Are there limits to selection in poultry ? theoretical, biological, ethical, environmental ?

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Preamble

Selection is at the beginning of the poultry chain :
Which types of animals are needed ?
how are the breeding goals defined ?
What diversity of genotypes should be offered ?

Does selection always reach its goals ?
Litterature on selection ‘plateaux’ :
→**Selection may exhaust genetic variability**
But
→**Evolutive mechanisms maintain variability**

Selection may reduce fitness ⇒ unrealized selection response

Main issues

- Selection theory and possible limits
  – Principles and Experimental evidence on poultry
- Biological limits and decreased fitness
  – Physiological constraints
  – Unfavorable correlated responses
- Ethical limits
  – Welfare issues and social acceptance
- Environmental limits
  - Climate change and limited natural resources

Quantitative genetics theory

An infinite number of genes with additive effects:

simple and powerful !

Selection response: **$R = h^2 S$** (h^2 heritability = σ^2_a / σ^2_p)

S selection differential

(function of σ^2_p and fitness)

Additive genetic variance at a locus $\sigma^2_a = 2 \Sigma_l p_l q_l (a_l - b_l)^2$

depends on allelic effects and allelic frequencies

(a - b) = effect of substituting one allele by the other

True for a population at *equilibrium* (no selection, mutation, migration)

⇒ Selection is modifying allelic frequencies

Effects of selection on genetic variance

Change in p: $\Delta p = i\, pq\, (a - b) / \sigma_p$

i = selection intensity,

Selection effect will be maximal for intermediate values of p and for large substitution effects (major gene)

When allelic frequencies are very unbalanced,

selection will be less and less effective

→ complete fixation seems very unlikely or very slow

→ AND a large number of loci is controlling selected traits

Deviations from the simple model of additivity

Dominance effect :

the genetic value of an heterozygous is different from the mean of the values of both homozygous → d may be negative or positive

$$\sigma^2_d = 4 \Sigma_l (p_l q_l d_l)^2$$

Interaction between genes : epistasis

Additive by additive or additive by dominance, or dominance by dominance

Interactions between genetic effects and environmental effects :

statistical G x E

epigenetic mechanisms

⇒ These sources of variation influence response to selection

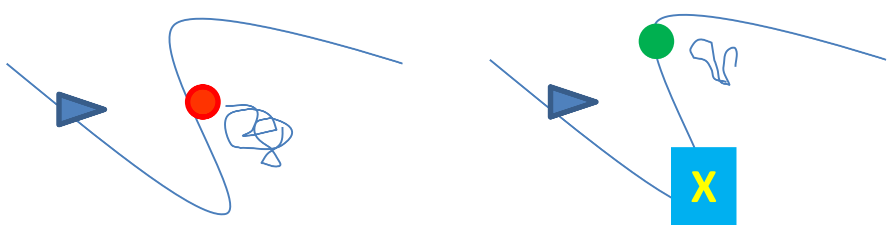
Genome dynamics

- **Mutation**: the typical evolutive force maintaining diversity,

  takes place at a low frequency, can generate genetic abnormalities

- **Recombination** : regular event, ‘the life of the genome’ !

Genes may act as clusters, some regulating the action of others, even at distance ; recombination may break such clusters and create new variation



This has been proven in plants, by genotyping molecular markers across generations

- Mobile elements, endogenous retroviruses

⇒additional reasons why selection limits may not be observed

Importance of population size for predicting selection response

Population size limits the gene pool

Small population size increases the impact of random events :
genetic drift may become as important as selection pressure

Ne: effective population size represents the size of a population in equilibrium showing the same **Δp** as the observed population
⇒ Prediction of ultimate selection response R according to Ne

Approximate value of Ne

N males	N females	Ne ≈	50% R at
50	200	160	224 gen
10	50	33	47 gen

Selection in practice

Several factors are preventing gene fixation during selection :

- Evolving selection objectives, adding new traits
- Moderate selection pressure, slow process
- Large base population
- New lines arising from crossbreeding
- at the opposite, inbreeding (F) is limiting the selection response
  - Within population σ^2_a is linearly decreasing with F
  - Increased frequency of genetic abnormalities

A higher ratio of deleterious mutations/neutral mutations in the most inbred of 3 layer lines (Derks et al., 2018)
$\Rightarrow$ may limit selection response by decreasing fitness

