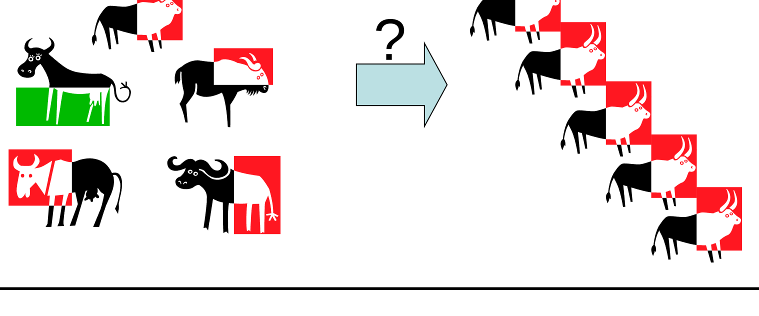
Uniformity

Inherited variability

Uniformity

Can we change phenotypic variability by means of breeding?



Opportunities to change variability

- In the classical framework
  - P = A + E
- When variability is a heritable trait in itself
  - Var(E) = A + E'

Opportunities within the classical frame work

- P = A + E
  - $\rightarrow$ Var(P) = Var(A) + Var(E)
  - Var(E) is not a heritable trait
  - Changes in Var(P) have to come from changes in Var(A)
- (1-Heritability) presents a limit to what can be achieved
  - Lowest possible std of trait $\sigma_E = \sqrt{(1-h^2)}\ \sigma_P$
  - E.g. $h^2 = 0.3 \rightarrow \sqrt{0.7} = 0.84 \rightarrow$ we cannot reduce the std by more than 16%
- Opportunities within the classical framework are limited

Using Inbreeding

$$Var(A)_F = (1-\overline{F})Var(A)_{\overline{F}=0}$$

- Problems when using inbreeding at the population level
  - F↑ → Var(A)↓ → response to selection ↓
  - Inbreeding depression
- Problems when using inbreeding as a mating strategy
  - F_{max} = 0.25 → the effect is very small
    - h^2 = 0.3 → $$sd(P) = \sqrt{0.75\times 0.3+0.7}\sigma_{P,0} = 0.96\sigma_{P,0}$$
  - Inbred individuals are more sensitive → Var(E) ↑
- Conclusion: inbreeding is not promising

Using an inbred parent

- Concept: Inbred parents have lower Mendelian sampling variance → less variability among offspring

$$Var(A_{off}) = \frac{1}{4}Var(A_S) + \frac{1}{4}Var(A_D) + Var(MS_S) + Var(MS_D)$$

- Use single fully inbred sire → $\frac{1}{4}Var(A_S) + \frac{1}{4}Var(A_{MS}) = 0$

$$sd(P) = \sqrt{0.5\times 0.3+0.7}\sigma_{P,0} = 0.92\sigma_{P,0}$$

- Using an inbred parent is not promising

Using in- & outbreeding

- Concept: outbred individuals show lower Var(E)
  - The effect is not very well known
- Use inbred but unrelated parents to produce an F1
- Theoretical maximum: Var(A_{parent}) = Var(MS) = 0
- Effect:

$$sd(P) = \sqrt{0.7}\sigma_{P,0} = 0.84\sigma_{P,0}$$

- Some reduction is possible, in particular when Var(E) also decreases
- Problem: How to get fully inbred sires and dams?

Use compensatory mating

- Concept: use opposite sires and dams
- Theoretical optimum: Corr(A_{Sire},A_{Dam}) = –1 $\rightarrow$ Var(A_{Sire} + A_{Dam}) = 0
- Effect: $sd(P) = \sqrt{0.5 \times 0.3 + 0.7}\sigma_{P,0} = 0.92\sigma_{P,0}$
- Problem 1: not feasible for multiple traits
- Problem 2: Corr(A_{Sire},A_{Dam}) = –1 requires 100% accuracy of EBV
- Not promising
- Compensatory mating is unimportant

Conclusions for the classical model

- Since $h^2 \approx 0.3$, the maximum reduction equals $1-\sqrt{0.7}$ = 16%, which is small
- Even this 16% is difficult to achieve
- There are trade-offs with response to selection and inbreeding depression
- Real effects must come from reducing Var(E)

