

## Module 2: mechanistic and statistical modelling of resilience and feed efficiency

### ➤ Allocation theory in farm animals: from concepts to code

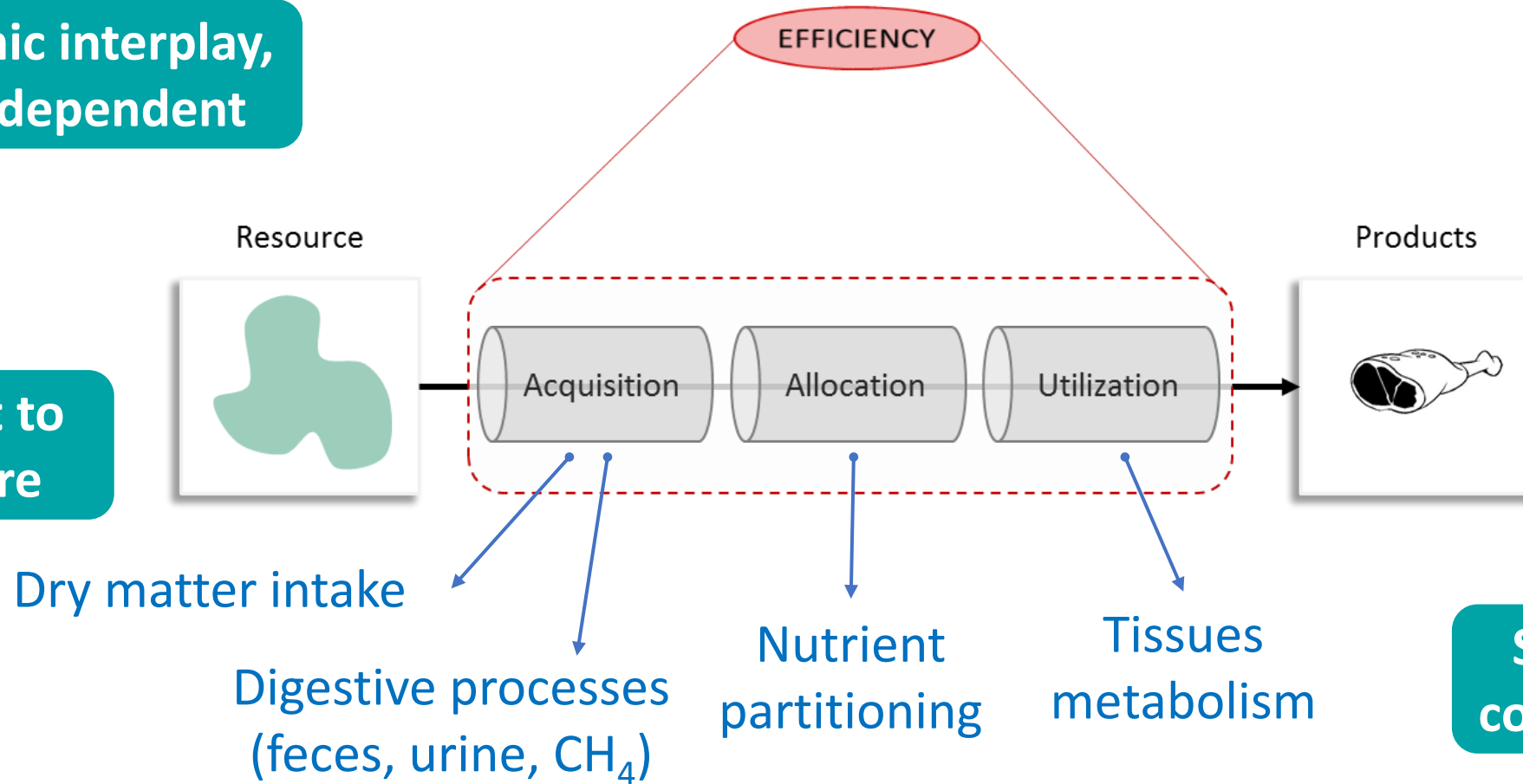
Laurence PUILLET  
(MoSAR unit)



# ➤ Complex features of feed efficiency

Dynamic interplay,  
time-dependent

Difficult to  
measure



Sub-traits  
combination

Trade-offs



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## ➤ Sustainable genetic selection for feed efficiency

- What are the long-term effects of selection?
- Is there any side effect?
- Are we selecting the mechanisms we want?
- High merit animals for FE → able to accommodate different environments?
- High merit animals for FE → still resilient?

**DISCLAIMER**

*One of the possible research avenue!*

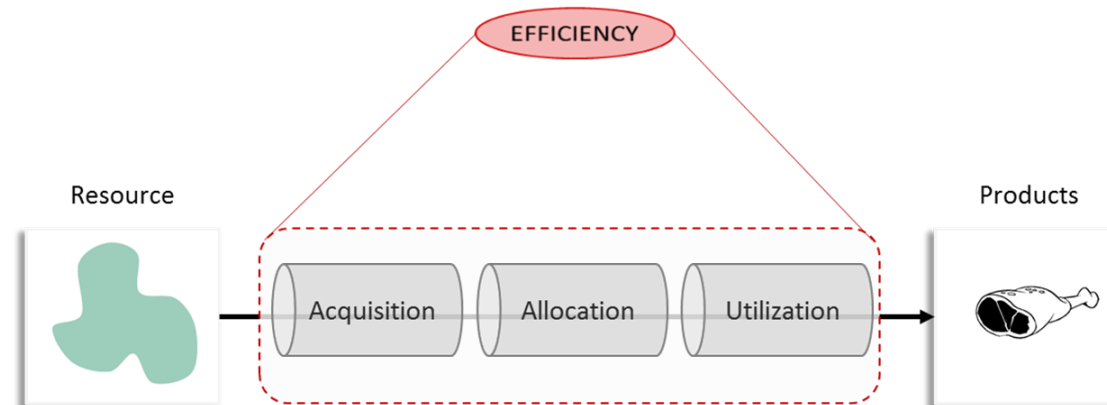
Part 2: link with  
nutrition modelling

Simulation model

Dynamic and  
process-based

Part 1: a concept  
from ecology

Incorporating  
allocation



# ➤ Resource allocation theory in ecology

Different life-history strategies exist

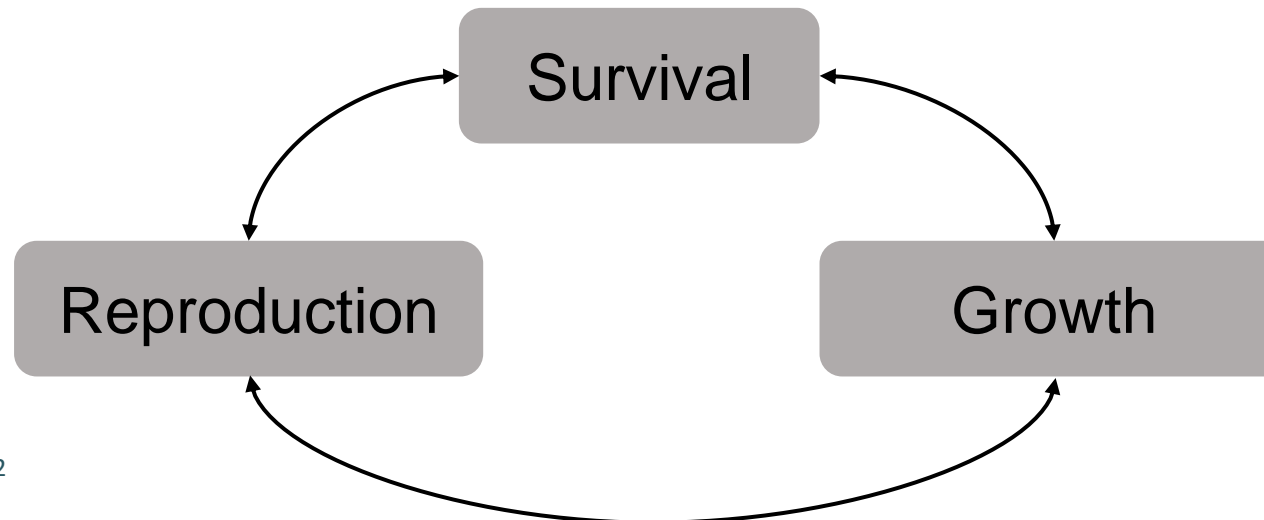
## Mus musculus

Lifespan: 3 y  
Age at maturity: 45 d  
Parturition: 6/y  
Litter size: 7



## Loxodonta africana

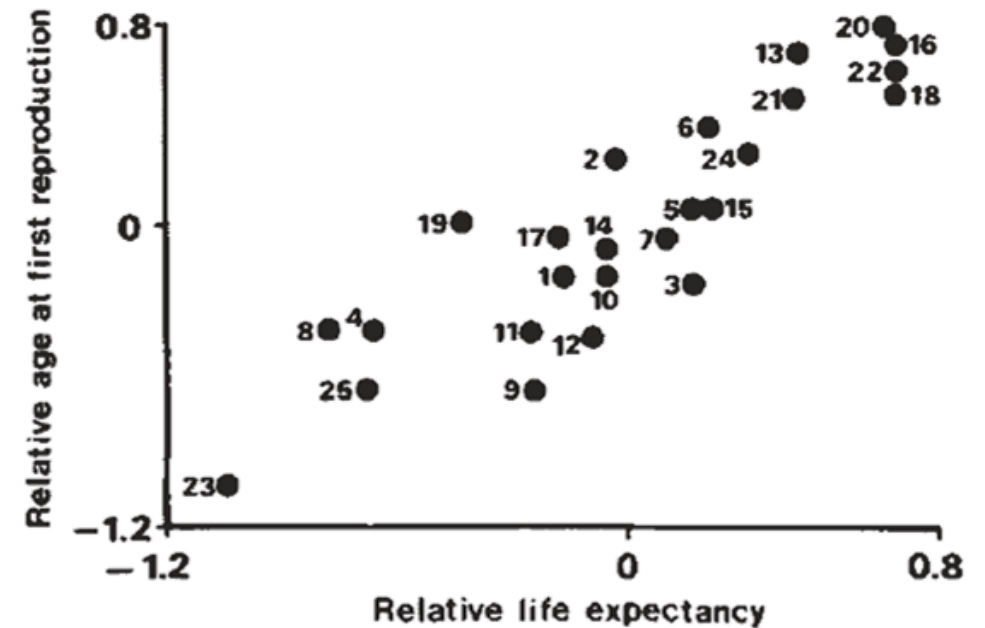
Lifespan: 60 y  
Age at maturity: 11y  
Parturition: 1/5y  
Litter size: 1