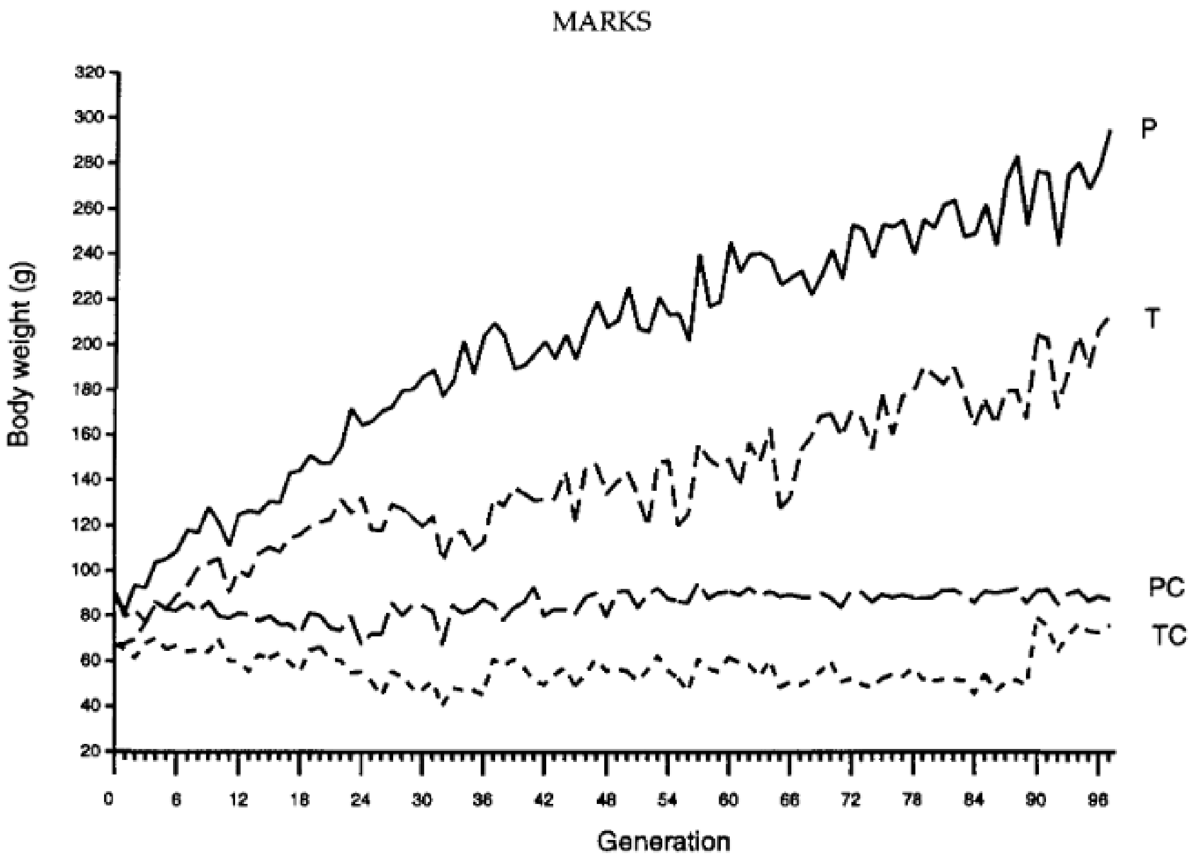
First take-home message

Selection is unlikely to exhaust all components of genetic variation

but inbreeding is the main risk for long-term selection response

Evidence from experimental lines

The longest selection experiment on 4 wk body weight in quails (Marks, 1996)



97 generations

P = control diet

28% CP

T = 20% CP

PC and TC : controls

Selection response

Still observed in P

Much lower in T

Realised heritability

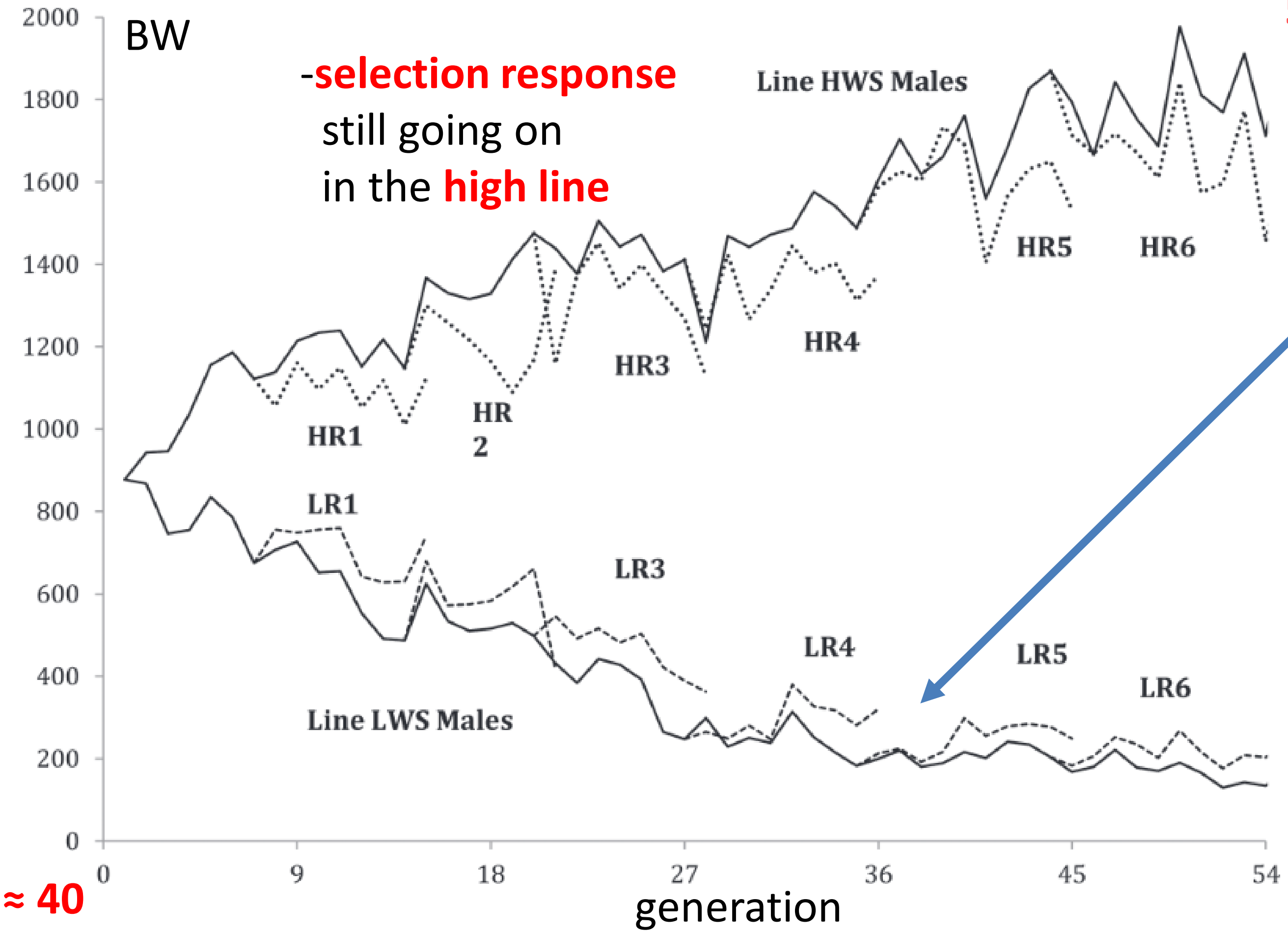
h^2 0.29 → 0.11 in P

h^2 0.22 to 0 in T ↗ ↘

Ne ≈ 72

Evidence from experimental lines

Long term selection experiment on 8 wk BW in chickens (Dunnington et al., 2013)



