

Quantitative characters II: components of the variance

The *variance* of a trait (x) is the average squared deviation of x from its mean:

$$V_p = (1/n) \sum (x - m_x)^2$$

This total phenotypic variance can be partitioned into components:

$$V_p = V_G + V_E \text{ (genetic and environmental)}$$

$$V_G = V_A + V_D + V_I \text{ (additive, dominance [between alleles], and interaction [between loci])}$$

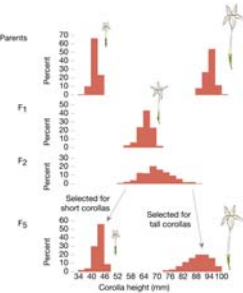
The broad-sense heritability is the fraction that's genetic:

$$H^2 = V_G / V_p$$

The narrow-sense heritability is the fraction that's *additive* genetic:

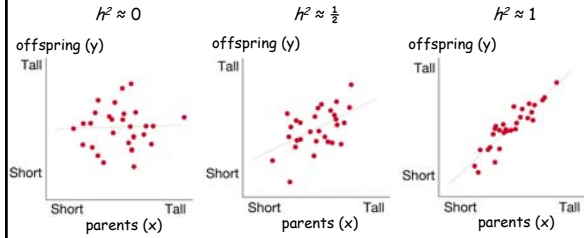
$$h^2 = V_A / V_p$$

h^2 determines (1) the *resemblance of offspring to their parents*, and (2) the *population's evolutionary response to selection*.



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h^2 is the regression (slope) of offspring on parents



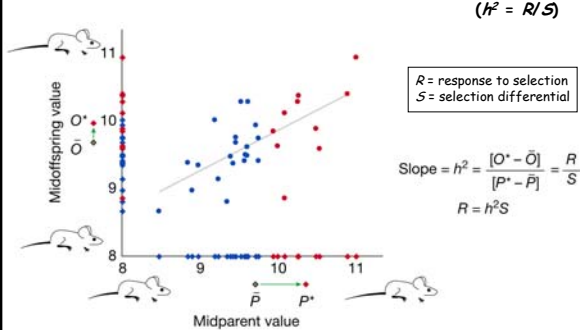
Definition of the regression coefficient (slope): $b_{yx} = cov(x,y) / var(x)$

Here x is the *midparent* value (parental mean), and y is the *offspring* value.

The higher the slope, the better offspring resemble their parents.

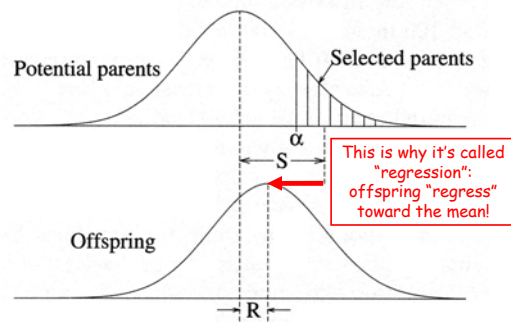
In other words, the higher the *heritability*, the better offspring trait values are *predicted* by parental trait values.

This "geometric" interpretation of heritability shows why $R = h^2 S$ ($h^2 = R/S$)



As it turns out, the *additive genetic variance* (V_A) is the part that makes offspring resemble their parents.

The Response to Selection



What's the heritability of height in humans?

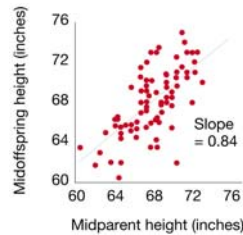


Scott Freeman and Jon Herron asked the students in their evolution course at the University of Washington to measure themselves, their siblings, and their parents.

Their *regression* plot is shown at the right.

The estimated heritability is 0.84.

That means 84% of the variance in height (V_A) is *additive genetic variance* (V_A).



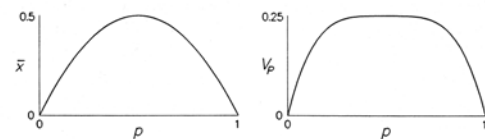
Not all *genetic* variance is *additive*! (A silly but instructive model.)

Consider a simple quantitative trait (x) controlled in a symmetrically overdominant manner by two alleles at one locus.

Assume that there is *no environmental variance*.

genotype	phenotype (x)	frequency
AA	0	p^2
Aa	1	$2p(1-p)$
aa	0	$(1-p)^2$

$$\text{Thus } \bar{x} = 2p(1-p), \text{ and } \text{Var}(x) = V_p = V_G = E(x^2) - [E(x)]^2 = 2p(1-p)[1-2p(1-p)].$$

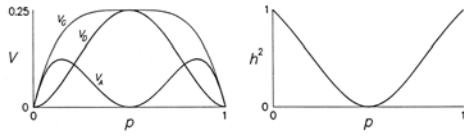


What happens if we *select for higher values of x* ?