## ➤ Resource allocation theory in ecology

- Variation among living organisms is not new: basis for evolution (see Darwin 1859)
- Covariance among traits
  - Slow-fast continuum of strategies
  - Trade-offs in resource allocation

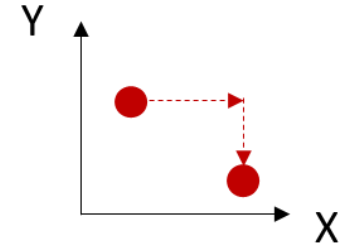
“Resources available for an individual are limited, so that individuals should allocate resources **optimally** among growth, survival, and reproduction in order to maximize their fitness” (Stearns 1992)



Harvey and Zammuto, 1985

# ➤ Resource allocation theory in ecology

- Trade-off
  - Increase in  $X \rightarrow$  decrease in  $Y$
  - “Darwinian demon” doesn’t exist
- Use of the concept by Cody (1966)
  - Clutch size in birds =  $f(\text{allocation predator avoidance} \mid \text{competition for resource})$
- Life history strategy is a genetically inherited pattern of resource allocation that has evolved through the process of natural selection
- Cost/benefit analysis to predict the optimal strategy (= maximize fitness) and therefore organisms that will adapt to the environment and evolve

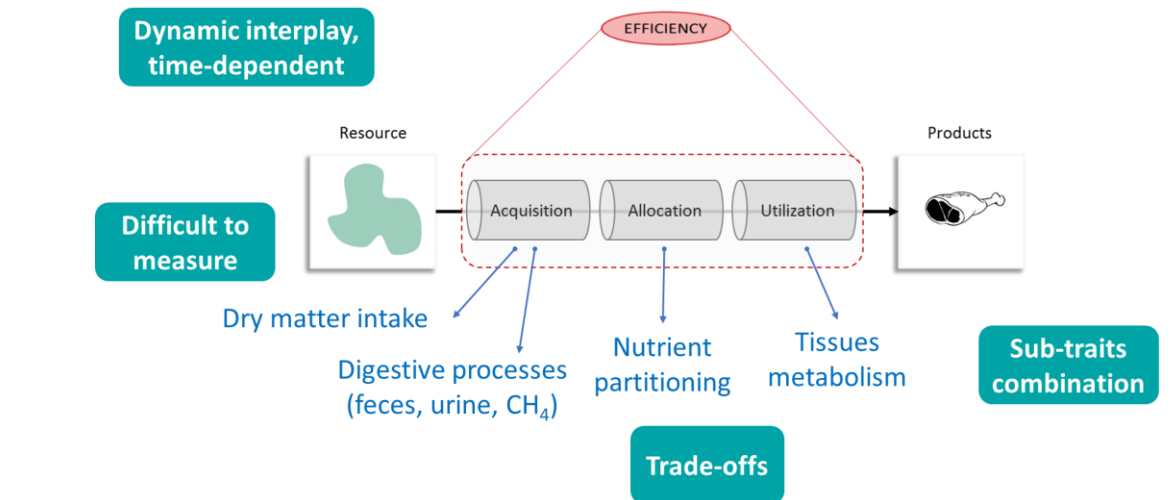
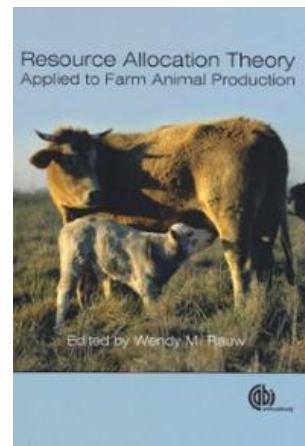


# ➤ Resource allocation theory in ecology

## Wrap-up: a framework useful for...

- Describing trade-offs, interactions among traits | functions
- Understanding variation among individuals
- Predicting long-term effect on fitness

Potential interest for sustainable genetic selection for feed efficiency!



Rauw, 2008

## ➤ Resource allocation in animal nutrition

- How to feed animals to obtain products (milk, meat...)?
- Nutritional energetics → how much energy lost | retained?
  - Relationships gas exchange / heat production
  - Evaluation of food to be related to requirements and expenditures
  - Causes of expenditures

Lactation 50%



Lactation 70%



- Nutrient partitioning ( $\approx$  resource allocation) → core of feeding tables/feeding systems
  - Starch Equivalent system (Kellner and Köhler, 1900)
  - Physiological Fuel Values system (Atwater and Bryant, 1900)



# ➤ Resource allocation in animal nutrition

A long-standing concern

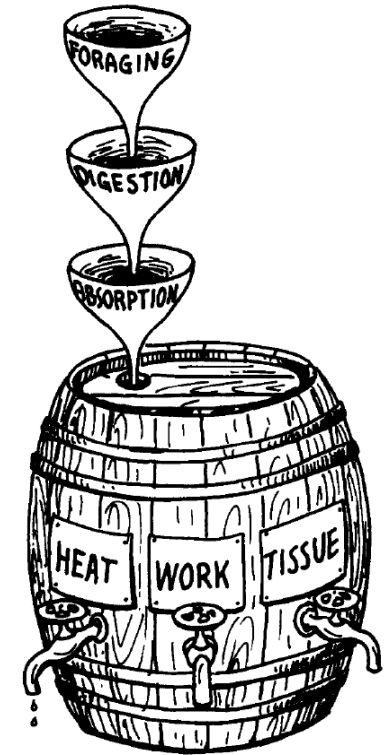
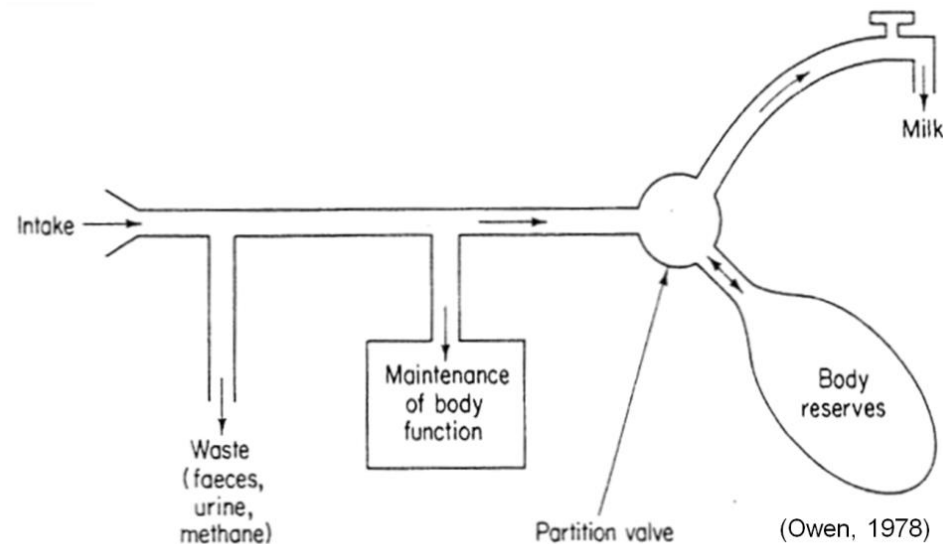
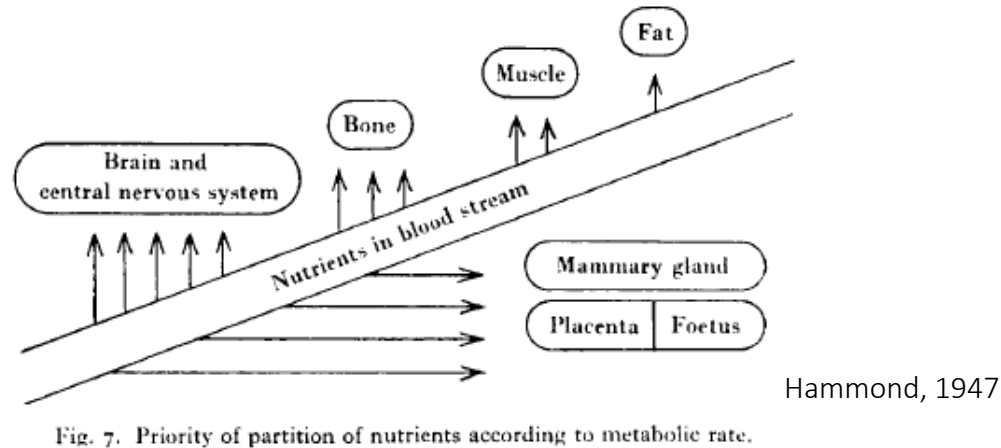


Fig. 2. The barrel model of an organism's energy balance. Input constraints (maximum rates of foraging, digestion, and absorption) are engaged in series; outputs (heat production, mechanical work, tissue growth) are parallel and independently controlled. If the sum of output rates does not match the input, the balance is buffered by the storage capacity of the system. Note that the first spigot always 'leaks' (basal heat loss of the organism).

