Estimation of genetic parameters

- Additive genetic variance / dominance deviation
- Heritability

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Quantitative genetics – the basic model

- Phenotype = Genotype + Environment + G*E + ??
- One assumes $P = G + E$

  ?

  - G (Genotypic value) = result of a number of loci that influence the trait

Quantitative genetics – the basic model

- Phenotype = Genotype + Environment + G*E + ??
- One assumes $P = G + E$

  ?

  - G (Genotypic value) = result of a number of loci that influence the trait
  - G is completely unknown, but estimated

- How?
  - Fisher (1918) developed statistical approach (‘analysis of variance’)
  - quantitative genetics allows one to make certain statistical inferences about the genetic basis of a trait given only the information on the phenotypic (co)variances in/between sets of known relatives

Quantitative genetics – the basic model

- Phenotype = Genotype + Environment + G*E + ??
- One assumes $P = G + E$

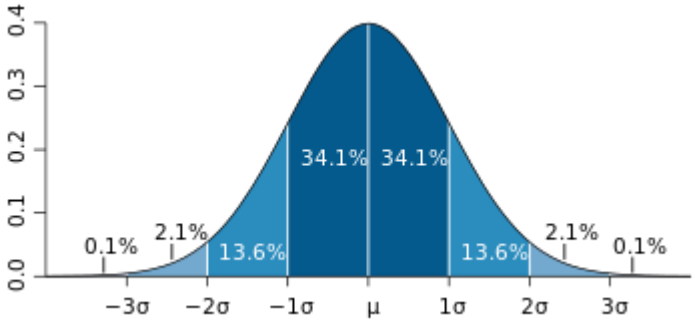
  ?
  - This is a statistical model !

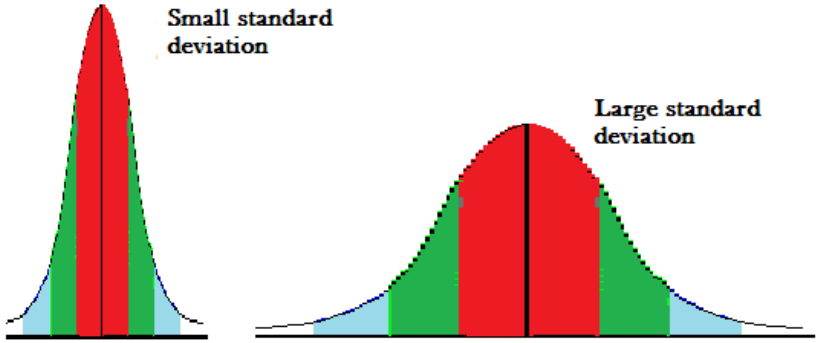
- Fisher: Variation in phenotype is dissected in variance components
  - This approach is based on phenotypic resemblance between relatives (see later)
    - e.g., offspring tend to have similar phenotypes as their parents if a trait is heritable

$$VarP = Var(G+E)$$

$$VarP = VarG + VarE \qquad (V_P = V_G + V_E)$$

Variance – how to interpret?





σ = SD, standard deviation

Gaussian curves are specified by two parameters: the mean, and the variance.

Variance (σ^2) measures how far a data set is spread out.

= *"The average of the squared differences from the mean"*

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Quantitative genetics – the basic model

- Phenotype = Genotype + Environment + G*E + ??
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  ?

  - G (Genotypic value) = result of a number of loci that influence the trait

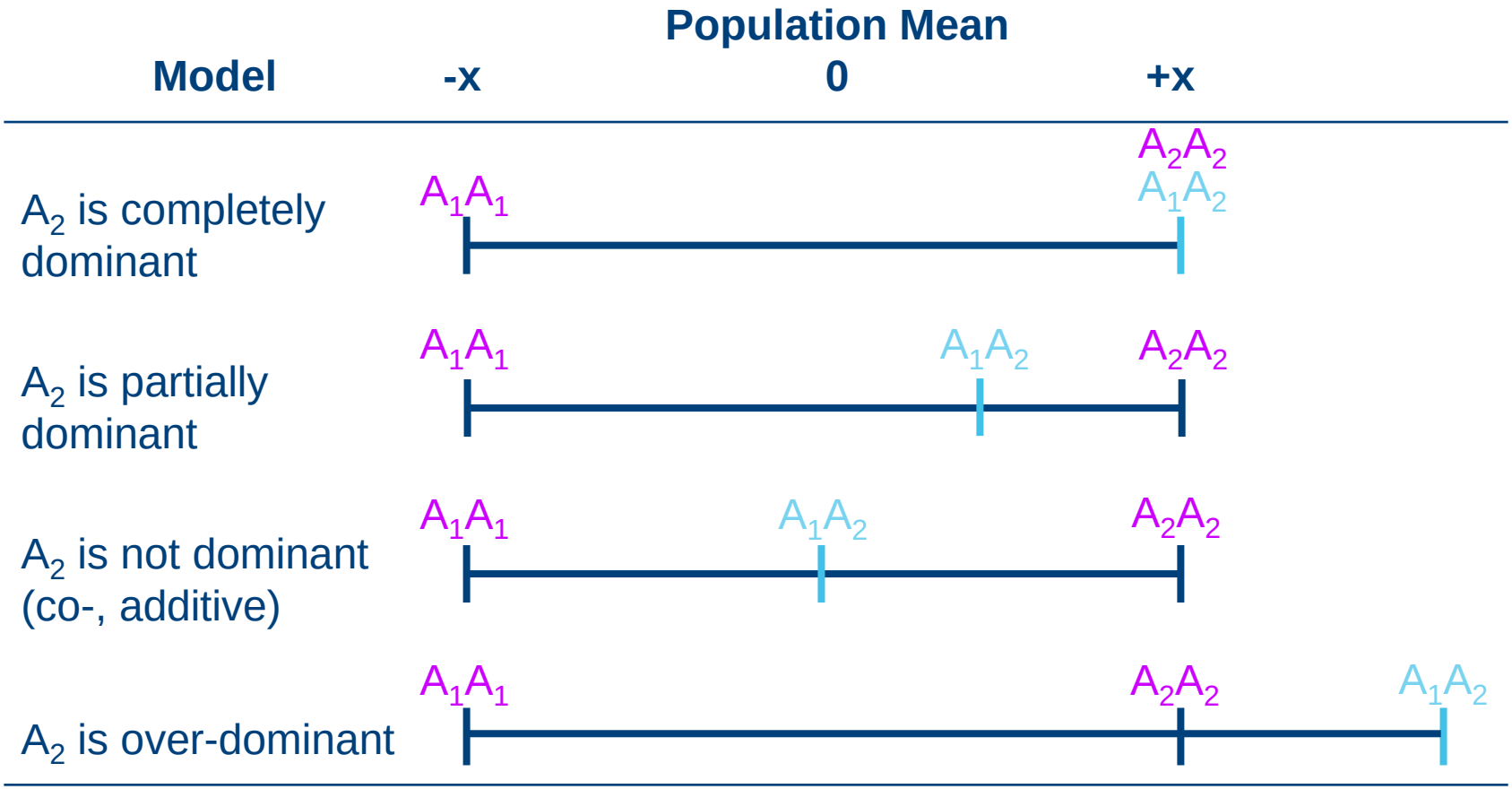
Contribution of a locus to the phenotypic value of a quantitative trait ?

Contribution of a locus to the phenotypic value of a trait

A_1 → x increase in height

A_2 → x decrease in height

Contribution of a locus to the phenotypic value of a trait



Contribution of a locus to the phenotypic value of a trait

- Suppose a single locus: A with alleles A_1 and A_2

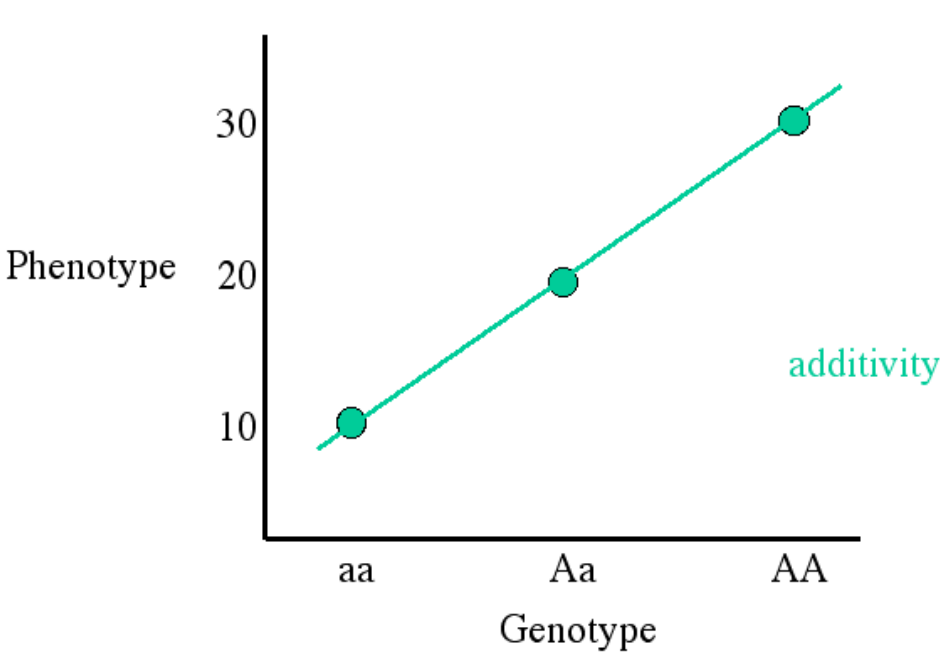
Genotypes	A_1A_1	A_1A_2	A_2A_2
Average trait value (X)	X	X+a+d	X+2a