Heritable variability

Treating Var(E) as a heritable trait

Var(E) as a heritable trait

- What do we mean?
  - Classical: Var(A) $\rightarrow$ genetic variance in the mean trait value of a genotype
  - E.g. a difference among sires in the mean trait value of their offspring
  - $Var_A(\sigma_E^2)$ $\rightarrow$ genetic variance in the (environmental) variability of a genotype
  - E.g. differences between sires in the variability among their offspring

Simplest possible case: clones

- Variation within a cloned genotype
- $P = A + E$, $Var(A_{clone}) = 0 \rightarrow Var(P_{clone}) = Var(E)$
  - E.g compare 1000 individuals of each of two genotypes
  - $Var(P_{clone1}) \neq Var(P_{clone2})$ $\rightarrow$ clones vary in Var(E) $\rightarrow$ genetic variance in variability
- Genetic variance in Var(E) does not necessarily mean <u>heritability</u> of Var(E)
  - Heterozygous genotypes may show lower Var(E) than homozygous genotypes $\rightarrow$ dominance effects

Key Question

1. Does $Var_g(\sigma_E^2) > 0$ occur?

2. Is this genetic variability in Var(E) heritable?

If the answer is YES, then we can breed for uniformity ☺

Modeling heritable variance in Var(E)

- The additive model (Hill and co-workers)
  - (the standard deviation model; briefly)

- The exponential model (SanChristobal et al.)

The additive model

- Additive effects for the mean trait value, A_m
- Additive effects for the variability of trait value, A_v

$$P_i = \mu + A_{m,i} + E_i$$
$$E_i \sim N(0, \sigma_E^2 + A_{V,i})$$
$$\sigma_{E,i}^2 = \sigma_E^2 + A_{v,i}$$

$A_{m,i}$ = breeding value of i for mean

$A_{v,i}$ = breeding value of i for residual variance

σ_E^2 = the mean environmental variance

$$\begin{bmatrix} A_{m,i} \\ A_{v,i} \end{bmatrix} \sim N\left(\begin{matrix} 0 \\ 0 \end{matrix}, \begin{matrix} \sigma_{A_m}^2 & \sigma_{A_m A_v} \\ \sigma_{A_m A_v} & \sigma_{A_v}^2 \end{matrix}\right)$$

Bivariate model:
Two normally distributed traits
that are correlated

This is an additive model because the breeding value is added to the mean var(E)

The additive model

- This model can also be written as

$$P_i = \mu + A_{m,i} + \chi\sigma_{E,i}$$
$$P_i = \mu + A_{m,i} + \chi\sqrt{\sigma_E^2 + A_{V,i}}$$
$$\chi \sim N(0,1)$$

- Conceptual problems with the additive model
  - "Heritability" of Var(E) is 100%

    $$\sigma_{E,i}^2 = \sigma_E^2 + A_{v,i} \quad \text{vs} \quad \sigma_{E,i}^2 = \sigma_E^2 + A_{v,i} + E_{v,i}$$

    - This is only an issue with repeated observations on the same individual, otherwise E_v and χ are fully confounded
  - Var(E_i) can become negative if $A_{v,i}$ is strongly negative
    - Probably unlikely for practical cases

The standard deviation model (briefly)

- This model specifies the breeding value on the SD instead of the variance (Garcia et al., 2009)

$$P_i = \mu + A_{m,i} + \chi\sigma_{E,i}$$

$$P_i = \mu + A_{m,i} + \chi(\sigma_E + A_{V,SD,i})$$

- Conceptual problems with the standard deviation model
  - SD(E_i) can become negative if $A_{v,SD,i}$ is strongly negative
    - Probably unlikely for practical cases
  - The average residual standard deviation does not equal σ_E

    $\overline{\sigma_E} = \sqrt{\sigma^2_{e,SD} + \sigma^2_{A_V,SD}}$
  - Part of the genetic variance in SD ends up in the mean residual SD.

