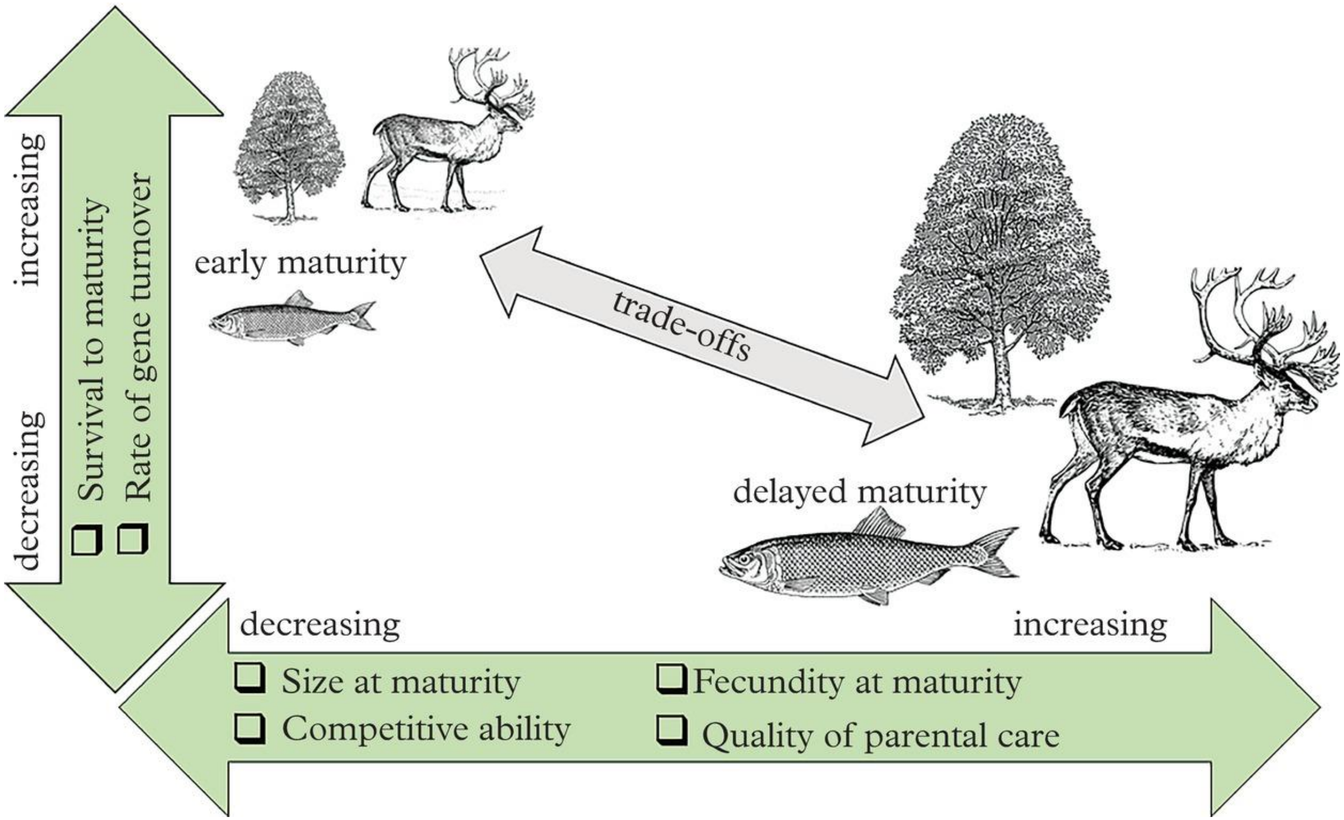
-- What prevents organisms from increasing fitness?

- Trade-offs
- Constraints

<u>What are trade-offs?</u>

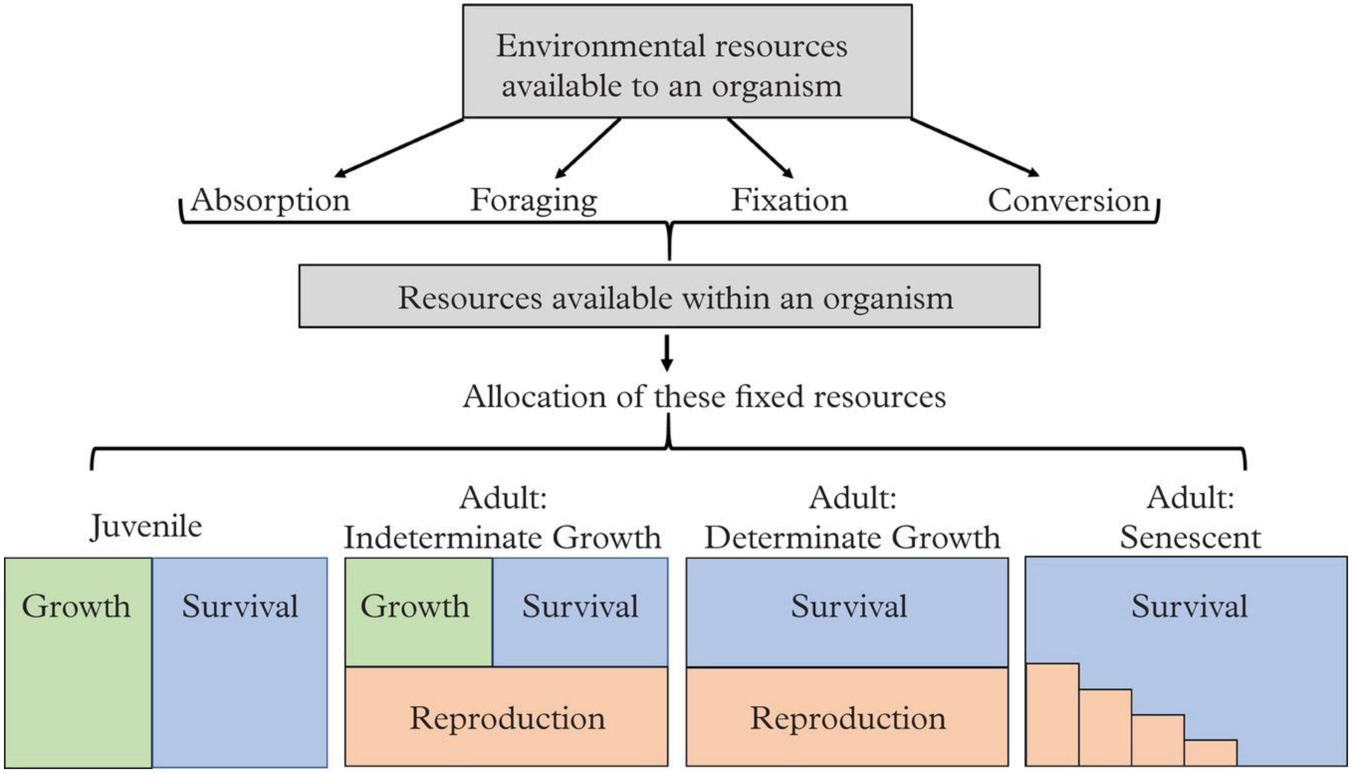
-- *Benefits* derived from making one LH "decision" are made at a *cost* of not realizing potential benefits associated with alternative decisions



Why trade-offs?

-- *Benefits* derived from making one LH "decision" are made at a *cost* of not realizing potential benefits associated with alternative decisions

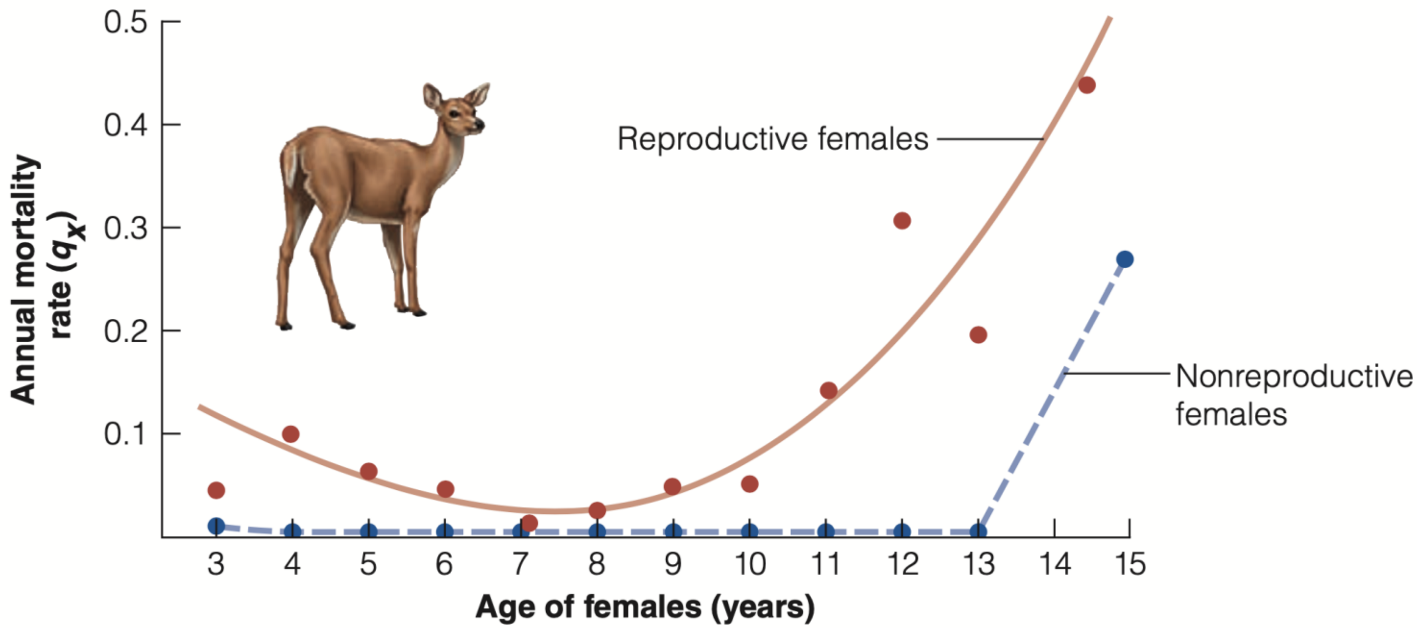
-- Trade-offs are the inevitable outcome of a constraint which prevents multiple positive outcomes from being simultaneously realized



<u>Major example: **Cost of reproduction**</u>

-- Reproduction causes reduced growth, future fecundity and/or increased mortality (immediately or later in life).

