DEB 2025

DEB meta theory: patterns in DEB par values

Bas Kooijman

salm.kooijman@gmail.com

A-Life, VU University Amsterdam

VU VRIJE UNIVERSITEIT AMSTERDAM

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University of Crete, Heraklion, Greece

deb2025.sciencesconf.org

Recognized patterns in DEB par values

- Metabolic acceleration
- Physical co-variation rules
- Waste to hurry
- Supply-demand spectra
- Altricial-precocial spectra
- Other relationships

Page DEBpapers on the AmP site
has a section on pattern papers
Github has SI for recent versions

Direct explanations for Kleiber's law are problematic

- Respiration has contributions from several metabolic processes

  Sousa et al 2008 From empirical patterns to theory:
  A formal metabolic theory of life. *Phil. Trans. R. Soc. B*, **363**:2453–2464.

- Body size is an emergent property of metabolism

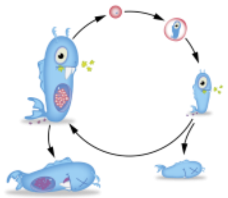
  Lika et al 2019 Body size as emergent property of metabolism. *J. Sea Res.*, **143**:8–17

- Allometric functions might be nice for description,
  but not for understanding

  Kooijman 2018 Models in stress research. *Ecological Complexity*, **34**:161–177

Implication: respiration, interpreted as THE metabolic rate, cannot be used to explain other traits

Kleiber 1932 Body size and metabolism. *Hilgardia*, **6**: 315-353
Rubner 1883 Uber den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Z. Biol.*, **19**:535–562



Physical co-variation rules for parameter values

- DEB parameters have a clear physical interpretation (fact)
- they are either intensive or extensive (fact)
- appropriate ratios of extensive parameters are intensive (fact)
- intensive parameters are equal among species (assumption)

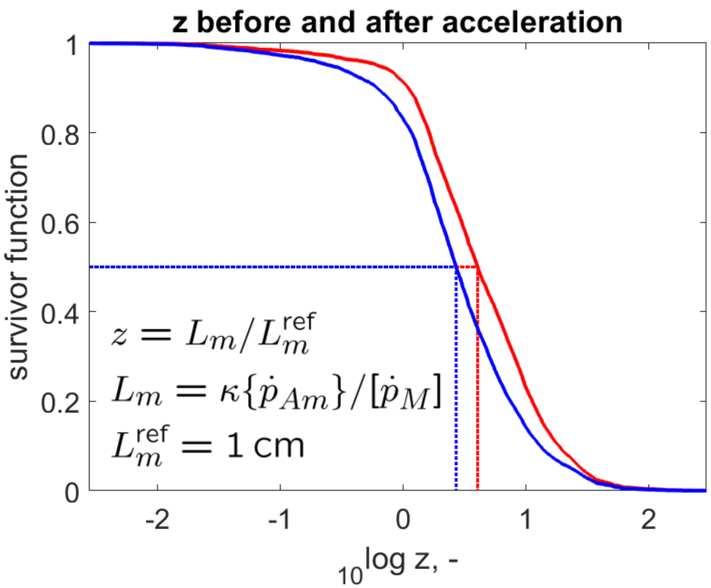
Implication:

- this links all parameters, leaving just 1 degree of freedom for variation
- write any physiological trait as function of parameters
  (including e.g. max body weight, respiration)
- evaluate this trait (e.g. respiration) as function of e.g. max body weight
- observe: no empirical argument is involved

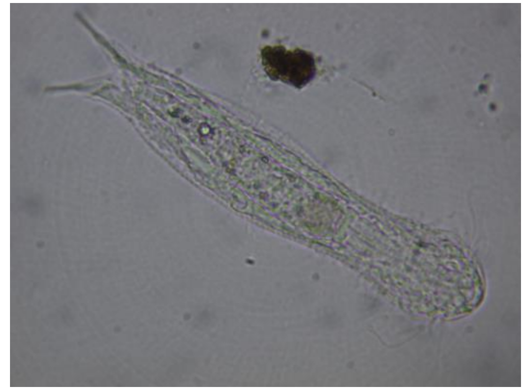
- adaptations cause deviations from the assumption that
  intensive parameters are equal among species

Kooijman 1986 Energy budgets can explain body size scaling relations *J. Theor. Biol.* **121**: 269-282

Zoom factor



z is the value with which 1 cm must be multiplied to arrive at maximum structural length

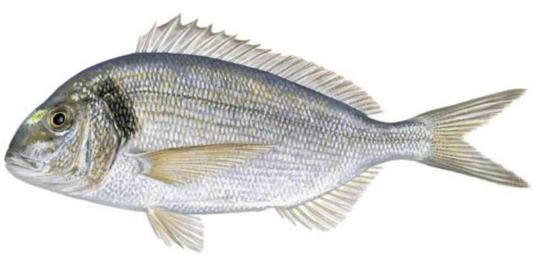


0.003 Aspidiophorus
8e-8 g

0.01 Brachionus plicatilis

0.04 Ferosagitta hispida

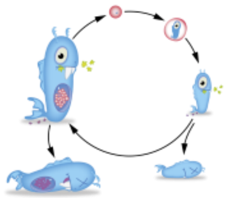
0.20 Pimephales promelas



1.25 Sparus aurata

77.3 Loxodonta africana

1.6e8 g
296 Balaenoptera musculus



Body size scaling

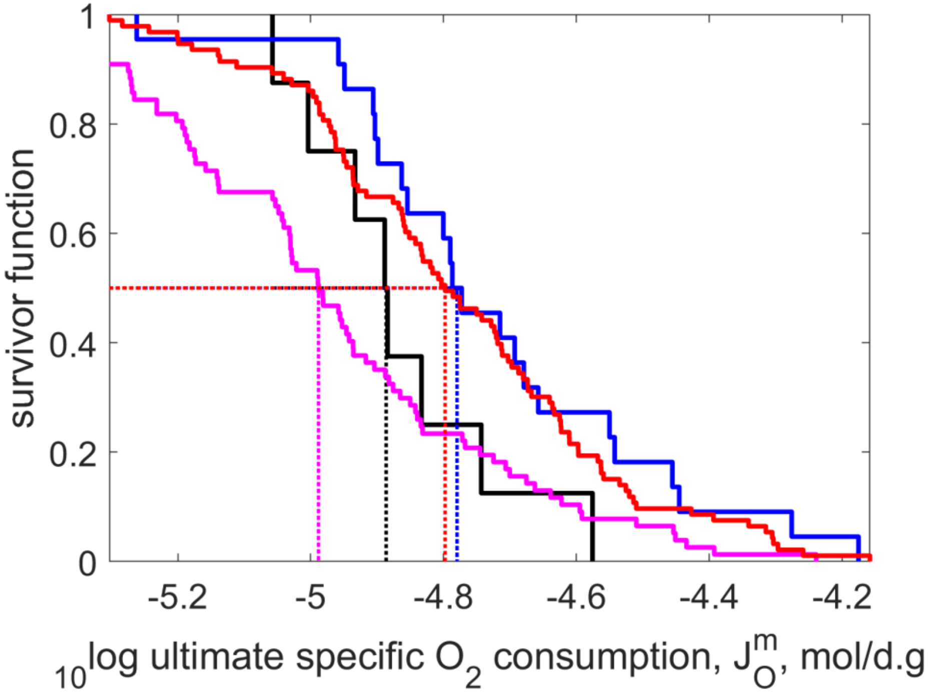
Intra-species: same parameters, different state variables
Inter-species: different parameters, ultimate body size
All cases: abundant food, constant temperature

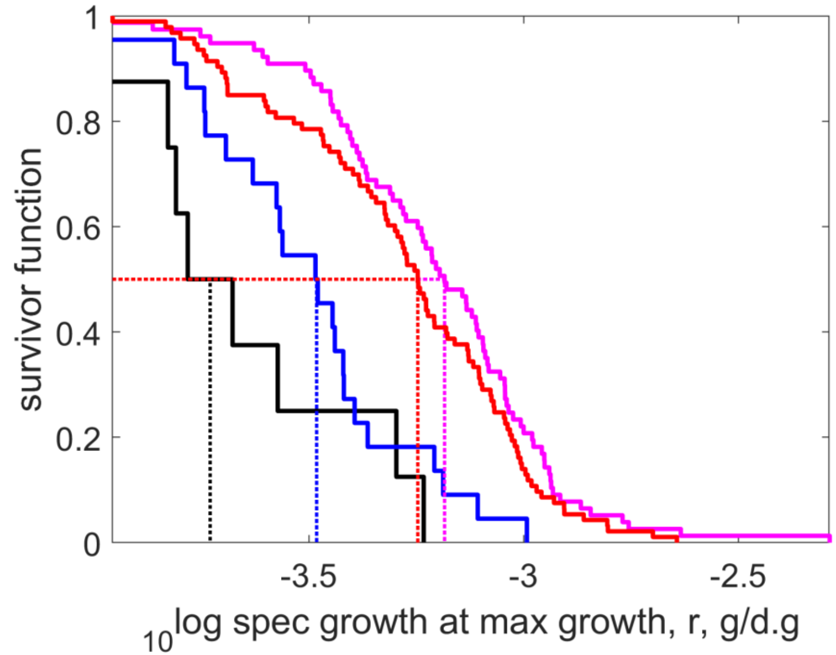
	intra-species	inter-species
som maint	$\propto L_T L^2 + L^3$	$\propto L_T L^2 + L^3$
growth	$\propto L_G L^2 - L^3$	0
$\frac{\text{reserve}}{\text{structure}}$	$\propto L^0$	$\propto L$
$\frac{\text{respiration}}{\text{weight}}$	$\propto \frac{L_s L^2 + L^3}{d_V L^3 + d_E L^3}$	$\propto \frac{L_T L^2 + L^3}{d_V L^3 + d'_E L^3}$
feeding	$\propto L^2$	$\propto L^2$
reproduction	$L_R L^2 + L^3$	$\propto L^{-1}$

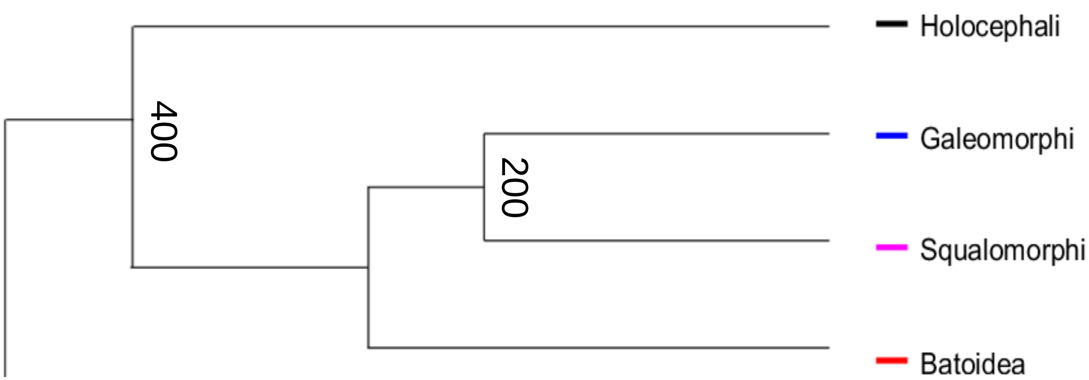
L	structural length
L_T,L_G,L_R,L_s	constant (dim: length)
d_V,d_E	specific density (struc, res)