The exponential model

- The exponential model specifies an additive breeding value on the log-scale

$$\ln(\sigma^2_{E,i}) = \ln(\sigma^2_E) + A_{v,i}$$

- Hence, $A_{v,i}$ is an additive breeding value for the log of the variance

- Taking the exponent $\rightarrow$ $\sigma^2_{E,i} = e^{\ln(\sigma^2_E) + A_{v,i}}$

- Since $e^x > 0$, this model avoids the problem that Var(E_i) can become negative

The exponential model

$$\sigma^2_{E,i} = e^{\ln(\sigma^2_E)+A_{v,i}} \Longrightarrow P_i = \mu + A_{m,i} + \chi \exp\left(\frac{\ln(\sigma^2_E)+A_{v,i}}{2}\right)$$

- The factor ½ comes from taking the square root of Var(E_i)

$$\left(e^x\right)^y = e^{xy}, \sqrt{} \rightarrow y = \tfrac{1}{2}, \rightarrow \left(e^x\right)^y = e^{x/2}$$

For example: $\sqrt{9} = \sqrt{3^2} = (3^2)^{½} = 3^{2x½} = 3$.

How to interpret the exponential model?

$$\sigma^2_{E,i} = e^{\ln(\sigma^2_E)+A_{v,i}} = e^{\ln(\sigma^2_E)}\, e^{A_{v,i}} = \sigma^2_E\, e^{A_{v,i}}$$

$$A_v \approx 0 \rightarrow e^{A_{v,i}} \approx 1 + A_{v,i} \rightarrow$$

$$\boxed{\sigma^2_{E,i} \approx \sigma^2_E (1 + A_{v,i})}$$

e.g. $e^{0.1} \approx 1.1$

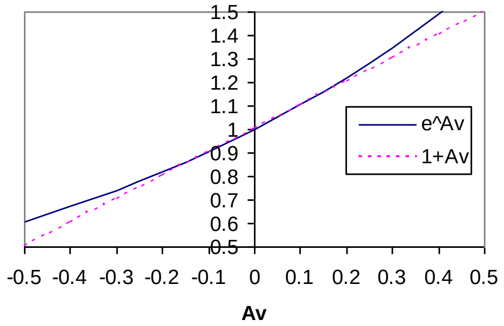
First-order Taylor series

- The breeding value in the exponential model is a multiplication factor
  - $A_v = 0.1 \rightarrow$ Var(e) is 10% increased
- The exponential model is additive on the log scale
- The exponential model is multiplicative on the observed scale

How to interpret the exponential model?

$$\sigma^2_{E,i} = \sigma^2_E \, e^{A_{v,i}} \approx \sigma^2_E (1 + A_{v,i})$$

approximation exp(Av) = 1+Av



The approximation is quite good
↓
Multiplicative interpretation is OK

A conceptual problem of the exponential model

- The mean environmental variance does not equal Var(E)

$$\sigma^2_{E,i} = e^{\ln(\sigma^2_E) + A_{v,i}}$$

$$\Rightarrow \overline{\sigma^2_{E,i}} = E\left[e^{\ln(\sigma^2_E) + A_{v,i}} \right]$$

$$\Rightarrow \overline{\sigma^2_{E,i}} = \sigma^2_E \exp(\tfrac{1}{2}\sigma^2_{A_v})$$

$$\exp(\tfrac{1}{2}\sigma^2_{A_v}) > 1 \Rightarrow$$

$$\overline{\sigma^2_{E,i}} > \sigma^2_E$$

Genetic variance ends-up in the mean
↓
This hampers comparison of studies
and interpretation of genetic trend

Relationship between both models

- Additive model: $\sigma^2_{E,i,ADD} = \sigma^2_{E,ADD} + A_{v,i,ADD}$
- Exponential model: $\sigma^2_{E,i,EXP} \approx \sigma^2_{E,EXP}(1 + A_{v,i,EXP})$
- $\rightarrow$ Relationship: $A_{v,i,ADD} \approx \sigma^2_{E,EXP} A_{v,i,EXP}$
- Breeding values differ approximately by a factor Var(E)
- Genetic variances differs approximately by a factor Var(E)^2

$$\sigma^2_{A_{V,ADD}} \approx \sigma^4_{E,EXP} \sigma^2_{A_{V,EXP}}$$

Exact relationships between both models

- Breeding values

$$\begin{aligned} A_{V,add} &= \sigma^2_{E,\exp} \exp(A_{v,\exp}) - \sigma^2_{E,add} \\ &\approx \sigma^2_{E,\exp} A_{v,\exp} + \left[\sigma^2_{E,\exp} - \sigma^2_{E,add}\right] \end{aligned}$$