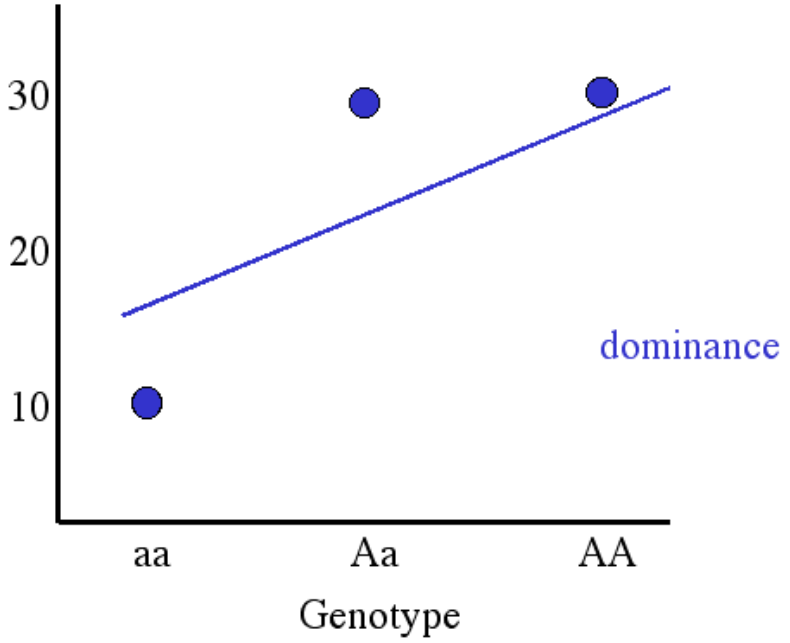
difference = 2a

a=additive effect, d=dominance effect

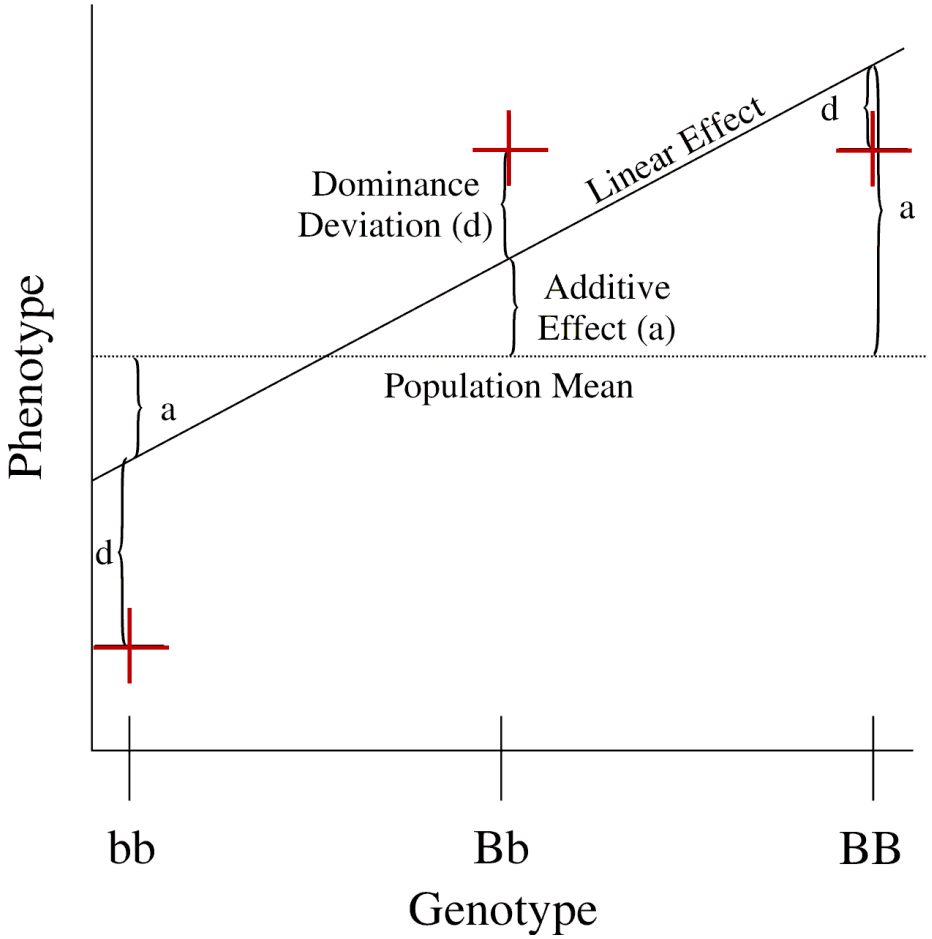
  - If d=0 : the alleles are additive
  - If d=a : allele A_2 is completely dominant to allele A_1
  - If d=-a : allele A_2 is completely recessive to allele A_1
  - If d>a : the locus shows over-dominance = heterozygote has a larger value than either homozygote

Additive and dominance effects



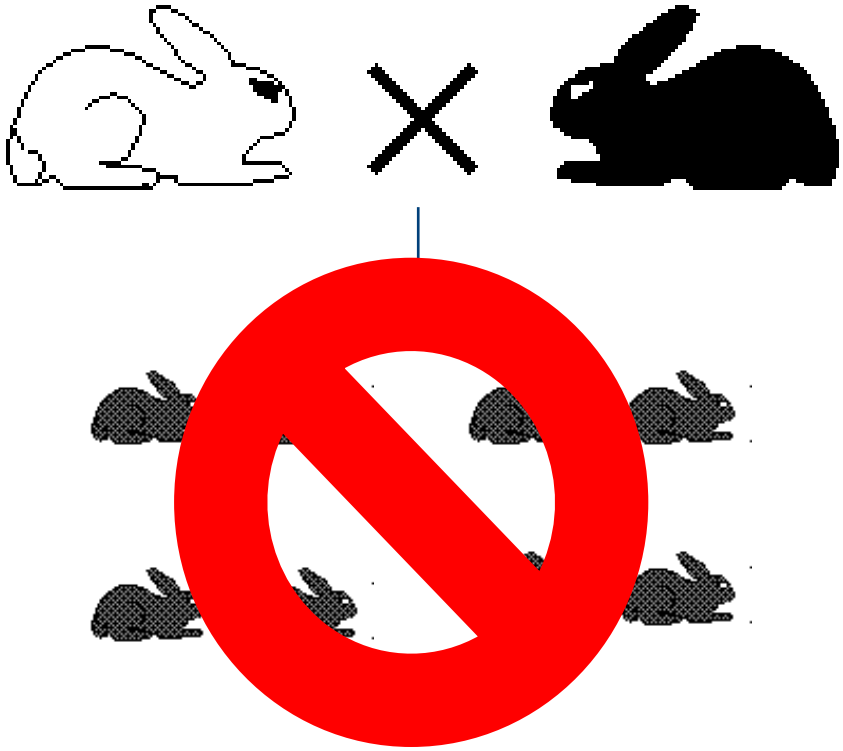


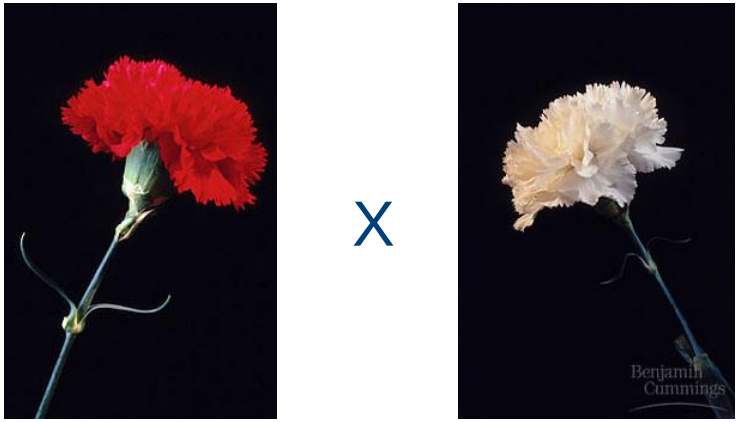
Additive and dominance effects



Dominance deviation = the degree to which one allele at a locus alters the effect of the allele on the complementary chromosome

Dominance deviation





Contribution of a locus to the phenotypic value of a trait – example

- Example: Apolipoprotein E (alleles E_1 and E_2) and age of onset of Alzheimer's disease
- Allele E_1 is associated with earlier age of onset for Alzheimer's disease :

Genotypes	E_1E_1	E_1E_2	E_2E_2
Age at onset	68.4	75.7	84.3

difference = 2a

- Additive effect of the E_2 allele is estimated by $a = \frac{84.3-68.4}{2} = 7.95$
- Dominance effect is estimated by $d = G_{E1E2} - \left(\frac{G_{E1E1}+G_{E2E2}}{2}\right)$

$$= 75.7 - \frac{68.4+84.3}{2} = -0.65$$

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Genotypic value – towards a general model