Kooijman 1986
J Theor Biol
121: 269-282

Galeans ↔ squaleans







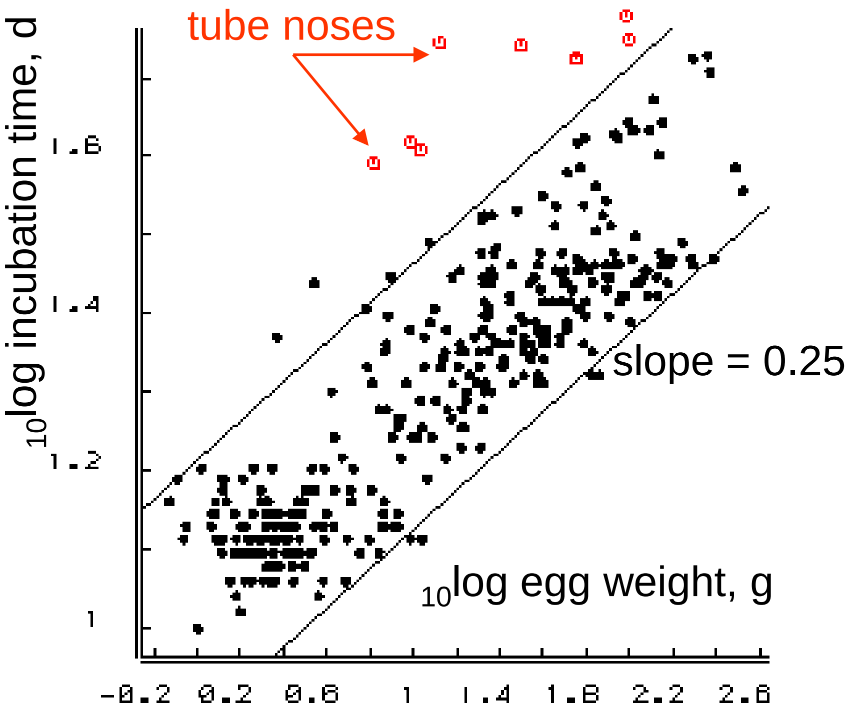
Although squaleans have the lowest specific respiration
they grow the fastest among the cartilaginous fish

Specific respiration is not necessarily a good predictor for other traits

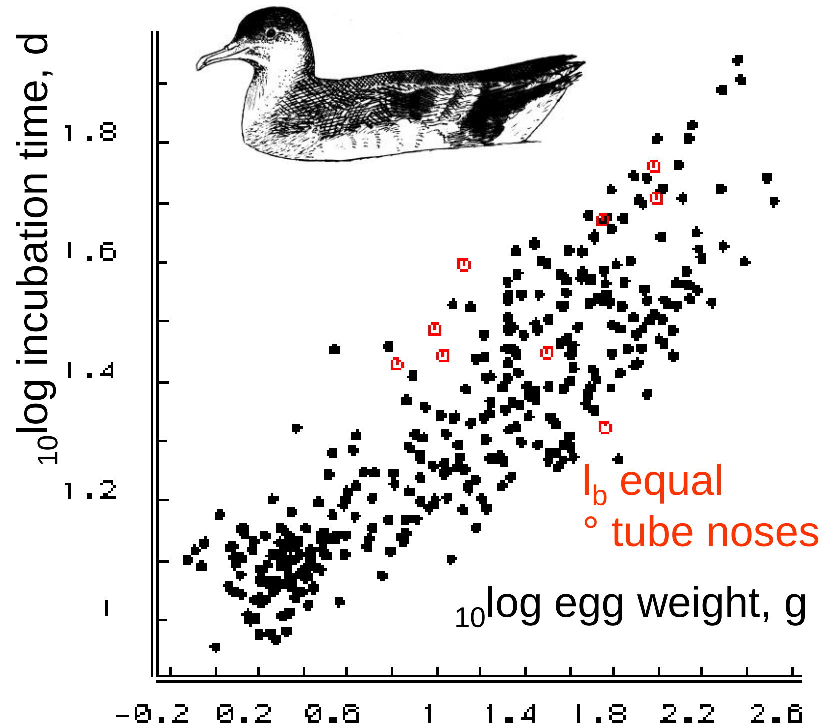
Augustine et al 2022
J Sea Res **185**: 102228

Incubation time

European birds



Data from Harrison 1975

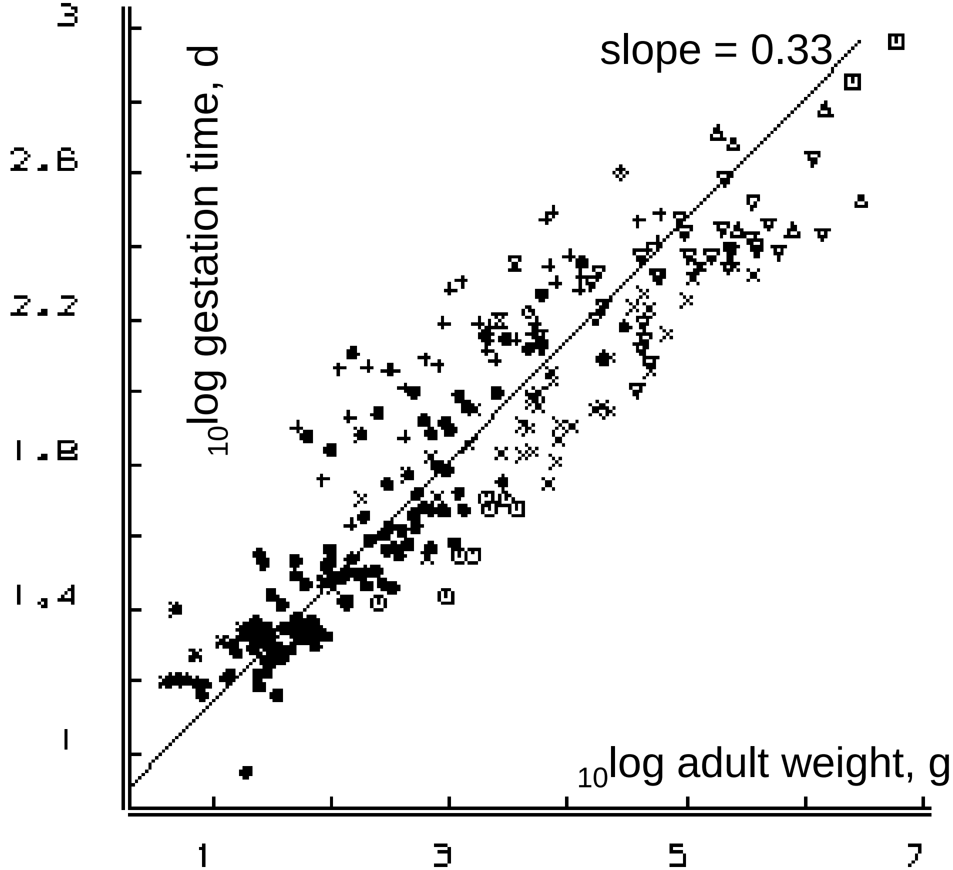


Incubation time $a_b \propto L_m$

Egg weight $E_0 \propto L_m^4$

$$a_b \propto E_0^{1/4}$$

Gestation time



Mammals

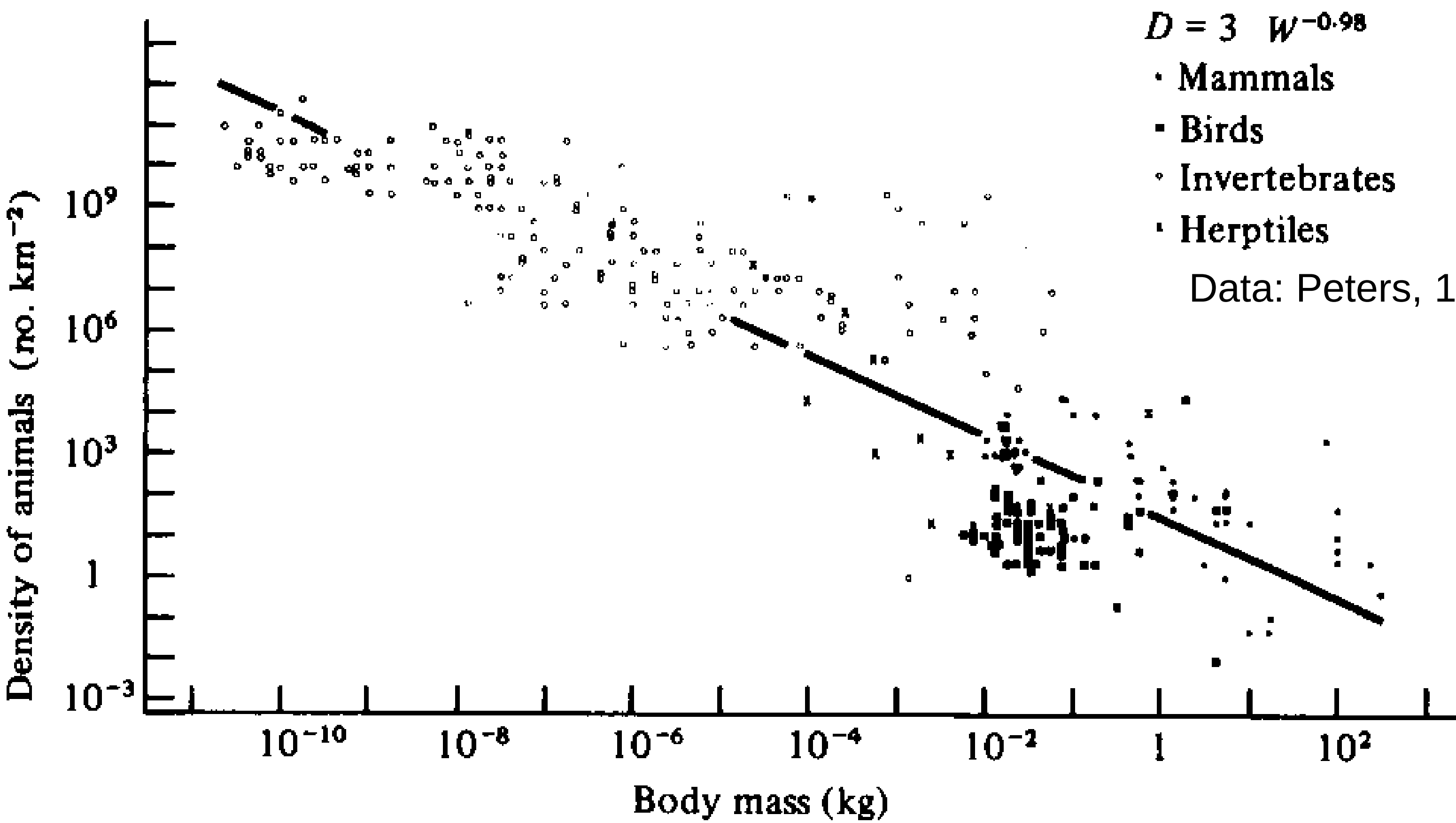
- * Insectivora
- + Primates
- ◊ Edentata
- ° Lagomorpha
- • Rodentia
- × Carnivora
- □ Proboscidea
- ⧖ Hyracoidea
- Δ Perissodactyla
- ∇ Artiodactyla

Data from Millar 1981

$$\text{gestation time} = \text{actual gestation time} \left(\frac{\text{adult weight}}{\text{birth weight}} \right)^{1/3} 0.396 \propto L_m$$

Kooijman 1986
J Theor Biol **121**: 269-282

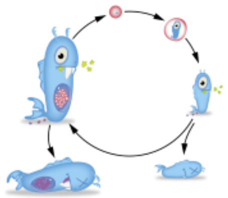
Abundance



feeding rate $\propto$ V
food production constant

$\Rightarrow$ Abundance $\propto V^{-1}$

Kooijman 1986
J Theor Biol
121: 269-282



Waste to hurry

- definition

  increase of $\{p_{Am}\}$ and $[p_M]$

- effect via κ-rule :

  ultimate structure remains small

  boosting of growth and reproduction

  increase of reserve capacity

- condition:

  food temporarily abundant (efficiency is not limiting)

  solution for starvation periods between blooms

  not available for large-bodied species

Futile cycles are well known
Qian & Beard 2006,
Stein & Blum 1978,
Steinberg 1963