Weiner, 1992

## ➤ Resource allocation in animal nutrition

A long-standing concern

One cow gave	1.85 kg.	more milk and	29 g.	more fat
Another	2.24	less	66	less
"	0.01	more	21	"
"	0.71	"	6	"

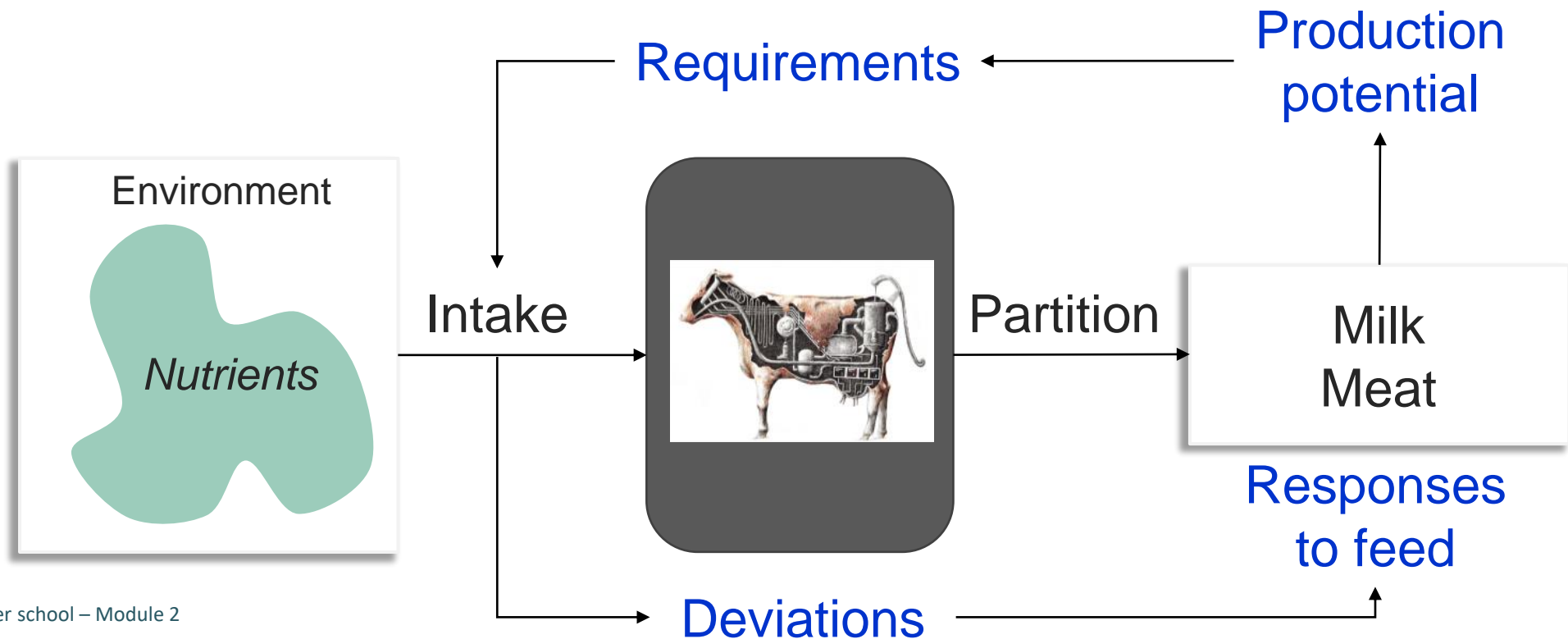
Observations of this kind, which anybody can make in practice, show how extraordinarily changeable is the influence of individuality upon the production of milk. They teach also how deceptive are the results of experiments carried out upon a small number of animals.

Kellner, 1908

# ➤ Resource allocation in animal nutrition

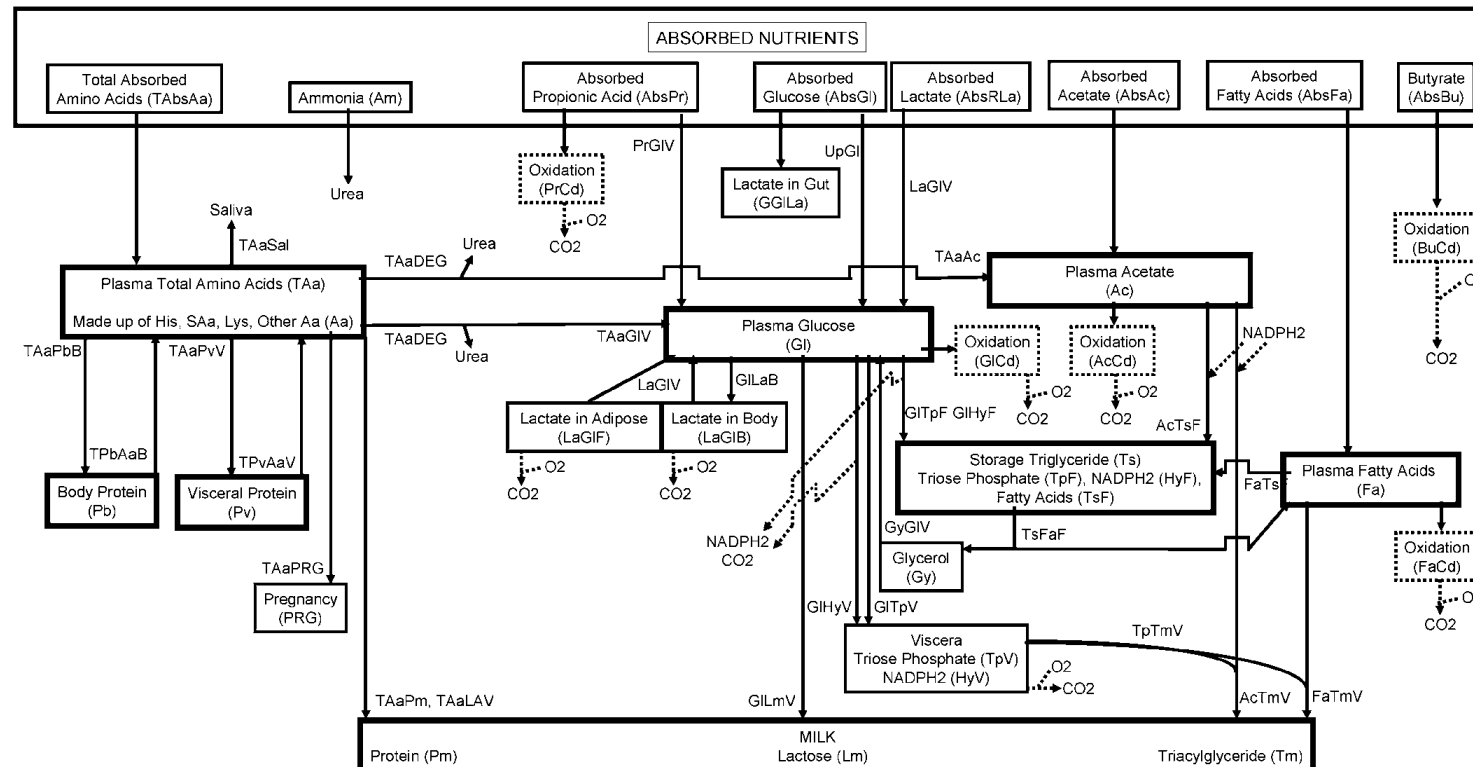
A concept that has evolved

- Starting point → the animal as biochemical convertor
- Nutrient partitioning → consequences of production potential



# ➤ Resource allocation in animal nutrition

- Biochemical models: for ex., dairy cow model Molly (Baldwin, 1987)
- Biological processes = metabolism



## ➤ Resource allocation in animal nutrition

- From a passive convertor to an active biological entity
  - The animal is a regulated organism
  - Short-term regulations: homeostasis (for ex. glucose regulations)
  - Long-term regulations: homeorhesis | teleophoresis