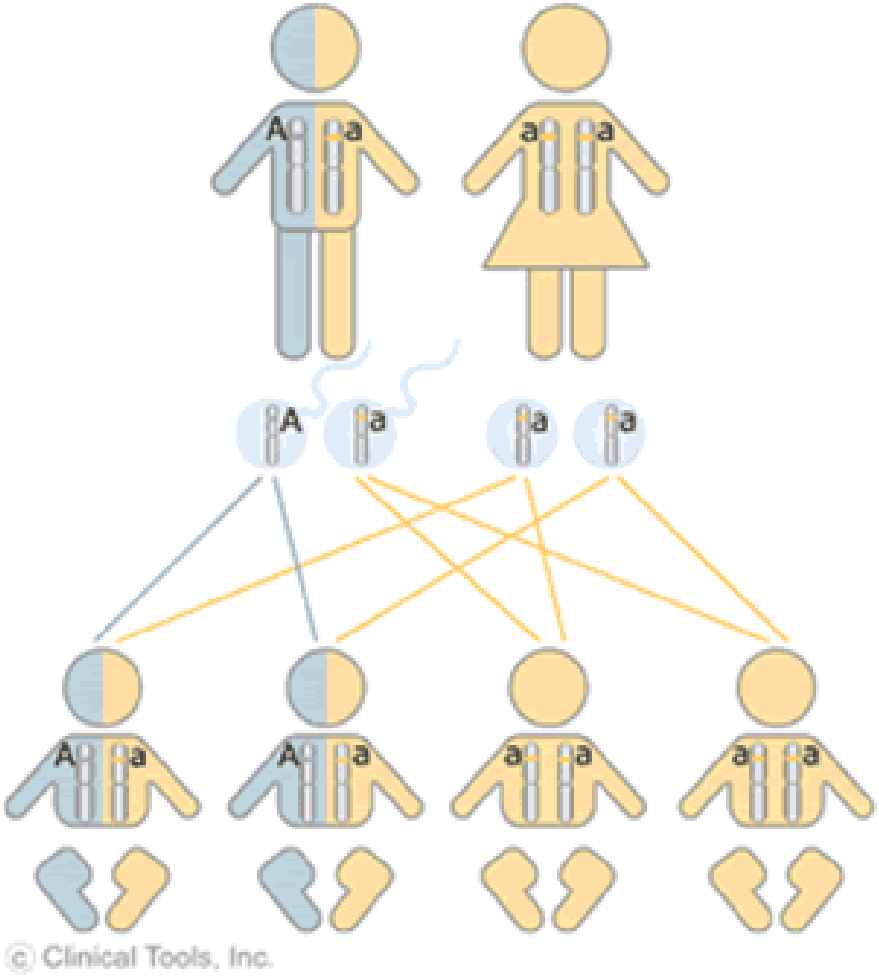
- The genotypic value G_{ij} of an individual carrying an A_iA_j genotype can be written in terms of
  - the average effect α for each allele
  - and δ (the dominance deviation)
- δ is the deviation of the actual value of this genotype from the value predicted by the average contribution of each of the single alleles

$$G_{ij} = \mu + (\alpha_i + \alpha_j) + \delta_{ij}$$

Fisher’s decomposition of the genotypic value

- Parents do not pass on their entire genotype to their offspring, but only one of the two possible alleles at each locus

Mendelian segregation



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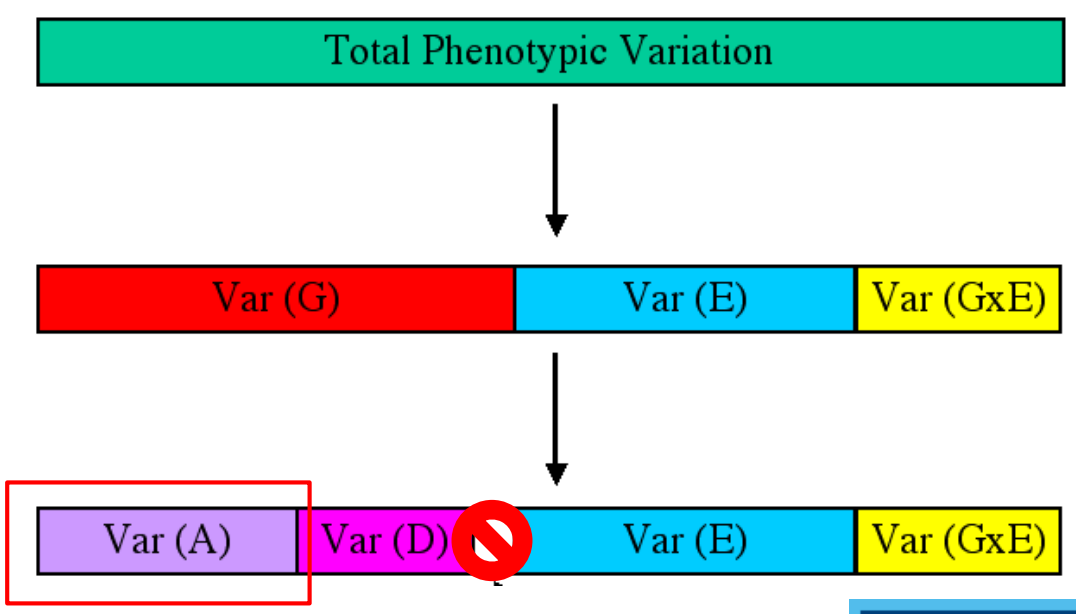
Fisher's decomposition of the genotypic value

- Parents do not pass on their entire genotype to their offspring, but only one of the two possible alleles at each locus

- Only a part of the genotypic value G is passed on
  → G is decomposed into several parts, some parts can be passed on while other parts cannot

Genetic sources of variation

- Basic model : P = G + E + G*E + ??
- Var(P) = Var(G) + Var(E)



Additive genetic variance

- = the inheritance of a particular allele from your parent
- and this allele's independent effect on the specific phenotype, which will cause the phenotype deviation from the mean phenotype

- = the source of heritable variation

- The resemblance between parents and offspring is entirely due to the additive effect that genes have on phenotype

Additive genetic variance

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- and this allele's independent effect on the specific phenotype, which will cause the phenotype deviation from the mean phenotype

- = the source of heritable variation

- The resemblance between parents and offspring is entirely due to the **additive effect** that genes have on phenotype

- **Why?**

Additive genetic variance

- The resemblance between parents and offspring is entirely due to the **additive effect** that genes have on phenotype

- **Why ?**
  - It are not the genotypes that are passed on from parents to progeny, but the alleles (at the loci that influence traits)
    - namely one allele from each locus from each parent

- = what selection can act upon

Genotypic value – towards a general model

- The genotypic value G_{ij} of an individual carrying an A_iA_j genotype can be written in terms of
  - the average effect α for each allele **(= inherited)**
  - and δ (the dominance deviation) **(= not inherited)**
- δ is the deviation of the actual value of this genotype from the value predicted by the average contribution of each of the single alleles

$$G_{ij} = \mu + (\alpha_i + \alpha_j) + \delta_{ij}$$

Fisher's decomposition of the genotypic value

- Parents do not pass on their entire genotype to their offspring, but only one of the two possible alleles at each locus

- Only a part of the genotypic value G is passed on
  → G is decomposed into several parts, some parts can be passed on while other parts cannot

➢ Phenotypic correlations among known relatives can be used to estimate variances of the components of G

Single locus model

- If the environment has no effect on a certain phenotype, the effect of the genotype (A_iA_j) equals the effect of the phenotype (P_{ij})

Genotype	Frequency	Phenotypic value
A_1A_1	p^2	P_{11}
A_1A_2	2pq	P_{12}
A_2A_2	q^2	P_{22}

- average value of the population $=$ $\mu = p^2 * P_{11} + 2pq * P_{12} + q^2 * P_{22}$

! Assuming avg environmental effect = 0

Single locus model

- If the environment has no effect on a certain phenotype, the effect of the genotype (A_iA_j) equals the effect of the phenotype (P_{ij})
- The genotypic value is expressed as a deviation to the population mean

Genotype	Frequency	Phenotypic value	Deviation from mean	Genetic deviation
A_1A_1	p^2	P_{11}	P_{11}-μ →	Y_{11}
A_1A_2	2pq	P_{12}	P_{12}-μ →	Y_{12}
A_2A_2	q^2	P_{22}	P_{22}-μ →	Y_{22}

- average value of the population = $\mu = p^2 * P_{11} + 2pq * P_{12} + q^2 * P_{22}$

! Assuming avg environmental effect = 0

- Mean of genetic deviation of all genotypes in the population = 0

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Single locus model – example 1

- Example : Fec-C locus in sheep
  - Influences the number of follicles that ovulate
  - Allele A_1 : **freq (p) = 0.3**
  - Allele A_2 : **freq (q) = 0.7**

Genotype	Frequency	Phenotypic value (ovulation rate)	Deviation from mean	Genetic deviation
A_1A_1	0.09	$V_{11} = 8.0$	$V_{11}-\mu$ →	$Y_{11} = +4.032$
A_1A_2	0.42	$V_{12} = 4.7$	$V_{12}-\mu$ →	$Y_{12} = +0.732$
A_2A_2	0.49	$V_{22} = 2.6$	$V_{22}-\mu$ →	$Y_{22} = -1.368$

μ = average value of the population

$$\mu = p^2 * V_{11} + 2pq * V_{12} + q^2 * V_{22} = 3.968$$

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Single locus model & effect of a gene

- Each genotype (A_iA_j) in the population has a genotypic value Y_{11}, Y_{12}, or Y_{22}, depending on the alleles it has

- General model to describe each genotype

$$A_iA_j = \alpha_i + \alpha_j + (\alpha\alpha)_{ij}$$

with α = the effect of one allele of the gene

- The effect of an allele = the difference between the mean value of all genotypes carrying this allele and the mean value of all genotypes in the population

Single locus model – example 1

- Example : Fec-C locus in sheep
  - Influences the number of follicles that ovulate
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  - Allele A_2 : **freq (q) = 0.7**

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μ = average value of the population

$$\mu = p^2 * V_{11} + 2pq * V_{12} + q^2 * V_{22} = 3.968$$

Average effect of alleles and allele pairs?