-**selection response** still going on in the **high line**

54 generations

-**selection limit** in the **low line**

fitness limits R

But molecular variation remains

(Lillie et al., 2018)

Relaxed lines

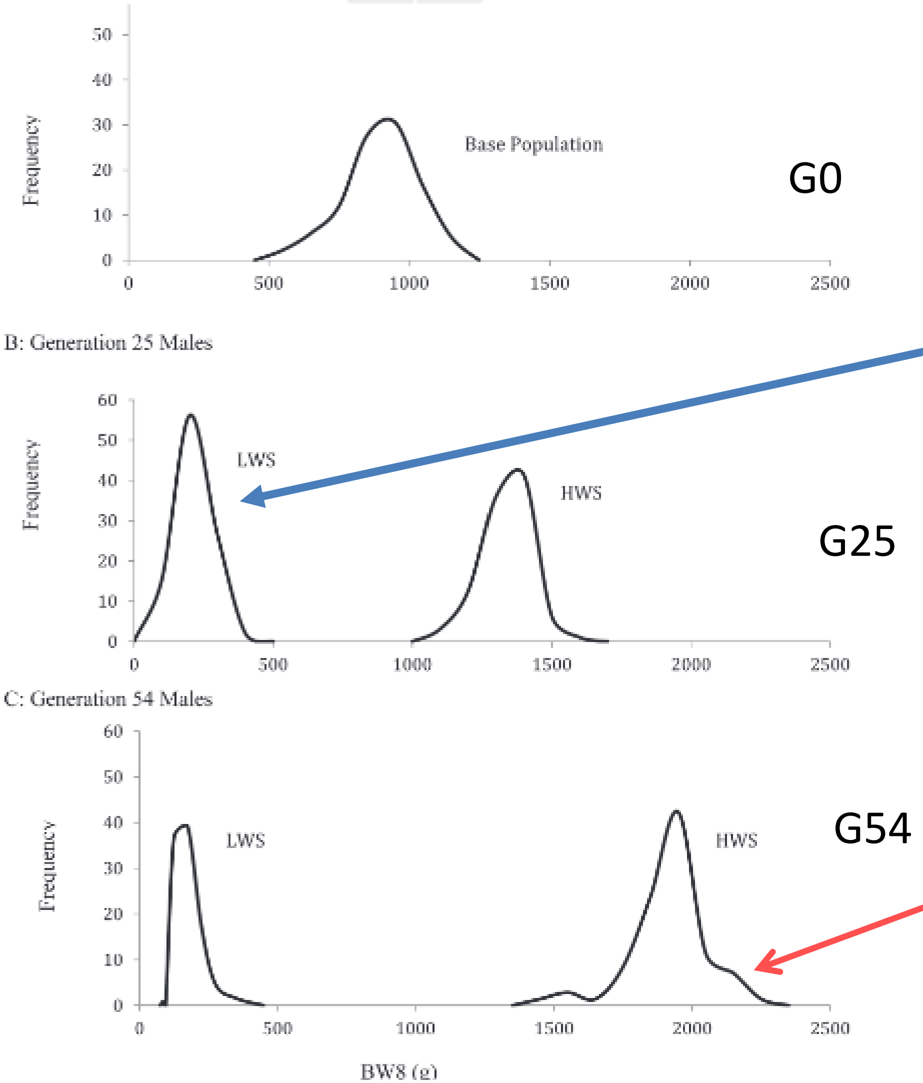
little regression

AND

Lower molecular variation : higher inbreeding

Ne ≈ 40

Evidence from experimental lines



Change in phenotypic variances
(Dunnington et al., 2013)

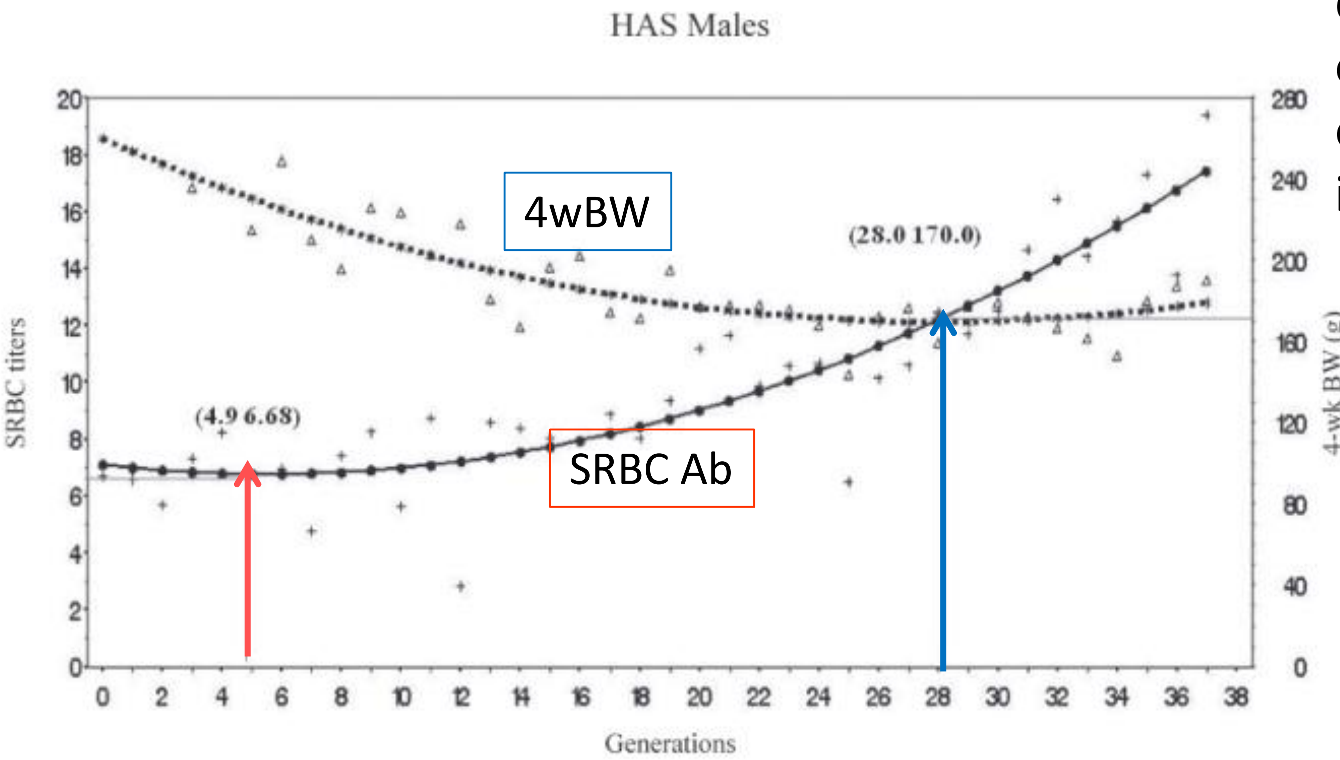
-**loss of phenotypic variance** in the **low line**
no overlap between lines