- Genetic variances

$$\begin{aligned} \sigma^2_{A_{V,add}} &= \sigma^4_{E,\exp} \exp(2\sigma^2_{A_V,\exp}) - \sigma^4_{E,add} \\ &\approx \sigma^4_{E,\exp} \sigma^2_{A_V,\exp} + \left[\sigma^4_{E,\exp} - \sigma^4_{E,add}\right] \end{aligned}$$

In addition to a multiplication factor, there is a (small) difference in mean

Conclusions on models

- Results from both models can be converted into each other
- Both models have conceptual issues
  - The exponential model is statistically more correct
  - The additive model better fits within the usual animal breeding framework

Interpreting the magnitude of $Var_g(E)$

- Coefficient of variation: CV = σ/μ
  - Standard deviation as fraction of the mean
  - Expresses variability relative to the mean
- Genetic coefficient of variation: GCV = σ_A / μ
  - Evolvability (Houle, 1992, Genetics 130: 195)
  - For classical breeding traits: GCV ≈ 3 - 10%
- Application to heritable variance in the additive model
  - μ = mean environmental variance = Var(E)
  - σ = genetic std in environmental variance = $\sigma_{A,v}$

$$GCV_v = \frac{\sigma_{A_V}}{\sigma_E^2}$$

Why evolvability makes sense

- Response to selection: $\Delta\mu = ir_{IH}\sigma_A$

$$\frac{\Delta\mu}{\mu} = ir_{IH}\frac{\sigma_A}{\mu}$$

- Relative change in mean trait value equals:
  - - the strength of selection (i)
  - - times the correlation between the criterion and the BV (r_{IH})
  - - times the GCV (σ_A/μ).
- Evolvability expresses the (biological) opportunity for response to selection, relative to the mean trait value

Interpreting the magnitude of Var_g(E)

The GCV of the residual <u>variance</u> (GCV_v):

The additive model:

$$\sigma^2_{E,i} = \sigma^2_E + A_{v,i} \rightarrow \mathrm{var}(\sigma^2_E) = \sigma^2_{A_v}$$

$$\rightarrow GCV_v = \frac{\sigma}{\mu} = \frac{SD(\sigma^2_E)}{\overline{\sigma^2_E}} = \frac{\sigma_{A_v}}{\sigma^2_E}$$

The ratio of the standard deviation in environmental variance
and the mean environmental variance

Interpreting the magnitude of $Var_g(E)$

The GCV of the residual <u>variance</u> (GCV_v):

The standard deviation model (Garcia et al. 2009):

$$\sigma_{E,i} = \sigma_E + A_{v,SD,i} \rightarrow .... \rightarrow$$

$$\rightarrow GCV_{v,SD} = \frac{\sigma}{\mu} = \frac{SD(\sigma_E^2)}{\overline{\sigma_E^2}} = \frac{2\sigma_{A_{v,SD}}}{\sigma_E^2}$$

The ratio of the standard deviation in environmental standard deviation
and the mean environmental variance,
multiplied by a factor of 2.

Interpreting the magnitude of $var_g(E)$

The GCV of the residual <u>variance</u> (GCV_v):

The exponential model:

$$\sigma_{E,i}^2 \approx \sigma_E^2 (1 + A_{v,i}) \Rightarrow GCV_{v,EXP} = \frac{\sigma}{\mu} = \frac{SD(\sigma_E^2)}{\overline{\sigma_E^2}} = \sigma_{A_{V,EXP}}$$

In the exponential model, the standard deviation of the residual variance
is an estimate of the genetic coefficient of variation

So you don't need to divide by the mean environmental variance

Interpretating the magnitude of var$_g$(E)

- Are we interested in the variance or in the standard deviation of the trait?
- **Issue: on the SD scale, the CV is only half as large!**

$$GCV_v = \frac{SD(\sigma_E^2)}{\overline{\sigma_E^2}} = \frac{\sigma_{A_V}}{\sigma_E^2}$$

but:

$$GCV_{SD} = \frac{SD(\sigma_E)}{\overline{\sigma_E}} = \frac{1}{2}\frac{\sigma_{A_V}}{\sigma_E^2}$$

This ½ holds irrespective of the model

It matters a lot (50%) for the interpretation of the importance of genetic variation in uniformity!