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Single locus model – example 1

- Average effect of alleles and allele pairs =

- $\alpha_1 = p * Y_{11} + q * Y_{21}$
- $\alpha_2 = p * Y_{21} + q * Y_{22}$
- $\alpha\alpha_{11} = Y_{11} - 2 * \alpha_1$
- $\alpha\alpha_{12} = Y_{21} - \alpha_1 - \alpha_2$
- $\alpha\alpha_{22} = Y_{22} - 2 * \alpha_2$

} = dominance effects

Genotype	Frequency	Phenotypic value	Genetic deviation	Additive effect	Dominance effect
A_1A_1	0.09	$V_{11} = 8.0$	$Y_{11} = +4.032$	$2*\alpha_1$	
A_1A_2	0.42	$V_{12} = 4.7$	$Y_{12} = +0.732$	$\alpha_1 + \alpha_2$	
A_2A_2	0.49	$V_{22} = 2.6$	$Y_{22} = -1.368$	$2*\alpha_2$	

Total genetic effect = value of genotype

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Single locus model – example 1

- Average effect of alleles and allele pairs =

• $\alpha_1 = p * Y_{11} + q * Y_{21}$	= 1.722
• $\alpha_2 = p * Y_{21} + q * Y_{22}$	= -0.738
• $\alpha\alpha_{11} = Y_{11} - 2 * \alpha_1$	= 0.588
• $\alpha\alpha_{12} = Y_{21} - \alpha_1 - \alpha_2$	= -0.252
• $\alpha\alpha_{22} = Y_{22} - 2 * \alpha_2$	= 0.108

= dominance effects

Genotype	Frequency	Phenotypic value	Genetic deviation	Additive effect	Dominance effect
A_1A_1	0.09	V_{11} = 8.0	Y_{11} = +4.032	$2*\alpha_1$ = 3.444	0.588
A_1A_2	0.42	V_{12} = 4.7	Y_{12} = +0.732	$\alpha_1 + \alpha_2$ = 0.984	-0.252
A_2A_2	0.49	V_{22} = 2.6	Y_{22} = -1.368	$2*\alpha_2$ = -1.476	0.108

Total genotypic effect = value of genotype

→ gene effects depend on allele frequencies !!

Single locus model – example 2

- Consider a single locus model where genotypic values (as deviations from the population mean) are
  - A_1A_1 (Y_{11}): -25
  - A_1A_2 (Y_{12}): 5
  - A_2A_2 (Y_{22}): 15
- Within the population the two alleles are **at equal frequency**

- *What is the average effect of A_1?*

- An A_1 gamete will meet either an A_1 or A_2 gamete at equal frequency
- Progeny are thus equally divided between A_1A_1 and A_1A_2
- The average value of the progeny is (-25 + 5) / 2 = -10
- Which is equal to α_{A1}

- α_{A1} = -10 units (*and α_{A2} = +10 units*)

Single locus model – Genetic variance

- Total genetic variance σ_G^2

$$\sigma_G^2 = p^2 * Y_{11}^2 + 2pq * Y_{12}^2 + q^2 * Y_{22}^2$$

- Additive genetic variance σ_A^2

$$\sigma_A^2 = p^2 * (2 * \alpha_1)^2 + 2pq * (\alpha_1 + \alpha_2)^2 + q^2 * (2 * \alpha_2)^2$$
$$= 2 * p * \alpha_1^2 + 2 * q * \alpha_2^2$$

- Dominance genetic variance σ_D^2

$$\sigma_D^2 = p^2 * (\alpha\alpha)_{11}^2 + 2pq * (\alpha\alpha)_{12}^2 + q^2 * (\alpha\alpha)_{22}^2$$

Single locus model – Genetic variance

- Back to the sheep example
  - Total genetic variance $\sigma_G^2 = 2.605$
  - Additive genetic variance $\sigma_A^2 = 2.542$
  - Dominance genetic variance $\sigma_D^2 = 0.063$

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2$$

$$\sigma_A^2 \gg \sigma_D^2$$

Genetic variance

- When two loci

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2$$

Homework - Litter Size in Merino Sheep

- For the three genotypes at the FecB gene, the mean litter sizes for 685 recorded pregnancies are

Genotype	Mean litter size
A1A1	2.66
A1A2	2.17
A2A2	1.48

- If the frequency of the FecB A2 allele is 0.1, what is the mean litter size of this sheep population?
- How does the mean litter size change if the frequency of the FecB allele is quadrupled in this sheep population?
- What is the average effect for the two alleles for the two frequencies?

Selection decisions

- P = G + E
- P = A + D + E

- Q : which component would you select on??

- A : A (additive genetic value) as neither D (dominance) or E (environment) can be passed to progeny

- A (additive genetic value) = sum of average effects of alleles an individual carries (α) = breeding value (Falconer & Mackay, 1996)

Single locus model

- Average effects of alleles and allele pairs → gene effects depend on gene frequencies

- $\alpha_1 = p * Y_{11} + q * Y_{21}$ = 1.722
- $\alpha_2 = p * Y_{21} + q * Y_{22}$ = -0.738
- $\alpha\alpha_{11} = Y_{11} - 2 * \alpha_1$ = 0.588
- $\alpha\alpha_{12} = Y_{21} - \alpha_1 - \alpha_2$ = -0.252
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= dominance effects

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Breeding value (BV)

Total genetic effect

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Single locus model

- Average effects of alleles and allele pairs → gene effects depend on gene frequencies

- $\alpha_1 = p * Y_{11} + q * Y_{21}$ = 1.722

! When no dominance effect, genetic and breeding values are equal

effects

Genotype	Frequency	Phenotypic value	Genetic deviation	Additive effect	Dominant effect
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Breeding value (BV)

Total genetic effect

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Breeding value versus Genotypic value

$$P = G + E$$

$$P = A + D + E$$

- Genotypic value (G) = the value of genes to self
  - Includes additive and non-additive effects (which can not be passed on to progeny)

- Breeding value (A) = the value of genes to offspring
  - = the additive genetic effect
  - = the (economic) value of an individual's genotype, as judged by the average performance of its offspring
  - From the size of the breeding value it is possible to choose suitable parents for future crosses

Cfr single locus model – example 2

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- Which is equal to α_{A1}

Breeding value ?

- α_{A1} = -10 units (*and α_{A2} = +10 units*)

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Cfr single locus model – example 2

- Breeding value = the sum of the average effect of alleles (α)

- In our single locus model example
  - If α_{A1} = -10 units & α_{A2} = +10 units
  - Breeding value A_1A_1 = -10 + -10 = -20
  - Breeding value A_1A_2 = -10 + 10 = 0
  - Breeding value A_2A_2 = 10 + 10 = 20

Estimation of genetic parameters

- Additive genetic variance / dominance deviation
- **Heritability**

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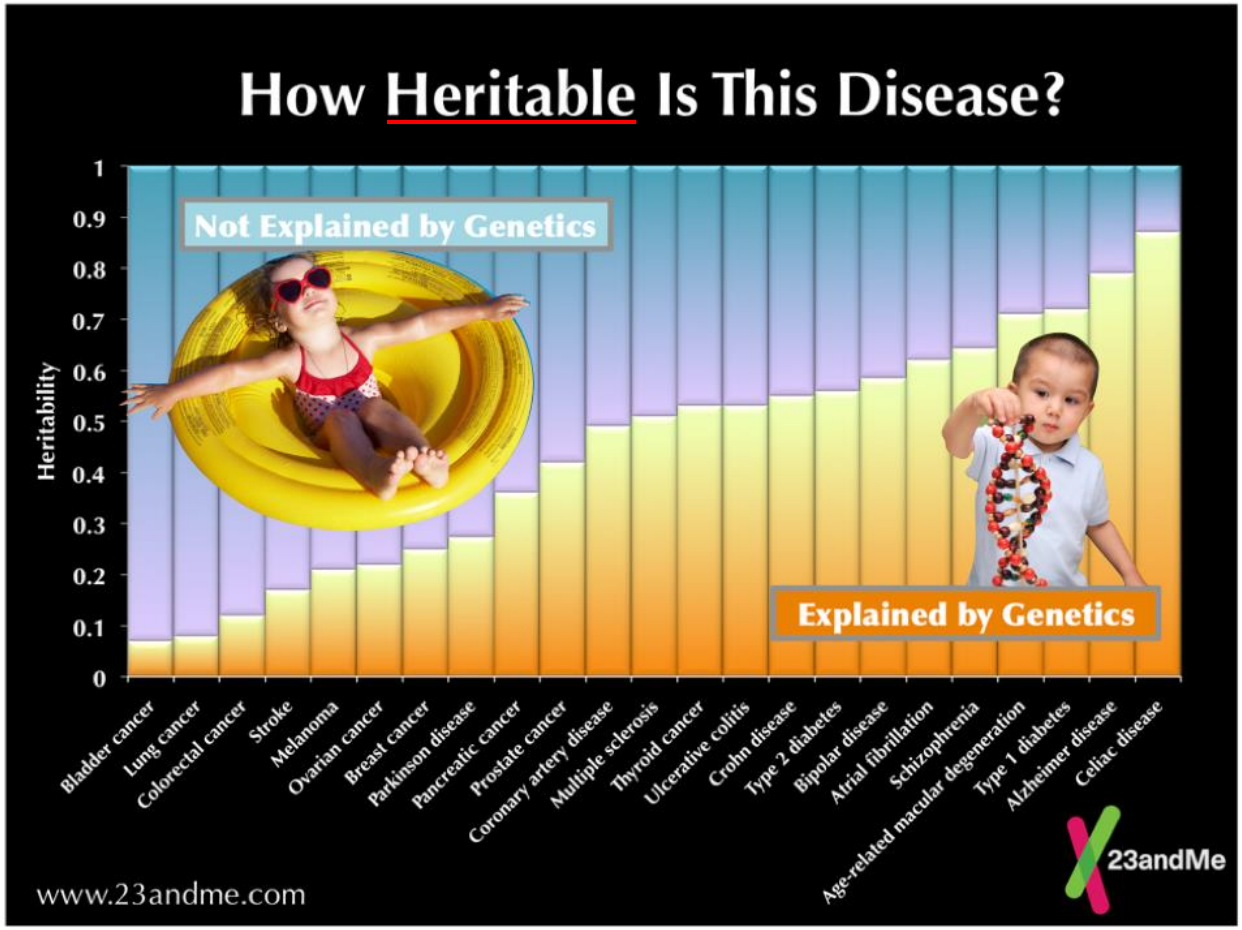
Genes and environment – to what extent??