Winter mortality of female red deer, Island of Rhum, Scotland

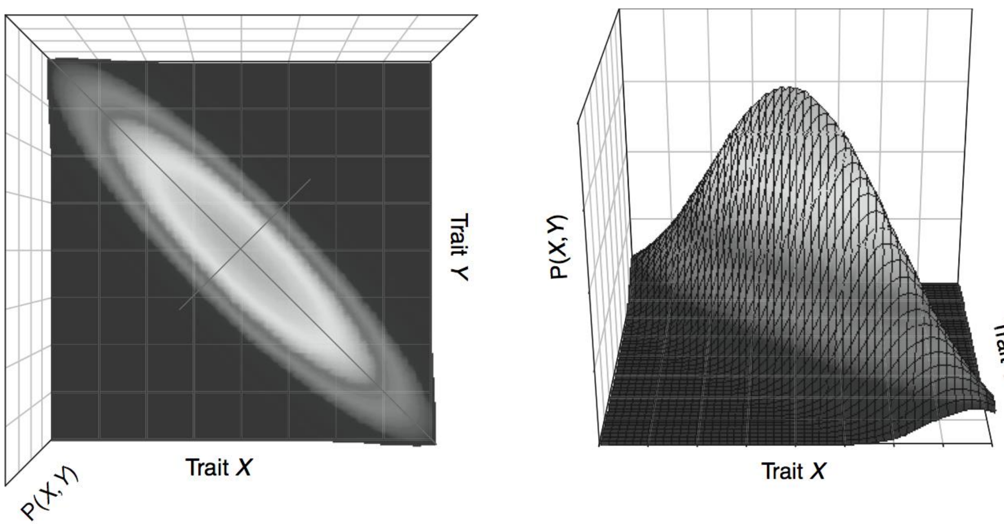


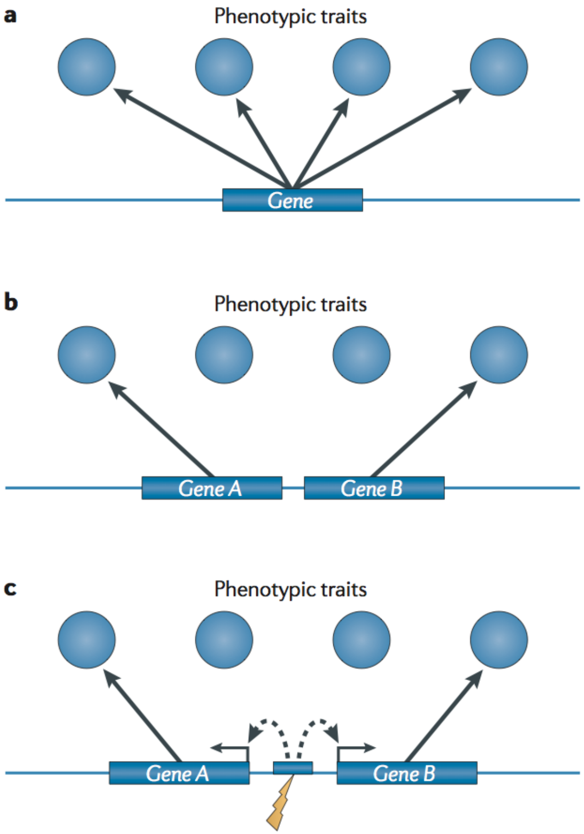
<u>Causes of trade-offs</u>

-- *Benefits* derived from making one LH "decision" are made at a *cost* of not realizing potential benefits associated with alternative decisions

-- Trade-offs are the inevitable outcome of a constraint which prevents multiple positive outcomes from being simultaneously realized

-- Causes: **genetic architecture**



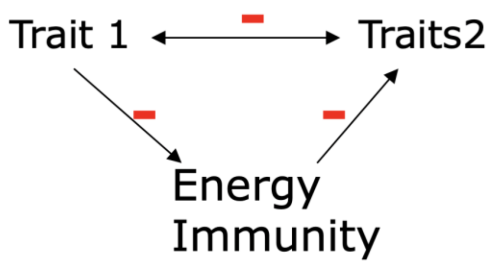


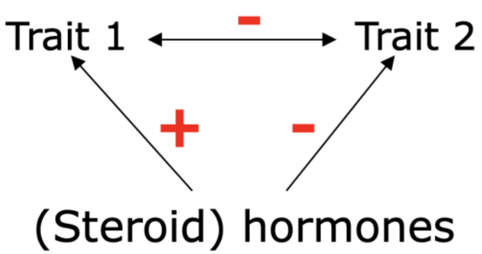
Causes of trade-offs

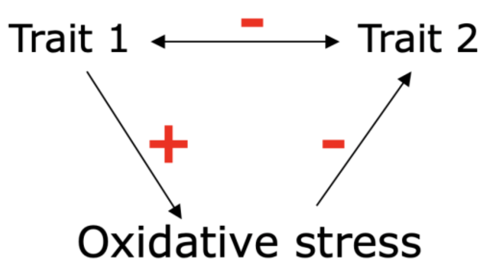
-- *Benefits* derived from making one LH "decision" are made at a *cost* of not realizing potential benefits associated with alternative decisions.

-- Trade-offs are the inevitable outcome of a constraint which prevents multiple positive outcomes from being simultaneously realized

-- Causes: genetic architecture, **finite or fixed resources**





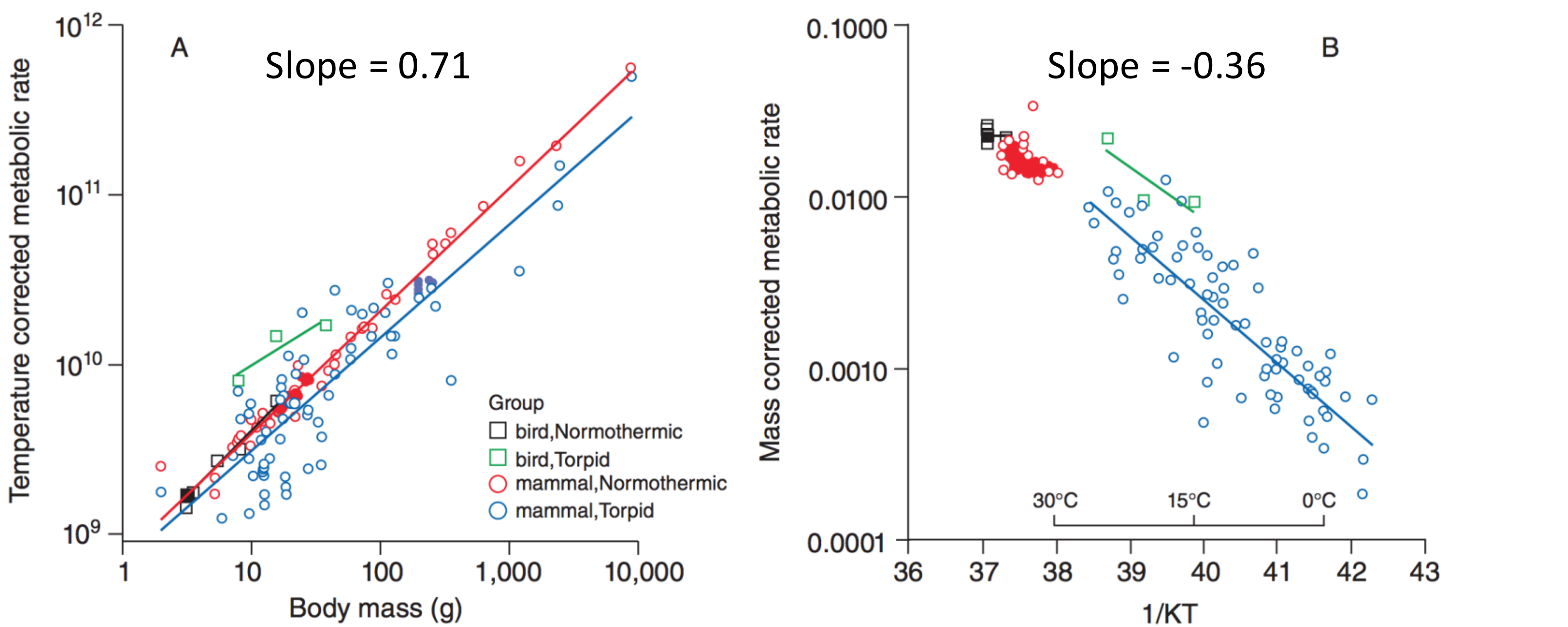


<u>Causes of LH variation</u>

-- Constraints: LH traits cannot take any value

- Metabolic ecology: metabolism and LH traits scale with body mass and temperature
- Physics of life (bone strength, distribution networks, viscosity of environments…)

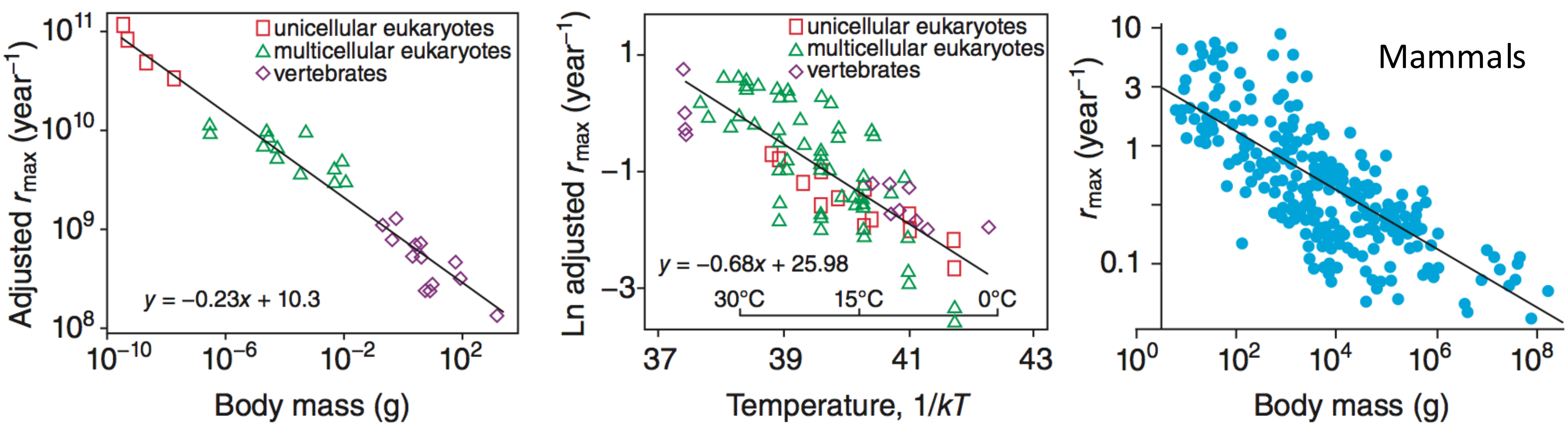
$$B = B_0 M^c e^{-\frac{E_a}{kT}}$$ → How would you "correct" for temperature or body mass?



