DEB Theory & Evolutionary Theories on Life-History

Charlotte Récapet

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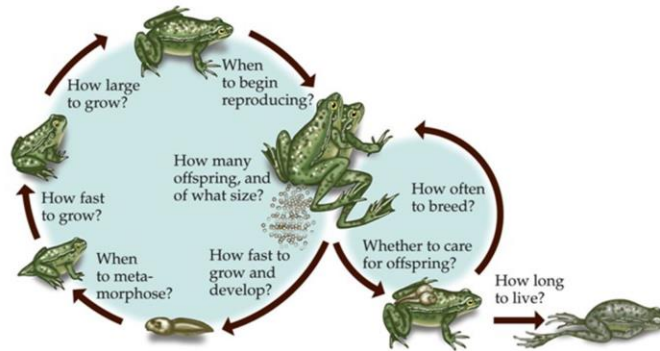
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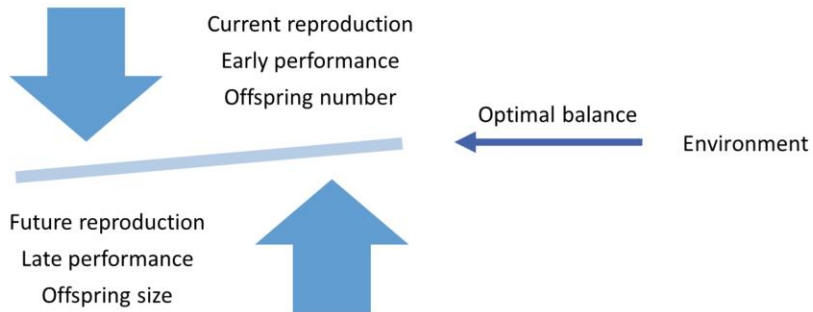
ECOBIOP
UMR 1224
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Explaining variation in life-cycles…

ECOLOGY, Figure 7.3   © 2008 Sinauer Associates, Inc.

…as optimization under constraints

Current reproduction
Early performance
Offspring number

Optimal balance

Environment

Future reproduction
Late performance
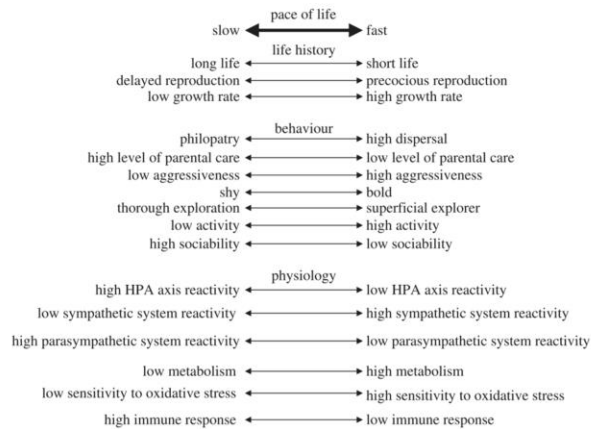Offspring size

1.
Empirical foundations
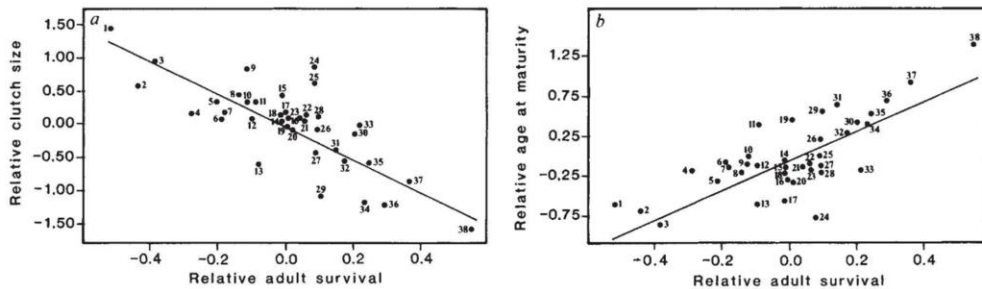
Relative adult mortality rate in relation to (a) relative clutch size and (b) relative age at maturity of different families of European birds. The points represent the deviations of each family from the predicted value of the regression of the life history trait on body weight, using the family averages (logarithmically transformed) as data entries. 1, Phasianidae; 2, Tytonidae; 3, Tetraonidae; 4, Turdidae; 5, Sturnidae; 6, Hirundinidae; 7, Motacillidae; 8, Corvidae; 9, Anatidae; 10, Muscicapidae; 11, Ciconiidae; 12, Fringillidae; 13, Columbidae; 14, Sylviidae; 15, Ardeidae; 16, Scolopacidae; 17, Strigidae; 18, Emberizidae; 19, Phalacrocoracidae; 20, Charadriidae; 21, Accipitridae; 22, Passeridae; 23, Falconidae; 24, Rallidae; 25, Paridae; 26, Pandionidae; 27, Gaviidae, 28, Recurvirostridae; 29, Sulidae; 30, Haematopodidae; 31, Laridae; 32, Stercorariidae; 33, Alaudidae; 34, Alcidae; 35, Sternidae; 36, Procellariidae; 37, Apodidae and 38, Hydrobatidae.