-**variation and outliers** in the **high line**

mutations
(G40 to G54 :
one molecular event could be traced)
or
gene x gene interactions

Evidence from experimental lines

Long term selection experiment on immune response in chickens (Zhao et al., 2012)



37 generations divergent selection on SRBC antibodies : effect on 4 wk BW in males

Trade-off with 4wk BW In males

different inflexion points according to trait

Ne ≈ 25

Lessons from selection experiments

Divergent selection experiments generally exhibit dissymetry :
Limit is reached more easily in one direction (**physiological limit**)
Whereas molecular variation remains

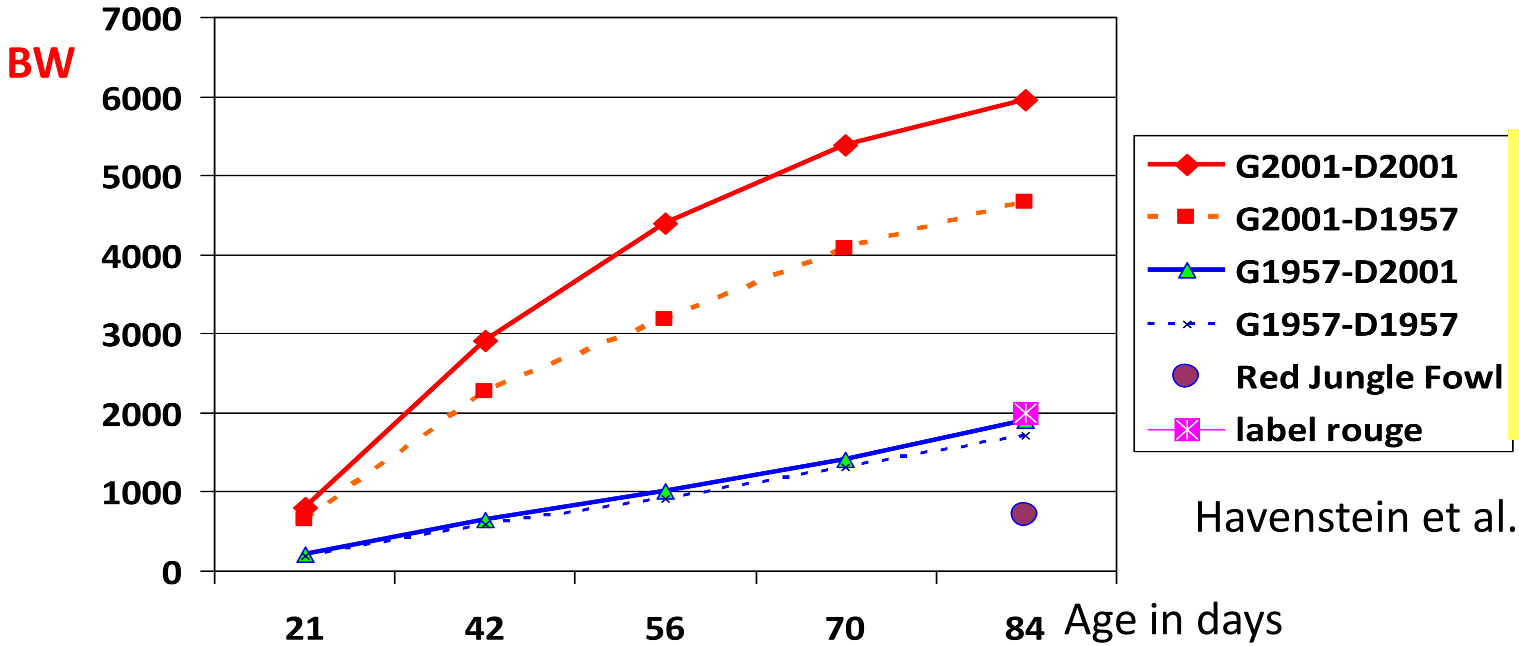
No evidence for selection plateau in lines selected for a high value,
in spite of a decrease in additive genetic variance
But number of generations generally still < 1.4 Ne