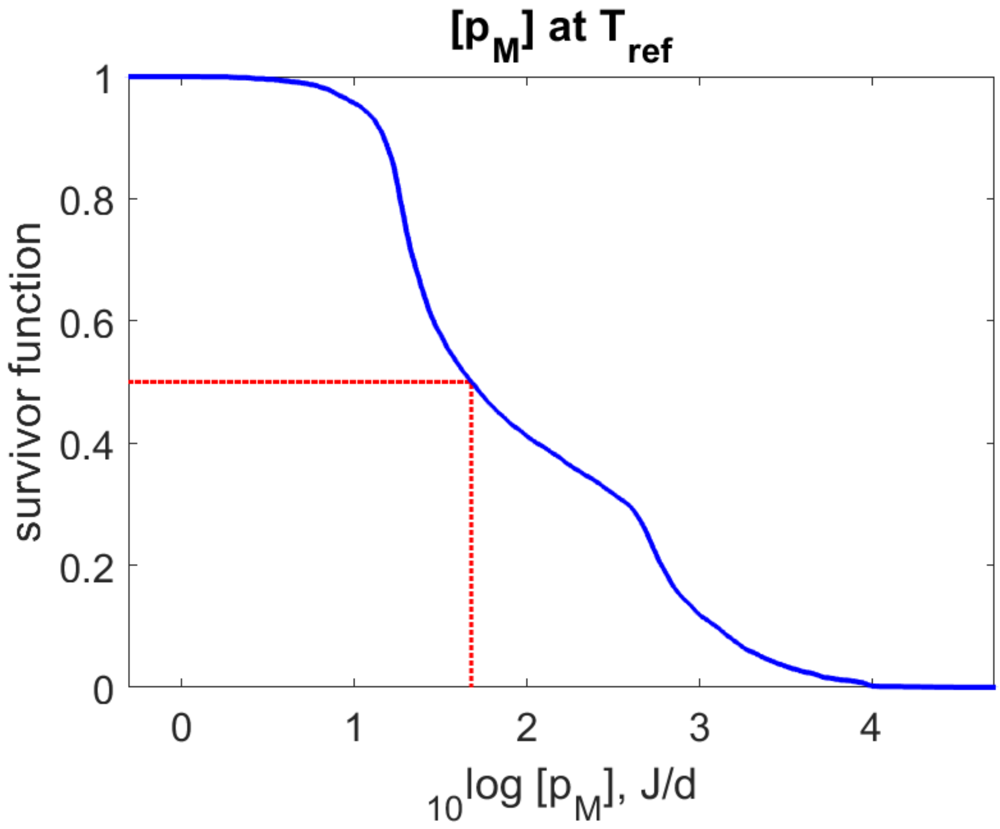
All species have the pathway
only function ATP→ADP+P

Reason remained a mystery
for biochemists

vBGR $r_B \propto [p_M]$

Kooijman 2013 Waste to hurry *Oikos* **122**: 348–357
Augustine et al 2019 Why big-bodied animal species cannot evolve a waste-to-hurry strategy
J Sea Res **143**: 1385-1101

Specific somatic maintenance

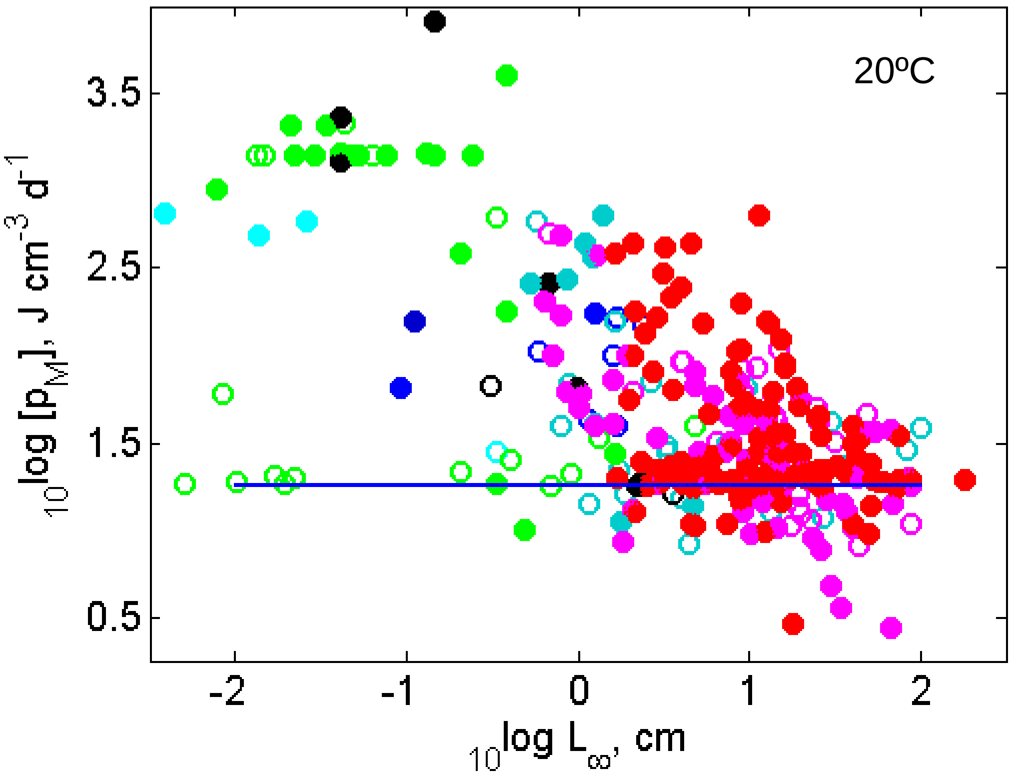


Typical value at 20 °C:
$[\dot{p}_M] = 18\,\mathrm{J\,d^{-1}cm^{-3}}$

The humps in the survivor function separate
the waste-to-hurry strategists from the rest.
$\dot{p}_M^\infty = [\dot{p}_M]^3 L_\infty^3$ follows a Weibull distribution

Waste to hurry

radiata
bilateria
platyzoa
lophotrochozoa
ecdysozoa
invertebrate deuterostomes
ectothermic vertebrata
endothermic vertebrata



$$L_m = \kappa\{\dot{p}_{Am}\}/[\dot{p}_M]$$

L_m	max structural length
κ	allocation fraction to soma
$\{\dot{p}_{am}\}$	max spec assimilation rate
$[\dot{p}_M]$	max spec somatic maintenance

Kooijman 2013
Oikos **122**: 348-357

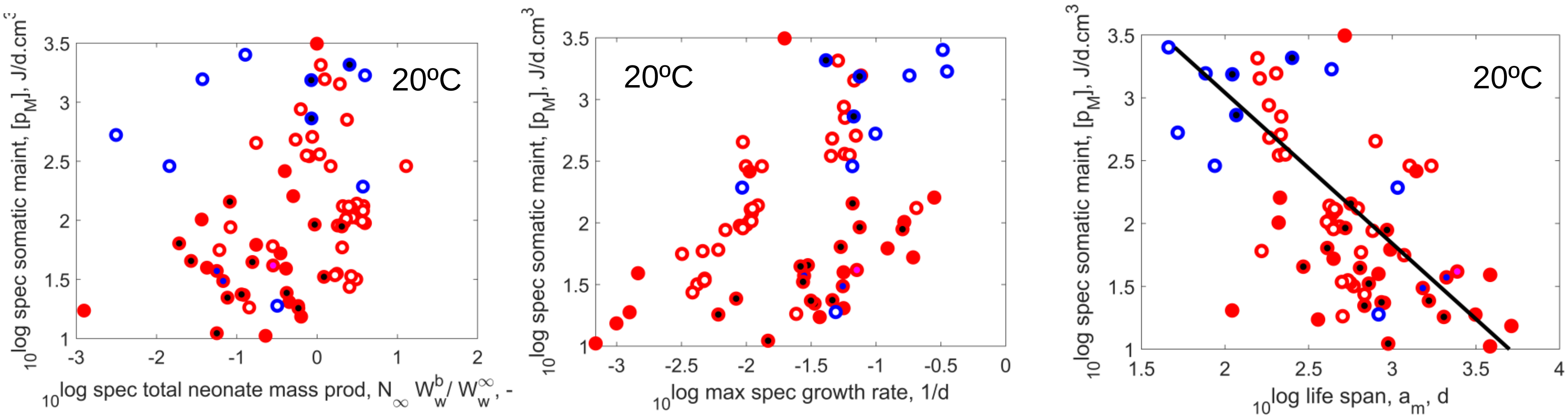
Exploiting blooming resources
requires blooming yourself

- high numerical response
- short life cycle
- small body size
- fast reproduction
- fast growth
- high feeding rate
- resting stages between blooms

κ-rule explains why
$[p_M]$ needs to be high

Ecosystem significance:
flux through basis food pyramid

Waste to hurry



Cyprinodontiformes

- Nothobranchiidae
- Rivulidae
- Fundulidae
- Goodeidae
- Valenciidae
- Cyprinodontidae
- Poeciliidae

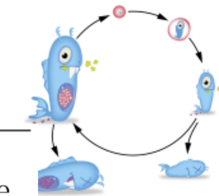
Valencia hispanica, Valencia toothcarp

For increasing spec som maintenance

- Life span decreases
- Max spec growth increases
- Reprod rate independent

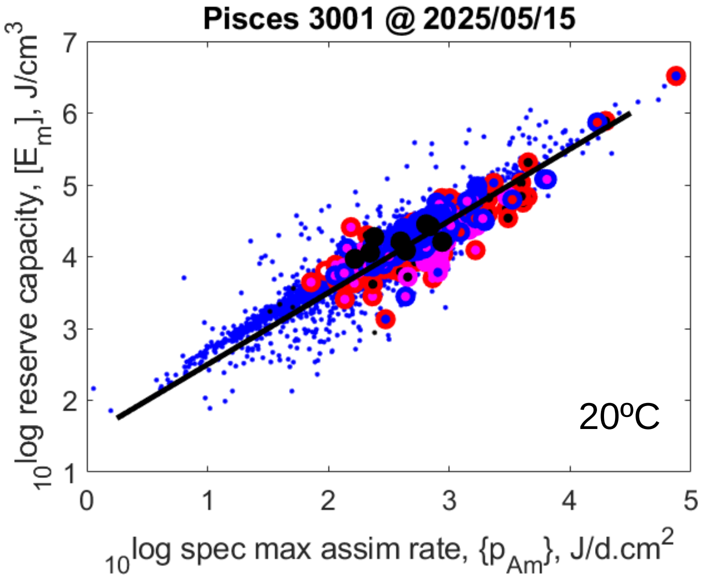
Lika et al 2022
Cons Physiol **10**: coac030