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Heritability (h^2)

- A measure of the degree to which observed phenotypic differences for a trait are due to genetic differences

→ how much of the phenotypic variance (V_P) is due to variance in genetic factors (V_G)?

  - $h^2 = 0$: differences between observed phenotype are not caused by genetic differences

  - $h^2 = 1$: only the genetic differences count for the observed phenotypical differences

Quantitative genetics – the basic model

- Phenotype = Genotype + Environment + G*E + ??
- One assumes $P = G + E$

- VarP = Var(G+E)
- VarP = VarG + VarE $(V_P = V_G + V_E)$
- $\text{Heritability} = \frac{V_G}{V_P}$

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Estimating heritability – how?

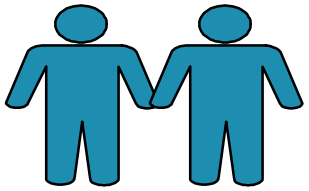
- Approaches are based on phenotypic resemblance between relatives
  - between twins

Twin studies

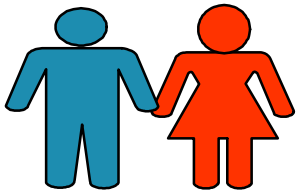
Identical twins
100%

Non-identical twins
50%

identical twins



non-identical twins



Concordance (correlation of trait)?

completely genetically determined

100% correlation cfr siblings

completely environmentally determined

variable, but identical = non-identical

***multifactorial**

variable, but identical > non-identical

=> calculation of *heritability*

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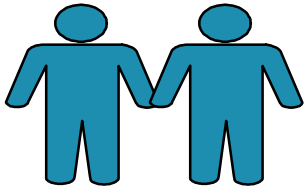
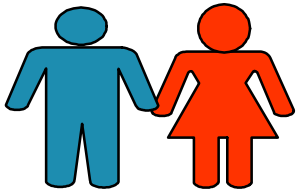
Example

identical twins



non-identical twins



Concordance (correlation of trait)?

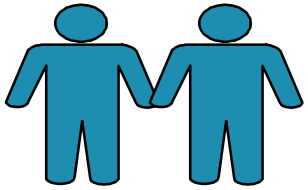
>90%

50-60%

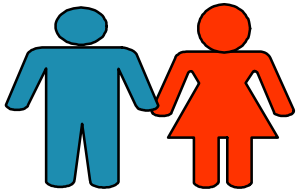
How define heritability from these numbers??

Example

identical twins



non-identical twins



Concordance (correlation of trait)?

>90%

50-60%

Difference in concordance = ± 35 %

⇒ Sharing a marginal half genome with your twin explains an additional 35%

⇒ In theory, sharing a full genome explains 2*35% = 70% heritability

⇒ 70% of the variation in example trait is genetically determined

heritability = $2(r_{MZ} - r_{DZ})$

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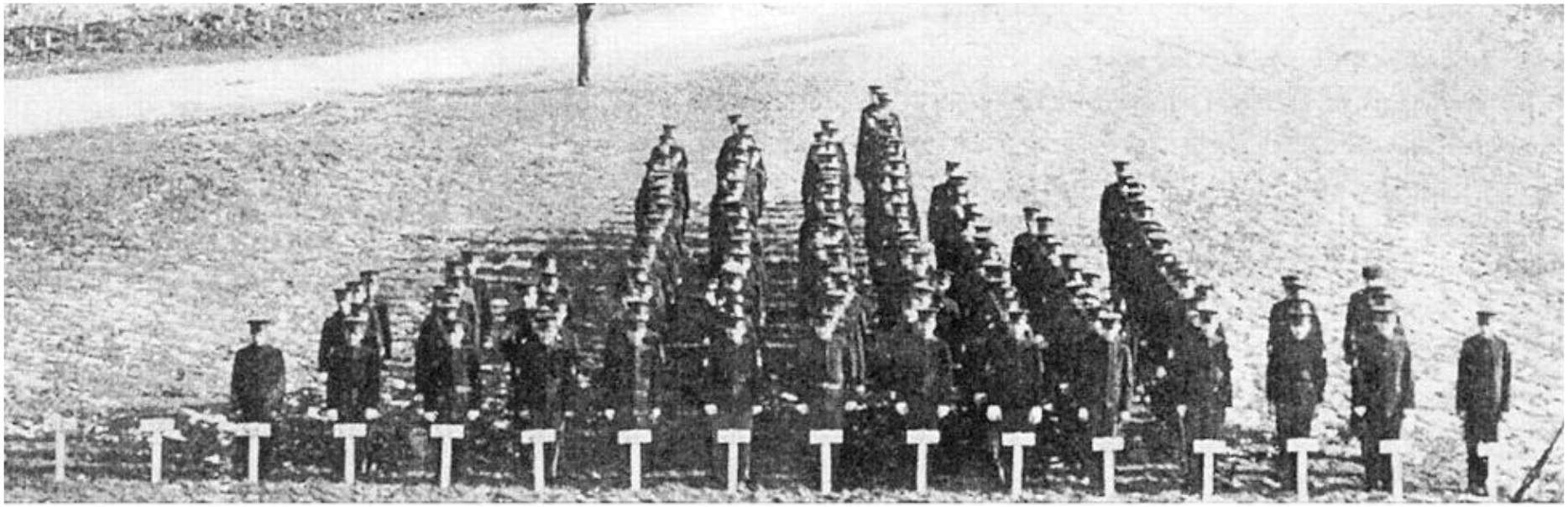
Variation of height in the normal population



4:11 5:0 5:1 5:2 5:3 5:4 5:5 5:6 5:7 5:8 5:9 5:10 5:11 6:0 6:1 6:2

To what extent is variation explained by

differences in genetic factors = heritability

differences in environment ?

Twin studies

~ 70%

~ 30%

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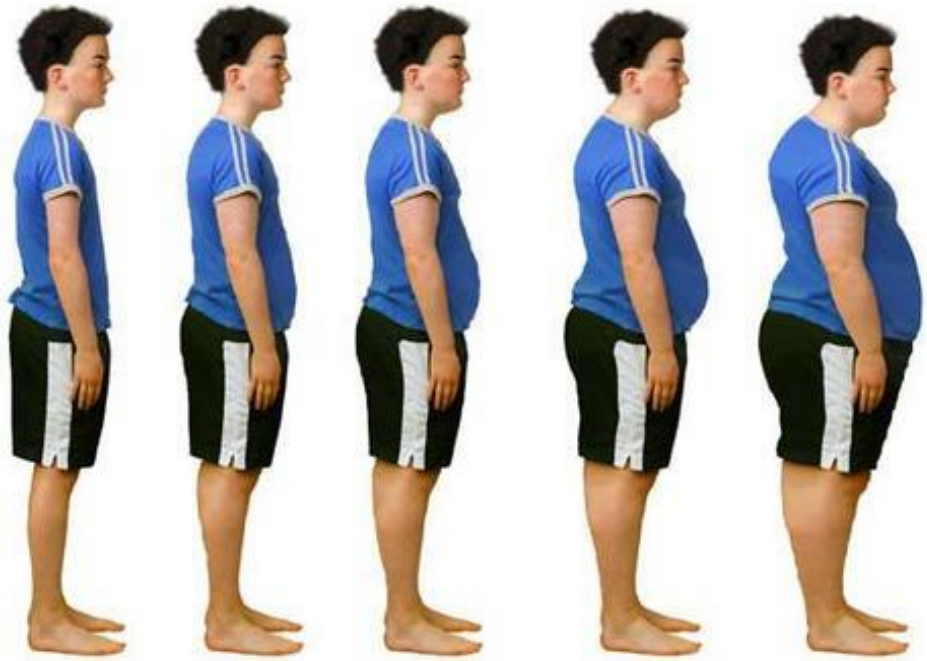
Variation in weight in the normal population



To what extent is variation explained by

differences in genetic factors = heritability → ~ 80%

differences in environment ? → ~ 20%

Twin studies

Heritability example - twin concordance

Disease	Monozygotic twin	Dizygotic twin
Rheumatoid arthritis	14.6	3.4
Ulcerative colitis	-	-
Type 1 diabetes	30.1	6.8
Graves disease	22.2	0
Multiple sclerosis	21.4	3.3
Lupus	22.2	2.4
Ankylosing spondylitis	-	-

Cooper, Environ Health Persp, 1999

Estimating heritability – how?