Allometry and temperature

-- LH traits correlate with body mass and temperature

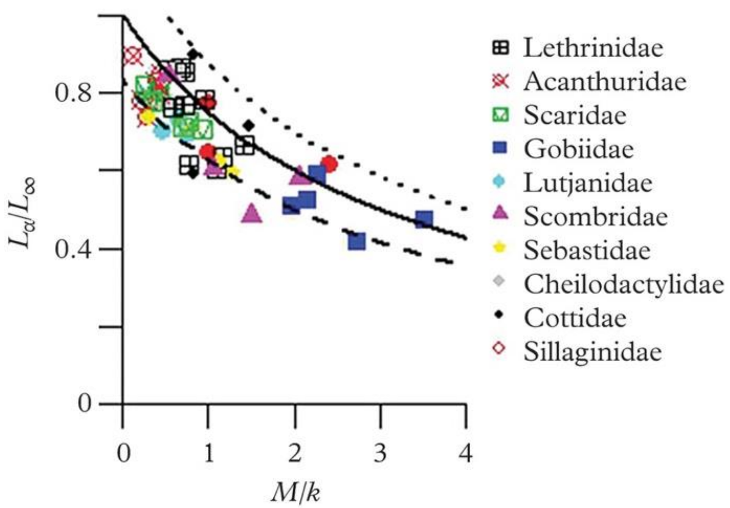
-- This carries over to potential population growth rates and other key characteristics

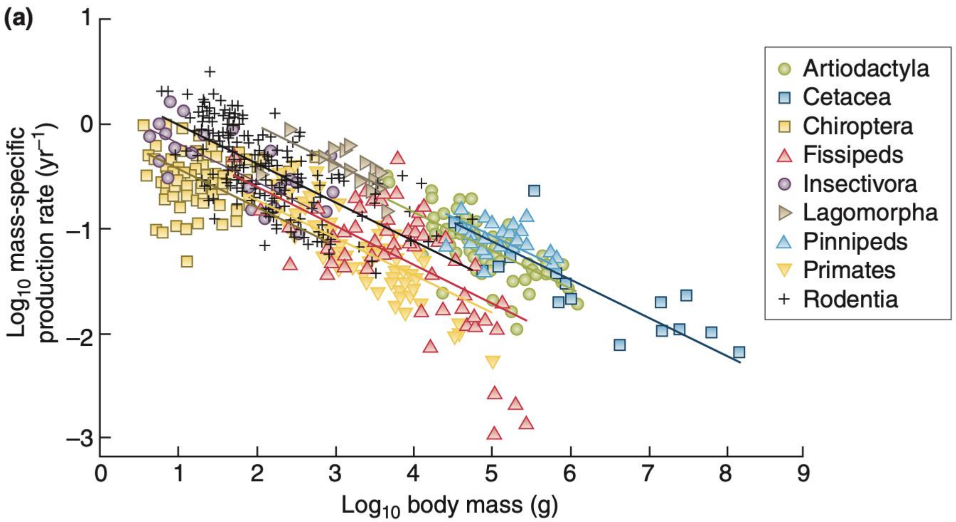


Phylogeny

-- Historical/phylogenetic effects = different solutions (conditioned on "body design") of maximizing fitness

-- This varies with taxonomic/phylogenetic resolution

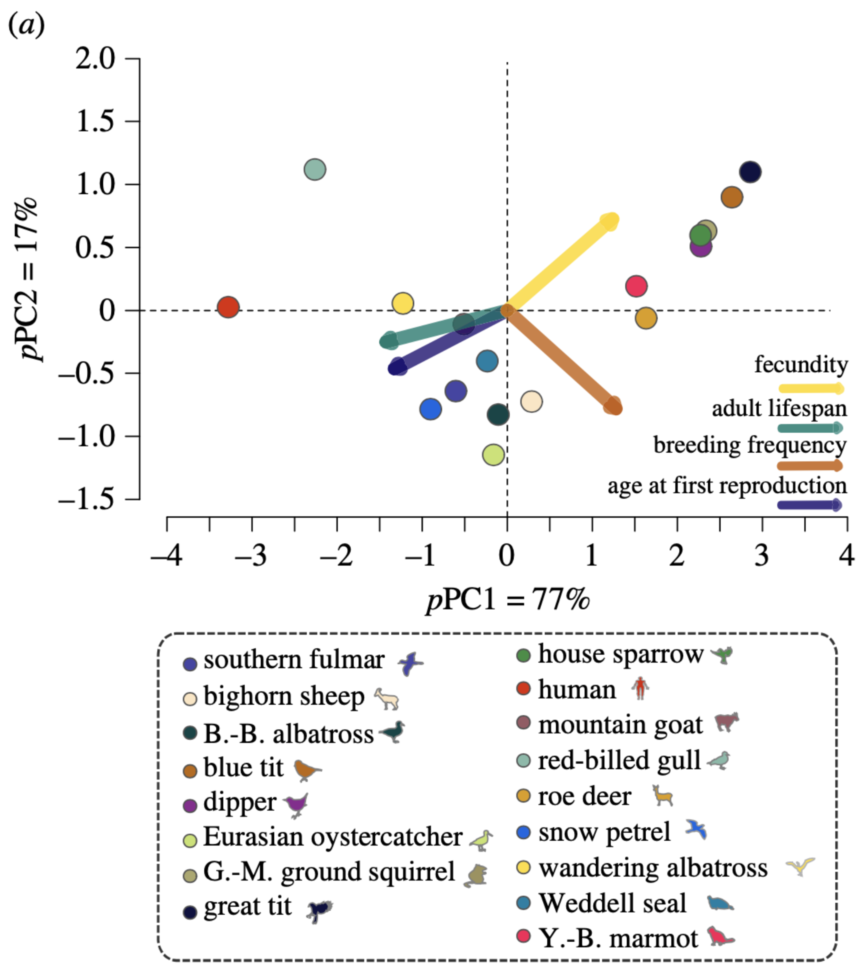




LH trait covariation

-- Life history traits co-vary systematically across species, even after accounting for allometry and phylogeny

-- Slow-fast continuum -> **pace of life**

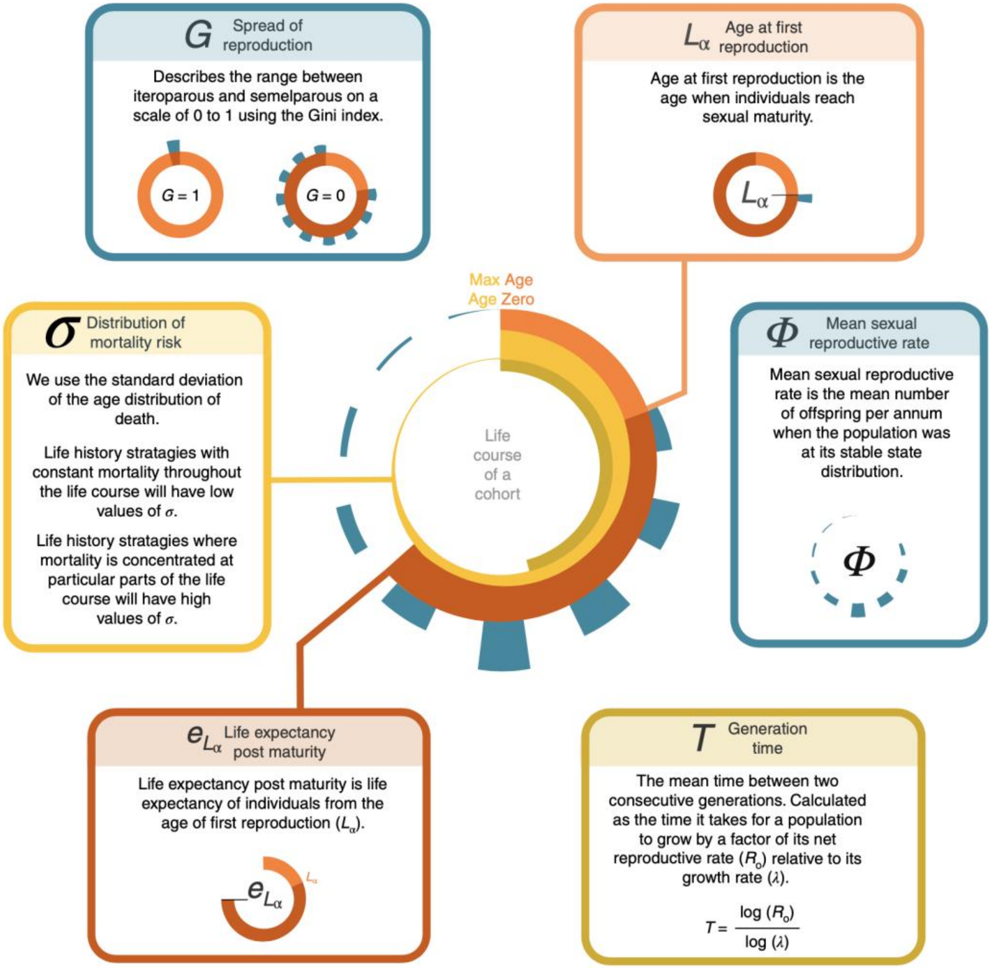


<u>LH trait covariation</u>

-- Life history traits co-vary systematically <u>across species</u>, even after accounting for allometry and phylogeny