Interaction: physical co-variation rules - waste to hurry



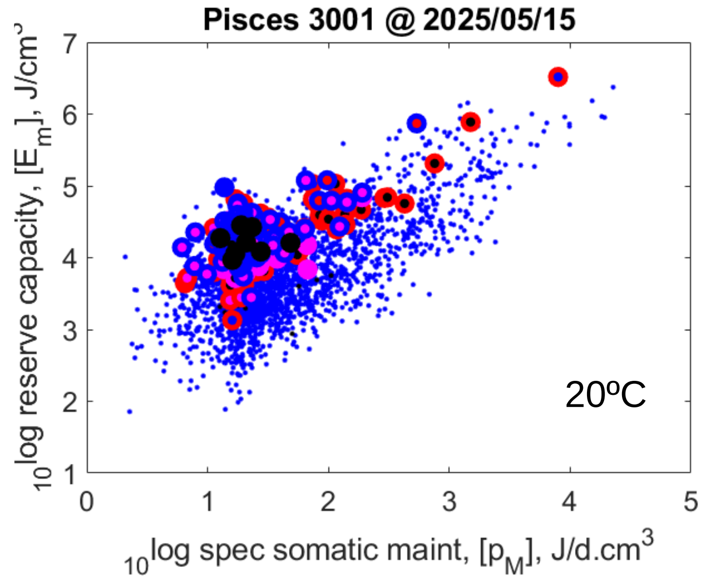
$$[E_m] = \{\dot{p}_{Am}\}/\dot{v}$$

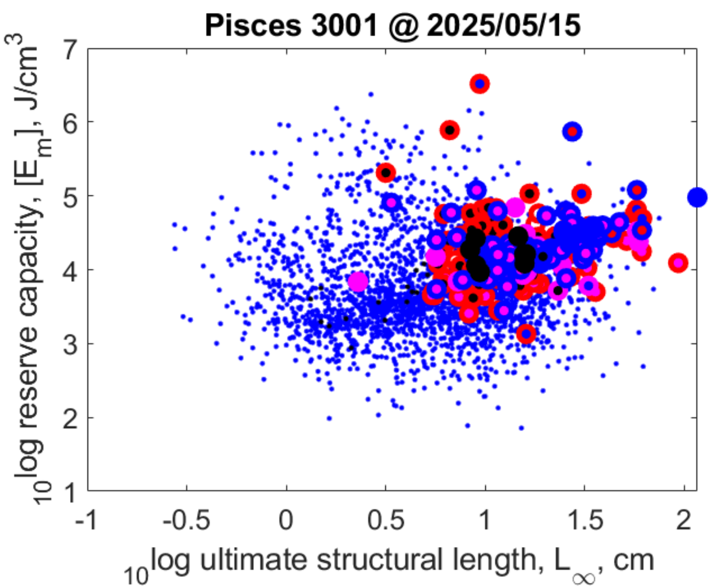
$\{\dot{p}_{Am}\}$	spec assimilation
$\dot{v}$	energy conductance



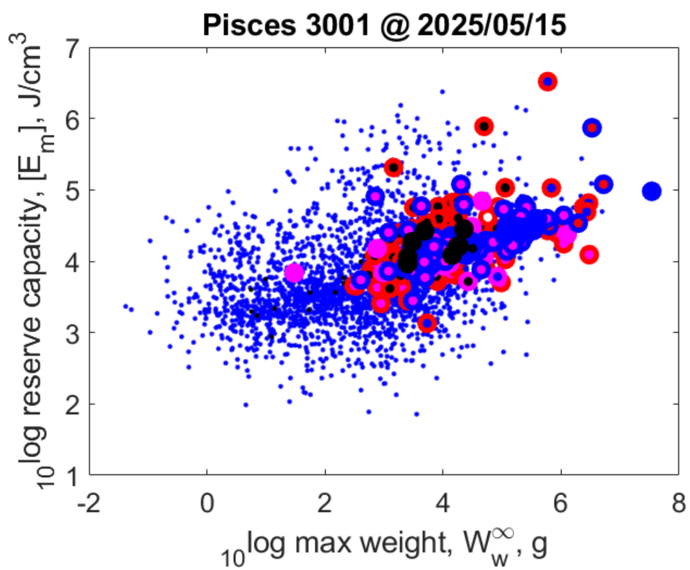
Pisces

- Chimaeriformes
- Heterodontiformes
- Orectolobiformes
- Carcharhiniformes
- Lamniformes
- Squatiniformes
- Pristiophoriformes
- Squaliformes
- Hexanchiformes
- Rajiformes
- Rhinopristiformes
- Myliobatiformes
- Torpediniformes
- Cyclostomata
- Actinopterygii
- Actinistia
- Dipnoi





Lika et al 2022
Cons Physiol **10**



Supply ↔ demand spectrum

Quantifier: supply stress $s_s = \frac{p_J p_M^2}{p_A^3}$

Can take values on (0,4/27)

Demand stress = 4/27 – supply stress

Derivation: puberty must be reachable at constant food

Spin off from research on bijection data *vs* parameters

Boundaries of data and parameter space

Used in filtering par combinations during estimation

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

Snakelocks anemone, *Anemonia viridis.* Bretagne 1981

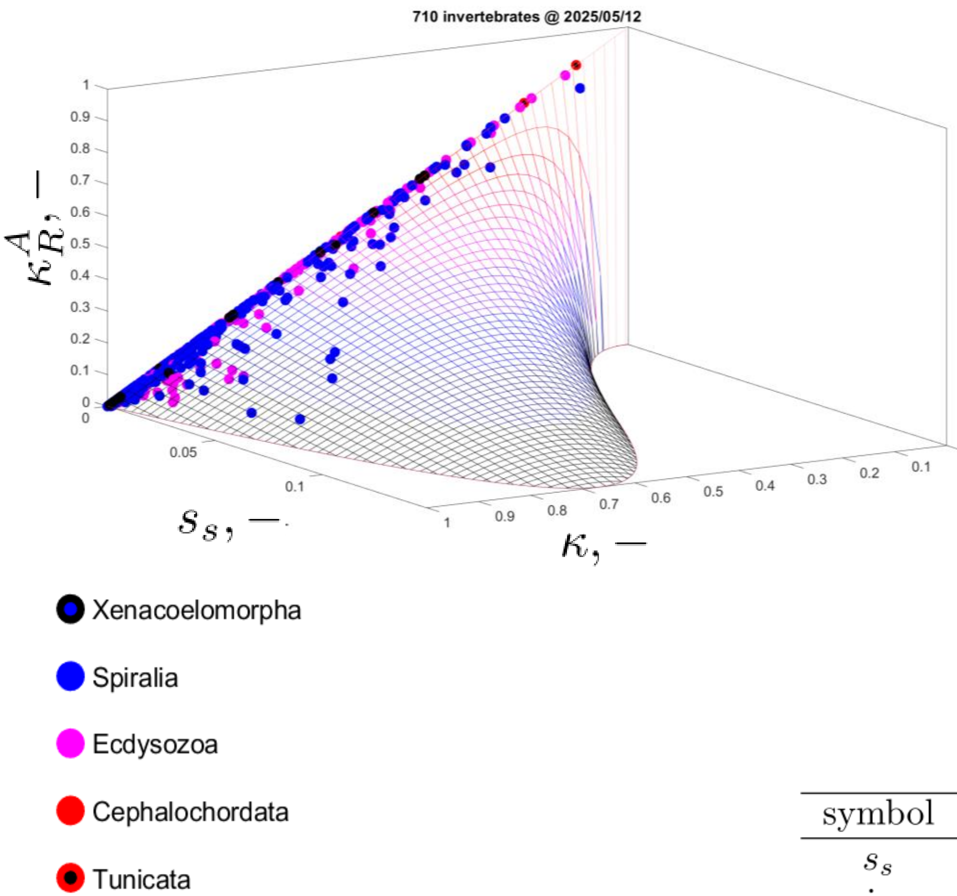
Can reversibly shrink to tiny size during starvation

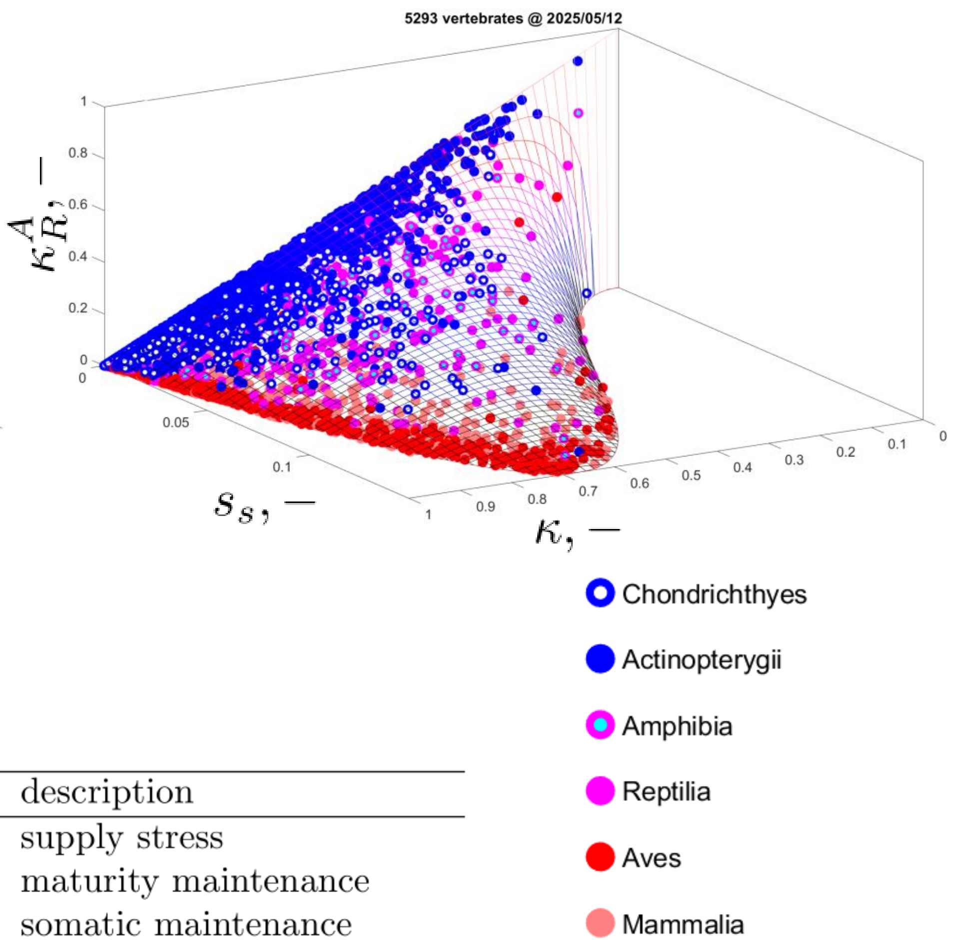
Supply ↔ demand

controls of energetics: environmental → internal

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 rejuvenate 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 (maintenance)	has supply components (some food must be available)

Supply stress





symbol	description
s_s	supply stress
$\dot{p}_J$	maturity maintenance
$\dot{p}_M$	somatic maintenance
$\dot{p}_A$	assimilation
κ	fraction of mobil to soma
κ_R^A	fraction of assim to reprod