- Approaches are based on phenotypic resemblance between relatives
  - between twins
  - between sibling pairs
    - Esp when phenotype is rare, you also want to include non-twin siblings
  - between offspring and parental phenotypes
    - Analysis of variance

Quantitative trait - heritability

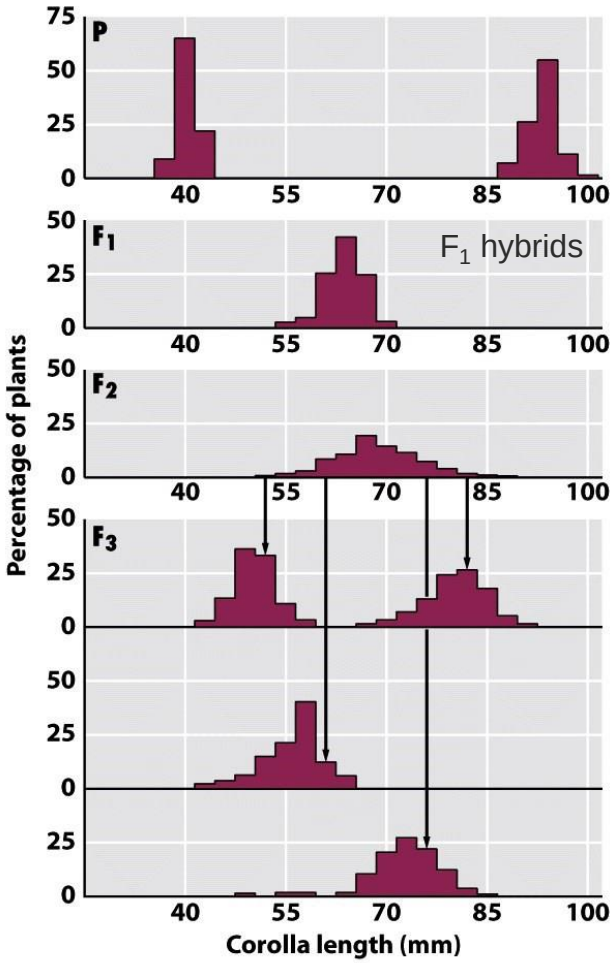


Figure 18-2
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- Crossing of two separate lines differing in a quantitative trait
  - Eg length of corolla (petal) in *Nicotiana longiflora*

- The F_1 generation
  - is intermediate in phenotype
  - same genotype ≠ exactly same phenotype → variation in phenotype ~ environment (V_E)
- The variance increases in the F_2 generation

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Estimating heritability – how?

- Approaches are based on phenotypic resemblance between relatives
  - between twins
  - between sibling pairs
    - Esp when phenotype is rare, you also want to include non-twin siblings
  - between offspring and parental phenotypes
    - Analysis of variance → cfr $\text{Heritability} = \frac{V_G}{V_P}$
    - Regression methods

Regression

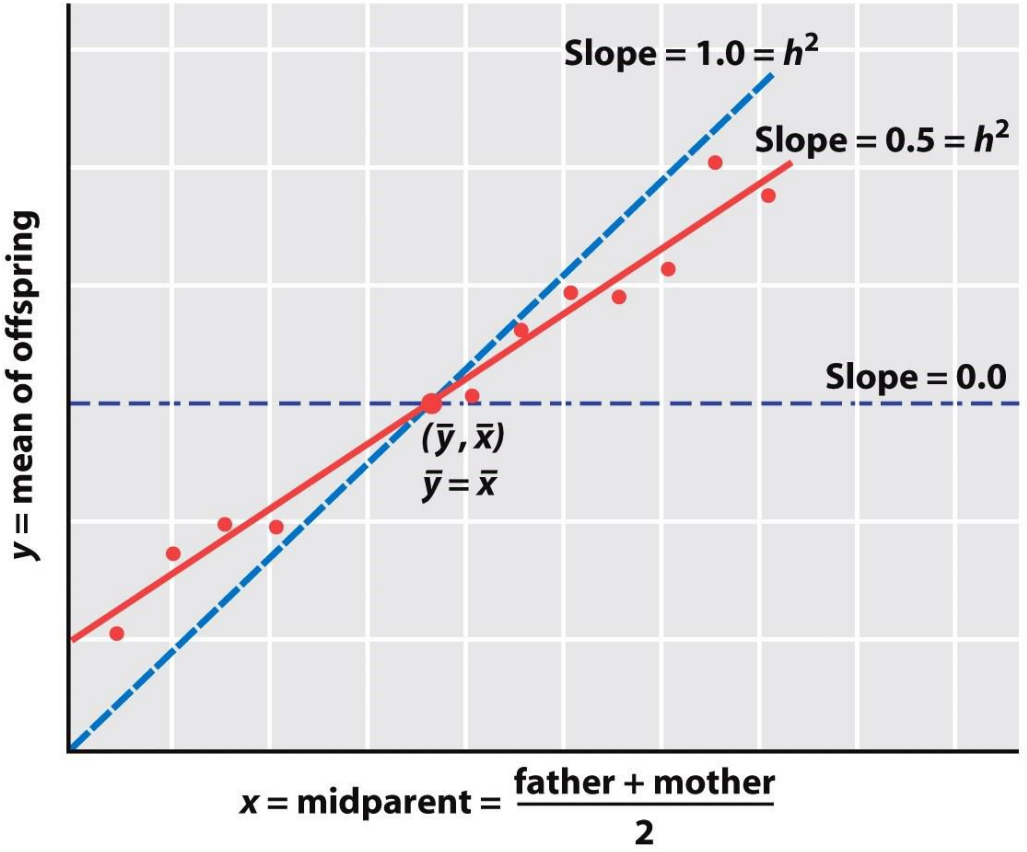

Figure 18-12
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Regression example

low heritability

high heritability

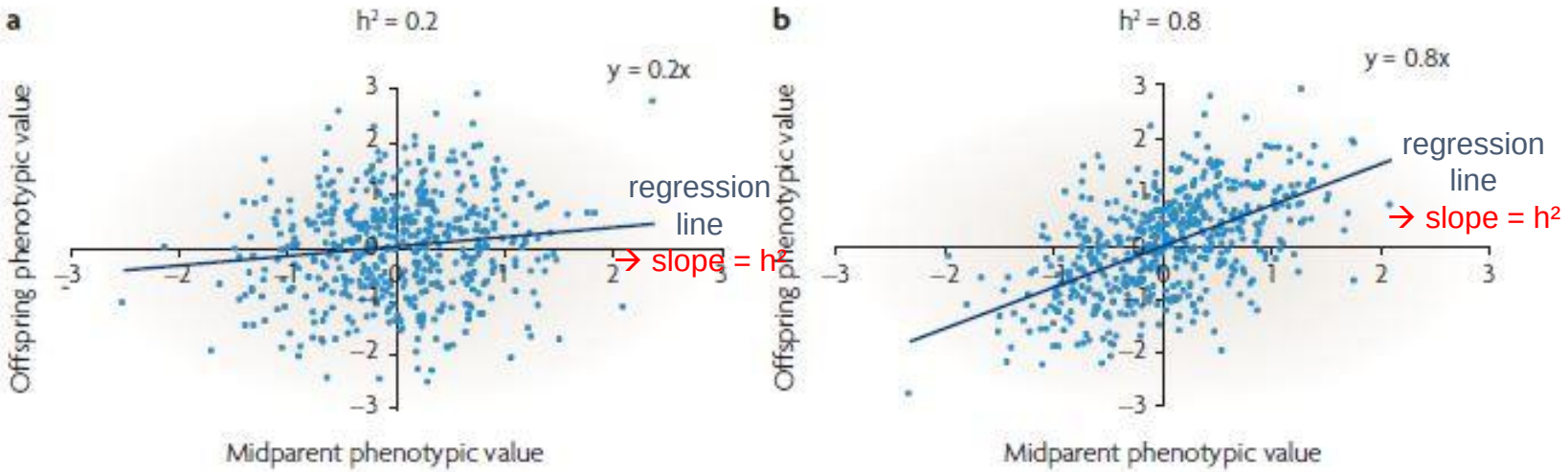


Figure 2 | **Estimation of heritability from the regression of offspring phenotype on the average phenotype of the parents.** The slope of the regression line is an estimate of the narrow-sense heritability for traits with a heritability of 0.2 (**a**) and 0.8 (**b**) and phenotypic variance of 1. The variances of the observations about the regression line are 0.98 (**a**) and 0.68 (**b**), demonstrating that the average phenotypic value of the parents (midparent phenotypic value) is a better predictor of the offspring phenotypic value if heritability is high.

Plot children's (offspring) traits against the average of their parents

Regression example

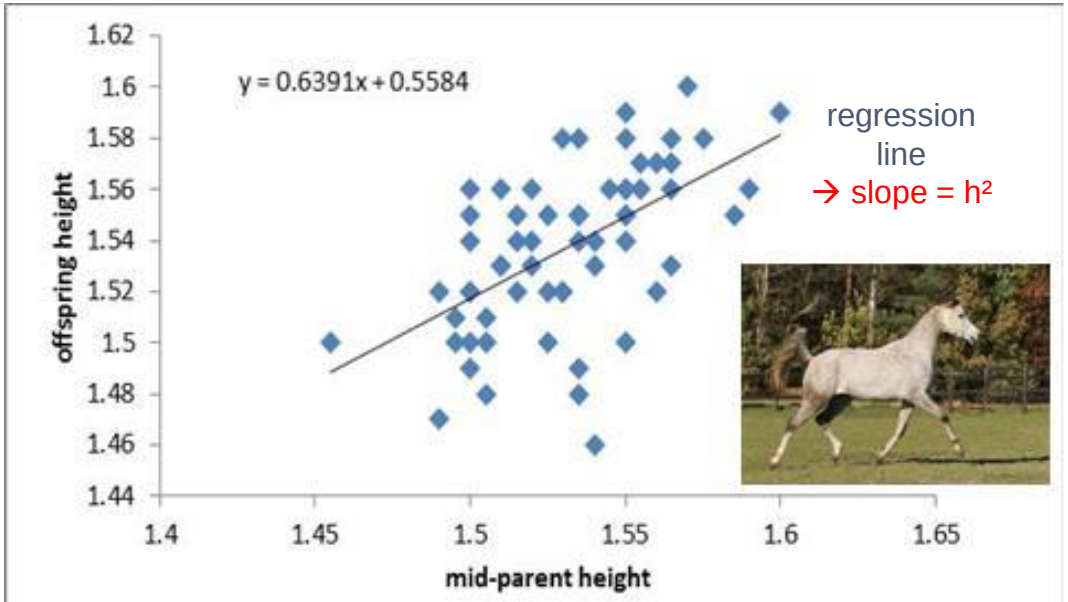
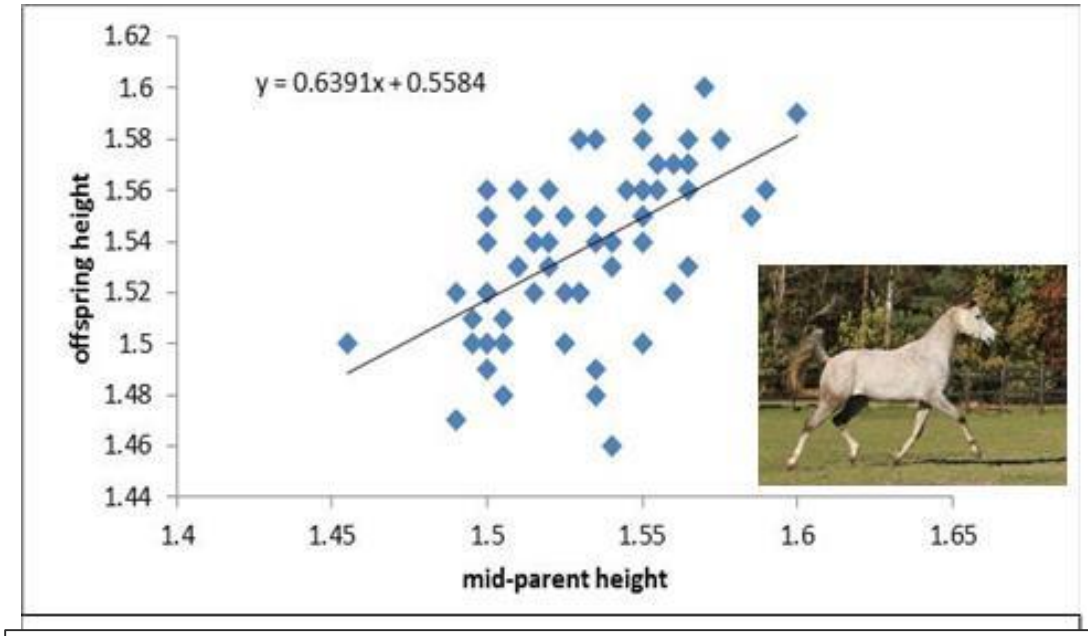