Long term selection show evidence of mutations

Changing environments can 'reveal' hidden variation

Evidence from commercial lines

Selection response has been taking place for > 50 generations still < 1.4Ne



GxD interaction ***
G significant
D significant
G >> D

Havenstein et al., Poult Sci, 2003

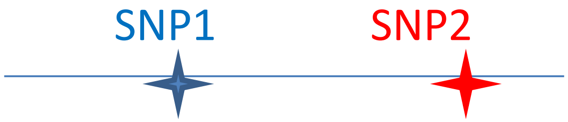
However, variation assessed by molecular markers indicates some loss of genetic variation particularly in layers

Within-population variability

(microsatellites Leroy et al., 2012)

Mean values	Unbiased Hetero-zygosity	Observed Hetero-zygosity	Population History	Mean Number of alleles	Effective Number of alleles
Broiler *(3 lines)*	**0.487**	**0.490**	Commercial GP	**3.26**	**2.21**
Layer *(2 lines)*	**0.351**	**0.328**	Commercial GP	**2.55**	**1.76**
Taïwan *(6 breeds)*	**0.489**	**0.488**	Conserved breeds	**3.33**	**2.20**
France **(14 breeds)**	**0.527**	**0.505**	Traditional breeds	**3.68**	**2.45**
West Africa ***(23 provinces 450 birds)***	**0.588**	**0.580**	Village Chickens	**4.64**	**2.96**

Impacts of selection on genome diversity patterns: linkage disequilibrium



LD: Does SNP1 provide information on SNP2 ?

Calculate correlation coefficient r^2 between adjacent markers

haploblock size for association studies = segment size where $r^2 > 0,3$

Differences reflect not only selection but also size of the base population

Qanbari et al., 2010,
Muir et al., 2008
Mwacharo et al., 2013
Qanbari et al., 2014

Biological limits to selection

✓**Physiological constraints** :

limiting value of a trait for survival or reproduction

as illustrated by selection experiments:

→selection limits on decreased BW or decreased antibody level

→**decreased fitness : limits the selection intensity**

✓**Unfavorable correlated responses to selection**:

question of resource allocation

→ opposition high growth/immune response high growth/reproduction

→ decoupling between 'muscular growth' and 'supply organs'

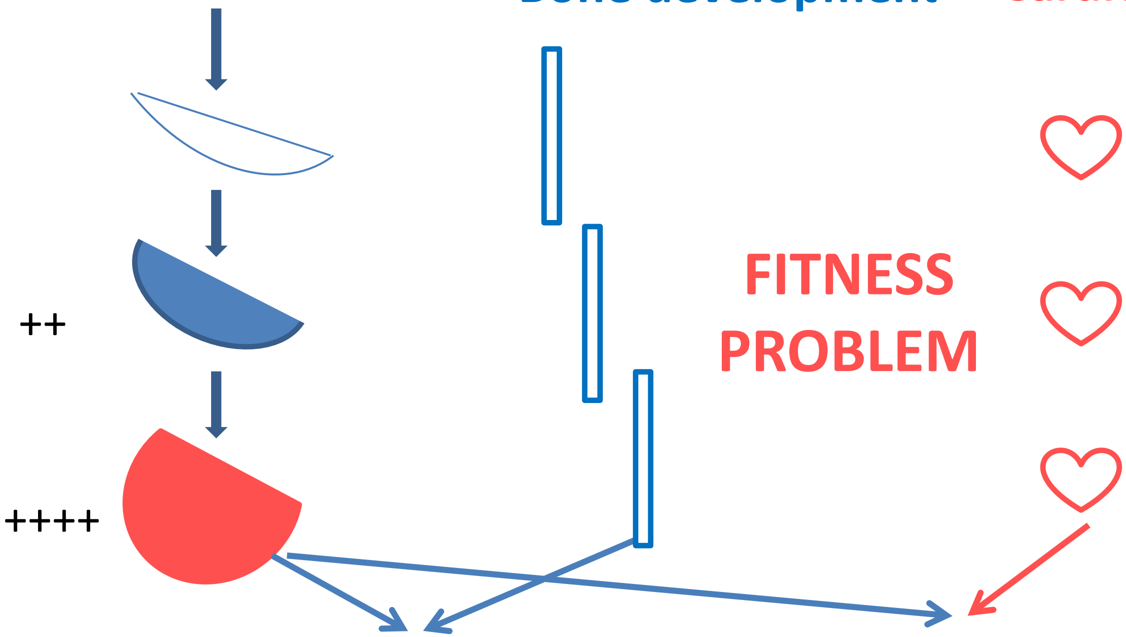
✓**Limit in the expression of a trait**: ex = ovulation rate

Resource allocation (broilers)

Selection on Breast meat

Unselected support tissue Bone development

Unselected supply tissue Cardio-vascular



Uncoupling: lameness, TD..

Ascites

Possible solutions to go beyond the limit

Management
(Tre, feed)

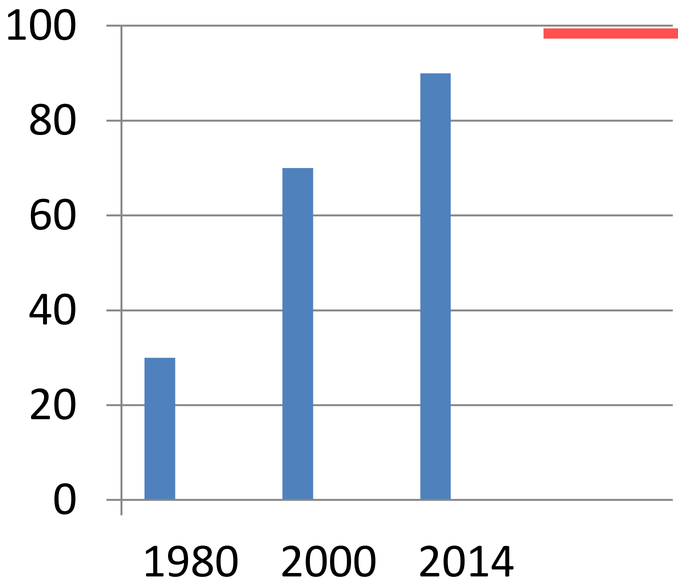
Selection in new environment

New selection criteria
bone score
O_2 saturation in blood

Antagonistic functions (broilers)