-- Slow-fast continuum -> **pace of life**

-- Distribution of survival and reproduction over lifetime -> **shape of life**



VARIATION IN LIFE HISTORIES

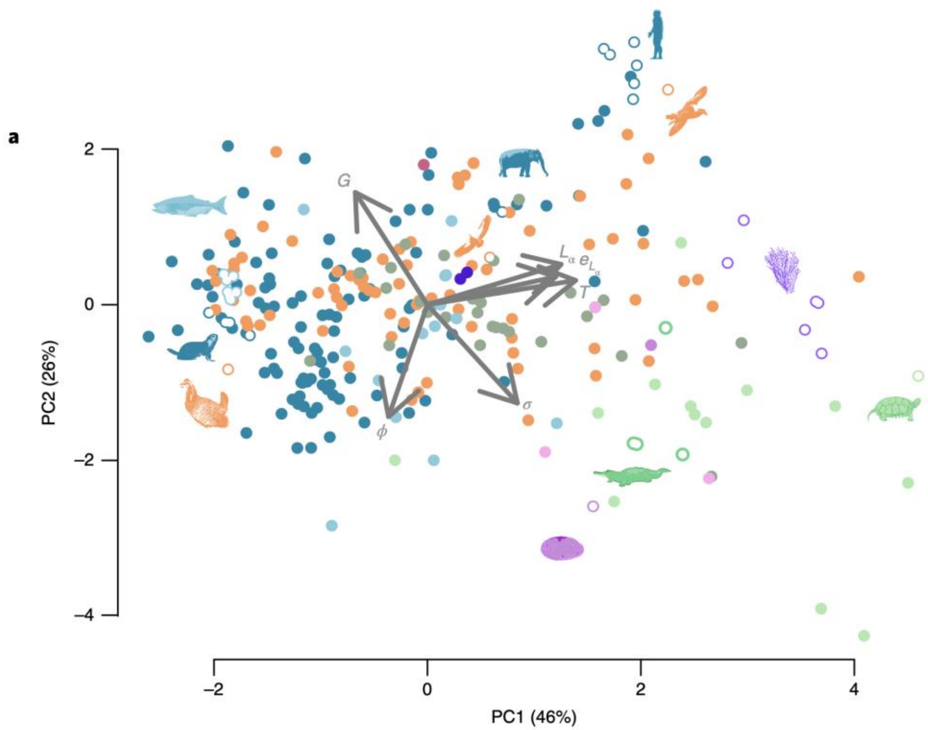
<u>LH trait covariation</u>

-- Life history traits co-vary systematically <u>across species</u>, even after accounting for allometry and phylogeny

-- Slow-fast continuum -> **pace of life**

-- Distribution of survival and reproduction over lifetime -> **shape of life**

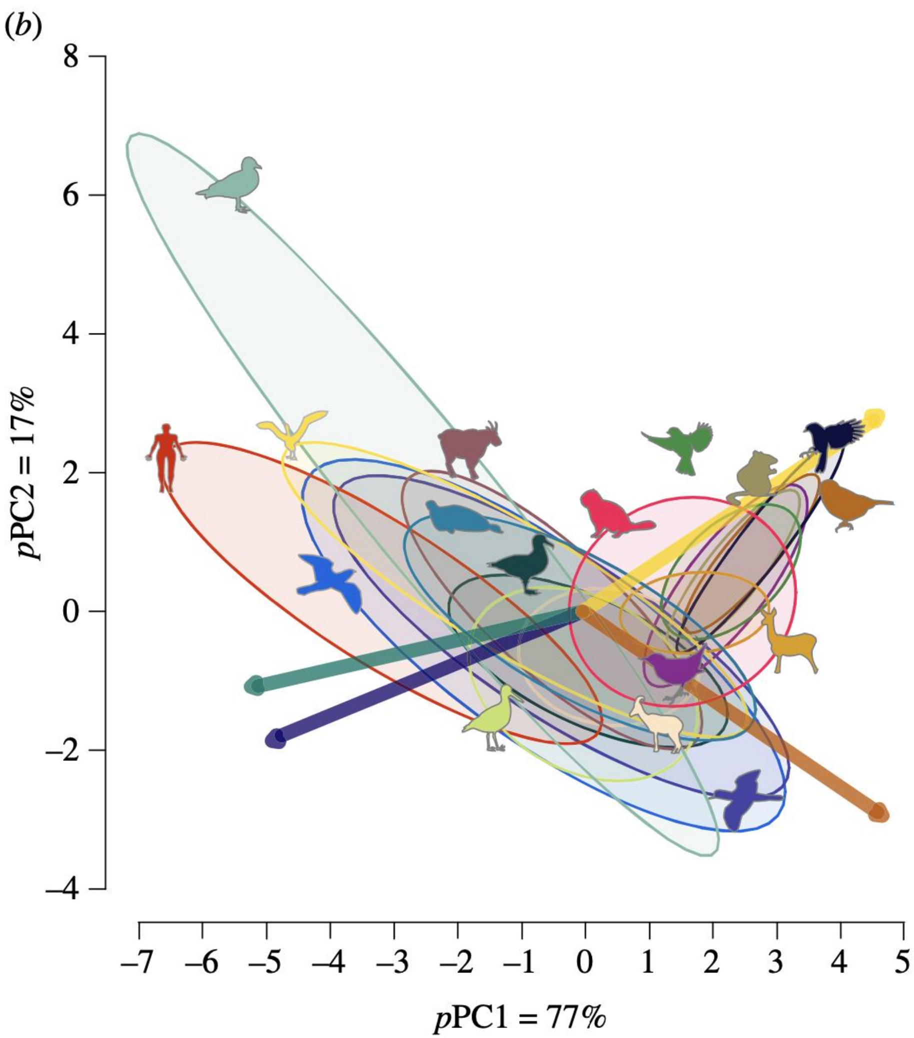
Low iteroparity,
low reproductive rate,
Constant mortality through life

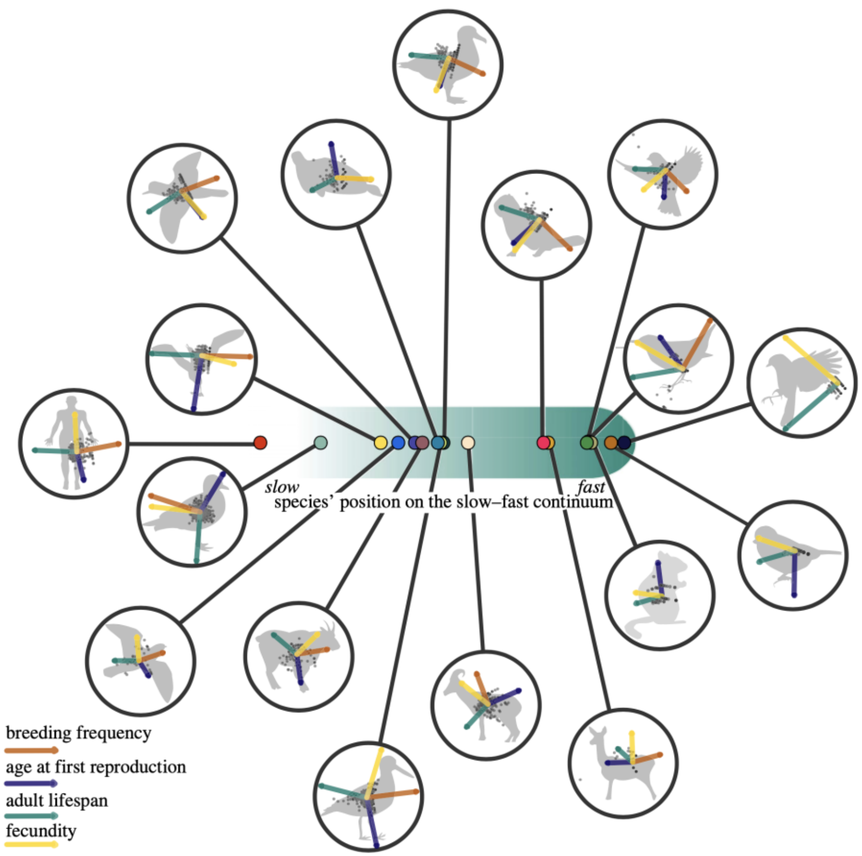


High age at first reproduction, high life expectancy, long generation time

<u>LH trait covariation</u>

-- Life history traits do not co-vary consistently <u>within species</u>





Causes of LH variation

-- Each allocation strategy has its costs and benefits (trade-offs)

-- LH trait is optimized for max. fitness under trade-offs and constraints

-- This process generates variation in LH among populations and species

Trade-offs
Constraints

Optimization
Adaptation

Environmental conditions
-- Food
-- Predation
-- Competitors, etc…

Evolution within populations

Interspecific variation

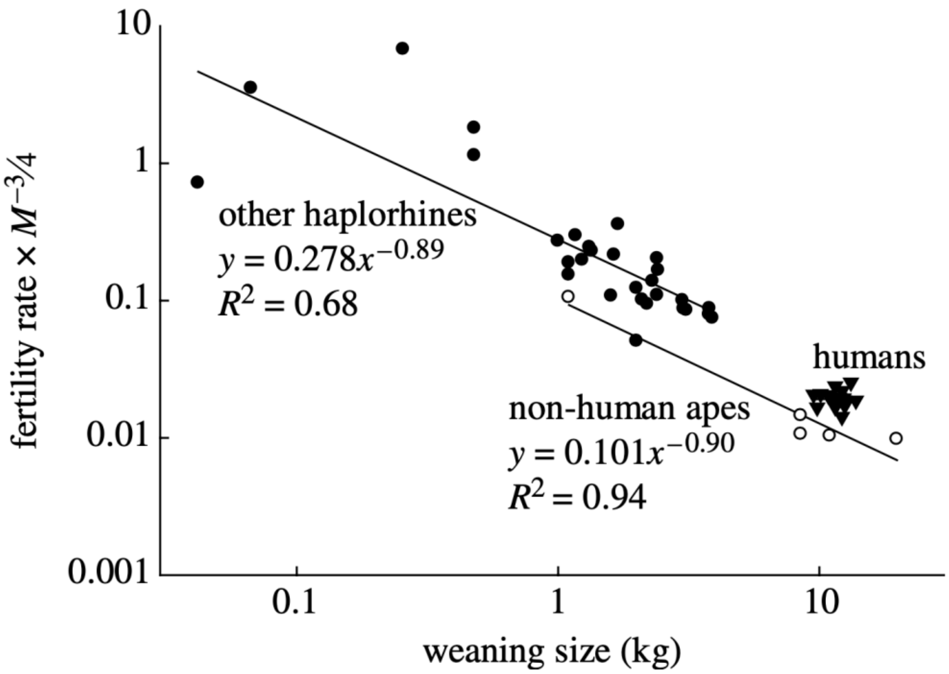
Main approaches

-- Observation (problem of acquisition vs. allocation)
-- Manipulative experiments ("clutch size manipulations")
-- Selection experiments, experimental evolution
-- Interspecific comparisons