Figure 4. Height at withers of offspring plotted against that in their mid-parents. The regression between the two indicates how heritable the trait (height at withers) in this population is.

Plot children's (offspring) traits against the average of their parents

Regression example



Note that even with high h^2, there is a lot of variation around regression line.

Why ?

Plot children's (offspring) traits against the average of their parents

Heritability examples

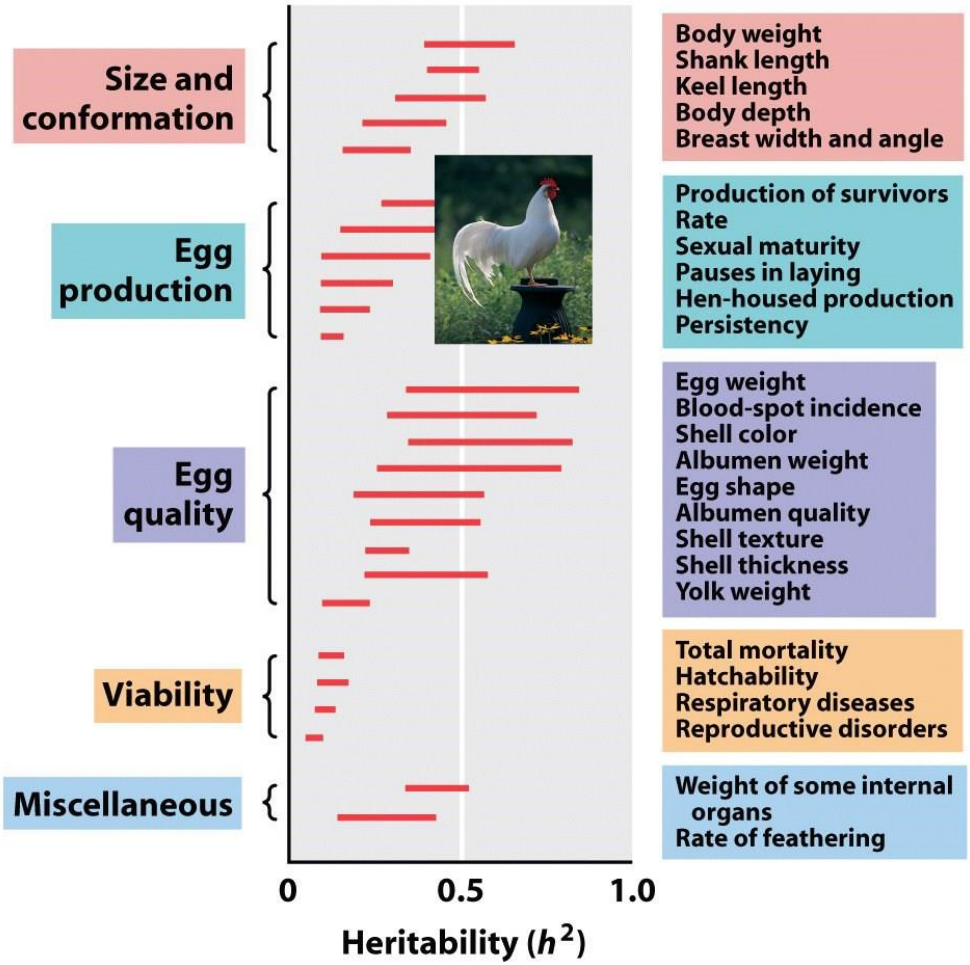


Figure 18-13
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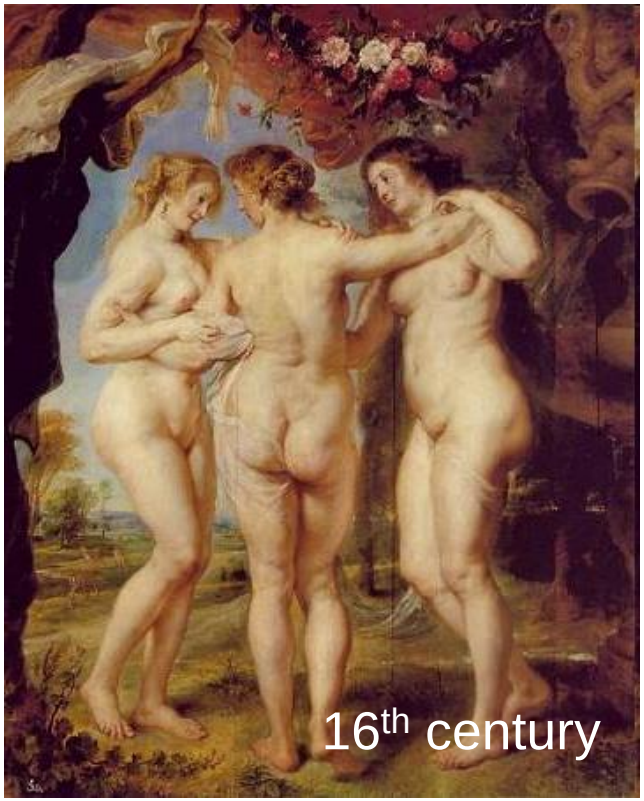
h_2 is not identical in different populations !

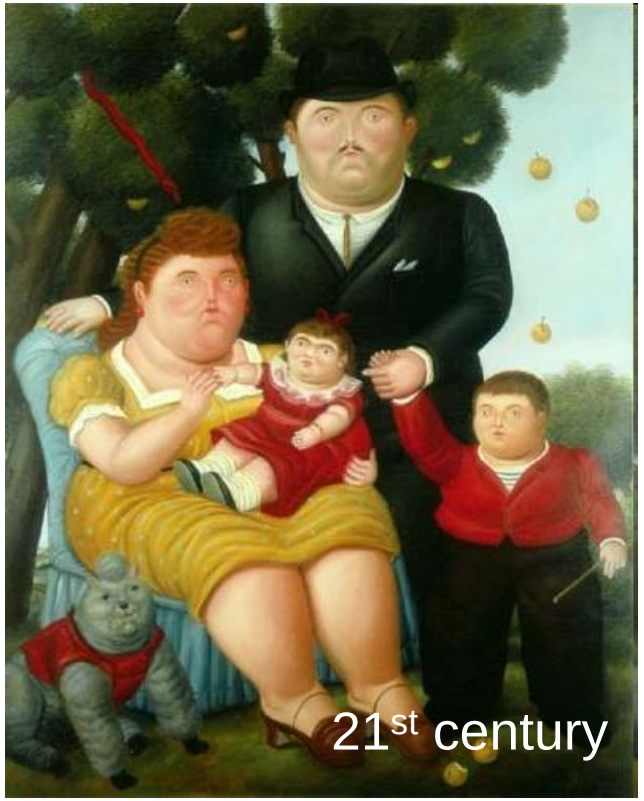
Heritability – need to knows

- Depends on the genetic variance AND the environmental variance
- Depends on structure of data and on estimation method
- Heritability ≠ constant
  - = property of a trait within a population at a certain moment
  - can change over time and can be different in different populations

Heritability ≠ constant - example



Weight mostly defined
by access to food



Weight mostly defined
by genetics

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Heritability ≠ constant - example

Unfavorable environment

- huge difference in environment
- variation = defined by environment
- heritability is lower

Optimal environment

- more equal environment
- variation = defined by genes
- heritability is higher

Heritability – need to knows

- Depends on the genetic variance AND the environmental variance
- Depends on structure of data and on estimation method
- Heritability ≠ constant
  - = property of a trait within a population at a certain moment
  - can change over time and can be different in different populations

- ! Heritability ≠ fraction of an individual's phenotype that is genetic, but rather
  - the proportion of phenotypic variance that is due to genetic factors
  - a population parameter → depends on population-specific factors (eg allele frequencies, variation in environmental factors…)