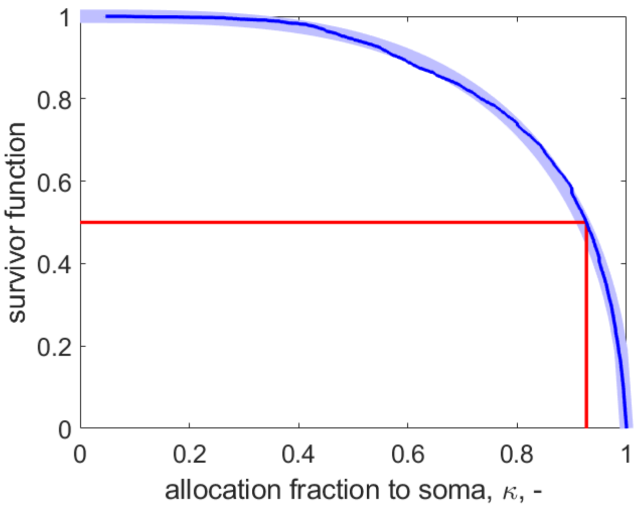
$$s_s = \frac{\dot{p}_J \dot{p}_M^2}{\dot{p}_A^3} = \frac{\dot{p}_J}{\dot{p}_A}\kappa^2; \quad \kappa = \frac{\dot{p}_M}{\dot{p}_A} \text{ for } L = L_\infty$$

mesh: $1 = \kappa_R^A + \kappa + s_s/\kappa^2$

tiny deviations are caused by supply stress depending on acceleration

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

Ratios of fluxes



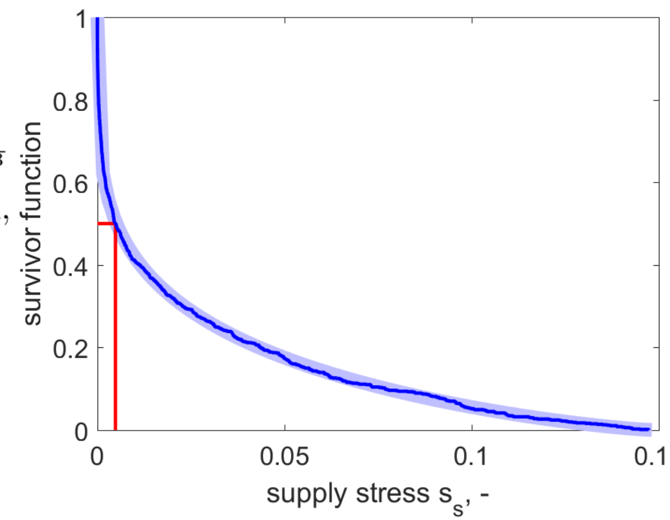
For fully growns: $\dot p_G = 0$, $\kappa \dot p_A = \dot p_M$

$\dot p_A = \dot p_M + \dot p_J + \dot p_R$; $\kappa = \frac{\dot p_M}{\dot p_M + \dot p_J + \dot p_R}$

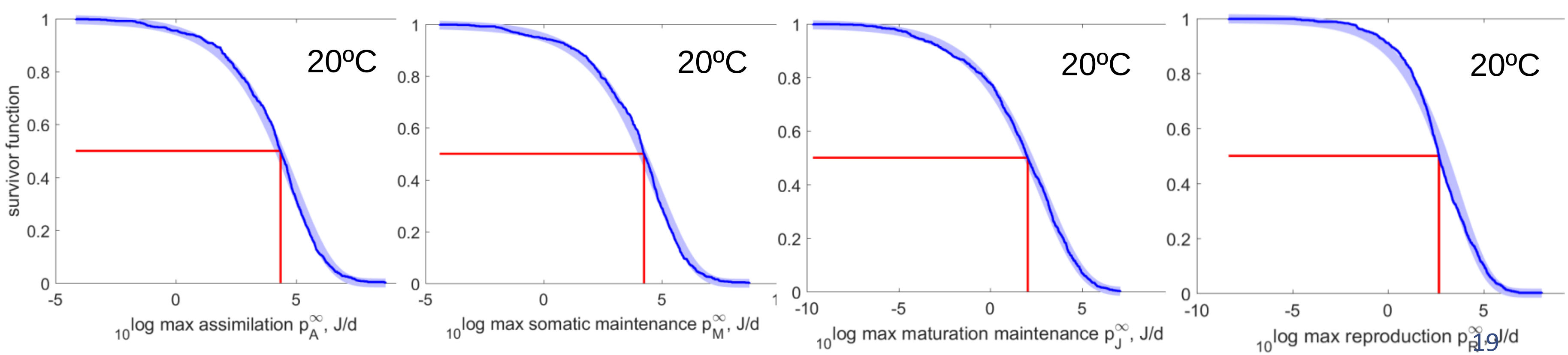
Supply stress $s_s = \frac{\dot p_J \dot p_M^2}{\dot p_A^3} = \frac{\dot p_J \dot p_M^2}{(\dot p_M + \dot p_J + \dot p_R)^3}$

$\dot p_A$, $\dot p_M$, $\dot p_J$, $\dot p_R$ are Weibull-distributed,
κ, s_s are beta-distributed

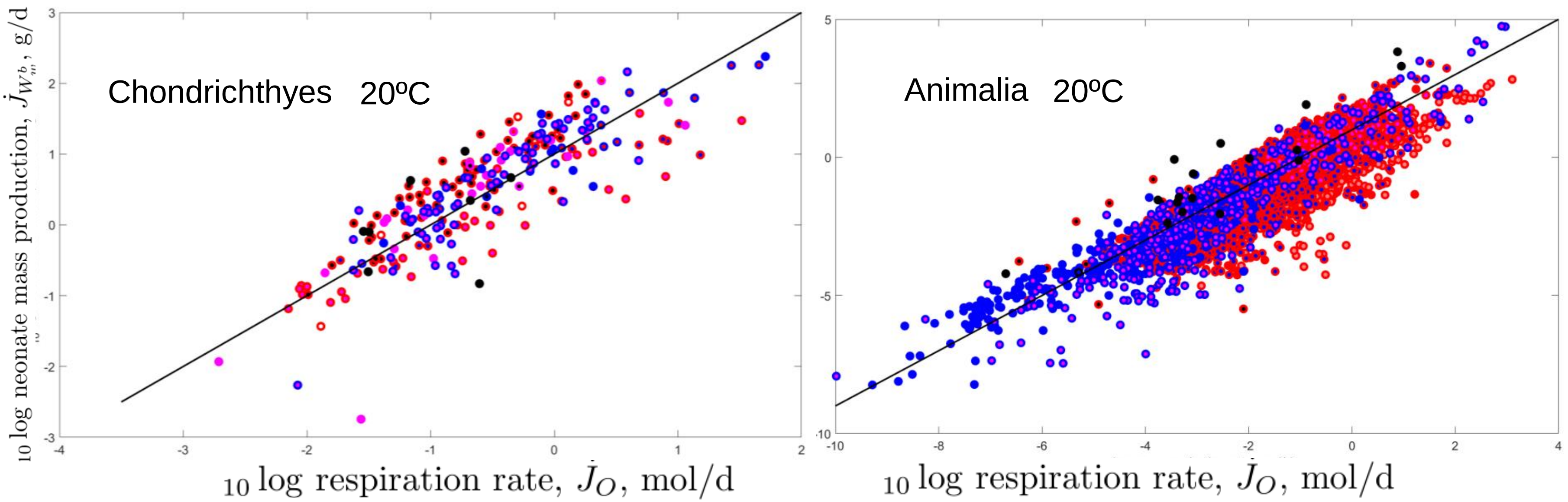
Median κ is 0.9;
animals with $\kappa \simeq 0.45$ can
reproduce 10 till 100 $\times$ faster



Lika et al 2019 *J Sea Res* **143**: 8-17
Kooijman & Lika 2014 *Biol Rev* **89**: 849-859
Lika et al 2014 *J Theor Biol* **354**: 35-47



Respiration ∝ neonate mass prod



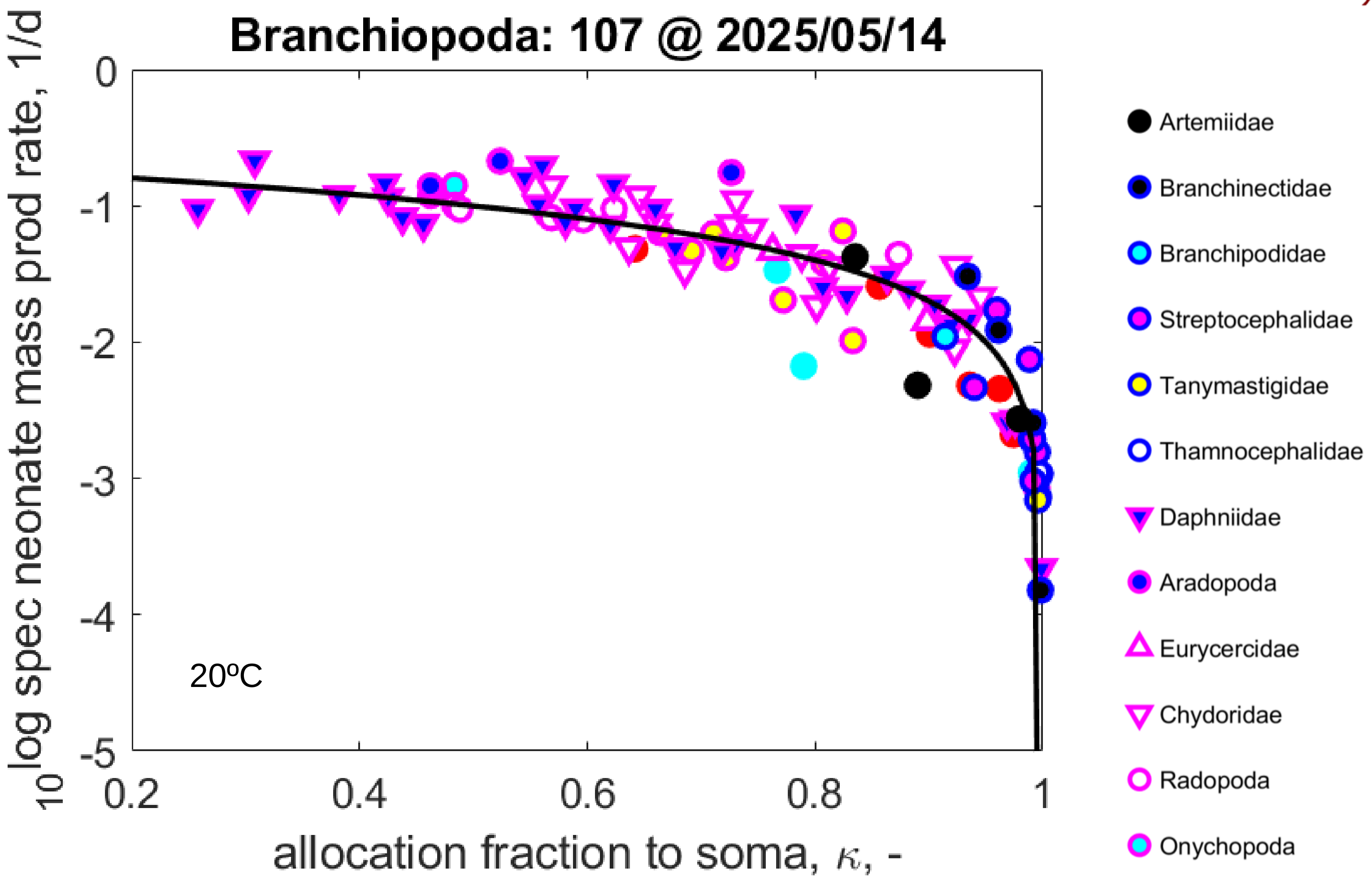
- Chimaeriformes
- Heterodontiformes
- Orectolobiformes
- Carcharhiniformes
- Lamniformes
- Squatiniformes
- Pristiophoriformes
- Squaliformes
- Hexanchiformes
- Rajiformes
- Rhinopristiformes
- Myliobatiformes
- Torpediniformes

Lines: $\dot{J}_{W_w^b} = w_R \dot{J}_O$ with $w_R = 10\,\mathrm{g/mol}$
Assumption: female length is at maximum for all species

- Radiata
- Xenacoelomorpha
- Spiralia
- Ecdysozoa
- Chondrichthyes
- Actinopterygii
- Mammalia
- Tetrapoda
- Deuterostomata