The Evidence

Does Var$_g$(E) exist?

Estimates of heritable variance in Var(E)

The evidence: “livestock”

Comparison of literature estimates of genetic variance in environmental variance

Source	Trait	$\sigma^2_{A_v,exp}$	$\sigma^2_{A_v}$ [b]	h^2_v [c]	GCV_E [d]
SanCristobal-Gaudy *et al.* (1998)	Fat/protein goat milk	0.000	0.000	0.000	0.000
	pH pig	0.150	1.2*E*-04	0.039	0.402
SanCristobal-Gaudy *et al.* (2001)	Litter size sheep	0.230	0.057	0.048	0.509
Sorensen and Waagepetersen (2003)[a]	Litter size pigs	0.090	4.291	0.026	0.307
Ros *et al.* (2004)[a]	Body weight (g) snails	0.290	0.368	0.017	0.580
Rowe *et al.* (2006)	Body weight (kg) broiler ♂	0.086	8460	0.029	0.299
	Body weight (kg) broiler ♀	0.096	5310	0.031	0.318

[a] Models included permanent environmental variance; environmental variance was taken from their model 1 estimates.
[b] Equation 17: $\sigma^2_{A_v} = \sigma^4_{E,exp}\exp(2\sigma^2_{A_v,exp}) - \sigma^4_E$.
[c] $h^2_v = \sigma^2_{A_v}/(2\sigma^4_P + 3\sigma^2_{A_v})$ = heritability of environmental variance.
[d] $GCV_E = \sigma_{A_v}/\sigma^2_E$, a measure of evolvability (Houle 1992).

Estimated GCV are quite high → suggests good prospects for improvement

The evidence: Drosophila

- Drosophila bristles and the nature of quantitative genetic variation
  - Mackay and Lyman (2005) Phil. Trans. R. Soc. 360: 1513
- ~300 inbred lines
- Crosses between those lines (uniform F1’s, i.e. heterozygous clones)
- Model: CV = sex + line + sex*line + e
- Var(line) > 0 → genetic variance in var(E)
  - Not necessarily heritable variance!

Table 1. Analyses of genetic variance of environmental plasticity for homozygous chromosome 2 substitution lines.

	sternopleural bristle number					abdominal bristle number			
source	d.f.[a]	MS[b]	F	p	σ^{2c}	MS[b]	F	p	σ^{2c}
sex	1	66.030	6.34	0.0122	fixed	44 182.0	167.86	<0.0001	fixed
line	325	14.544	1.40	0.0013	1.089	1117.717	4.23	<0.0001	220.481
sex × line	320	10.403	0.97	0.6117	−0.155	264.288	1.47	<0.0001	43.429
error	623	10.706			10.706	179.235			179.235

[a] Degrees of freedom. The design is unbalanced as some lines produced individuals of only one sex.
[b] Type III mean squares.
[c] Variance component.

Table 2. Analyses of genetic variance of environmental plasticity for homozygous chromosome 3 substitution lines.

	sternopleural bristle number					abdominal bristle number			
source	d.f.[a]	MS[b]	F	p	σ^{2c}	MS[b]	F	p	σ^{2c}
sex	1	75.868	7.84	0.0054	fixed	9031.54	80.69	<0.0001	fixed
line	322	12.863	1.33	0.0056	0.840	425.600	3.80	<0.0001	78.483
sex × line	320	9.693	1.18	0.0451	0.737	112.130	1.19	0.0373	8.936
error	625	8.240			8.240	94.518			94.518

[a] Degrees of freedom. The design is unbalanced as some lines produced individuals of only one sex.
[b] Type III mean squares.
[c] Variance component.