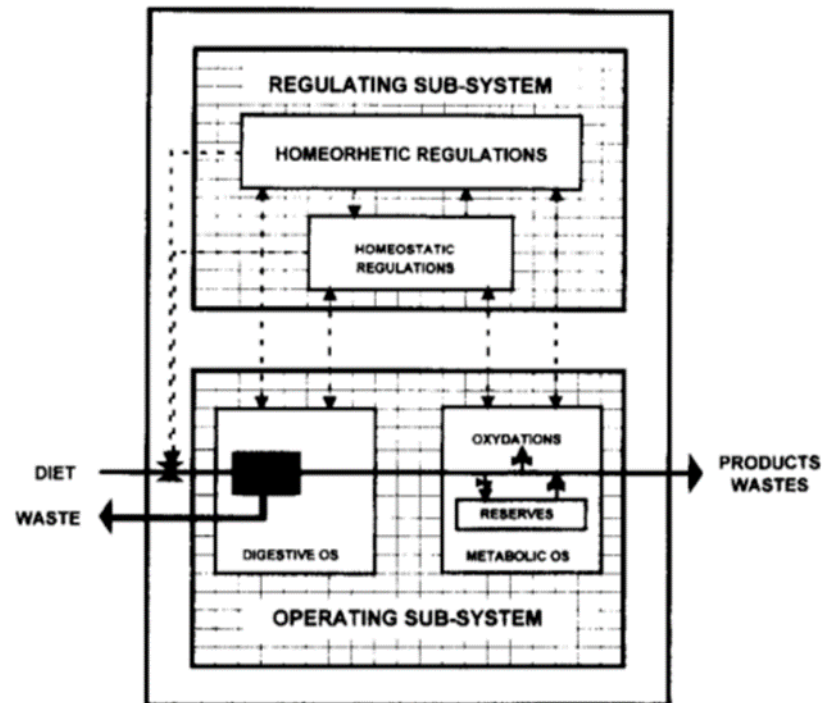
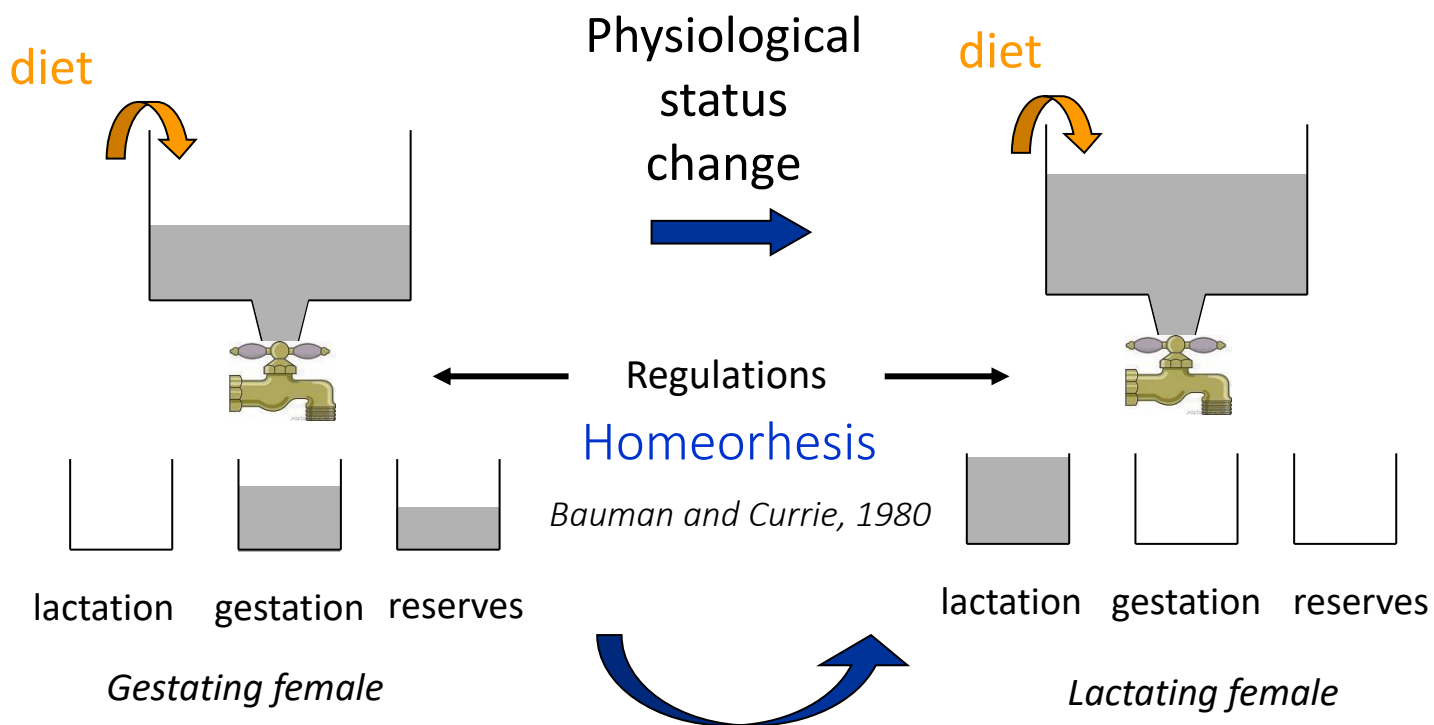


Fig. 1. The live organism as a regulated system.

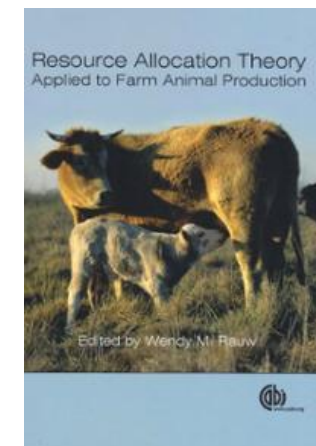
Sauvant, 1994

# ➤ Resource allocation in animal nutrition



👍 Trade-offs among biological functions

👍 Key role of body reserves



Genetic differences in nutrient partitioning?

Starting point to connect nutrition/genetics



Priority change between functions

Dynamic expression of genes throughout life

Genetically-driven trajectories

Friggens and Newbold, 2007

# ➤ Resource allocation in animal nutrition

## Example of body reserves mobilization in early lactation

- Classical view: intake doesn't increase as fast as lactation energy requirements

Mobilization is a consequence

- Experimental evidence: rich diet doesn't abolish mobilization

See review by Friggens and Newbold, 2007; Friggens et al., 2011

- Mobilization has a genetic component

Evolutionary role of body reserves in lactation

The dairy female is a mammal!

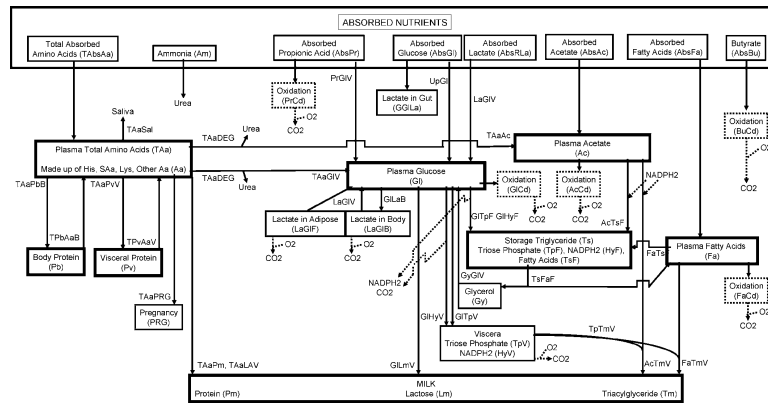
→ Life history strategy is a **genetically inherited pattern of resource allocation** that has evolved through the process of natural selection



## ➤ Resource allocation in animal nutrition

# Homeorhesis regulations reflect genetic drives of nutrient partitioning

How to introduce this level of control in nutrition models? (and up scaling at lifetime level!)



Bottom-up approach:  
let regulations emerge

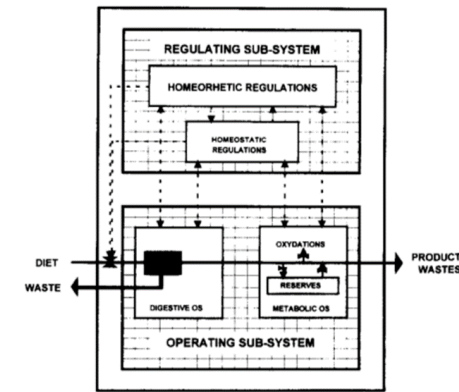
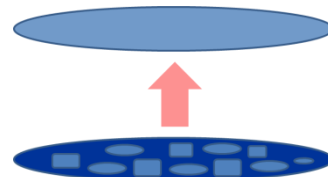
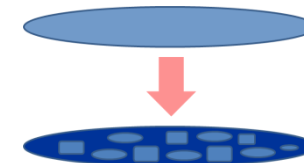


Fig. 1. The live organism as a regulated system.

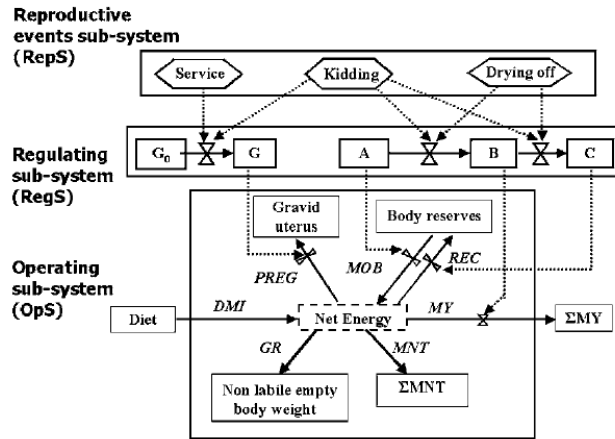
## Top-down approach: impose regulations



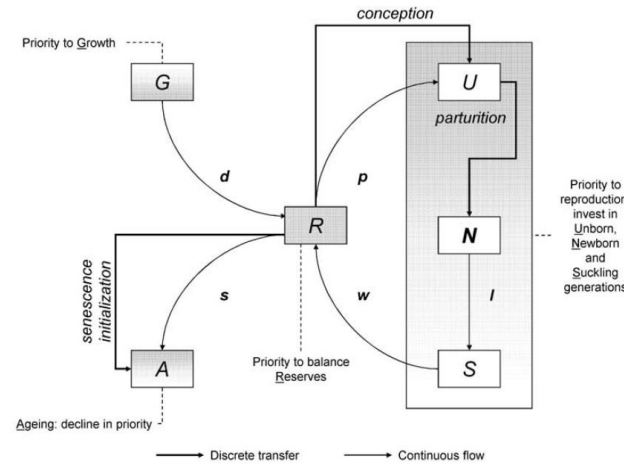
See Friggens et al.,  
2011 for review



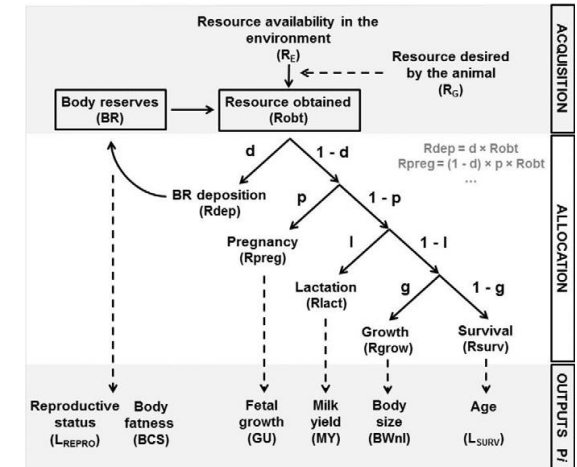
# ➤ Resource allocation in animal nutrition