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Observed links between metabolism and POL
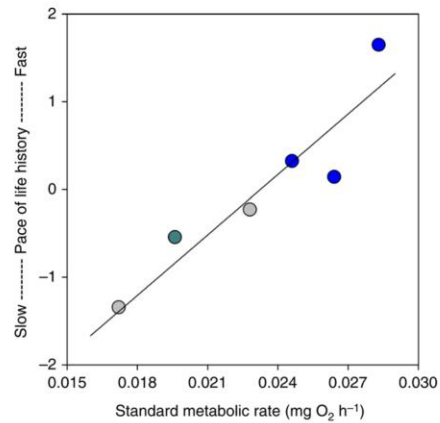
Auer et al. 2018. *Nature Com* 9, 14

A generalized POL syndrome?

	pace of life	
slow	◄──────►	fast

	life history	
long life	◄────────►	short life
delayed reproduction	◄────────►	precocious reproduction
low growth rate	◄────────►	high growth rate

	behaviour	
philopatry	◄────────►	high dispersal
high level of parental care	◄────────►	low level of parental care
low aggressiveness	◄────────►	high aggressiveness
shy	◄────────►	bold
thorough exploration	◄────────►	superficial explorer
low activity	◄────────►	high activity
high sociability	◄────────►	low sociability

|	physiology	
high HPA axis reactivity	◄────────►	low HPA axis reactivity
low sympathetic system reactivity	◄────────►	high sympathetic system reactivity
high parasympathetic system reactivity	◄────────►	low parasympathetic system reactivity
low metabolism	◄────────►	high metabolism
low sensitivity to oxidative stress	◄────────►	high sensitivity to oxidative stress
high immune response	◄────────►	low immune response

Réale et al. 2010. *Phil Trans Roy Soc B* 365(1560), 4051-4063

Schematic of the potential integration of different traits along a pace-of-life continuum. Double arrows illustrate presumed continuous variation in life-history strategies among individuals in a population, and its assumed relationship with personality and physiological traits.

Links to behaviour are less supported by data.
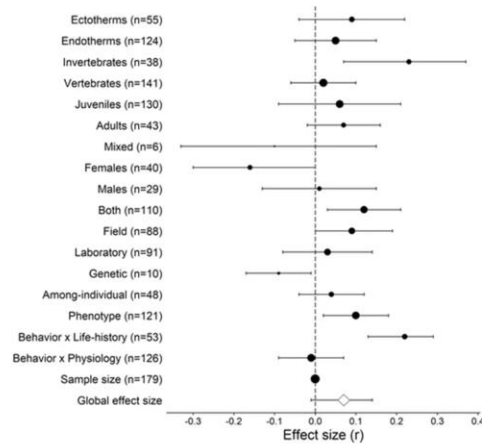
Royauté et al. 2018. *Behav Ecol Sociobiol* 72, 64

Forest plot of estimated effect sizes (*r* ± 95% CI) for all moderator categories based on moderator contrasts. Positive values indicate stronger support for the pace-of-life hypothesis. The effect size and confidence interval from the intercept only model (white diamond) indicates whether there is an overall support for the pace-of-life hypothesis. Point size is proportional to the sample size in the dataset

2.

A central debate in life-history evolution

"The general theoretical problem is to predict which combinations of traits will evolve in organisms living in specified circumstances."

Stearns, 1977

EB

Diverse approaches

Optimality reasoning

Calculate which combination of traits maximise an estimate of fitness:

- Life-time reproductive success
- Malthusian/intrisic rate of increase
- Reproductive value (relative to other genotypes)

Evolutionary models

Explicitely model evolution

- Variant invasion models
- Demo-genetic models

What differences would you expect?

Brommer 2000. *Biol Rev Cambridge Phil Soc* 75(3), 377-404

Predictability and density-dependence...