These results show large genetic variance in Var(E)
Largely due to recessive effects

More evidence

Genetic variance in micro-environmental sensitivity laying hens/broilers

Species	Trait	varav	GCV ve	**GCV sd**	GCV vp	GCV sdp	h2v
Laying hens	Egg color purebreds	0.08	0.28	**0.14**	0.11	0.05	0.01
	Egg color crossbreds	0.07	0.26	**0.13**	0.13	0.07	0.01
	Egg weight	0.10	0.32	**0.16**	0.17	0.09	0.03
Broilers	Body weight males	0.10	0.32	**0.16**	0.26	0.13	0.03
	Body weight females	0.14	0.37	**0.19**	0.30	0.15	0.04
	Body weight males	0.24	0.49	**0.25**	0.36	0.18	0.05
	Body weight females	0.32	0.57	**0.29**	0.36	0.18	0.05

Genetic variance in micro-environmental sensitivity pigs

Species	Trait	varav	GCV ve	**GCV sd**	GCV vp	GCV sdp	h2v
Pigs	Piglet birth weight LW	0.04	0.19	**0.09**	0.15	0.07	0.01
	Piglet birth weight LR	0.04	0.21	**0.10**	0.16	0.08	0.01
	Carcass weight P	0.08	0.28	**0.14**	0.17	0.09	0.03
	Carcass weight Spain	0.12	0.34	**0.17**	0.15	0.08	0.01
	Litter size Denmark	0.09	0.31	**0.15**	0.23	0.12	0.03

Genetic variance in micro-environmental sensitivity dairy cattle

Species	Trait	varav	GCV ve	**GCV sd**	GCV vp	GCV sdp	h2v
Dairy cattle	milk NL	0.03	0.19	**0.09**	0.04	0.02	<0.01
	milk Sweden	0.05	0.22	**0.11**	0.07	0.03	0.01
	SCS Sweden	0.05	0.21	**0.11**	0.10	0.05	0.01
	SCS Robustmilk farms	0.08	0.28	**0.14**	0.08	0.04	0.01
	milk Belgium	0.03	0.17	**0.09**	0.06	0.03	<0.01
	SCS Belgium	0.03	0.16	**0.08**	0.08	0.04	<0.01
	SFA Belgium	0.01	0.12	**0.06**	0.04	0.02	<0.01
	UFA Belgium	0.02	0.12	**0.06**	0.08	0.04	<0.01
	C18:1 cis-9 Belgium	0.02	0.12	**0.06**	0.09	0.04	<0.01

Genetic variance in micro-environmental sensitivity fish

Species	Trait	Varav	GCV ve	**GCV sd**	GCV vp	GCV sdp	h2v
Fish	Salmon	0.17	0.42	**0.21**	0.26	0.13	0.03
Tilapia	Harvest weight			**0.18**			
	length			**0.12**			
	width			**0.17**			
	Depth			**0.17**			

Genetic correlation phenotype and micro-environmental sensitivity

Analysis	$r_{A_m A_v}$	se
Egg color purebreds	-0.06	0.09
Egg color crossbreds	0.48	0.11
Piglet birth weight LW	0.62	0.12
Piglet birth weight LR	0.55	0.14
Carcass weight	0.13	0.16
Dairy cattle milk	0.74	

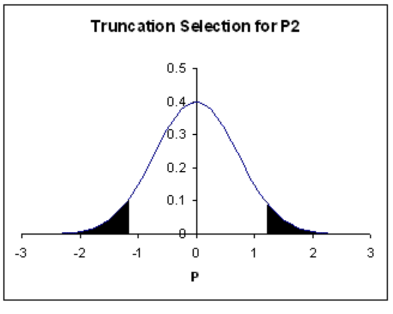
Estimates tend to be positive: higher trait values go together with more variation

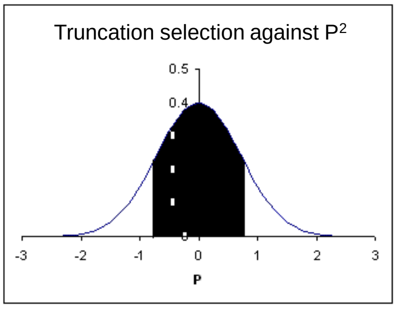
Heritability of Var(E)

Heritability of Var(E)