Empirical

-- Graphical analysis (implicitly mathematical!)
-- Mathematical modeling

Theoretical



Mathematical models

-- Model = Purposeful simplification of reality

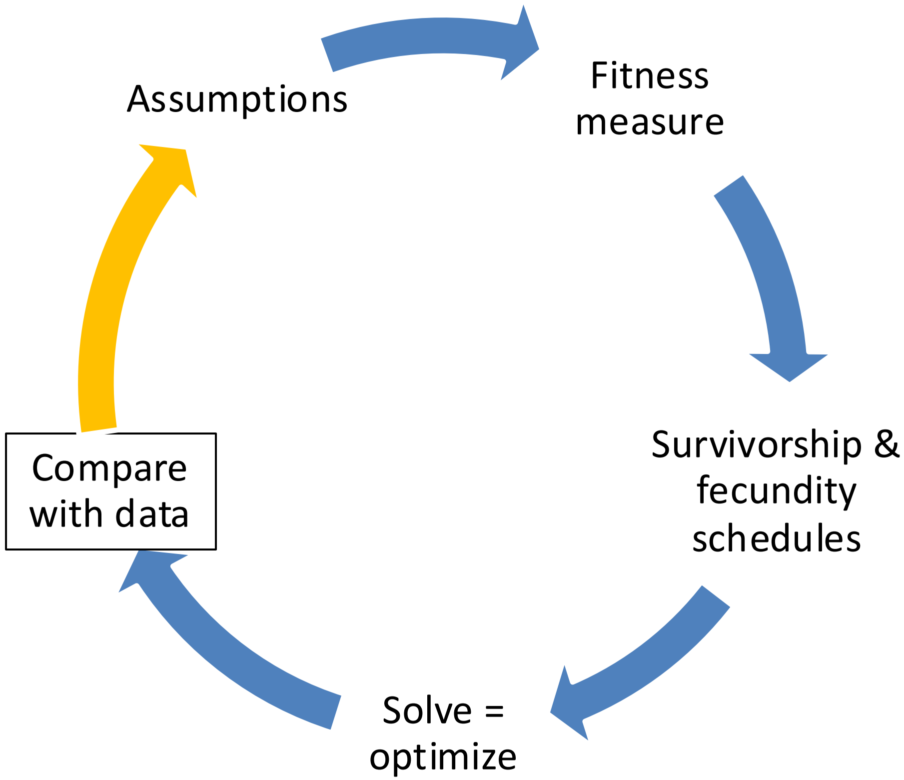
-- A logical engine to turn **assumptions** into consequences ("Thinking aid")

-- Models try to determine equilibrium trait values under the influence of natural selection

Model type	Main assumptions & advantages
Fisherian optimality analysis	Stable age distribution No density- or frequency-dependence
Invasibility analysis	Age- or stage-structure Density dependence
Genetic models	Genetic architecture of traits Evolutionary trajectory
Game theoretic models	Constant populations Frequency-dependence
Dynamic programming	Constant populations Sequential decisions (MDPs)

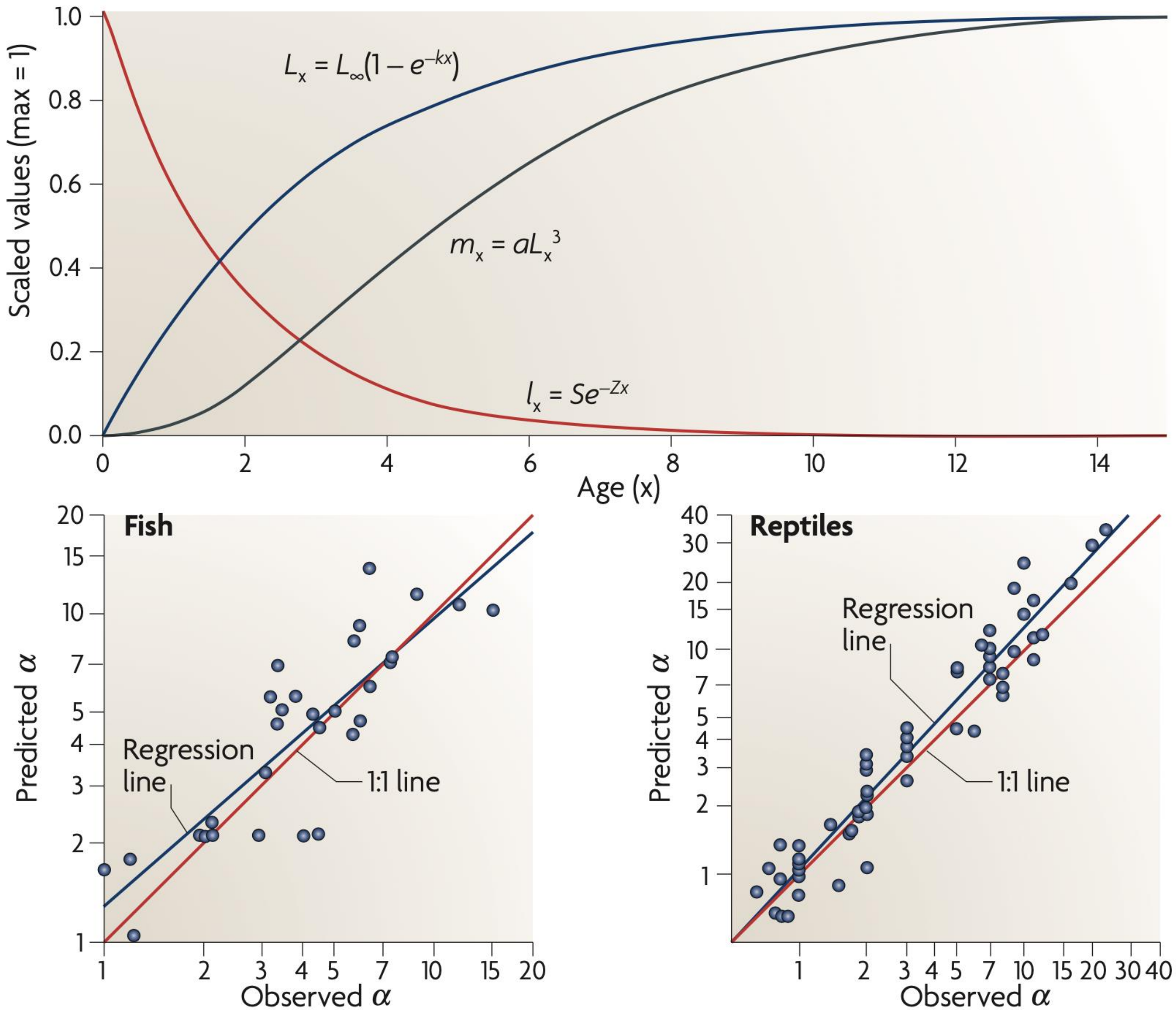
Mathematical models

-- General approach: the modeling cycle



Mathematical models

-- Example: Fisherian model of optimal age at maturity in **ectotherms**



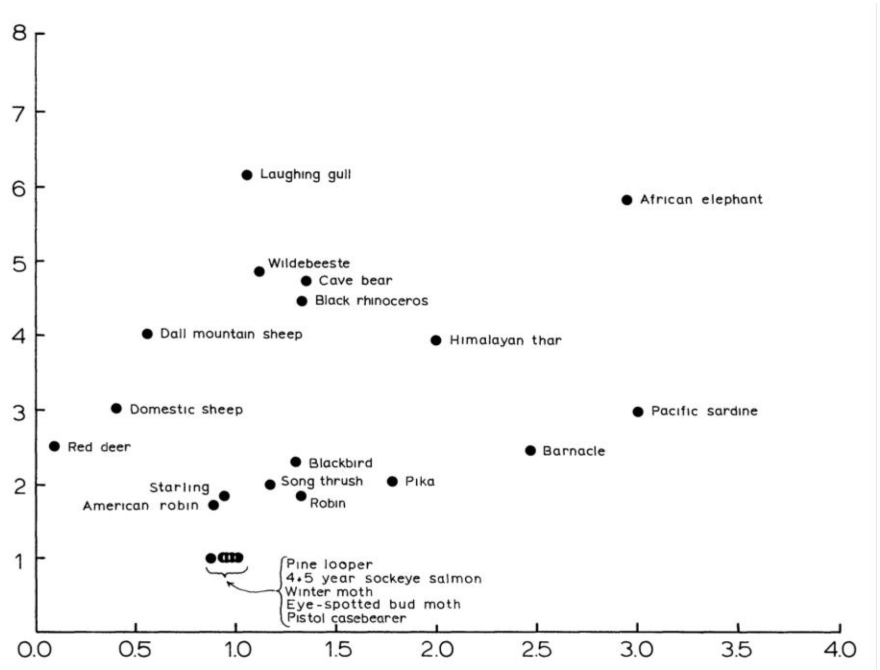
<u>Reproductive scheduling</u>

-- **Semelparity vs. iteroparity**: Cole's paradox and its solution

- No cost of reproduction, constant fecundity and survival
- We get $m_{semel} = m_{itero} + \frac{S}{s}$
- Cole assumed $S = s = 1$, thus $m_{semel} = m_{itero} + 1$, hence the famous "paradox"

-- <u>Modification 1</u>: **Extrinsic mortality** drives *S* and *s* (= degree of iteroparity)