Density-dependent processes
Predictable environment

Selective pressures

Density-independent processes
Unpredictable environment

CHARACTERISTICS OF K-SELECTED AND r-SELECTED SPECIES

K-selected equilibrium species

r-selected opportunist species

population size (vs time): K

population size (vs time): r

population size:
- limited by carrying capacity (K)
- density dependent
- relatively stable

organisms:
- larger, long lived
- produce fewer offspring
- provide greater care for offspring

population size:
- limited by reproductive rate (r)
- density independent
- relatively unstable

organisms:
- smaller, short-lived
- produce many offspring
- provide no care for offspring

Predictability and density-dependence…

Wright et al. 2019. *Biol Rev* 94(1), 230-247

A simple hypothetical representation of a pace-of-life continuum in life-history variation across species or populations. In (A) reproductive rates (e.g. per breeding attempt) decline in all types more-or-less equally (for simplicity) with population density (N); with (B) subsequent negative effects on lifespan ofthese different type-specific reproductive rates mediated by differential effects ofN; and (C) the resultant pace of life (POL) negative trade-off between (current) reproductive rate and (future) lifespan. Predicted lines are shown for fast (orange), medium (brown) and slow (green) types, with coloured circles indicating phenotypic values (filled to indicate values of highest fitness). In (D) Malthusian fitness is shown as a function ofN for only the fast-selected and slow-selected types. Fast types have higher intrinsic reproduction (high r0), but suffer from more density-dependent effects (γfast), giving them greater fitness (r0-γN) at lower mean population densities (μlow). Slow types have lower intrinsic reproduction (low r0), but fewer density-dependent effects (γslow), giving them higher total fitness at higher mean population densities (μhigh) closer to the population carrying capacity (K). See text for further explanation and Engen, Lande & Sæther (2013).

...or age-related mortality processes?
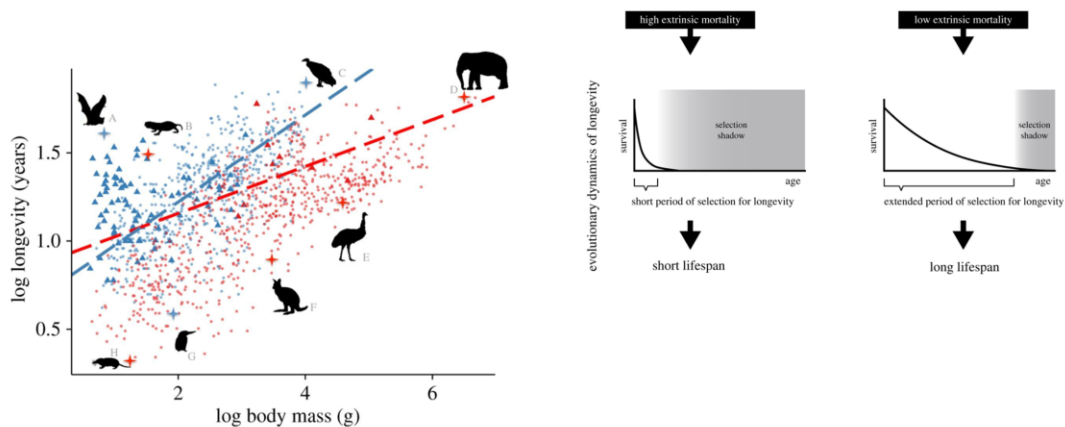
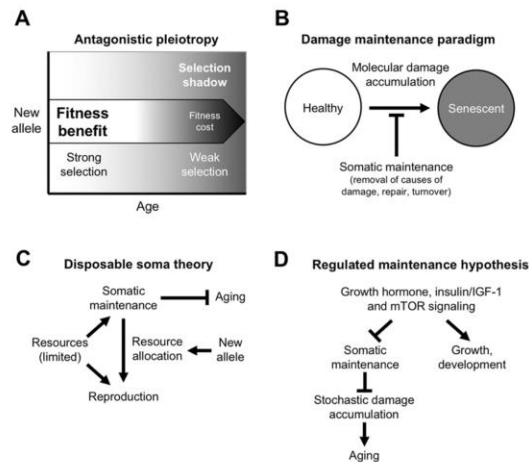Healy et al. 2014. *Phil Trans R Soc B* 281(1784), 20140298   Tasaki et al. 2021. *Phil Trans R Soc B* 376(1823), 20190740   13

Left: Relationships between body mass and maximum lifespan in birds and mammals. Silhouettes highlight a selection of species with much longer or shorter lifespans than expected given their body size. These species are (A) *Myotis brandtii*, Brandt's bat; (B) *Heterocephalus glaber*, naked mole rat; (C) *Vultur gryphus,* Andean condor; (D) *Loxodonta Africana*, African elephant; (E) *Dromaius novaehollandiae*, emu; (F) *Dorcopsulus macleayi*, Papuan forest-wallaby; (G) *Ceryle rudis,* pied kingfisher and (H) *Myosorex varius*, forest shrew. Blue points and line represent volant birds and mammals (n = 662; slope = 0.25, intercept = 0.73). Red points and line represent non-volant birds and mammals (n = 706; slope = 0.13, intercept = 0.89). Blue triangles represent bat species and red triangles represent non-volant bird species. Estimates of slopes and intercepts represent back transformed values from mean centred values given in table 1.