- Consider the additive model:
- Classical heritability as a regression coefficient
  - Heritability is the regression coefficient of breeding value on phenotype
  - "Realized heritability"
  - $E(A|P) = h^2(P-P_{avg})$
  - $h^2 = Cov(A,P)/Var(P) = Var(A)/Var(P)$
- Extension to the variance scale
  - Observation on the variance scale: P^2
  - h_v^2 is the regression of A_v on P^2
  - Reflects opportunities for changing the variance by selecting on P^2

Selection on P^2





Heritability of the variance relates to the change in variance with disruptive or stabilizing selection

Realized heritability of the variance: $h_v^2 = R_v / S_v$ for selection on P^2

Heritability of Var(E)

- Consider the additive model:
- Classical heritability as a regression coefficient
  - Heritability is the regression coefficient of breeding value on phenotype
  - $E(A|P) = h^2(P-P_{avg})$
  - $h^2 = Cov(A,P)/Var(P) = Var(A)/Var(P)$
- Extension to the variance scale
  - Observation on the variance scale: P^2
  - Heritability: regression of A_v on P^2

$$h_v^2 = b_{A_V,P^2} = Cov(A_V, P^2)/Var(P^2) \rightarrow\rightarrow\rightarrow$$

$$h_v^2 = \sigma^2_{A_V}/Var(P^2) \rightarrow\rightarrow\rightarrow$$

$$\Rightarrow \quad h_v^2 = \frac{\sigma^2_{A_V}}{2\sigma^4_P + 3\sigma^2_{A_v}}$$

Heritability of Var(E)

- The accuracy of mass selection on P^2

$$h_v^2 = \frac{\sigma^2_{A_V}}{2\sigma^4_P + 3\sigma^2_{A_v}}$$

You can do this because h_v^2 is defined as a regression coefficient

$$\Downarrow$$

$$r_{IH,mass(P^2)} = \sqrt{\frac{\sigma^2_{A_V}}{2\sigma^4_P + 3\sigma^2_{A_v}}}$$

Interpretation of h_v^2

- h_v^2 refers to
  - Inheritance of P^2 from parent to offsping
  - Accuracy of selection on P^2
- h_v^2 does **not** refer to
  - the proportion of variance in Var(E) that is heritable

$$\sigma^2_{E,i} = \sigma^2_E + A_{v,i} \Leftrightarrow \sigma^2_{E,i} = \sigma^2_E + A_{v,i} + E_{v,i} \qquad h_v^2 \neq \frac{\sigma^2_{A_V}}{\sigma^2_{A_V} + \sigma^2_{E_V}}$$

- h_v^2 is a measure for response and accuracy of mass selection on P^2
- GCV_v is a measure for genetic variability in variance

Estimates of h_v^2

Comparison of literature estimates of genetic variance in environmental variance

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Ros *et al.* (2004)[a]	Body weight (g) snails	0.290	0.368	0.017	0.580
Rowe *et al.* (2006)	Body weight (kg) broiler ♂	0.086	8460	0.029	0.299
	Body weight (kg) broiler ♀	0.096	5310	0.031	0.318

[a] Models included permanent environmental variance; environmental variance was taken from their model 1 estimates.
[b] Equation 17: $\sigma^2_{A_v} = \sigma^4_{E,exp}\exp(2\sigma^2_{A_v,exp}) - \sigma^4_E$.
[c] $h_v^2 = \sigma^2_{A_v}/(2\sigma^4_P + 3\sigma^2_{A_v})$ = heritability of environmental variance.
[d] $GCV_E = \sigma_{A_v}/\sigma^2_E$, a measure of evolvability (Houle 1992).

These values are quite low → accuracies of mass selection on P^2 ≤ ~0.2
Mass selection is not a powerful tool to increase uniformity

Conclusions on genetic parameters for variance

- Estimated GCV_g is high
  - Substantial genetic variance in var(E)
  - In principle, substantial improvement is possible
  - On the SD scale, differences are half as large!
- Estimated h_v^2 is low
  - Response and accuracy of mass selection on P^2 are low

- Hence: there is large genetic variation, but this is difficult to use because of low accuracy
  - We need something better than mass selection on P^2
  - Lectures Han Mulder