Number of breeding seasons



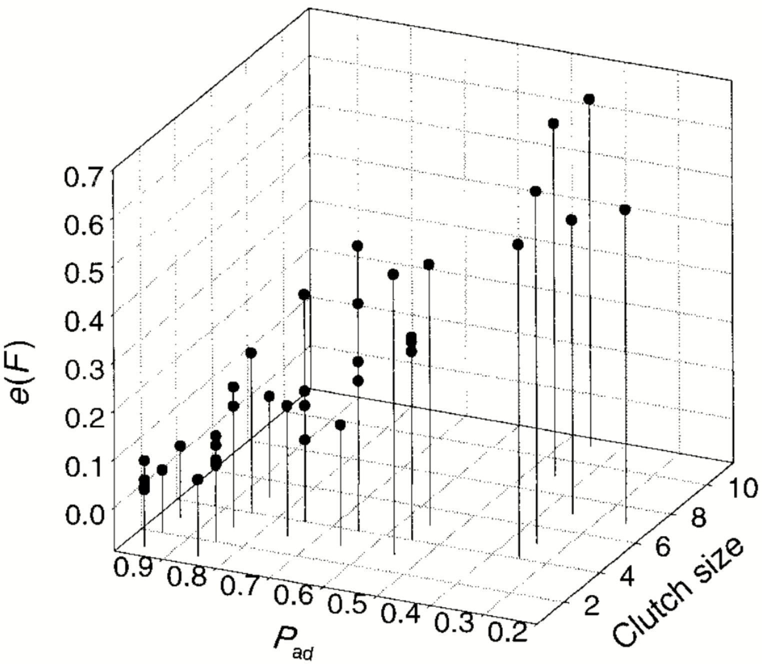
Adult survival (S) / Juvenile survival (s)

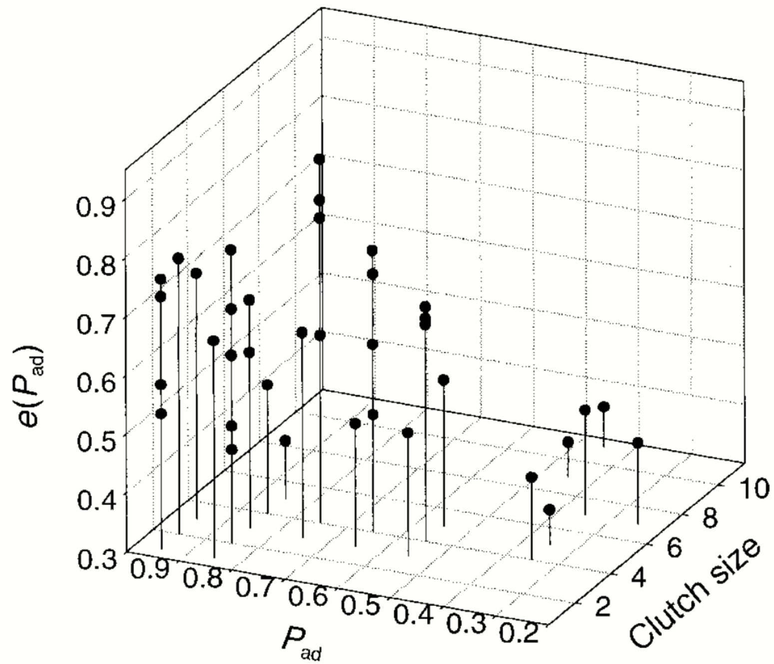
Reproductive scheduling

-- **Juvenile vs. adult survival** $m_{semel} = m_{itero} + \frac{S}{s}$

-- Modification 1: Imagine **extrinsic mortality** drives *S* and *s* (= degree of iteroparity)

–> **Fitness sensitivity** of different vital rates in long- vs short-lived species





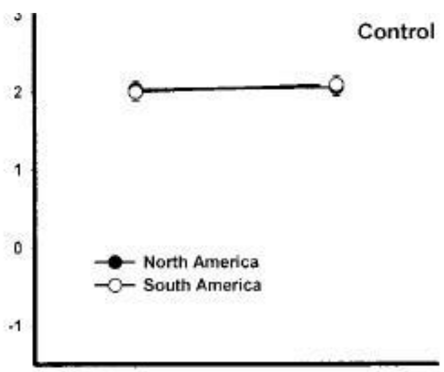
Reproductive scheduling

-- **Juvenile vs. adult survival** $m_{semel} = m_{itero} + \frac{S}{s}$

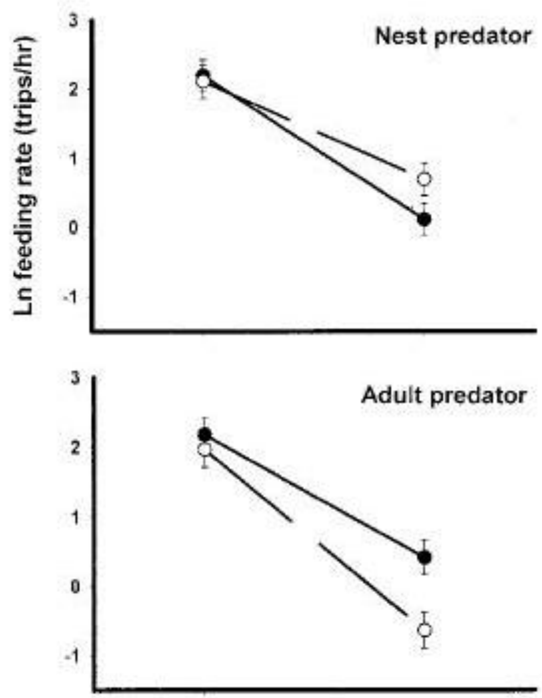
-- Modification 1: Imagine **extrinsic mortality** drives *S* and *s* (= degree of iteroparity)

–> **Fitness sensitivity** of different vital rates in long- vs short-lived species

–> "**Behavioral sensitivity**" to predators of adults vs. juveniles



Pre-presentation Model presentation



Pre-presentation Model presentation

Steller's jay (*C. stelleri*), Plush-capped jay (*C. chrysops*)

Sharp-shinned hawk (*A. striatus*)

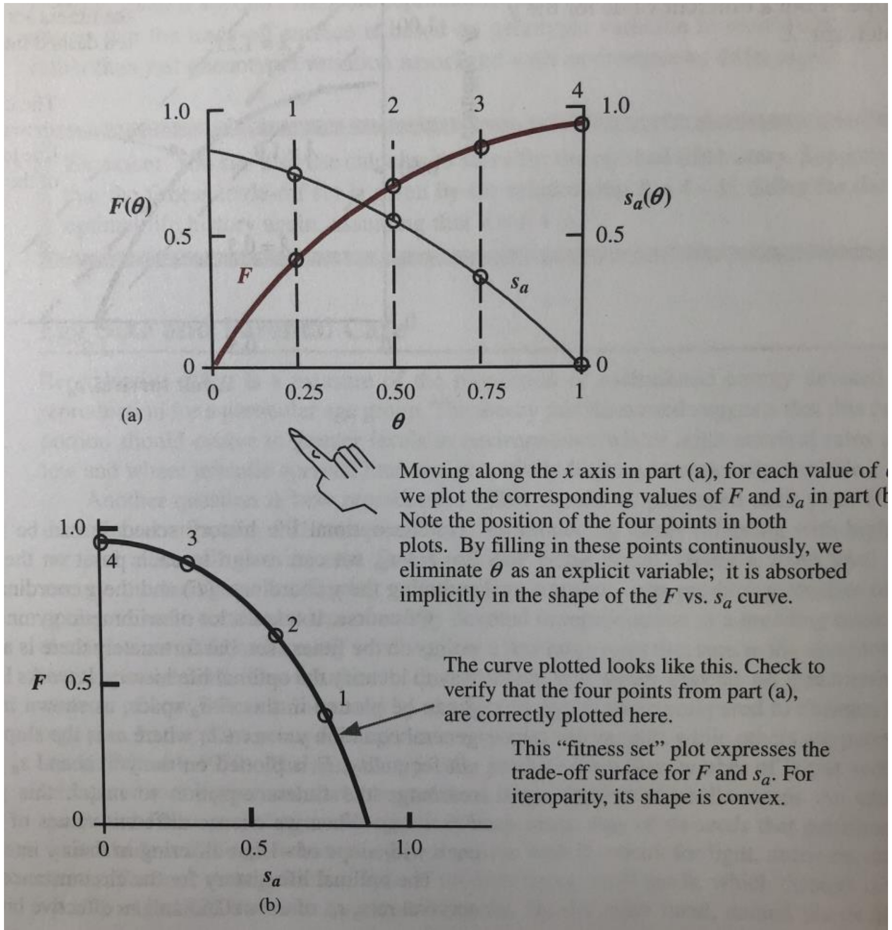
MAIN TRAITS AND TRADE-OFFS

Reproductive scheduling

-- We defined (for iteroparity): $\lambda = ms + S = F + S$

-- Modification 2: Imagine a **trade-off** between *F* and *S* (**cost of reproduction**)

- assume F and S are functions of **reproductive effort**: $F(\theta)$ and $S(\theta)$
- derive a **trade-off curve** (options set)



<u>Reproductive scheduling</u>

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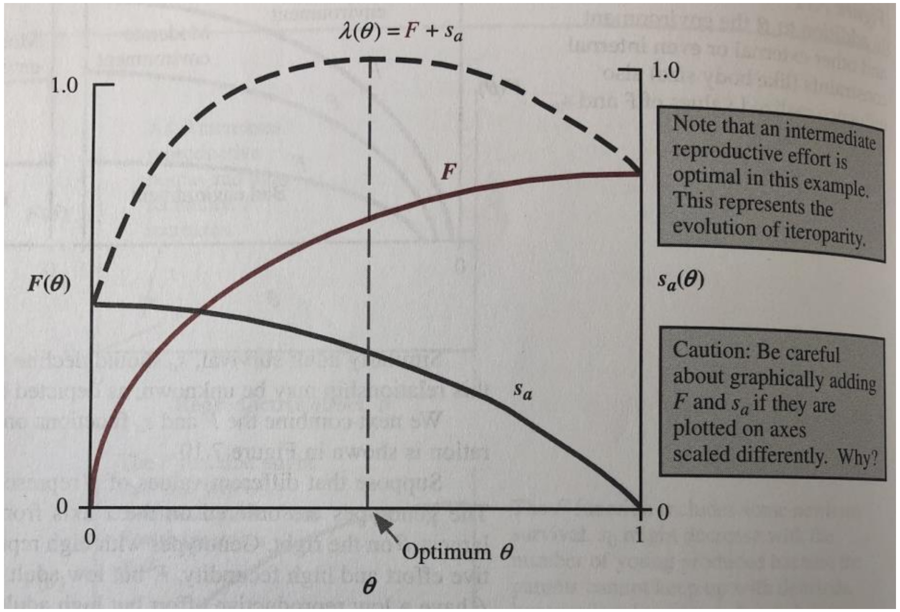
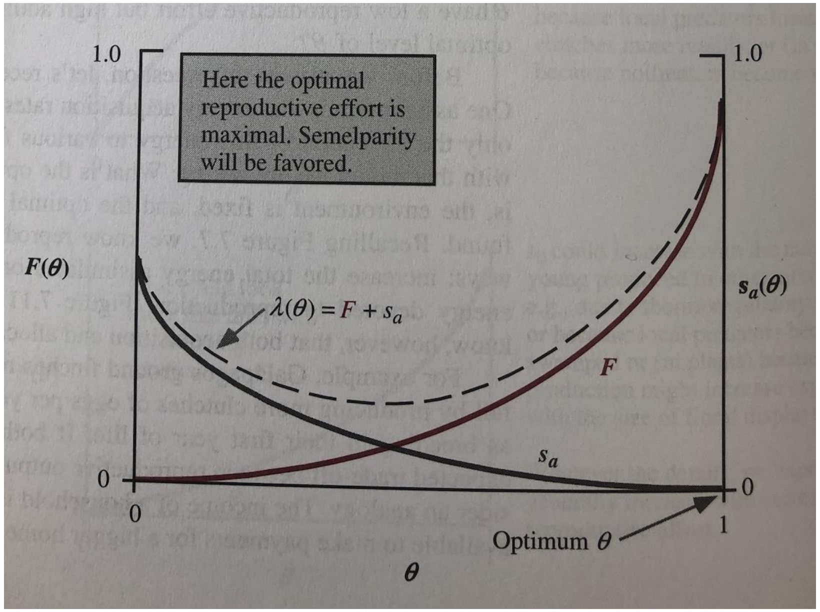
-- <u>Modification 2</u>: Imagine a **trade-off** between *F* and *S* (**cost of reproduction**)