Augustine et al 2022, *J. Sea Res.* **184**:102228

kappa - neonate mass prod



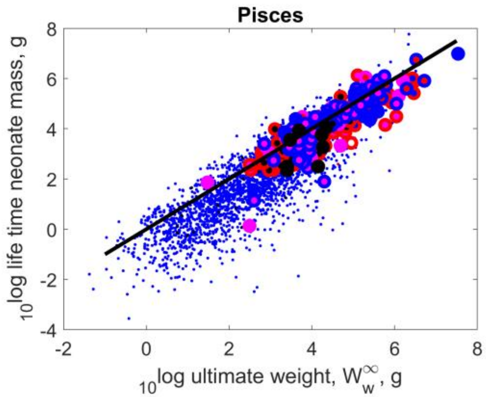
Curve: $$\dot{R}_\infty W_w^b / W_w^\infty(\kappa) = (1-\kappa)/5$$

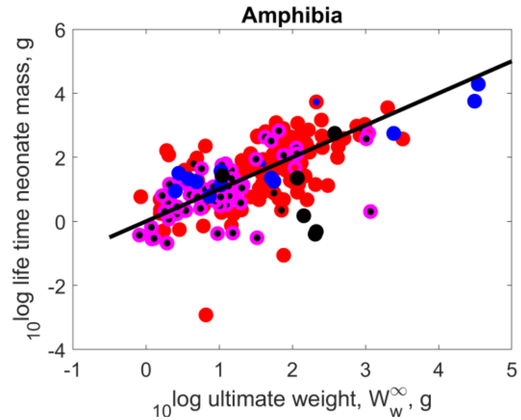
Assumption: female length is at maximum for all species

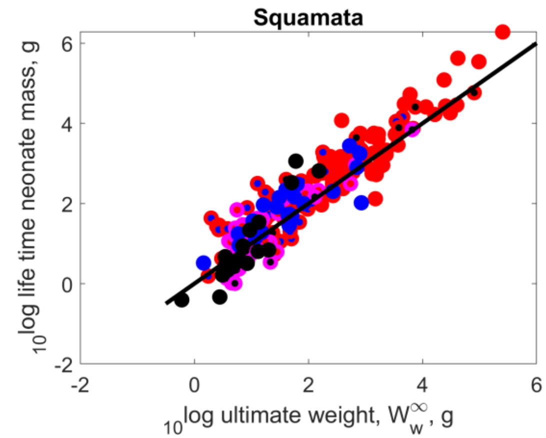
κ	alloc frac to soma
$\dot{R}_\infty$	max reprod rate
W_w^b	weight at birth
W_w^∞	ultimate weight

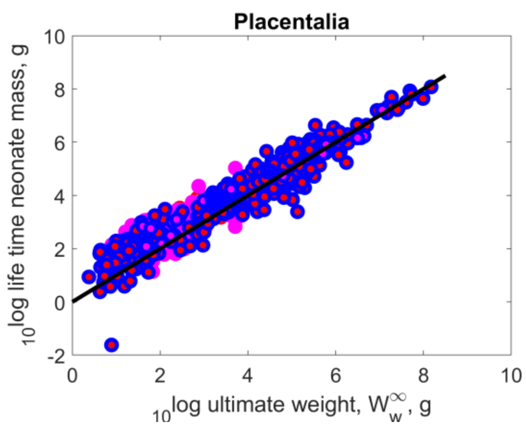
Kooijman 2024, *Ecol. Mod.* **488**: 110721

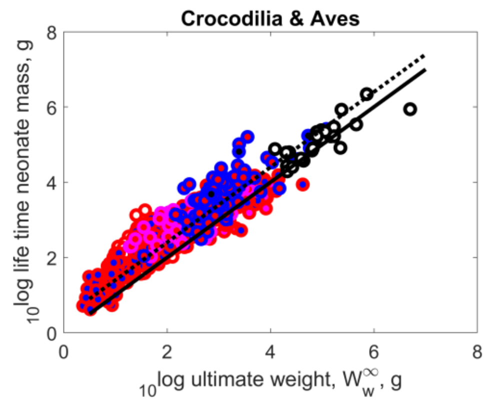
Life-time neonate mass = ultimate weight

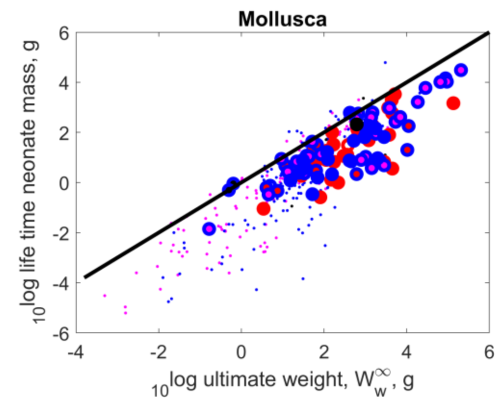


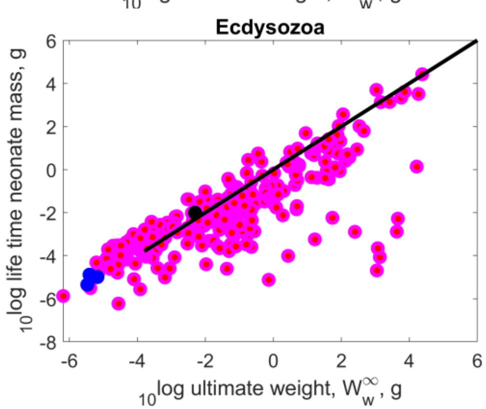


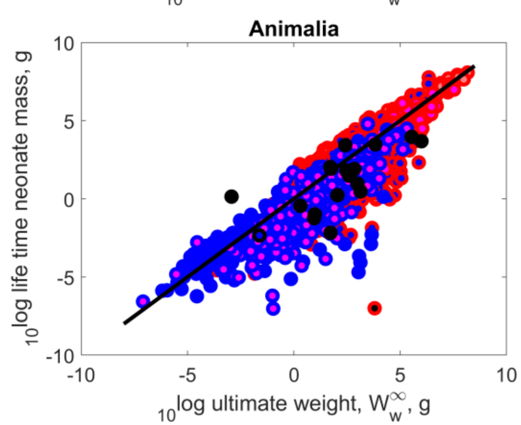










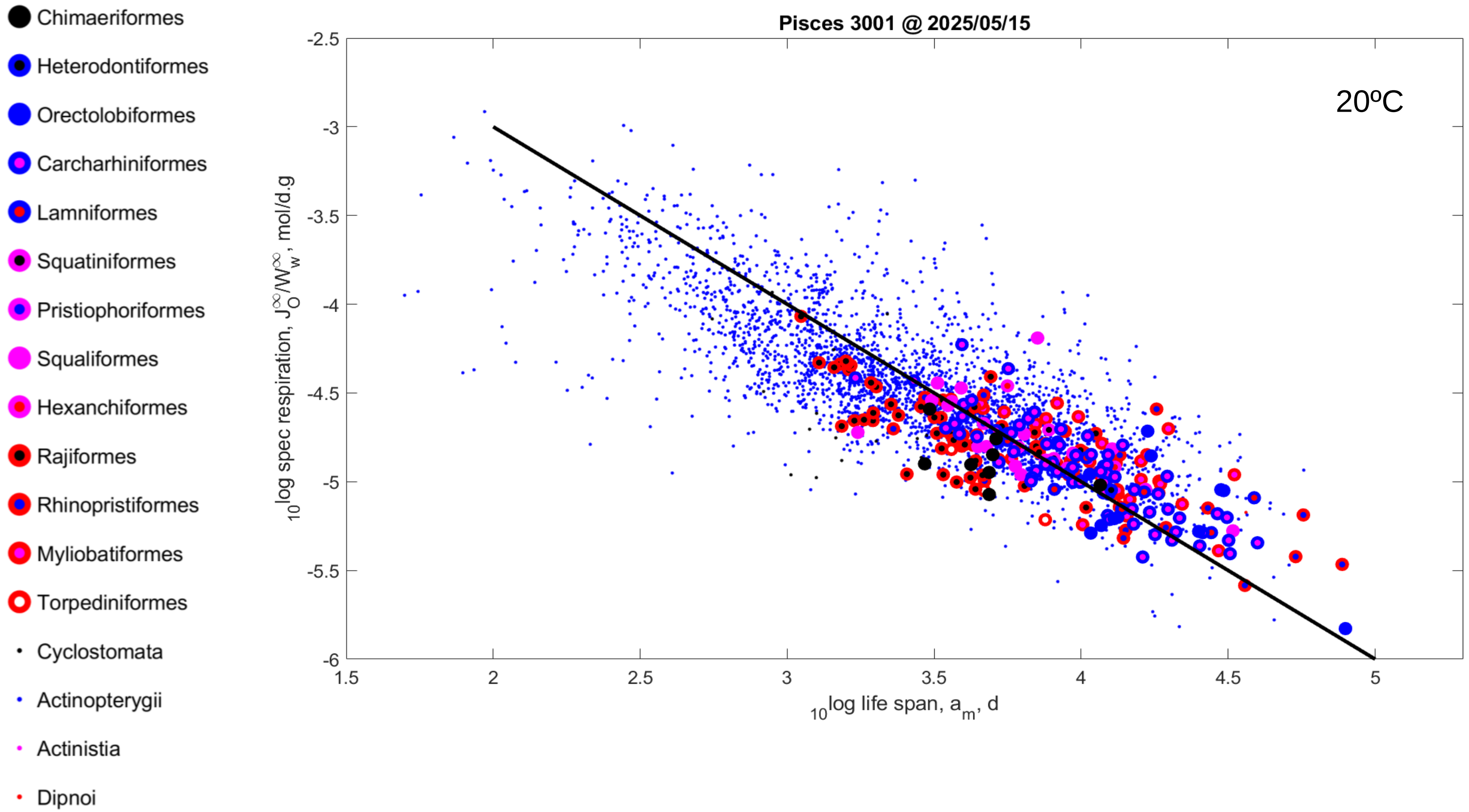


Lines indicate equality (no fitting)
Dotted line for crocs & birds
indicates an extra factor 2.5

Augustine et al 2022,
J. Sea Res. **184**:102228

Life span ∝ 1/spec respiration

Pisces



Line: $a_m^{-1} = w_O \dot{J}_O^\infty / W_w^\infty; \quad w_O = 10^5 \text{ g/mol}$

Augustine et al 2022,
J. Sea Res. **184**:102228

Altricial ↔ Precocial spectrum

Definition: birth early-late in maturation
DEB quantification $s_H^{pb} = E_H^p / E_H^b$

In literature applied to birds & mammals
Birds: precocial → altricial
Mammals: altricial → precocial

Significance: budget dictates reproduction investment
Evolutionary choice:
a few large bodied neonates or many small ones

s_H^{pb}	altriciality coefficient
E_H^b	maturity at birth
E_H^p	maturity at puberty

Augustine et al 2019,
J. Sea Res. **143**:27-34

Animal nitrogen wastes

more expensive
less toxic

nitrogenous waste	formula	solubility (mM)	insects	crustaceans	fish	birds	mammals
ammonia	NH_3	52.4		○	○		
amm. bicarbonate	NH_4HCO_3	1.5		○			
urea	$CO(NH_2)_2$	39.8					○
allantoin	$C_4H_6O_3N_4$	0.015					○
allantoic acid	$C_4H_8O_4N_4$	slight					○
uric acid	$C_5H_4O_3N_4$	0.0015				○	
sodium urate	$C_5H_2O_3N_4Na_2$	0.016	○			○	
potassium urate	$C_5H_2O_3N_4K_2$	slight	○			○	
guanine	$C_4H_5ON_5$	0.0013	○			○	
xanthine	$C_5H_4O_2N_4$	0.068	○			○	
hypoxanthine	$C_5H_4ON_4$	0.021	○			○	
arginine	$C_6H_{14}O_2N_4$	3.4	○			○	

Withers 1992 *Comparative Animal Physiology*. Saunders.