Fast early growth / excessive appetite /fatness / poor reproduction

→ **Management solution : severe feed restriction of future breeders**



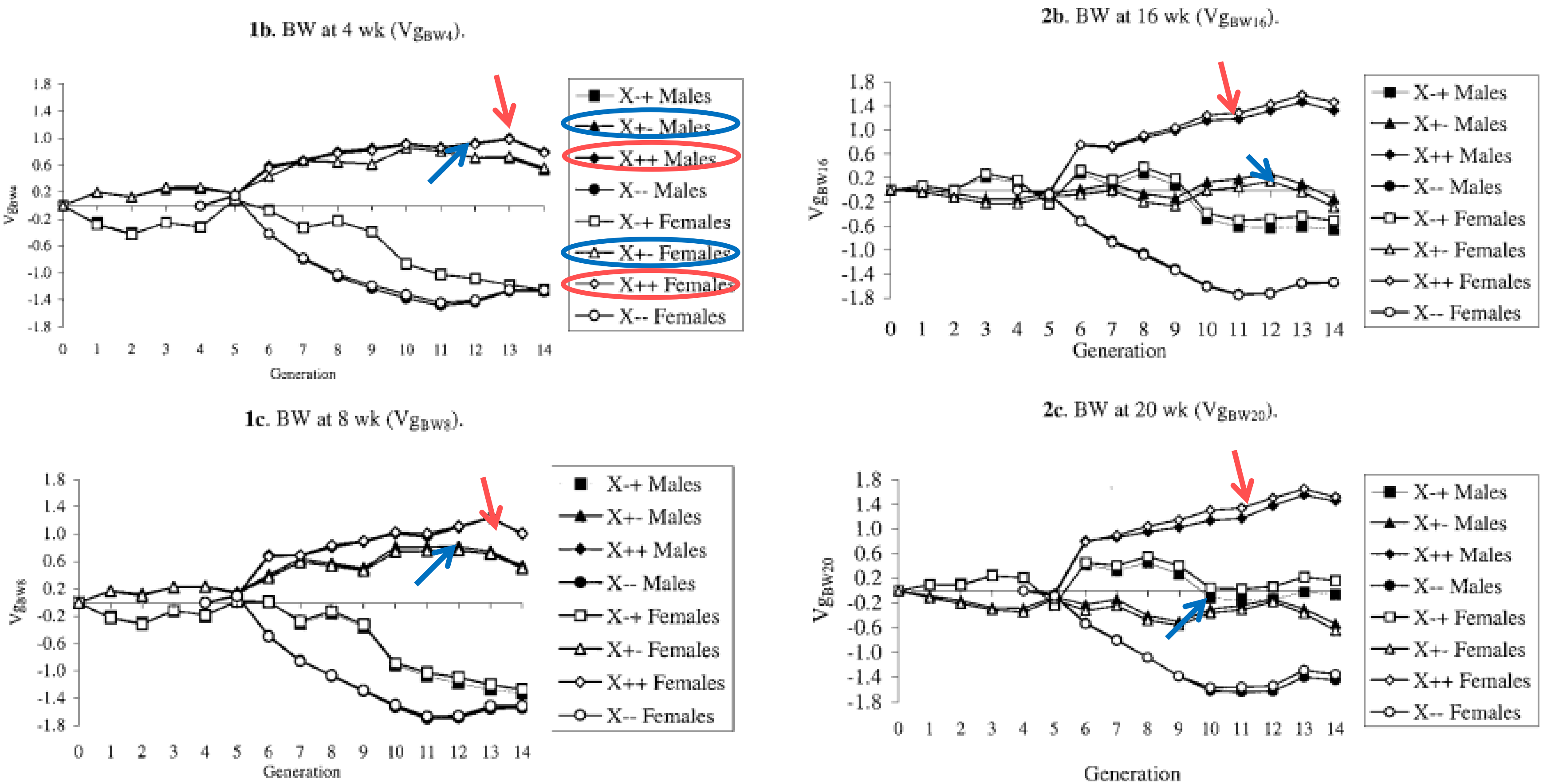
Physical limit to feed restriction !

Welfare issue: hunger

The **genetic correlation between growth and reproduction is not linear:** too small or too large BW : poor reproduction

Antagonism growth/reproduction

→ genetic solution : modify growth curve (broilers)