- assume F and S are functions of **reproductive effort**: $F(\theta)$ and $S(\theta)$
- derive a **trade-off curve** (options set)
- gives an alternative graphical method of **optimization analysis**





Explore interactively: https://www.desmos.com/calculator/hlr61wjxky

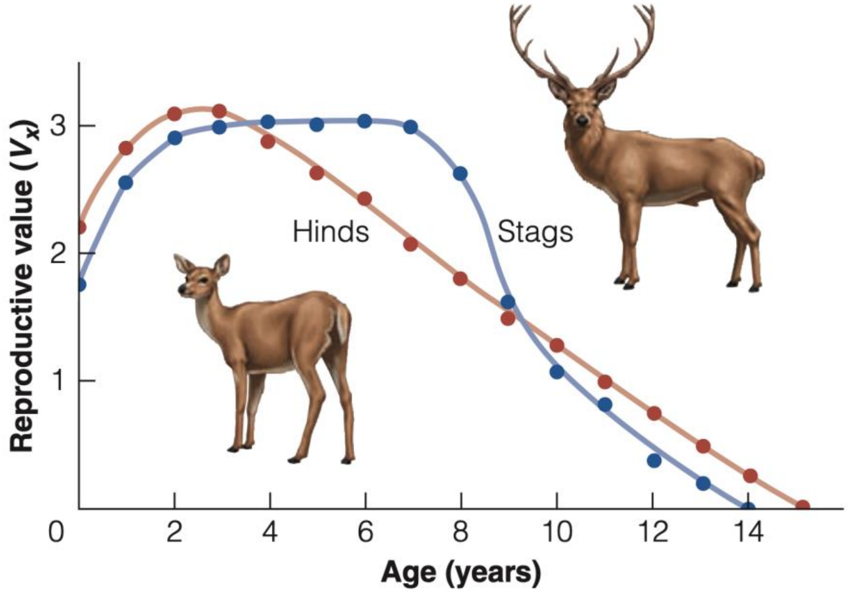
Senescence

-- Actuarial and/or reproductive ”decay” – but what does it mean?

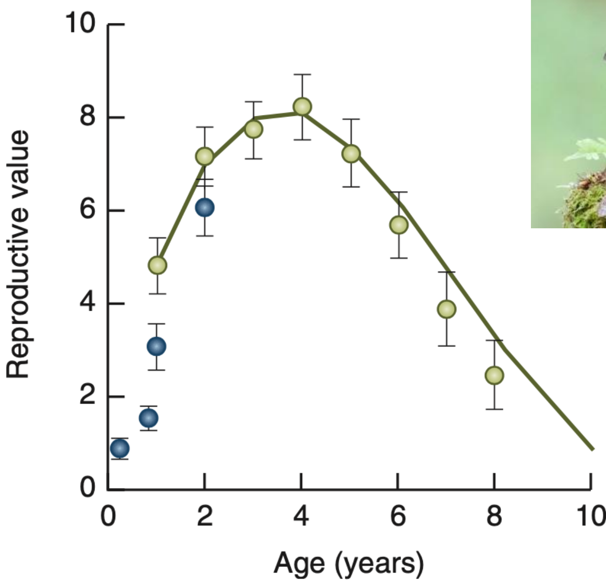
-- **Reproductive value**: Which age classes contribute the most to pop. growth?

–> Sensitivity of fitness to survival and fecundity at different ages

v_x of red deer (Island of Rhum, Scotland)



v_x of sparrowhawks (Scotland)

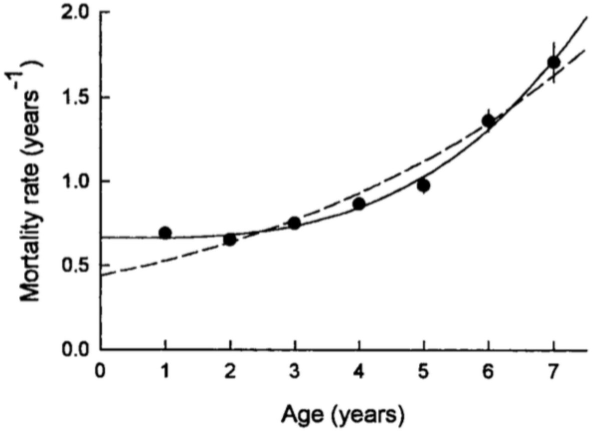


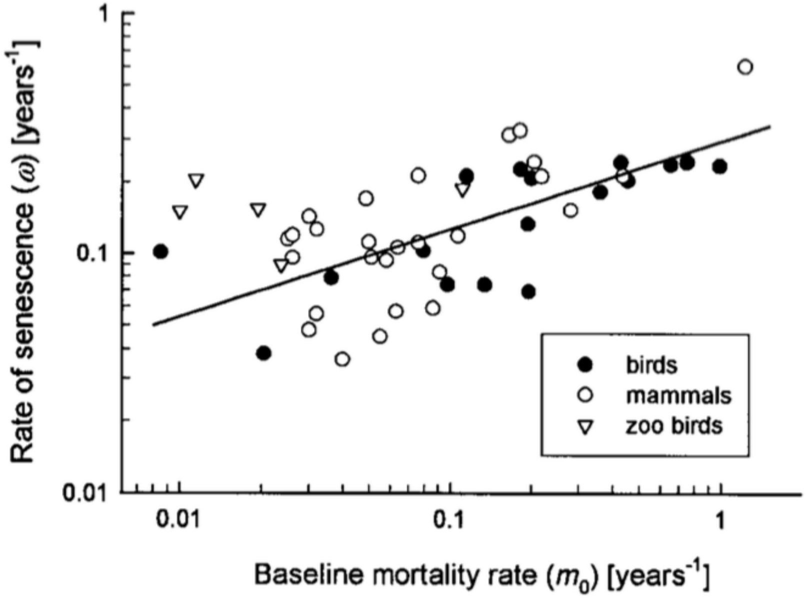
<u>Senescence</u>

-- Actuarial and/or reproductive ”decay” – but what does it mean?

-- **Mutation accumulation, antagonistic pleiotropy**

-- **Extrinsic mortality** molds senescence

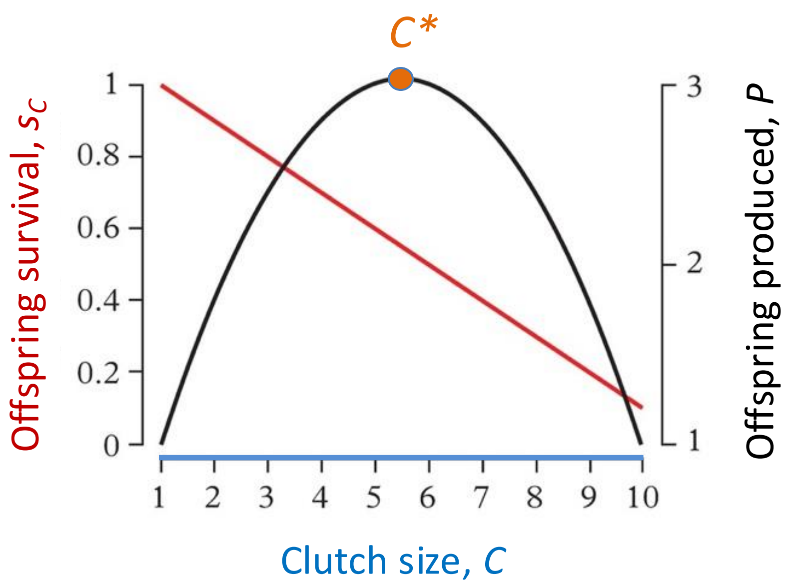




<u>Size and number of offspring</u>

-- <u>Tradition 1</u>: the number of offspring = **Lack's clutch size**

- D. Lack considered only m_x, which is problematic
- Offspring size only implicitly
- No cost of reproduction