Altricial–Precocial spectrum


Paleognat
Struthio camelus
ostrich
precocial


Passerine
Turdus merula
blackbird
altricial

Altricial & Precocial Finfoots 2.5.2e

Heliornis fulica,
American finfoot



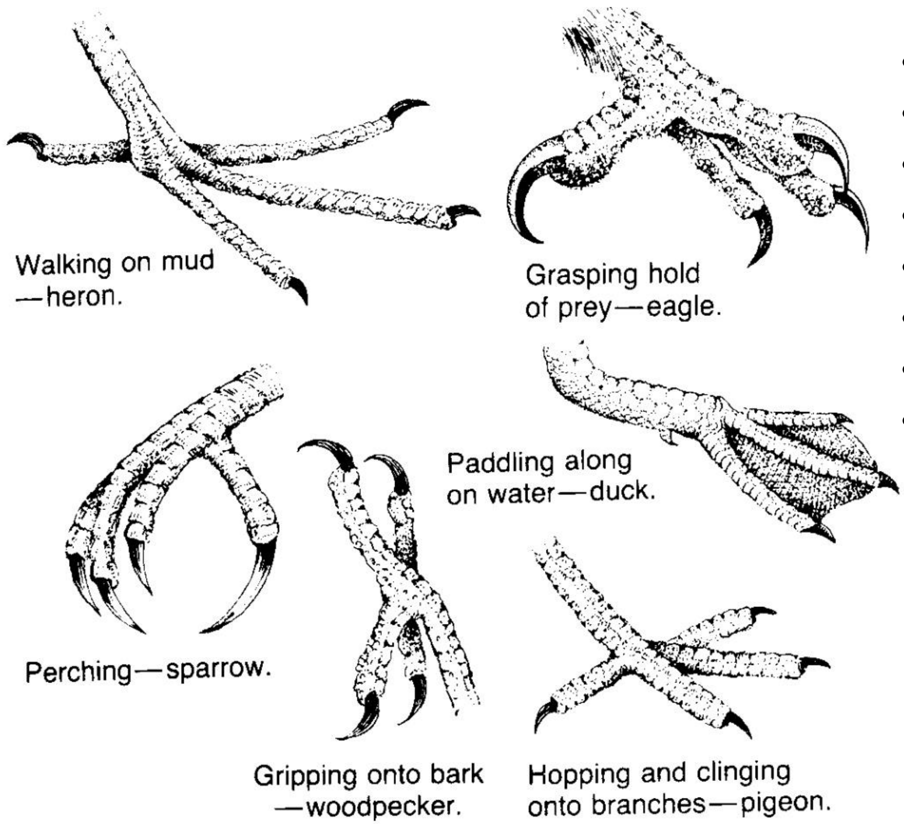

Podica senegalensis,
African finfoot



Heliopais personata,
Asian finfoot

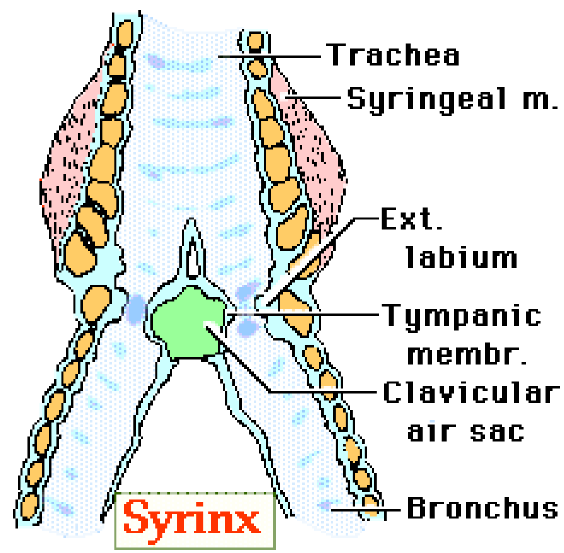


Altricial–Precocial spectrum



Bird adaptations to life in forest

- altricial development + demand species
- advanced parental care
- colour inner mouth, bagging, fecal sacks
- high water content of neonate tissues
- small body size for forest birds
- short round wings, maneuverable tail
- anisodactyl feet (perching)
- advanced singing (sight blocked by leaves)



Altricial–Precocial spectrum

Marsupial
Phalanger gymnotis
ground cuscus
altricial

Primate
Carlito syrichta
Phillippine tarsier
precocial

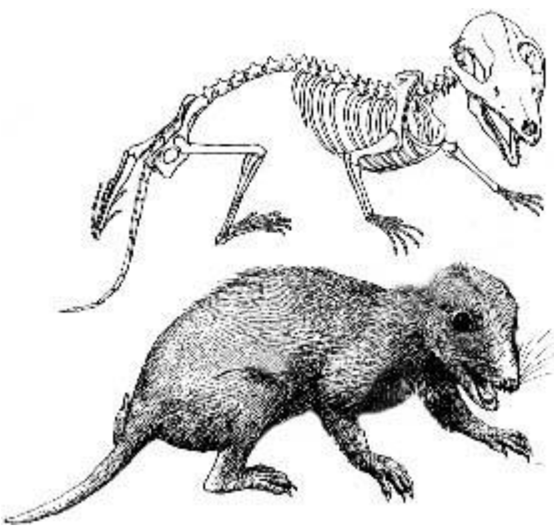
Reptile-Mammal transition

caseine synthetase 200-310 Ma
vitellogenin-encoding lost 30--70 Ma
Brawand *et al* 2008: **Plos Biol 6**:0507

Moschops (*Dinocephalia*)

Cynognathus (*Cynodontia*)

Lystrosaurus (*Dicynodontia*)



Megazostrodon (*Triconodonta*)

Ptilodus (*Multituberculata*)

nursing *Platypus*

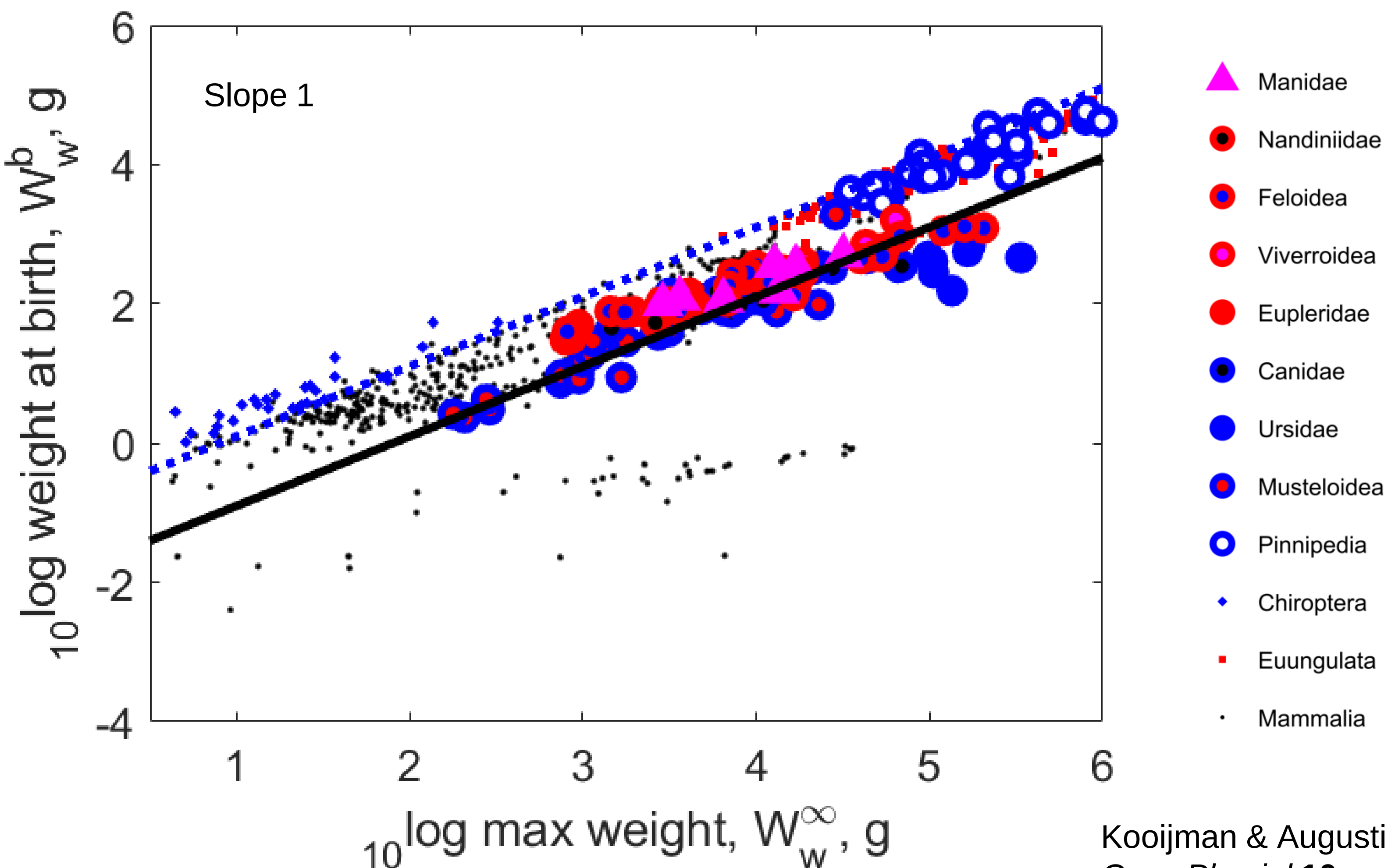
Altricial ↔ precocial in birds & mammals

Dinosaurs/birds could make large eggs because
they used expensive, but non-toxic, N-wastes
Birds became altricial due to adaptation to life in trees,
trees drove dinosaurs into extinction: precocial →altricial

Mammals had to make small eggs because
they used urea as N-waste
They became precocial after the invention of placental
development, 30-70 Ma ago: altricial → precocial

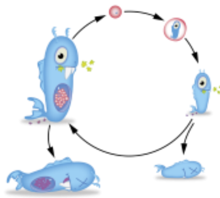
Dinosaurs & mammals evolved in (roughly) the same period,
birds & placental mammals evolved in the same period
Embryo development was bottleneck in aqua/terra transition