Right: Evolutionary dynamics of longevity in short-lived solitary insects (left) and long-lived termite reproductives (right). The black solid curves indicate survival levels in the wild, and the grey areas the 'selection shadows'. The reduced extrinsic mortality of termite reproductives extends the period available for longevity selection.

Ultimate and proximate mechanisms of aging (traditional interpretations). **A**, Antagonistic pleiotropy. A new allele that causes a fitness benefit in early life but a fitness cost (e.g. increased pathology) in later life may cause a net benefit in overall fitness due to the selection shadow (Williams, 1957). **B**, The damage/maintenance paradigm. Aging is caused by accumulation of stochastic molecular damage, whose levels can be controlled by somatic maintenance functions. **C**, The disposable soma theory. Investment of resources in reproduction more than somatic maintenance can increase fitness due to the selection shadow (Kirkwood, 1977). Genes promoting such resource allocation will exhibit antagonistic pleiotropy (Partridge and Gems, 2002a). **D**, Regulation of aging by nutrient pathways. Traditional view based on damage/maintenance paradigm (Partridge and Gems, 2006). The hyperfunction model argues that it is in fact the growth, development function that plays the main role in promoting aging.

Still a live debate!

Opinion

Evolutionary Ecology of Senescence and a Reassessment of Williams' 'Extrinsic Mortality' Hypothesis

Senescence: why and where selection gradients might not decline with age

Mark Roper ✉, Pol Capdevila and Roberto Salguero-Gómez

The selection force weakens with age because ageing evolves and not vice versa

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Alternative explanations to LH syndromes

Selection

Correlational selection should favor some combinations of behavioral/physiological and life history traits.

Constraints

The correlation between traits provides no fitness benefit but is rather the results of constraints to their independent expression.

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3.
Why integrate physiology with LH theory?

Beyond trade-offs: the importance of resource acquisition
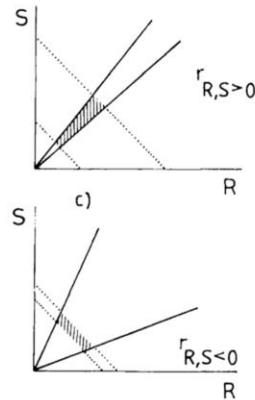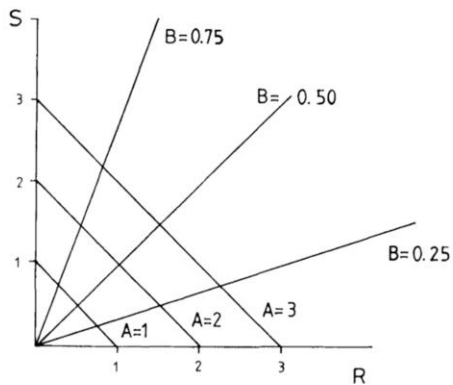
van Noordwijk & de Jong 1986. *Am Nat* 128(1), 137-142

An illustration of the model: a, the components A for the total investment and B for the allocation between life history traits R and S; b, the variation in A is large and the variation in B is small, such that R is positively correlated with S (observations lie in the hatched area); c, the opposite case.

... and its interplay with allocation
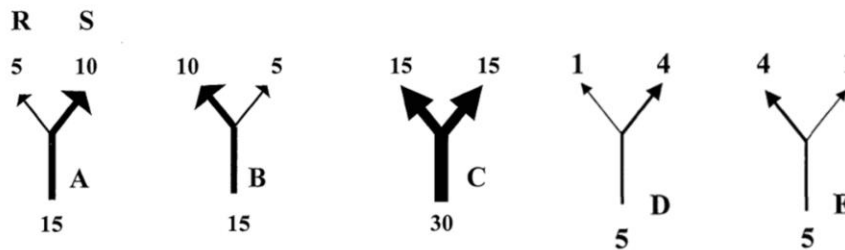
Zera & Harshman 2001. *Ann Rev Ecol Syst* 32, 95-126

Diagrammatic representation of trade-offs. Each "Y allocation tree" illustrates the amount of resource input (acquisition; number at the base) and the pattern of resource allocation (numbers at the tips of the branches) for a particular phenotype or genotype. R denotes allocation to reproduction, while S denotes allocation to soma. In trees A–E, maximal allocation to (maximal physiological cost of) R or S is 15 resource units. Trees A and B illustrate a standard trade-off (differential allocation of a limiting internal resource). Relative to trees A and B, tree C illustrates the obviating effect of increased resource in- put on a trade-off (resource input matches physiological costs of both traits), while trees D and E illustrate the exacerbating effect of decreased nutrient input on a trade-off. Trees A and B, relative to D and E, illustrate plasticity of a resource-based trade-off.