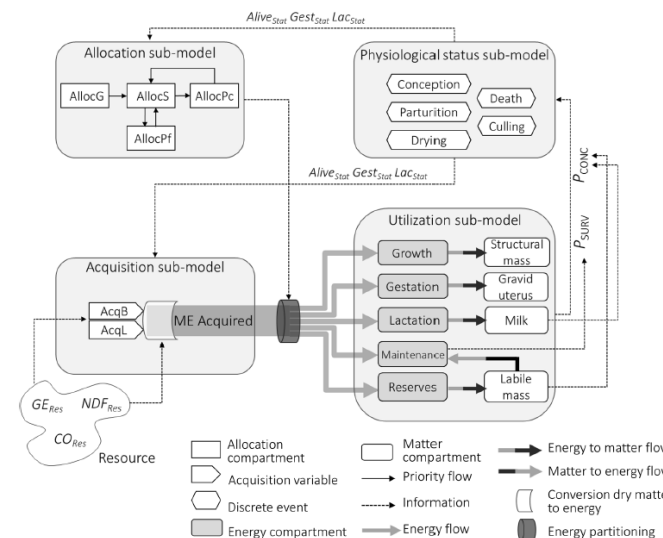
Puillet et al., 2008



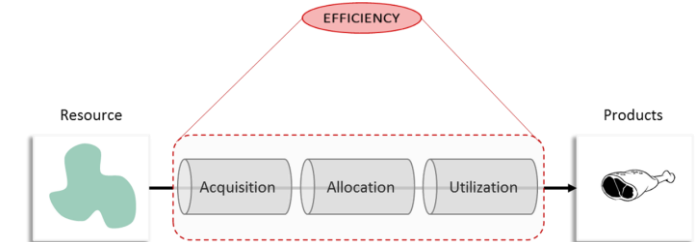
Martin et Sauvant, 2010



Douhard et al., 2014



AQAL model,  
next part



Effort to split acquisition and allocation to introduce genetics at both levels

Puillet et al., 2016

# ➤ Resource allocation in animal nutrition

What about resilience?

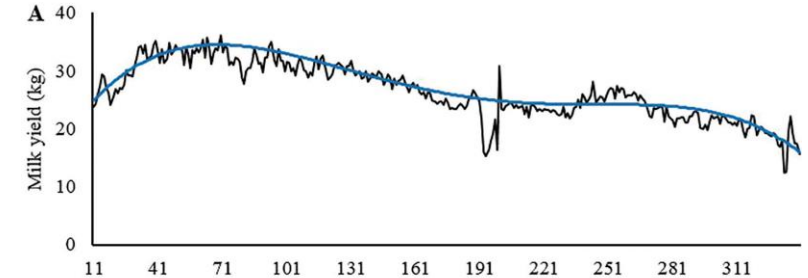
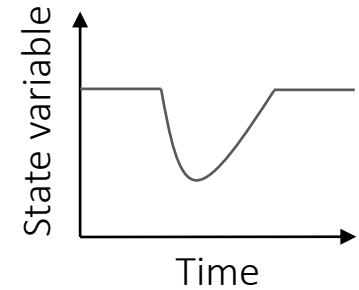
Ability to cope with short-term challenge

Deviation from the **baseline trajectory**, induced by a perturbation

Allocation models provide this baseline trajectory

State of reserves at the time of perturbation

Re-allocating nutrients



Poppe *et al.*, 2020

Development for dairy goat thanks to SMARTER project  
Research effort for health and reproduction functions!



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## ➤ Manipulating acquisition and allocation parameters to generate variability in production trajectories

- Get your hands dirty!

A little bit, due to short time...

More details in articles

Puillet, L., Réale, D. & Friggens, N.C. Disentangling the relative roles of resource acquisition and allocation on animal feed efficiency: insights from a dairy cow model. *Genet Sel Evol* 48, 72 (2016) <https://doi.org/10.1186/s12711-016-0251-8>

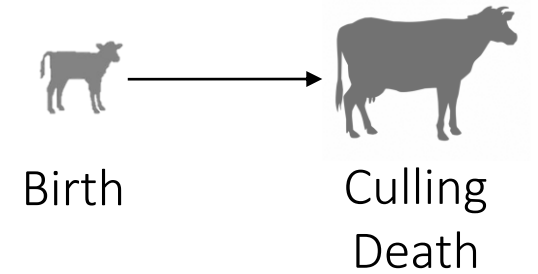
Puillet L., Ducrocq V., Friggens N.C., Amer P. Exploring underlying drivers of genotype by environment interactions in feed efficiency traits for dairy cattle with a mechanistic model involving energy acquisition and allocation. *Journal of Dairy Science*, 104, 5, 5805-5816 (2021) <https://doi.org/10.3168/jds.2020-19610>

- Play with AQAL model to generate concrete simulations of allocation trajectories

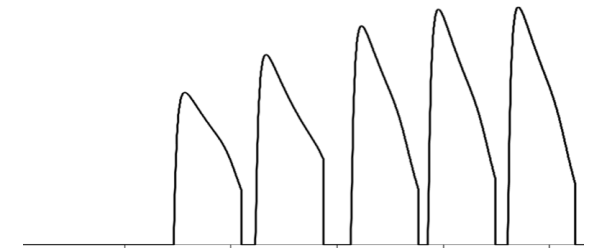
## ➤ AQUAL model (Acquisition-Allocation)

A dynamic model, simulating traits through life

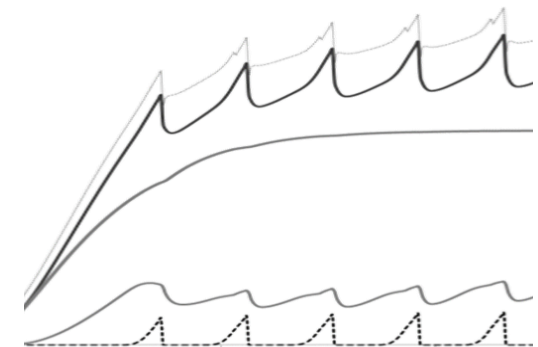
Feed resource converted into traits based on energy processes



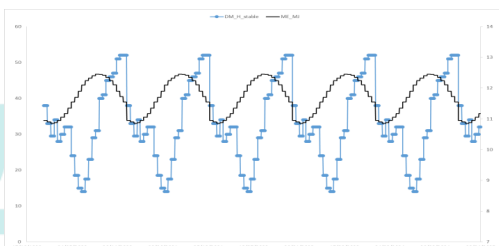
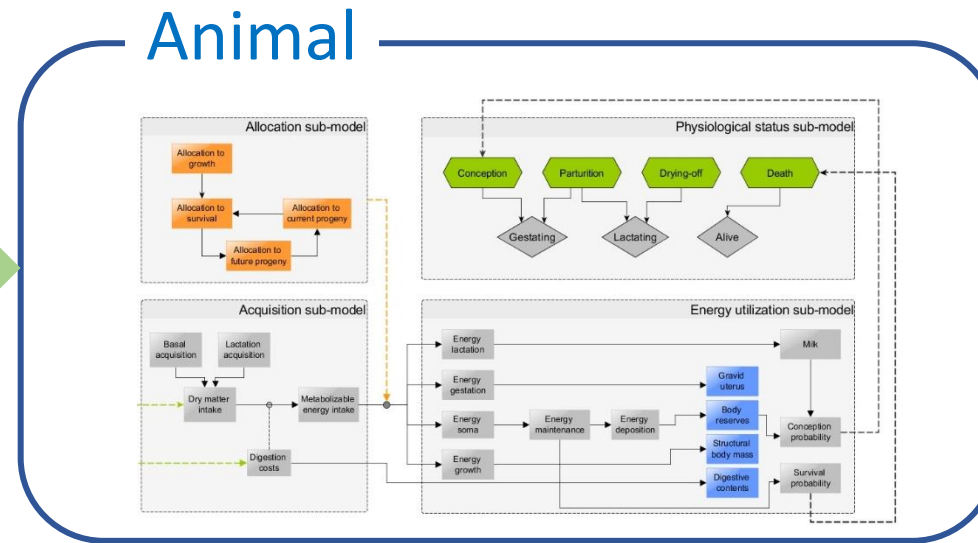
*Milk production*



*Body mass component*



Dry matter  
offer (kg/d)  
Energy content  
(ME/kg DM)



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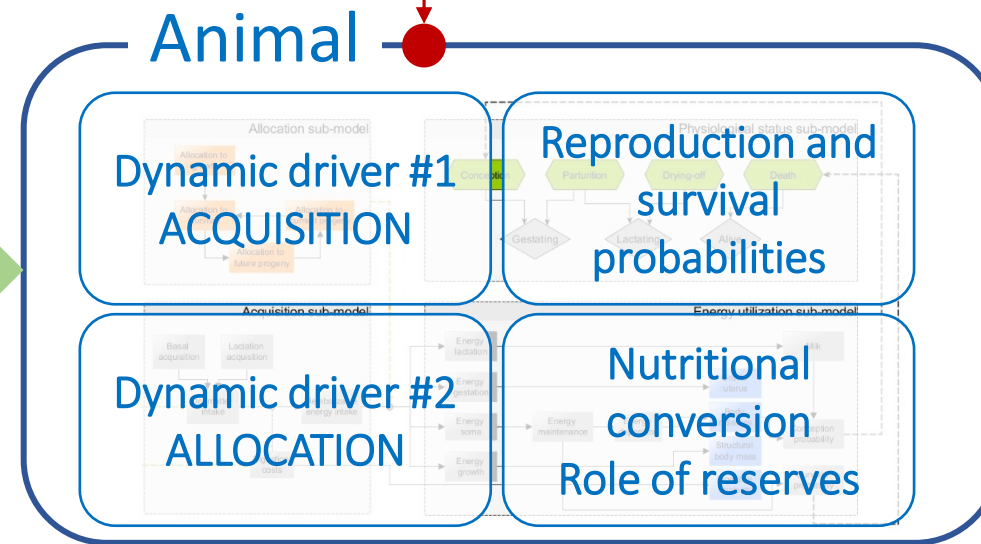
# ➤ AQUAL model (Acquisition-Allocation)

How many feed resource can get the cow ?