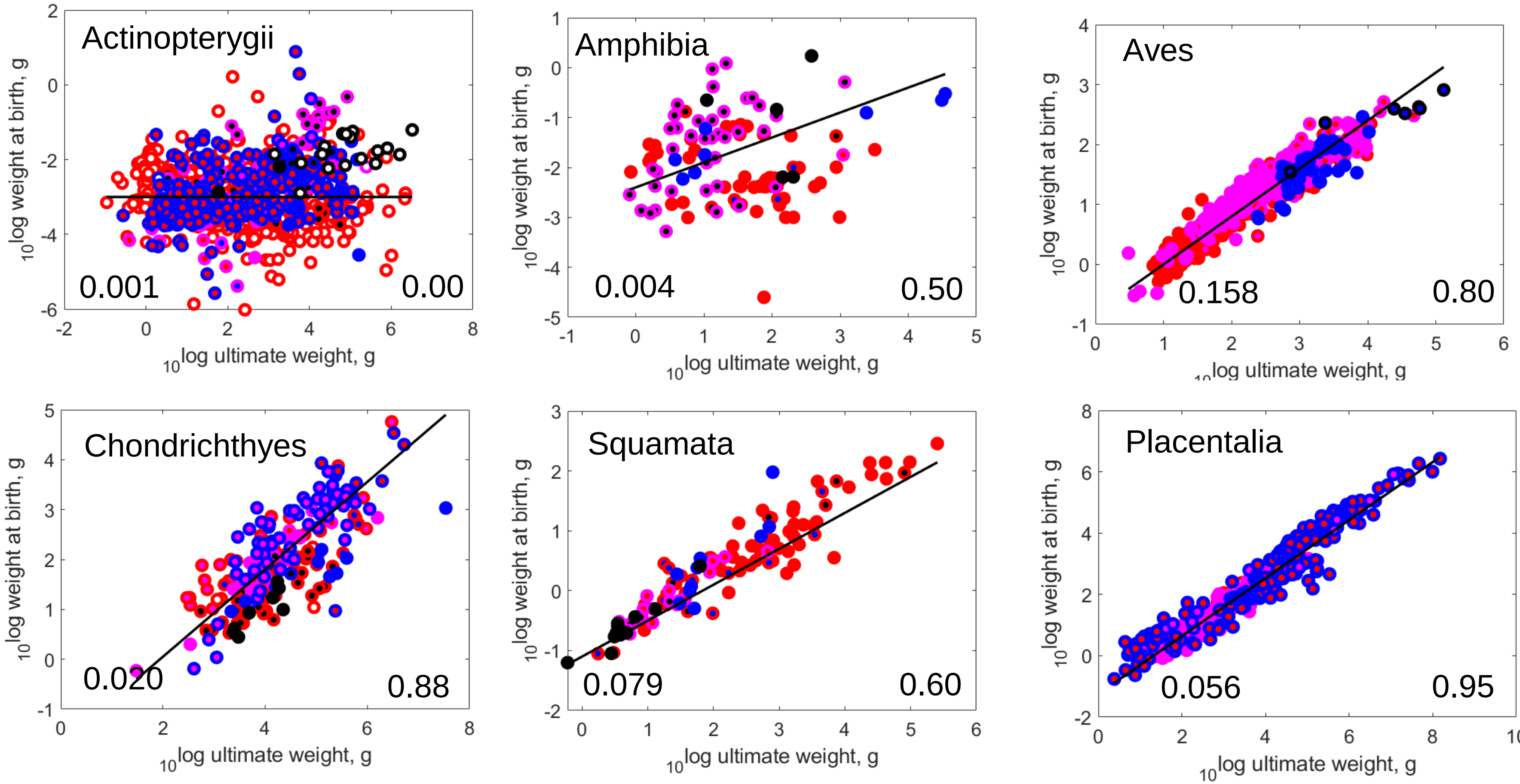
Relative birth weight in carnivorens



Kooijman & Augustine 2022
Cons Physiol **10**

Relative weight at birth

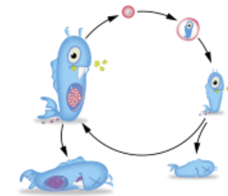


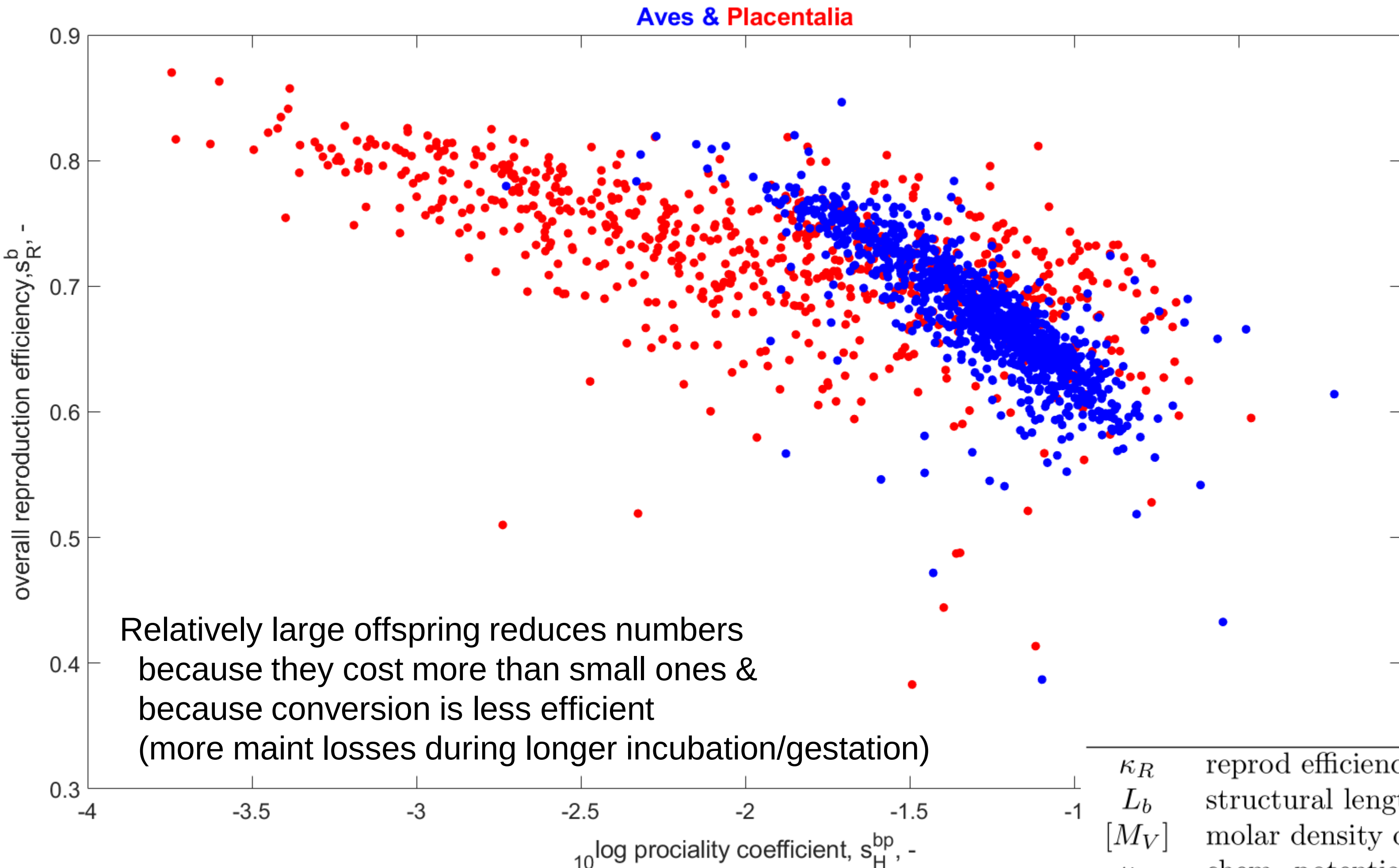


$W_b = \alpha \, (W_\infty/W_{ref})^\beta$ with W_{ref} =1 g and α lower left and β lower right
Factor α is smallest in fish, largest in birds
Slope β quantifies N-waste problem, in squamata & birds, 1 = no problem
Dioxygen use might be limiting egg size in amphibians
Ray-finned fish evolved a planktonic larval stage

Augustine et al 2022
J Sea Res **185** 102228

Overall reproduction efficiency





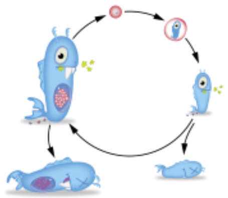
precociality coefficient: $s_H^{bp} = E_H^b / E_H^p$

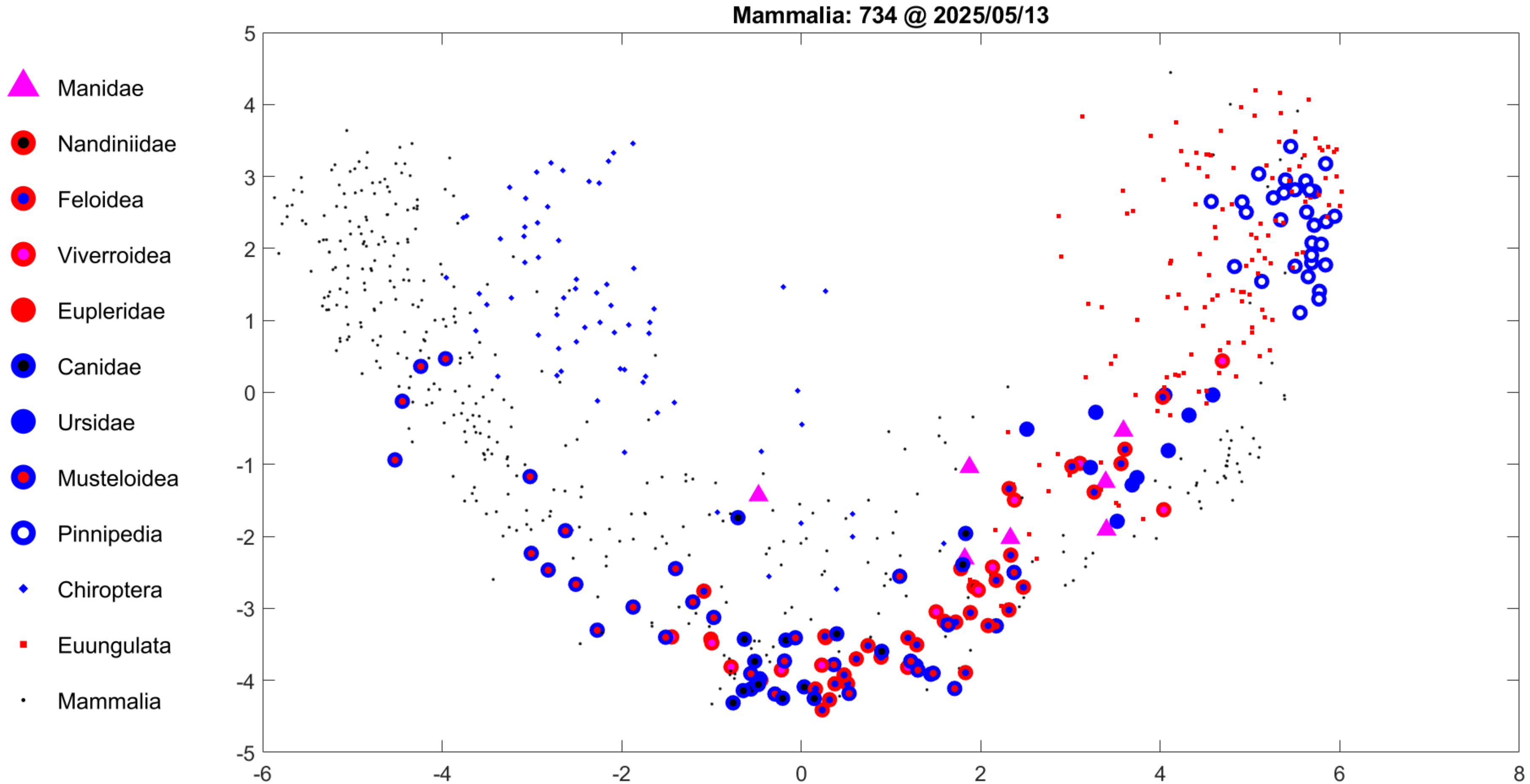
overall reproduction efficiency: $s_R^b = \kappa_R L_b^3 ([M_V]\mu_V + [E_m])/E_0$

κ_R	reprod efficiency
L_b	structural length at birth
$[M_V]$	molar density of structure
μ_V	chem. potential of structure
$[E_m]$	max reserve capacity
E_0	energy content of egg
E_H^b	maturity at birth
E_H^p	maturity at puberty

Multi-dimensional scaling

carnivora highlighted





14 traits at 20ºC: $a_m, a_p, a_b, W_w^\infty, W_w^p, W_w^b, \dot{R}_\infty, s_s, s_H^{bp}, [\dot{p}_M], \dot{v}, \kappa, E_H^b, E_H^p$

Final slide

Thank you for your attention

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Questions/remarks are very welcome

Also later during breaks