Generally, environmental effect on LH trait expression...
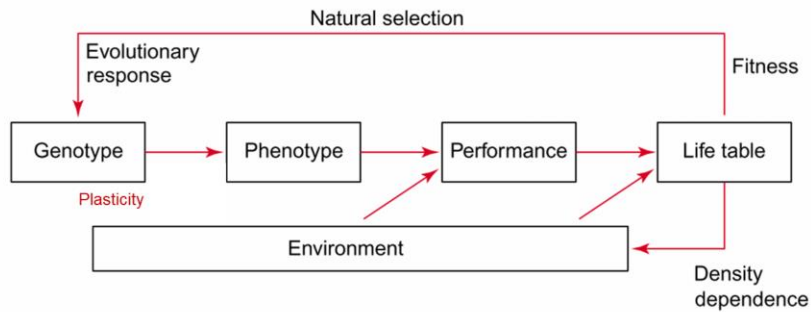
Ricklefs & Wikelski 2002. *TREE* 17(10), 462-468

...is poorly accounted for in LH models
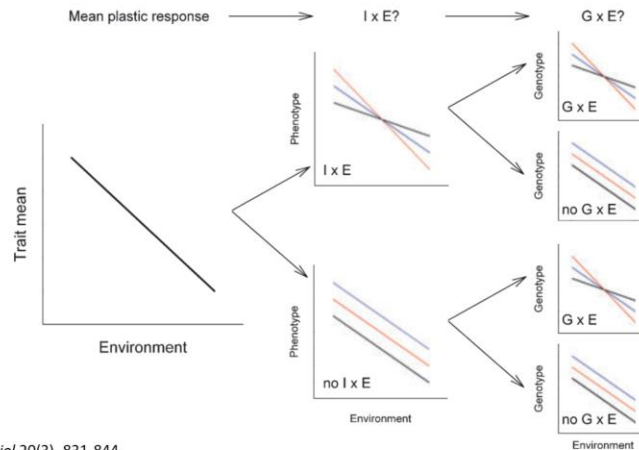
Nussey et al. 2007. *J Evol Biol* 20(3), 831-844

Three different levels of analysis are involved in understanding individual plasticity in labile life history traits. Cross-sectional studies examine population-level responses to the environment (left most graph), which can be underpinned by variation between individuals in their plastic response to the environment (I · E) or not. The presence or absence of I · E can itself be accompanied by underlying variation in plasticity at the additive genetic level (G · E) or not.
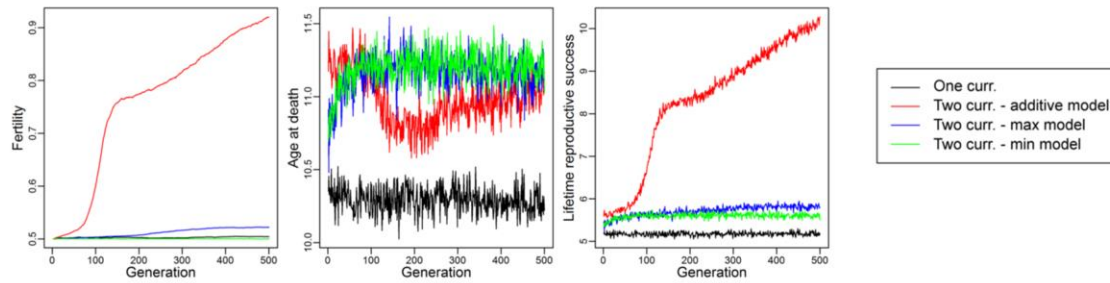
Different resources generate different trade-offs...
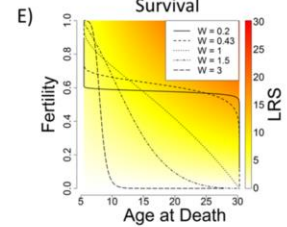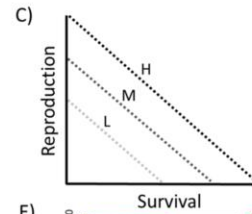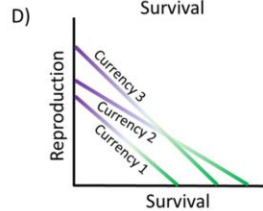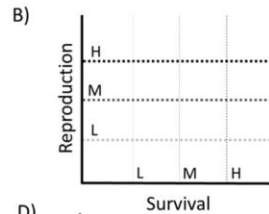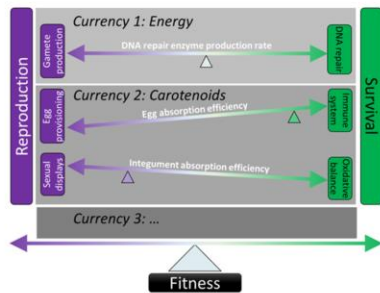
Cohen et al. 2017 *Plos ONE 12(12),* e0189124