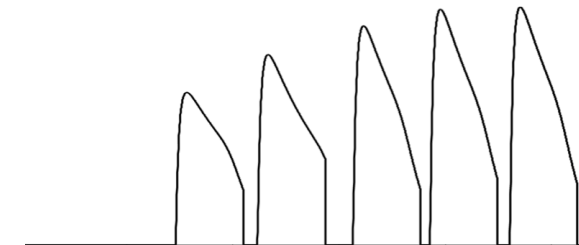
What is the cow strategy to distribute energy among functions?

2 parameters of acquisition      **Dynamic drivers**      2 parameters of allocation

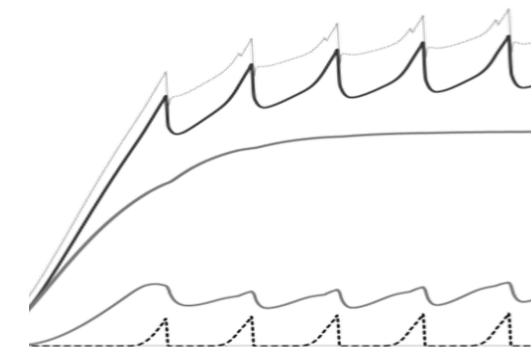
Dry matter offer (kg/d)  
Energy content (ME/kg DM)



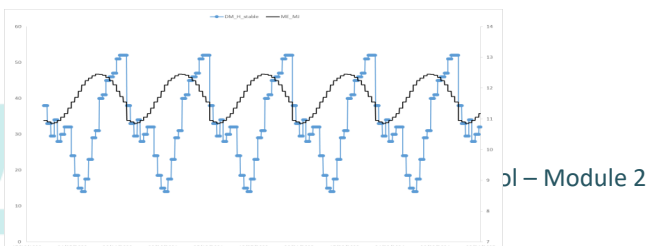
*Milk production*



*Body mass component*

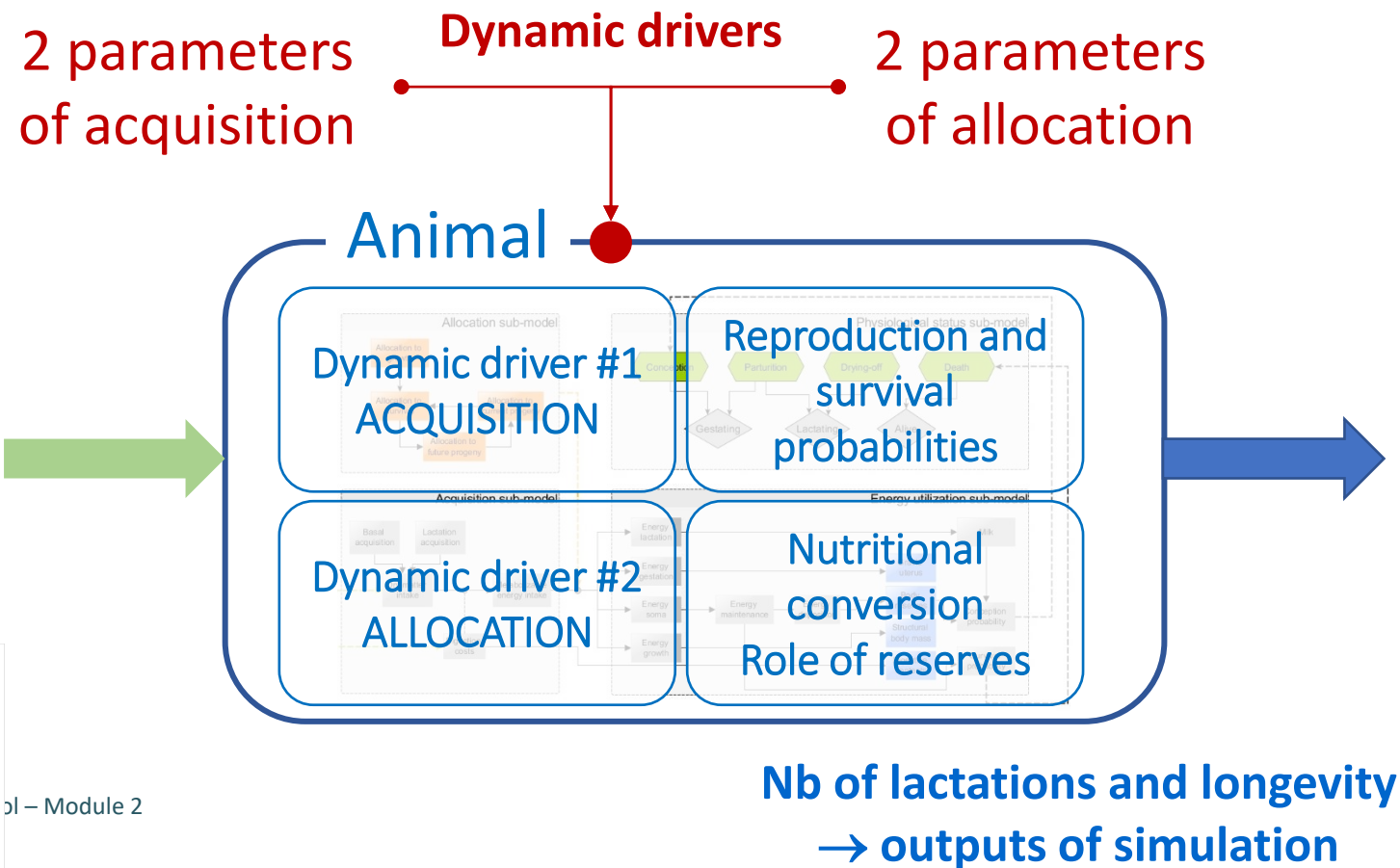


**Nb of lactations and longevity  
→ outputs of simulation**



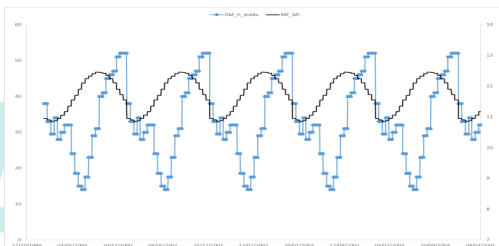
# ➤ AQUAL model (Acquisition-Allocation)

Genetic-scaling parameters, used to  
simulate ≠ animals

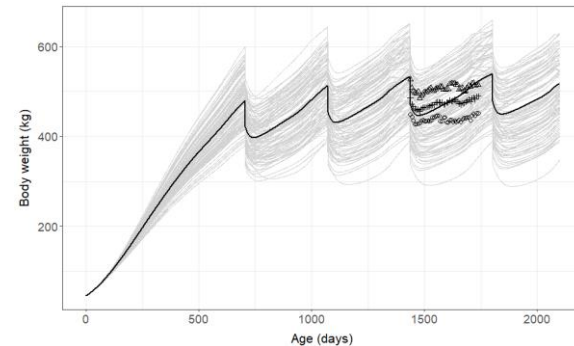
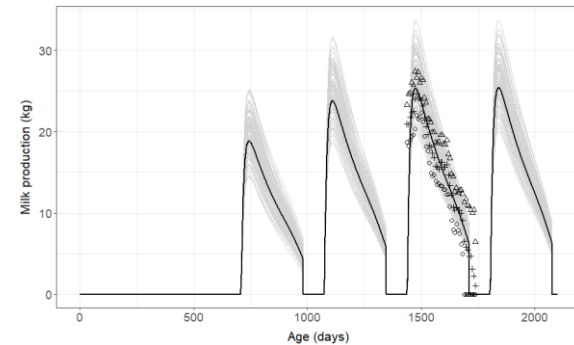


Dry matter  
offer (kg/d)

Energy content  
(ME/kg DM)



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## ➤ AQUAL model (Acquisition-Allocation)

### General (nutritional) principles

$$ME_{intake} = DryMatter_{intake} \cdot GE_{resource} \cdot \%MEinGE$$

kcal                      kg                      kcal/kg                      Proportion of energy lost in feces, urine and methane