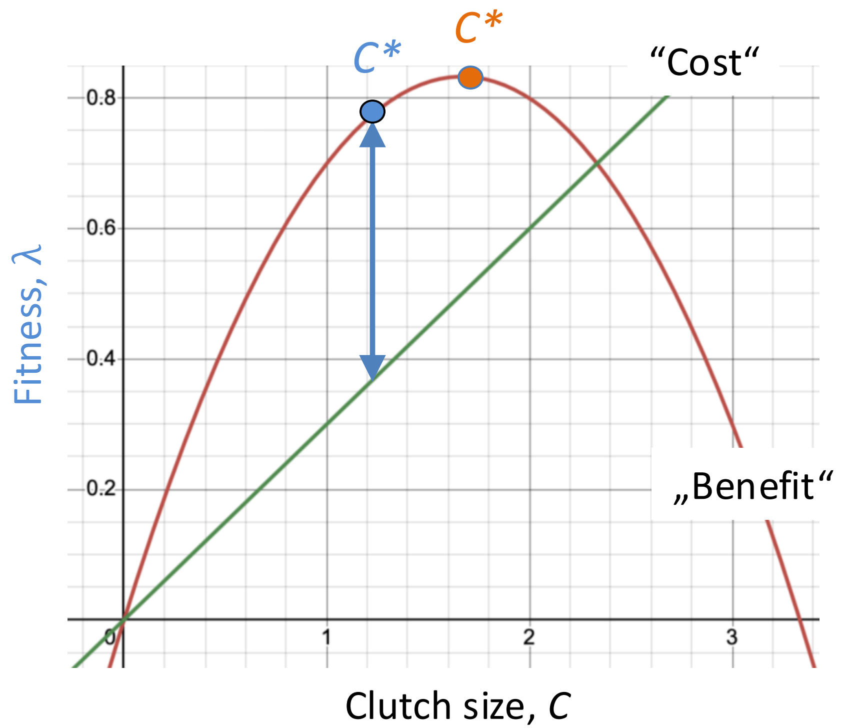


Explore interactively: https://www.desmos.com/calculator/nwyfji2q5x

Size and number of offspring

-- Tradition 1: the number of offspring = **Lack's clutch size**

- D. Lack considered only m_x, which is problematic
- We must study the $\boldsymbol{l_x m_x}$ **function** ("effective age-specific fecundity")



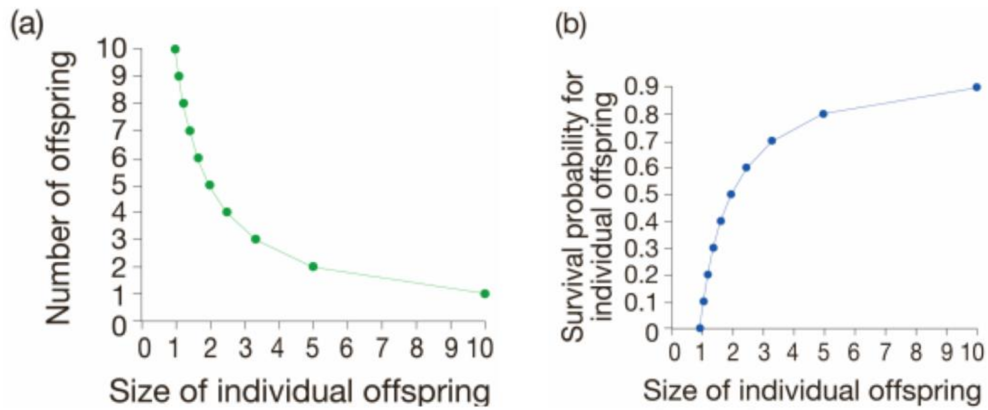
Explore interactively (linear survival fun.): https://www.desmos.com/calculator/jewmlptqim

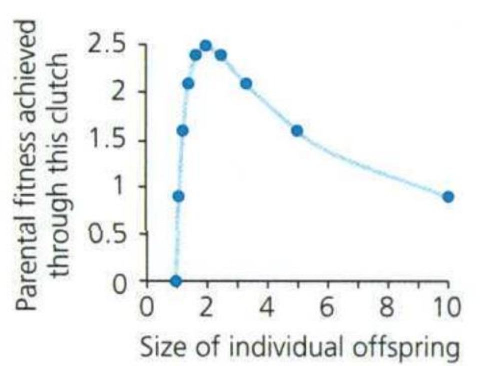
Explore interactively (exp. survival fun.): https://www.desmos.com/calculator/znirvzdndv

<u>Size and number of offspring</u>

-- <u>Tradition 2</u>: size of individual offspring = **Smith-Fretwell model**

- Considered only propagule size (propagule number only implicitly)
- No cost of reproduction



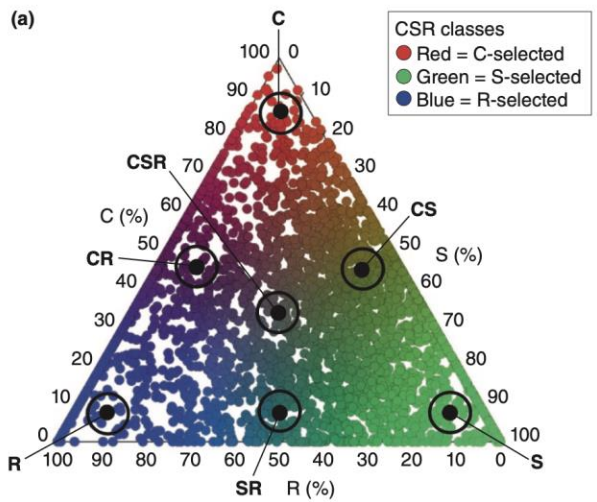


Explore interactively: https://www.desmos.com/calculator/fvgeiypbtj

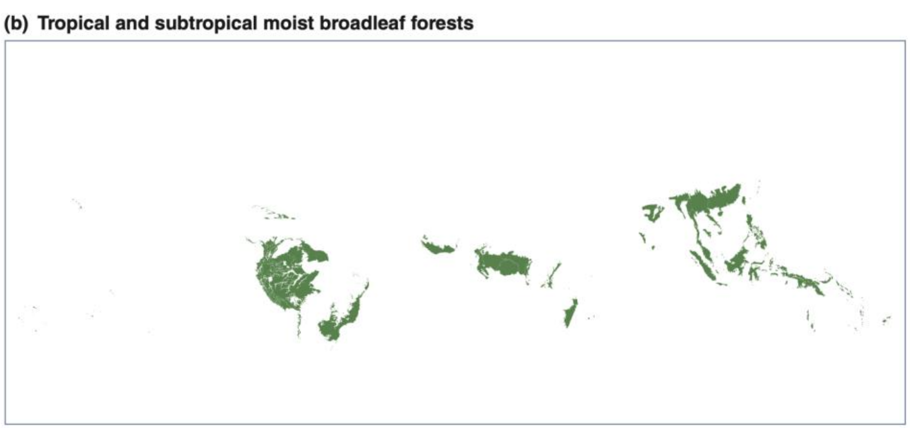
<u>"Habitat templet"</u>

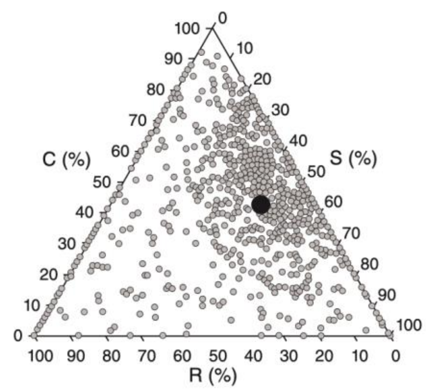
-- Similar LH repeatedly found in similar environments

-- r/K system, CSH system for plants, slow-fast continuum, pace of life syndromes



Leaf traits (3068 terrestrial plants)	**C**	**S**	**R**
Leaf area	high	low	low
Specific leaf area		low	high
Dry matter content		high	low
Leaf economics		conservative	acquisitive





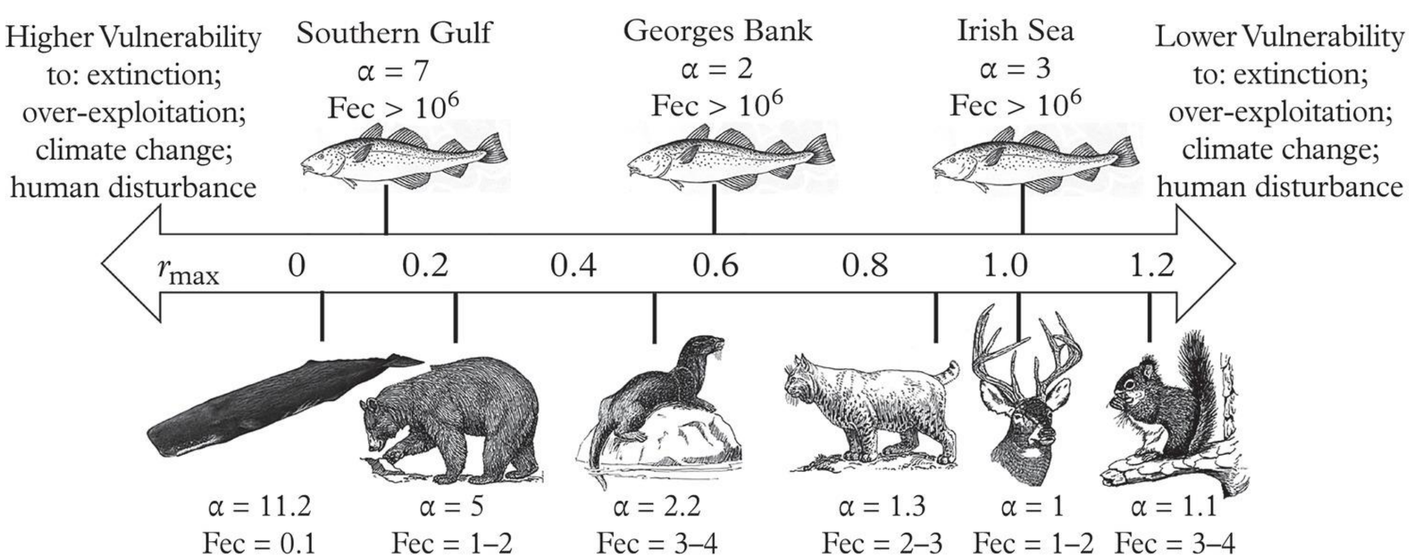
LH in conservation and natural resource management

-- LH traits (mainly body mass, age at maturity) as correlates of r_{max} (see above)

-- Predictors of species vulnerability and recovery potential

-- Vulnerability to fisheries collapse -> Maximum sustainable yield

-- Harvest-induced evolution



SOURCES

Sources of figures in this presentation

Undergraduate textbooks:
-- Begon et al. (2021) Ecology, Wiley.
-- Hutchings (2021) A primer of life histories, OUP.
-- Krebs (2009) Ecology, Pearson.
-- Sibly et al. (2012) Metabolic ecology, Wiley.

Graduate textbooks:
-- Case (1999) An illustrated guide to theoretical ecology, OUP.
-- Roff (2002) Life history evolution, Sinauer.
(Also includes these two classics: Roff (1992) The evolution of life histories, Chapman Hall; Stearns (1992) The evolution of life histories. OUP.)

Other sources:
-- Ricklefs (1998) Am. Nat. 152:24.
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