...with large consequences on evolutionary outcomes
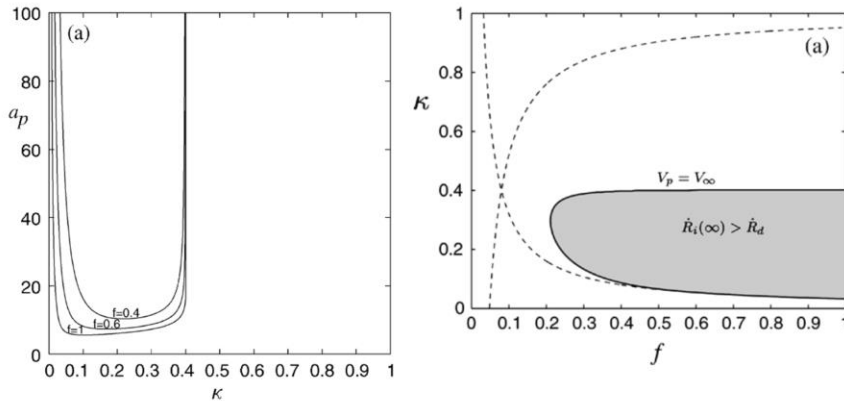

Cohen et al. 2017 *Plos ONE 12(12),* e0189124

4.

A few examples of mingling DEB and LH theory

DEB

Provide a null model for possible variation in LHT

Lika & Kooijman 2003. *Bull Math Biol* 65, 809–834

Left: The age at puberty a_p (a) (and length at puberty $V^{1/3}_p$ (b, cropped)) as functions of the partition coefficient κ, for different food levels.
Right: The dashed curves represent boundaries for which the neonate just can pay somatic and maturity maintenance costs. The grey areas indicate combination of values for the scaled functional response f and the partitioning fraction κ, for which the organism is reproductively active; size at puberty equals the ultimate size at its border (solid lines).
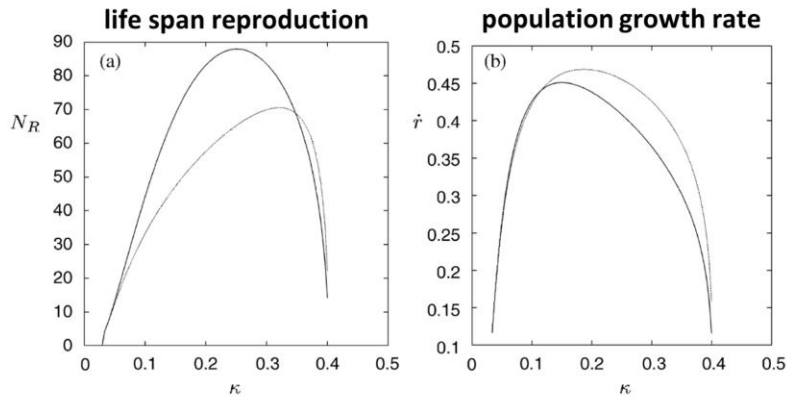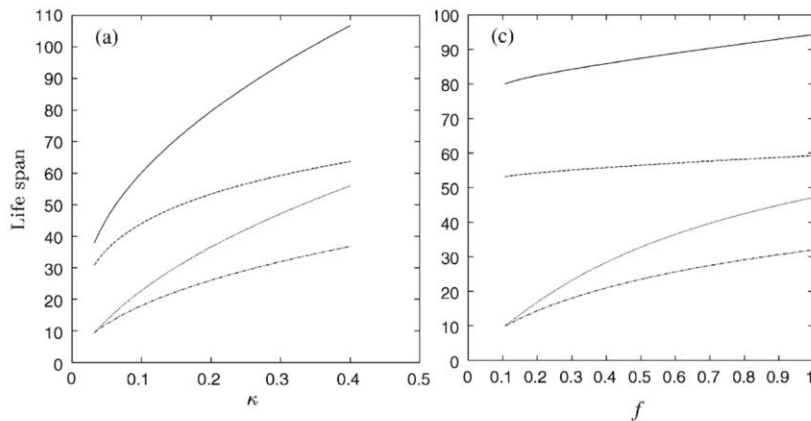
Figure 6. The life span reproduction *NR* (a, c) and the population growth rate ˙ *r* (b, d) of the indeterminate (solid) and the determinate (dotted) animals as a function of the partitioning fraction *κ* at abundant food *(f =* 1*).* Upper panel (a, b): constant mortality (*m˙* 0 = 0.2, *μ* = 0). Lower panel (c, d): size-dependent mortality (*m˙* 0 = 0.5, *μ* = 0.1).