Static view here but the model is dynamic (daily time-step)

$$ME_{survival} = ME_{intake} \cdot Alloc_{survival}$$

$$ME_{growth} = ME_{intake} \cdot Alloc_{growth}$$

$$ME_{lactation} = ME_{intake} \cdot Alloc_{lactation}$$

$$ME_{gestation} = ME_{intake} \cdot Alloc_{gestation}$$

$$\sum ME_{functions} = ME_{intake} \cdot \boxed{\sum Alloc_{function}} = 1 \rightarrow \text{energy conservation}$$

$$NE_{lactation} = ME_{lactation} \cdot k_{lactation}$$

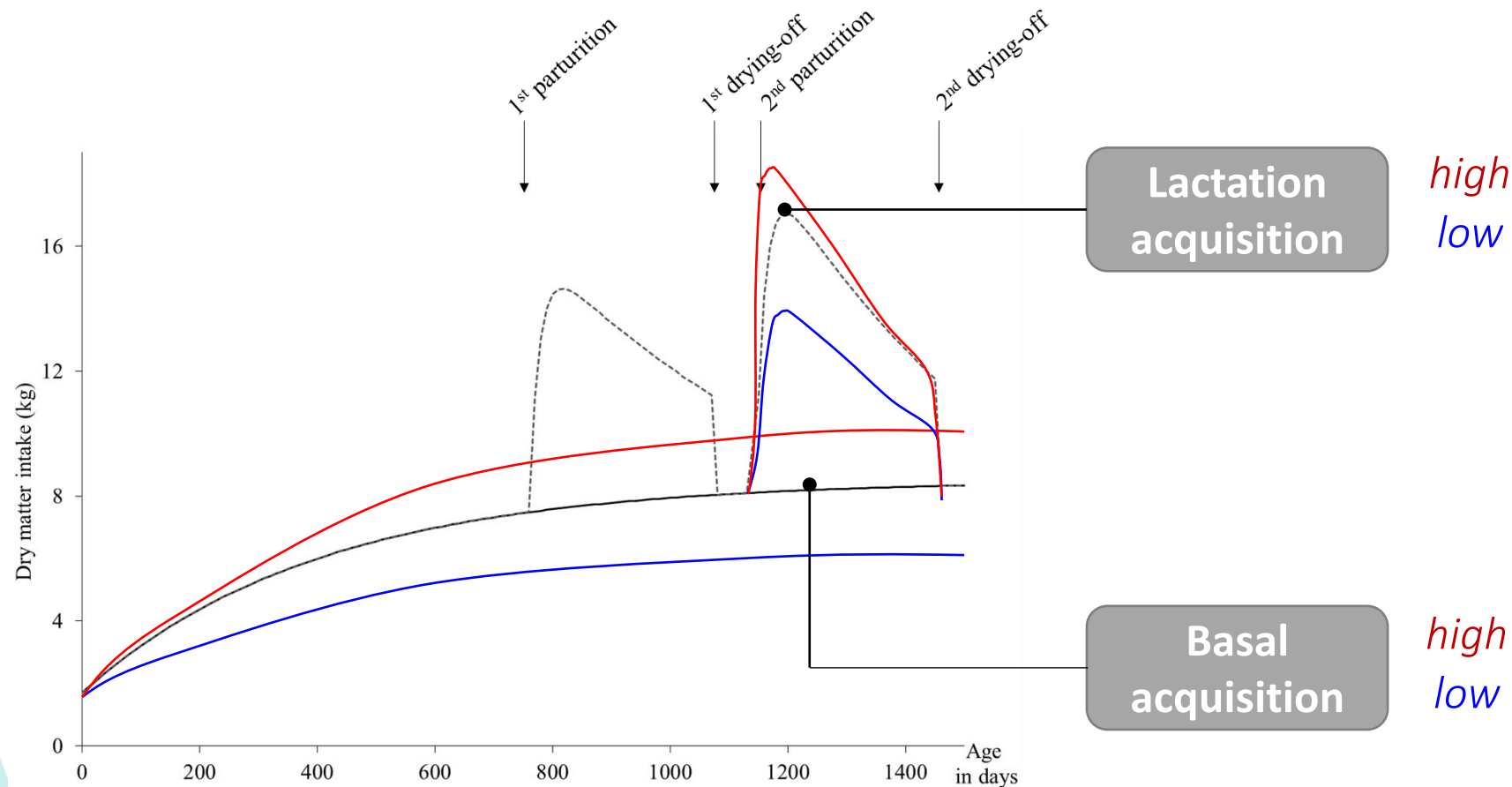
Heat production

$$Milk = \frac{NE_{lactation}}{EV_{milk}}$$

kcal                      kcal/kg  
 kg

## ➤ AQAL model (Acquisition-Allocation)

### Focus on acquisition



≠ combinations of parameters → variability of cow's capacities to acquire resource

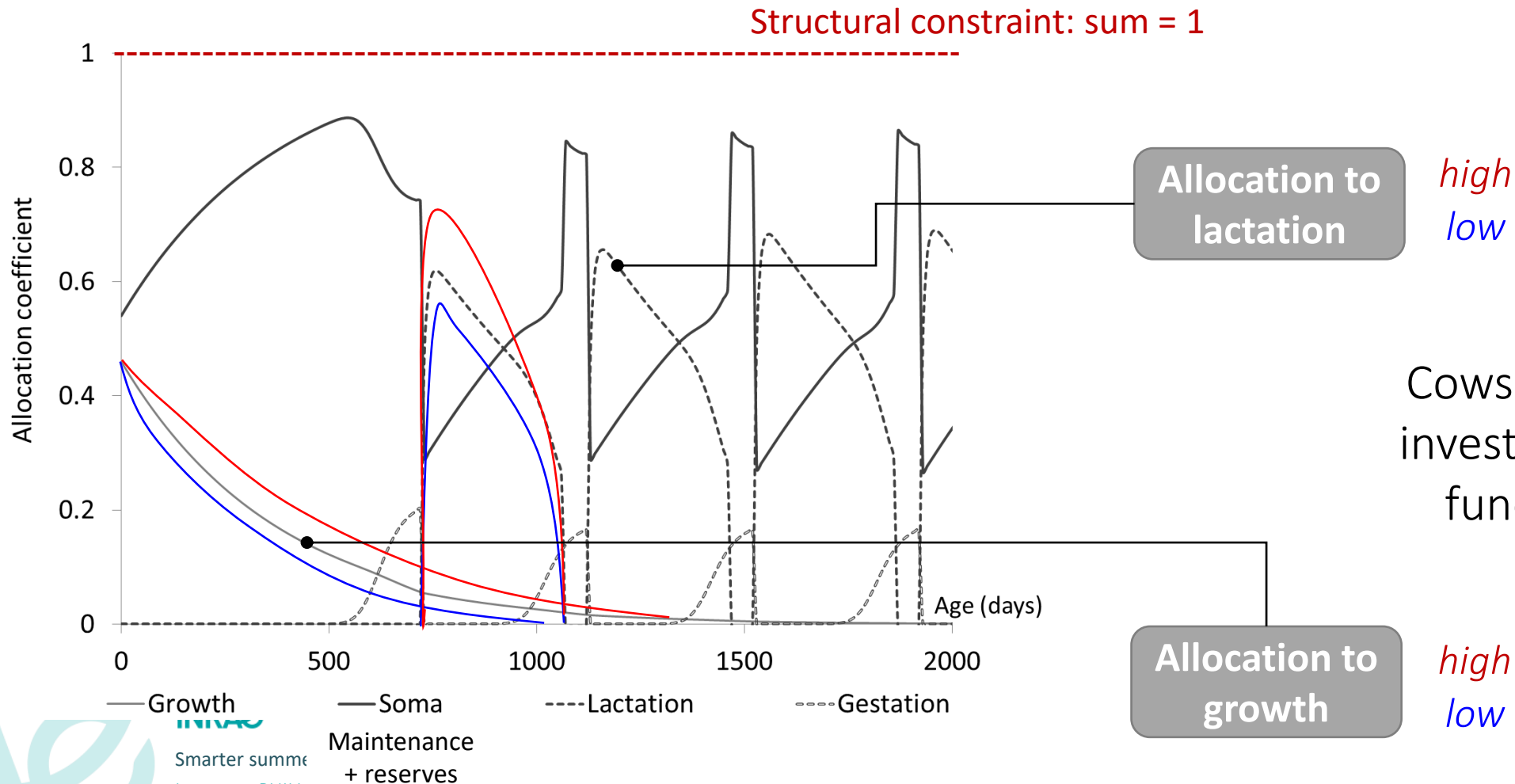
$$basal_{acq} = \frac{GSP}{1 + \alpha \cdot e^{-\beta \cdot age}}$$



## ➤ AQUAL model (Acquisition-Allocation)

### Focus on allocation

Dynamics of priorities among functions  
Inherited patterns of energy allocation



## ➤ AQUAL model (Acquisition-Allocation)

### Focus on allocation

A closed network of 4 compartments, with a quantity of 1 (virtual, dimensionless) flowing

→ At any time step, sum of compartments = 1 (no leak)

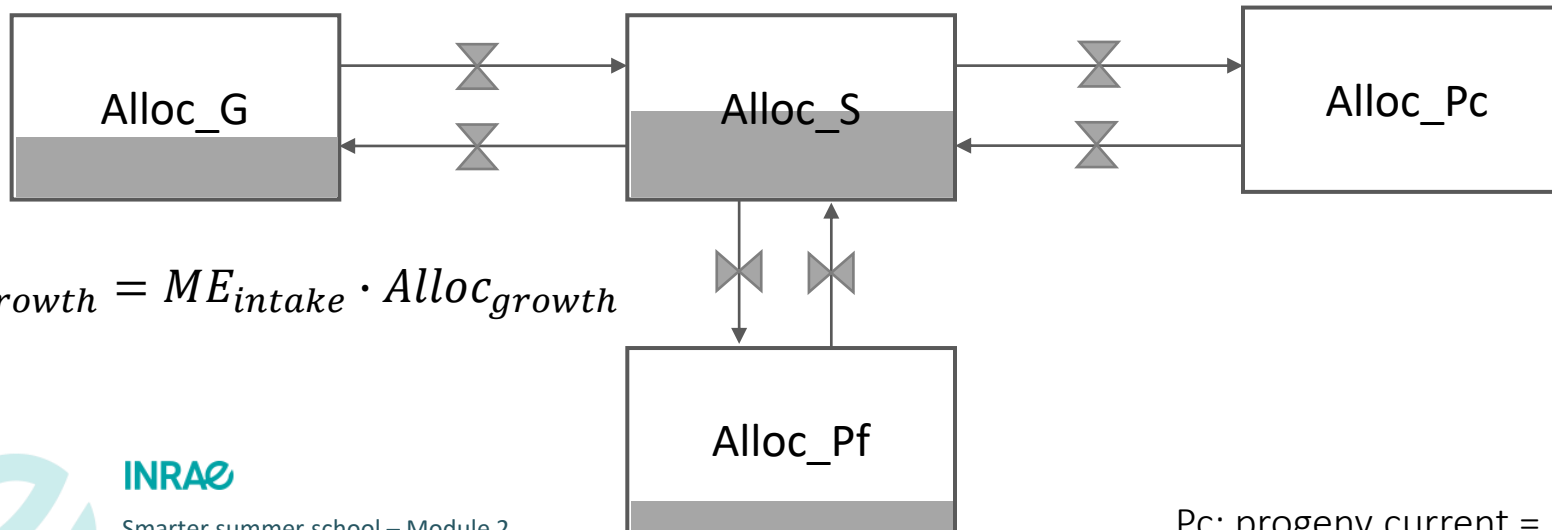
Compartment value = allocation coefficient value (level of priority)