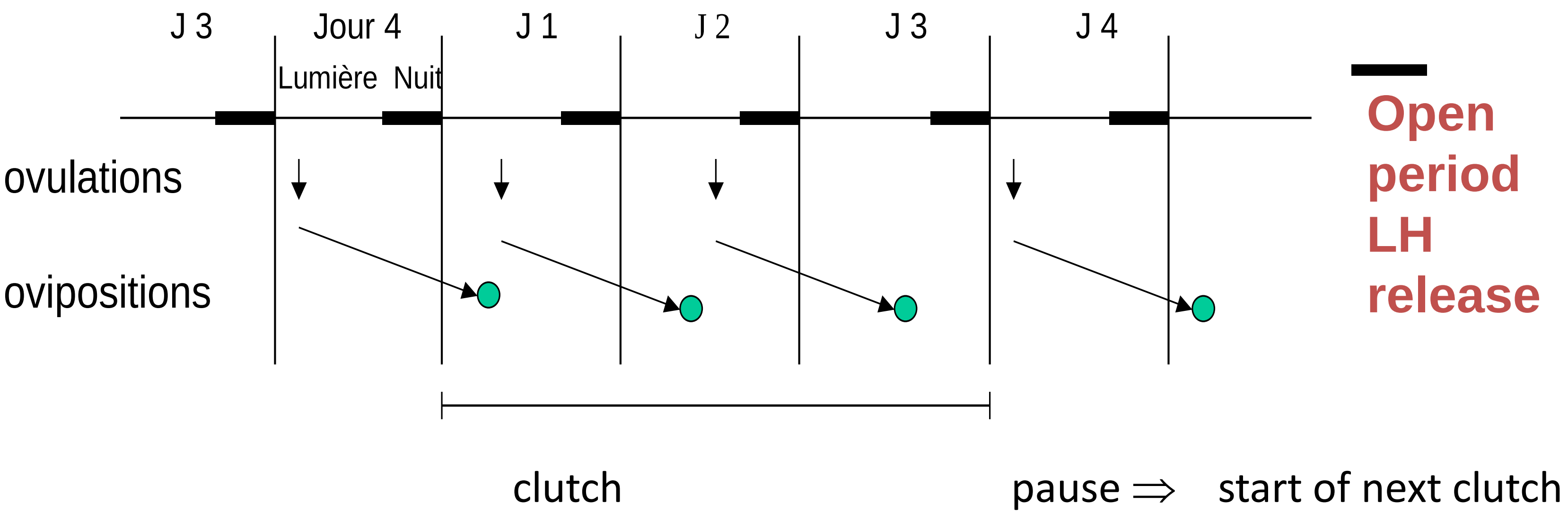


Mignon-Grasteau et al., 2001

towards a biological compromise ?

Biological limit (layers)
24h cycle and ovulatory cycle

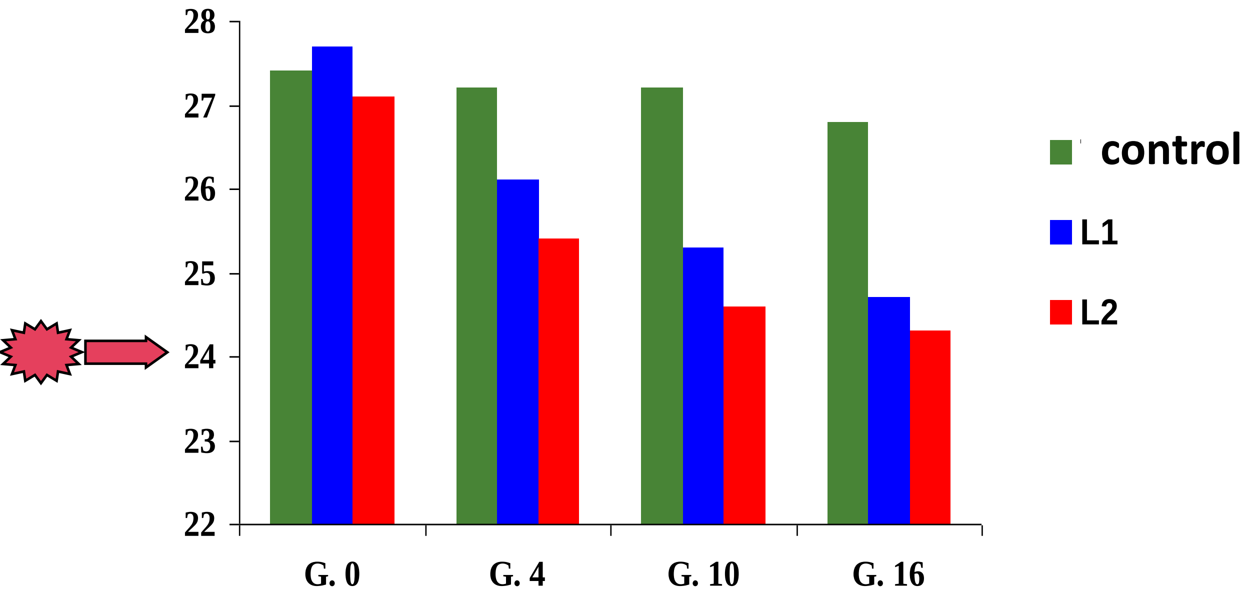
Endogenous cycle is constrained by the day-light external cycle



Biological limit (layers)
24h cycle and ovulatory cycle

Selection on clutch length in a dwarf brown egg-layer

→ **Effect on interval between ovipositions with a 16 L/ 8 D external cycle**



(Chen & Tixier-Boichard, 2003)

Solutions to go beyond the limit:

-**continuous lighting**
(Yoo et al., 1986)
> 1 egg /24 hours

-**Extended laying production**
→ 70 wks of lay
more days
with one egg a day

Take-home messages about biological limits

Several examples of such biological limits illustrate that selection response can be limited by a decreased fitness

Increased frequency of metabolic disorders :
Prevents selection of individuals with high breeding value for growth

Management solutions: short term

Genetic solutions (new trait in the breeding goal):
cumulative, long term, more complex programme
with a price to pay on the progress of the other traits

Ethical limits

- **Ethics raises questions, does not impose answers**

  →moral values and a more general view on the living world

- **There are ethical issues raised by intensive selection :**

-welfare : hunger in fed-restricted broiler breeders
Cannibalism / debeaking in layers

⇒ **Who does feel responsible** for this in the production chain ?
breeder? Producer? Slaughter-house, retailer ? Consumer ?

⇒ What is the main justification : to feed human population

Reactions from society : example in The Netherlands with the 'Wakker Dier' welfare association against the 'Plofkip'


Mijn burger bij
McDonald's?
Hoe dan ook
zónder
plofkip!!
WAKKER
DIER


AH-KLANTEN OPGELET
Deze verpakking bevat plofkip.
KIP
PLOFKIP
3.18


Een kilo plofkip is
geen stuntartikel.


PAS OP! BEVAT PLOFKIP

From the 'Plofkip'
to the Chicken of to-morrow

Media campaign + Pressure on supermarkets

Agreement on

Maximal growth rate allowed for the chicken: **50 g/day**

Has increased its market share (50% retailer) in a few years

Real limit to the selection goal

Leave room to select on other traits

Ethical limits

➢ **Relative perceptions according to countries and culture**

➢ Technology often considered as the solution, indeed, but

« **Higher technology calls for higher responsability »**

to be considered for genome editing !
Just take some time to think of consequences !