Define the shape of reaction norms

Lika & Kooijman 2003. *Bull Math Biol* 65, 809–834

The life span of the indeterminate animal as a function of the partitioning fraction κ at abundant food (f = 1) (a, b) and as a function of the functional response f with κ = 0.3 (c, d). The curves represent different mortality rates: aging only (—), aging and size-independent mortality (- - -, $\dot{m}_0$ = 0.01, μ = 0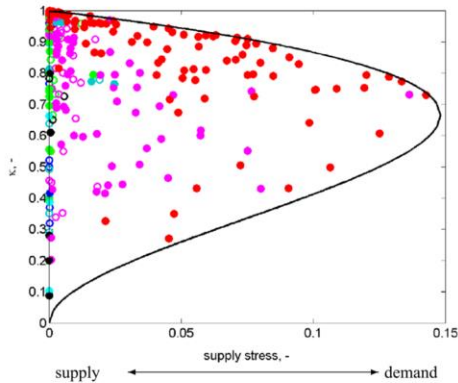), aging and size-dependent mortality ($\cdot\cdot\cdot$, $\dot{m}_0$ = 0.1, μ = 1; - · -, $\dot{m}_0$ = 0.1, μ = 0.7).
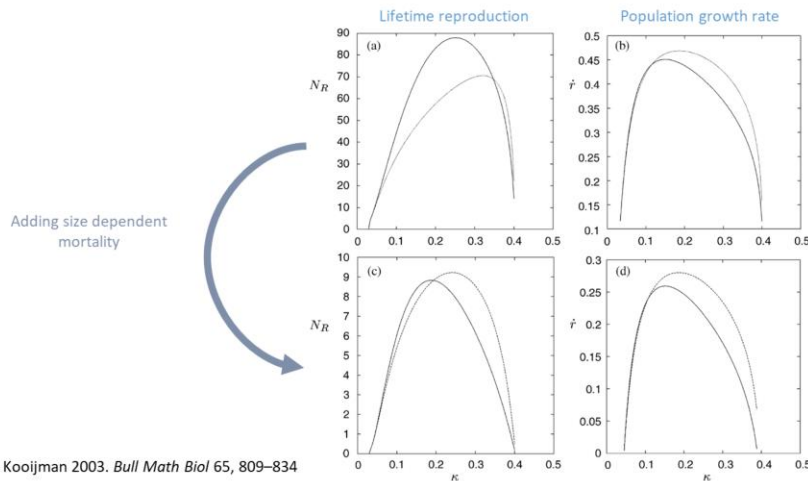
The life span reproduction *NR* (a, c) and the population growth rate $\dot{r}$ (b, d) of the indeterminate (solid) and the determinate (dotted) animals as a function of the partitioning fraction κ at abundant food *(f = 1)*. Upper panel (a, b): constant mortality ($\dot{m}_0 = 0.2$, $\mu = 0$). Lower panel (c, d): size-dependent mortality ($\dot{m}_0 = 0.5$, $\mu = 0.1$).

Explaining broad life-history patterns

| Supply	Demand
Eat what is available	Eat what is needed
Large half saturation coefficient	Small half saturation coefficient
Rather passive, simple behaviour	Rather active, complex behaviour
Sensors less developed	Sensors well developed
Can handle large range of intake	Can handle small range of intake
Low peak metabolic rate	High peak metabolic rate
Open circulatory system	Closed circulatory system
Iso- & centro-lecithal eggs	A- & telo-lecithal eggs
Typically ectothermic	Typically endothermic
Reserve density varies strongly	Reserve density varies little
Large range of ultimate sizes	Small range of ultimate sizes
Survives some shrinking well	Survives shrinking badly
Survives rejuvenation well	Survives rejuvenation poorly
Energetic birth control	Behavioural birth control
No upregulation for reproduction	Upregulation for reproduction
No acceleration of ageing	Acceleration of ageing
Evolutionary original	Evolved from supply systems
Has demand components	Has supply components
(maintenance)	(some food must be available)

Lika et al. 2014. *J Theor Biol* 354, 35-47

Allocation fraction κ as a function of supply stress ss for over 300 species of the add_my_pet collection. It can only take values between the two black curves and the maximum supply stress is 4/27. Colours indicate high-level taxa: blue for radiata, brown for bilateria, turquoise for platyzoa, dark turquoise for lophotrocho- zoa, green for ecdysozoa, black for invertebrate deuterostomes, magenta for ectothermic vertebrata and red for endothermic vertebrata. Open symbols indicate acceleration.