System dynamics approach (Forrester diagram)

Flows control = (genetic-scaling) parameters | boolean (physiological status)

ODE formalism, with numerical integration

$$\frac{dAlloc_G}{dt} = k_G \cdot Alloc_G$$



Modeller's choice: where to put genetics = GSP versus "normal" parameter

$$ME_{growth} = ME_{intake} \cdot Alloc_{growth}$$

Pc: progeny current = lactation

Pf: progeny future = gestation



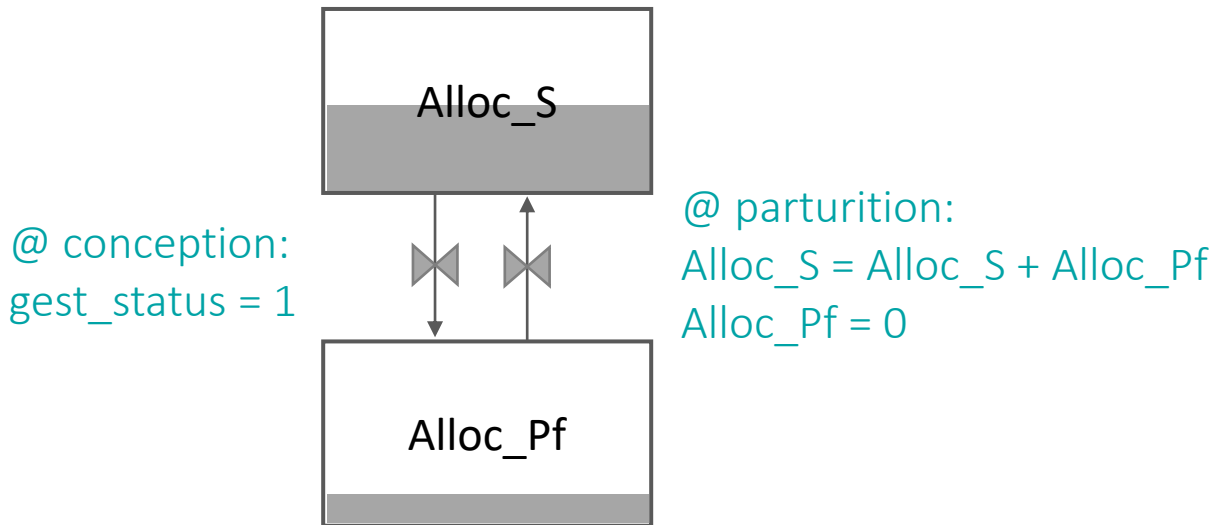
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## ➤ AQUAL model (Acquisition-Allocation)

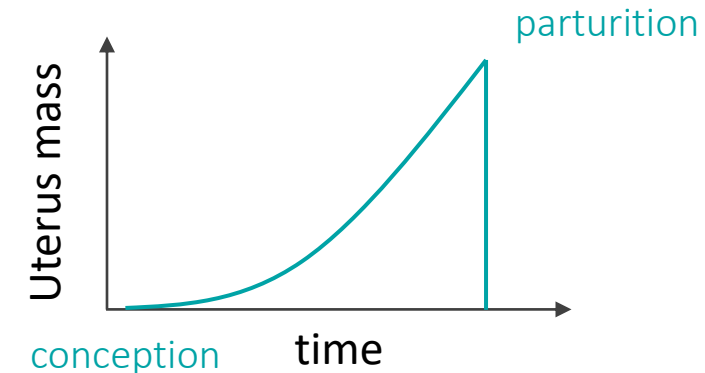
### Dynamic transmission: example of gestation



$$NE_{gestation} = ME_{intake} \cdot Alloc_{gestation} \cdot k_{eff}$$

$$flow_{GravidUterus} = \frac{NE_{gestation}}{EV_{GravidUterus}}$$

$$\frac{dMass\_Uterus}{dt} = flow_{GravidUterus}$$



## ➤ AQUAL model (Acquisition-Allocation)

Need a “minimal” environment

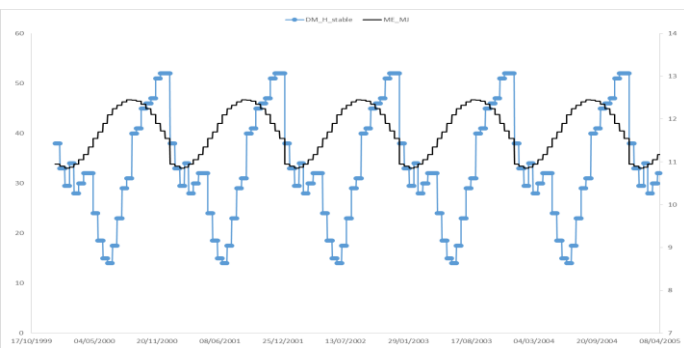
Changes in  
physiological stages

$$P_{\text{conception}} = f(\text{MY}, \text{BCS}, \text{EB}) \quad \text{Reproduction management}$$

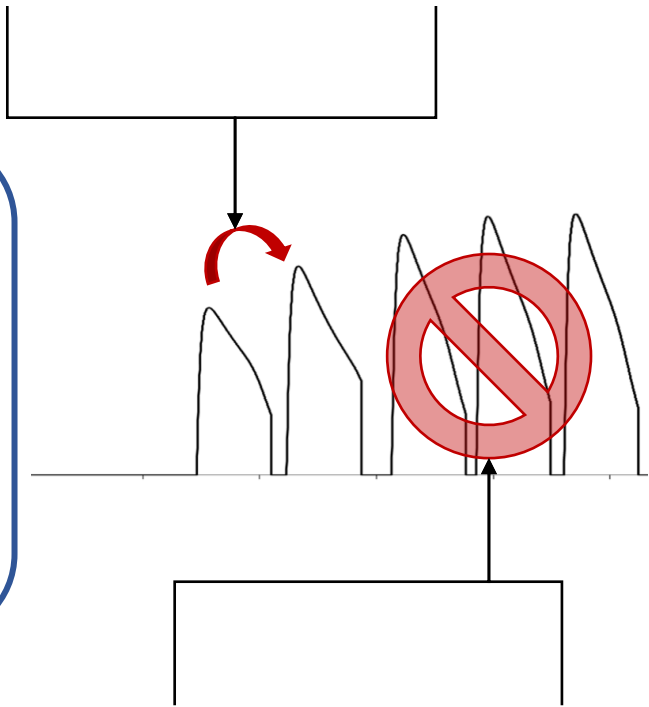
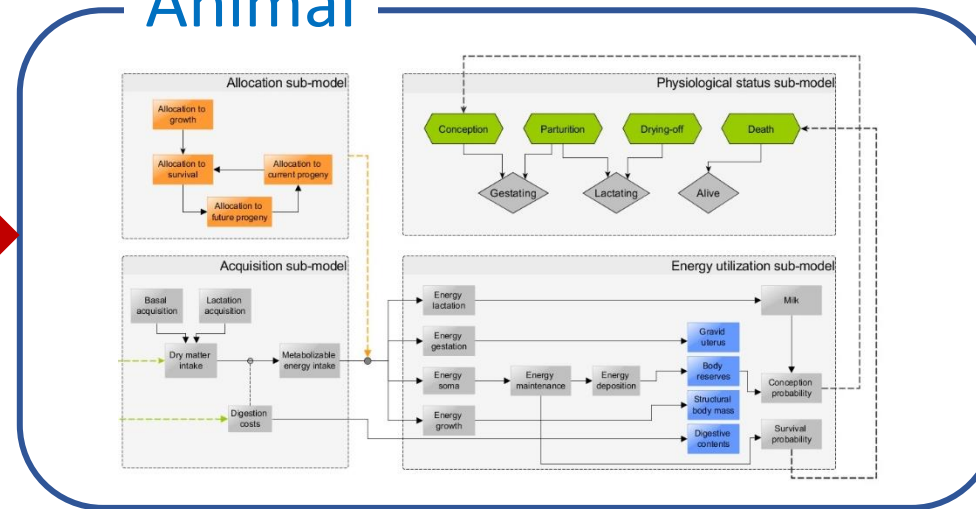
Potential  
limitation of  
acquisition

Dry matter  
offer (kg/d)

Energy content  
(ME/kg DM)



Animal



$$P_{\text{death}} = f(\text{cover maintenance})$$

Culling  
rules

- Manipulating acquisition and allocation parameters to generate variability in production trajectories

Thanks for your attention and let's move to the *in silico* part of the lecture!