The heritability disappears when the genetic variance is greatest!

Now we can calculate the heritability, which is

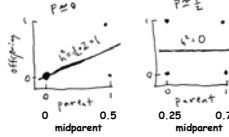
$$h^2 = V_A/V_p = (1-2p)^2/[1-2p(1-p)]$$



At $p = 0.5$, all of the genetic variance is dominance variance, not additive variance.

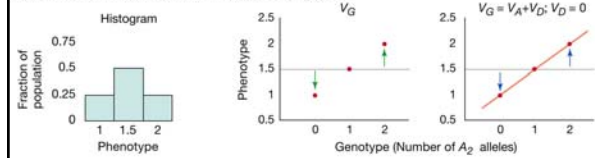
This means that parents and offspring strongly resemble each other when p is near 0 or 1, but not when p is near $1/2$. How can we understand this?

Suppose a is rare. Then most individuals are AA homozygotes and the mean phenotype is near 0. A heterozygous father (phenotype = 1) will almost always mate with a homozygous AA mother (phenotype = 0). Half of their offspring will be AA and half will be Aa (like him). On average, the offspring of the rare Aa heterozygotes will have a phenotype of 0.5. But most fathers will be AA homozygotes who mate with AA homozygote females and produce exclusively AA offspring. So the regression slope is $1/2$ and $h^2 = 2b = 1$.

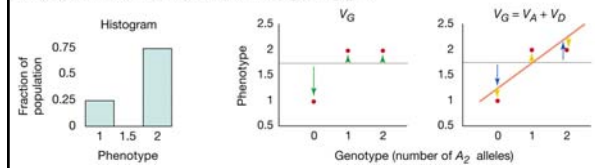


Dominance variance arises from non-additive relationships between the "dosage" of an allele (number carried) and the resulting phenotype

No dominance. Phenotypes: $A_1A_1 = 1; A_1A_2 = 1.5; A_2A_2 = 2$

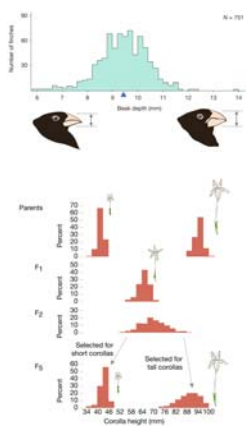


Complete dominance. Phenotypes: $A_1A_1 = 1; A_1A_2 = 2; A_2A_2 = 2$



How to estimate the components of the phenotypic variance (V_p)

1. Measure phenotypes (trait values) in a large random sample of the population.
2. Calculate the mean and variance: the variance is V_p .
3. Estimate the heritability, either of two ways:
 - (a) regress offspring on midparent values
 - (b) measure the response to selection: $h^2 = R/S$
4. The additive variance (V_A) is the heritable fraction of the total: $V_A = h^2 V_p$.
5. The remainder is environmental (V_E) and dominance variance (and other minor stuff).
6. If we can clone or closely inbred members of the species, or find identical twins, then we can *directly* estimate the environmental variance.



7. The dominance variance can be separated from the additive variance by exploiting the different ways these components appear in the covariances between different kinds of relatives. For example:

$$\begin{aligned} \text{cov}(\text{parent-offspring}) &\approx \frac{1}{2} V_A \\ \text{cov}(\text{half sibs}) &\approx \frac{1}{4} V_A \\ \text{cov}(\text{full sibs}) &\approx \frac{1}{2} V_A + \frac{1}{4} V_D \end{aligned}$$

An interesting and general finding is that traits closely related to *fitness* tend to have *little* additive variance but *more* dominance and interaction variance (epistasis) than typical morphological traits.

What might be the explanation?

Partitioning of the variance of four characters in *Drosophila melanogaster*. Components as percentages of the total, phenotypic, variance.

	Character	Character			
		(1)	(2)	(3)	(4)
Phenotypic	V_p	100	100	100	100
Additive genetic	V_A	52	43	30	18
Non-additive genetic	$V_D + V_I$	9	6	40	44
Environmental	V_E	39	51	30	38

Characters:

- (1) Number of bristles on 4th + 5th abdominal segments (Clayton, Morris, and Robertson, 1957; Reeve and Robertson, 1954).
- (2) Length of thorax (F. W. Robertson, 1957b).
- (3) Size of ovaries, i.e. number of ovarioles in both ovaries. (F. W. Robertson, 1957a).
- (4) Number of eggs laid in 4 days (4th to 8th after emergence) (F. W. Robertson, 1957b).