Explaining broad life-history patterns
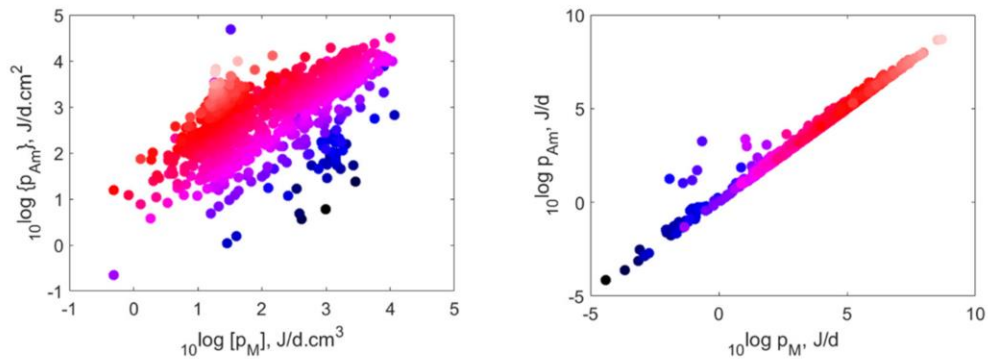
Augustine et al. 2019. *J Sea Research* 143, 18-26

Specific assimilation as a function of specific somatic maintenance at 20 °C (left) and the absolute ones (right), where the colors from black to white, via blue and red, are proportional to log ultimate length. Some insects (partly hidden in the cloud left, but more exposed on the plot right) behave as outliers, which is no surprise, since their ultimate length does not correspond with a balance between assimilation and maintenance. The steepest colour-gradient in the left panel, which indicates ultimate length, is from lower-right to upper-left.

5.
Other perspectives?
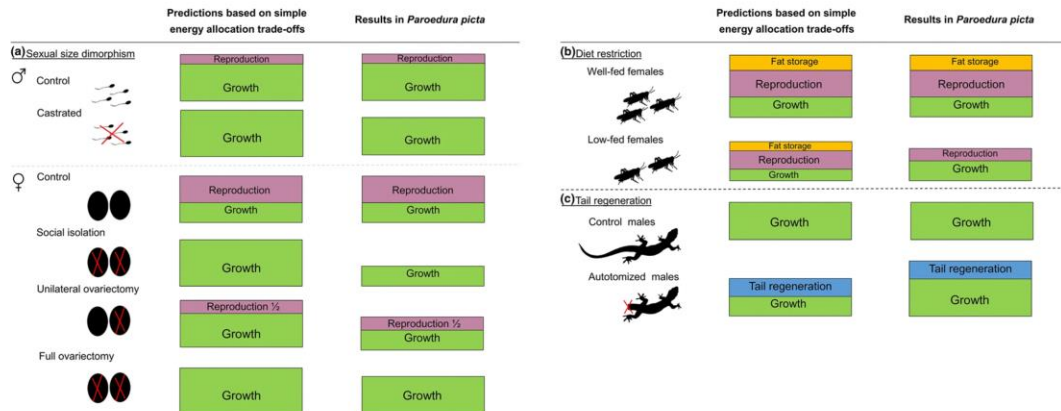
Meter et al. 2020. *Evol Ecol* 34, 469–481

Summary of the results from case studies in *Paroedura picta* that show that growth does not seem to be influenced by variations in allocable energy. **a** The "reproductive cost" hypothesis predicts that removal of the costs of reproduction should lead to higher allocation to growth in both sexes. However, castrated males attained the same size as non-castrated control males (Starostová et al. 2013). Socially isolated non-reproducing females and females with highly decreased allocation to reproduction due to unilateral ovariectomy maintained similar body size (SVL) and growth rate as control regularly egg-laying females (Kubička et al. 2017). Only full ovariectomy led to higher allocation to structural growth in females, which indicates that ovarian hormones, not directly allocable energy, controls ontogeny of sexual size dimorphism via negative effect on growth in females (Kubička et al. 2017). **b** In the case of food restriction, we expected that restricted diet would lead to reduced allocation to reproduction, growth and fat storage. However, structural growth was not affected by food limitations, which reduced only allocation to reproduction and fat storage (Kubička and Kratochvíl 2009). **c** The simple energy allocation trade-off predicts that growth should be decreased in the lizards during tail regeneration. Nevertheless, geckos with and without growth regeneration had similar growth rates and reached

similar structural body size (Starostová et al. 2017).

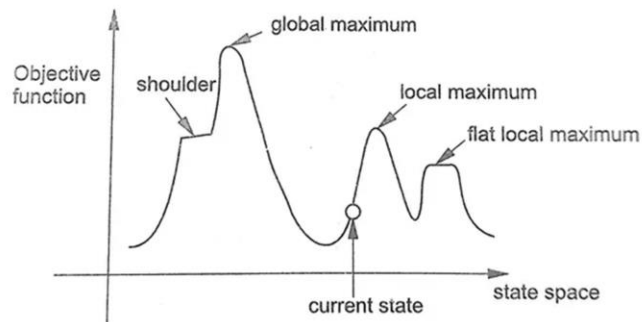# Investigate historical constraints and "hill climbing"

Fig: Hill Climbing

To take away!

✓ Different approaches to fitness/selection can yield different answers.

✓ Historically, the focus was on selective forces, while crudely accounting for constraints through (often static) « trade-offs ».

✓ Mechanistic models have the potential to truly investigate the interplay between selective forces and contraints.

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Thank you for your attention

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