Heritability examples

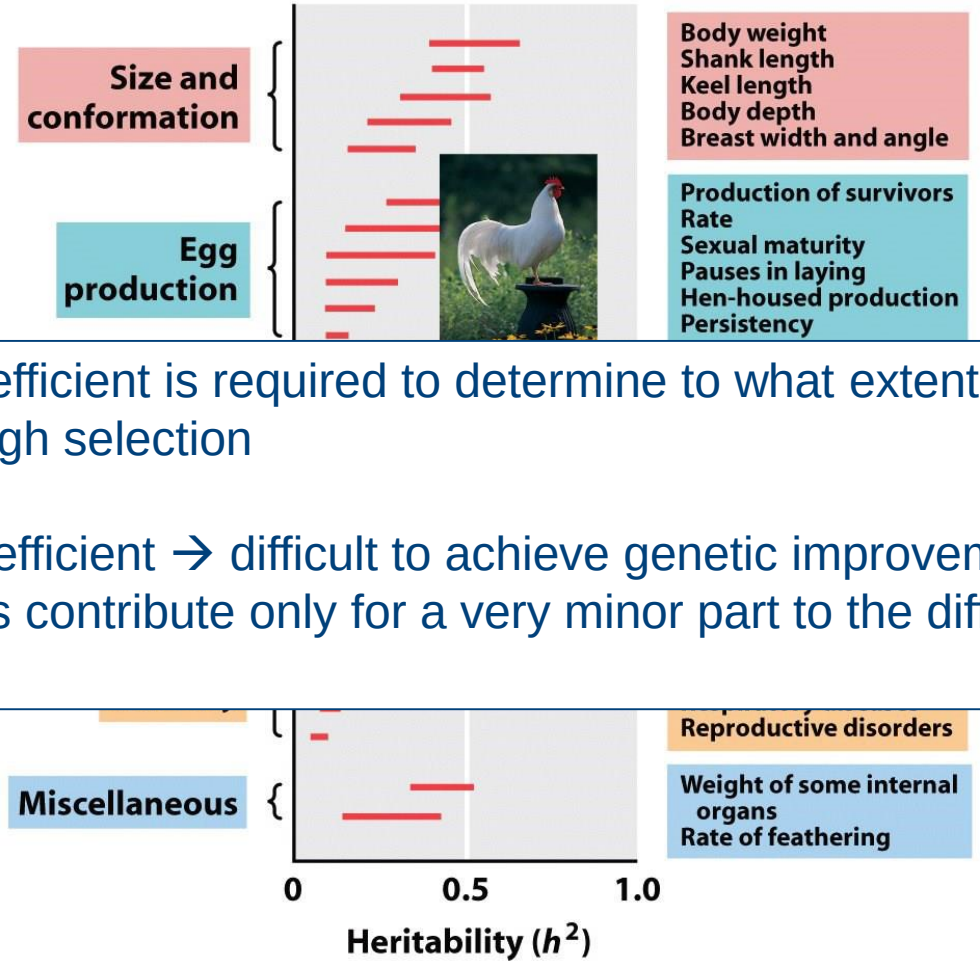

Figure 18-13
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The heritability coefficient is required to determine to what extent a population can be improved through selection

Low heritability coefficient → difficult to achieve genetic improvement, since genetic differences contribute only for a very minor part to the difference in phenotypes

Prediction of breeding values

- In real life we observe P, but want to estimate A (breeding value)
  - Ie to know the value of genes to progeny

➢ Estimate A from phenotype

$$h2 = \frac{Var(A)}{Var(P)} \quad \rightarrow \quad Var(A) = h^2 * Var(P)$$

Expresssed as deviations from their population means !

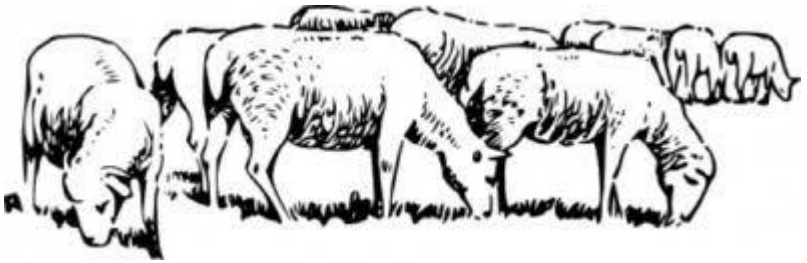
From : http://jvanderw.une.edu.au/gene251-351_lec5.pdf

Breeding Value : example

- Ram = 90 kg
- Ewe = 80 kg
- Average of flock = 70 kg

- $h_2 = 0.25$

- Breeding value ??



From : http://jvanderw.une.edu.au/gene251-351_lec5.pdf

Breeding Value : example

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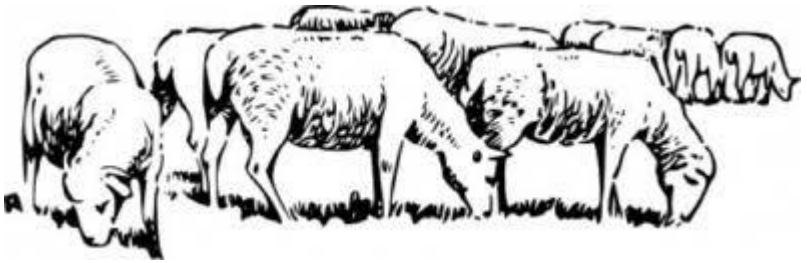


- Breeding value ??

$$h2 = \frac{Var(A)}{Var(P)} \quad \rightarrow \quad Var(A) = h^2 * Var(P)$$

From : http://jvanderw.une.edu.au/gene251-351_lec5.pdf

Breeding Value : example

- Ram = 90 kg
- Ewe = 80 kg
- Average of flock = 70 kg

- $h_2 = 0.25$

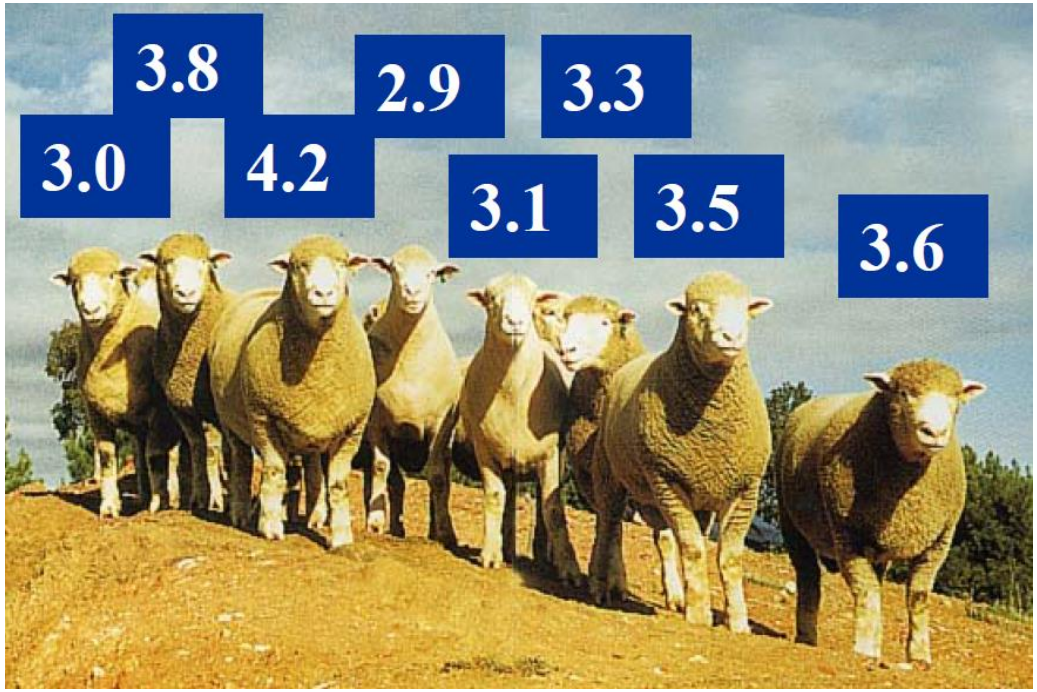
- Estimated BV Ram = P * h_2 = 20 * 0.25 = +5.0 kg (with P = deviation from population mean)
- Estimated BV Ewe = P * h_2 = 10 * 0.25 = +2.5 kg (with P = deviation from population mean)

- Expected genotypic value of progeny

  =(5.0 + 2.5)/2 = +3.75 kg (above average)

Breeding Value : example

- ! Not all progeny will be + 3.75 kg
- This is the average we expect for a large group



From : http://jvanderw.une.edu.au/gene251-351_lec5.pdf

Heritability - important note

- ‘narrow sense heritability’ (h^2) is defined as the proportion of trait variance that is due to additive genetic factors

- ‘broad sense heritability’ (H^2) is defined as the proportion of trait variance that is due to all genetic factors including dominance and gene-gene interactions

Heritability

- Basic model : P = G + E
- Var(P) = Var(G) + Var(E)
- $H2 = \frac{Var(G)}{Var(P)} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2}$ $h2 = \frac{Var(A)}{Var(P)} = \frac{\sigma_A^2}{\sigma_G^2 + \sigma_E^2}$

→ If you know the total amount of genetic variance responsible for a trait, you can calculate the trait heritability

Basic model in quantitative genetics

- P = G + E

- G is unknown, but estimated
  - based on variance components : Var(P) = Var(G) + Var(E)
  - Heritability, genotypic value, additive genetic variance, breeding value

- More recently, technological advances have made it possible to localize the underlying loci contributing to genetic variation (molecular markers, GWAS, NGS…): search for QTL/disease susceptibility loci