Environmental limits

➢ **Bird metabolism and ambient temperature :**

A very fast growing broiler ⇒ high metabolic heat

Confort zone : temperature range where the animal does not need to use evaporation or adapt its metabolism to maintain its normal body temperature

20 years ago : confort around 22-23°C ambient

Nowadays: confort zone of fast growing broilers ≈ 16-18 °C ambient

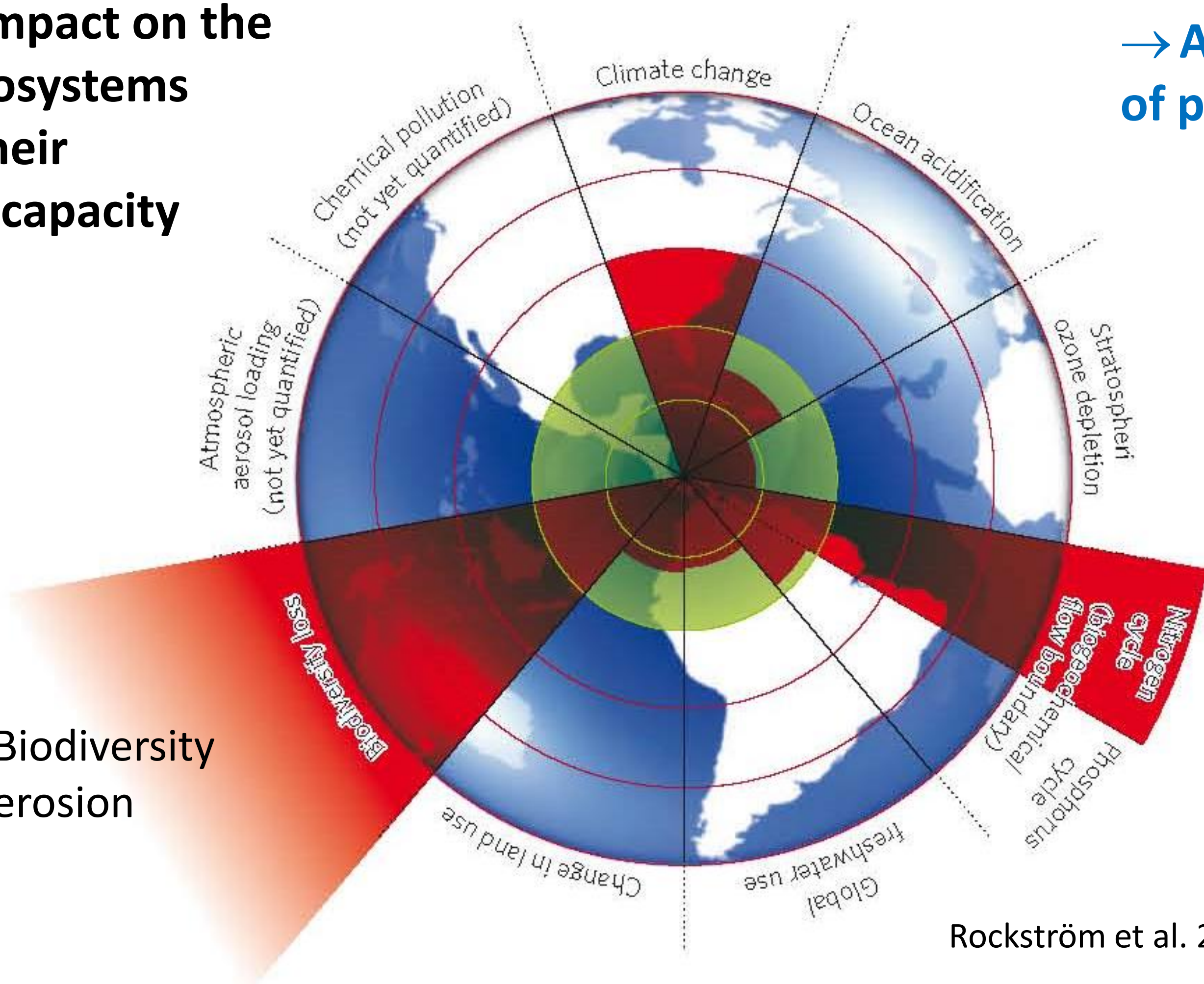
Higher ambient T^res will limit growth

What to do ? → decrease body weight objective
→ use naked animals (Sc mutation)
→ air conditionning (energy cost,
(humans don't get it ...)

Not unlimited resources on the planet

Human activities have an impact on the planet ecosystems beyond their buffering capacity

++ Demography:
→ Another way of producing food



Nitrogen cycle
Pollutions

Biodiversity
erosion

Rockström et al. 2009, Nature

Environmental limits and selection goals

Green-house-gas emissions: poultry on the safe side

Feed efficiency selected with high quality feed

$\Rightarrow$ **dependency on arable lands for high quality feed,**

$\Rightarrow$ select on ability to digest other feeds

Competition food/feed : stronger for poultry than for ruminants

Optimization of animal proteins in human diets: 15 to 45% proteins (Van Zanten et al., 2016; Van Kernebeek et al., 2016)

Data on cattle or pig production, but **few studies on chickens**

Conclusions

Selection response is still taking place

Acceleration with genomics

⇒ **careful monitoring of effects on genetic variance and deleterious variants**

Limit 1: extreme performance level is decreasing fitness

Genetics should be more predictive of such consequences

Selection objectives should consider **trade-offs between fitness and production**

Limit 2 ethical responsability regarding the living world ?
awareness of dependency on environment ?

➢ Which food systems do we want ?

- ➢ **update breeding goals**
- ➢ **manage diversity, gene bank or live populations**
- ➢ **propose a Portfolio of genotypes**

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