

Quantitative characters I: polygenes and environment

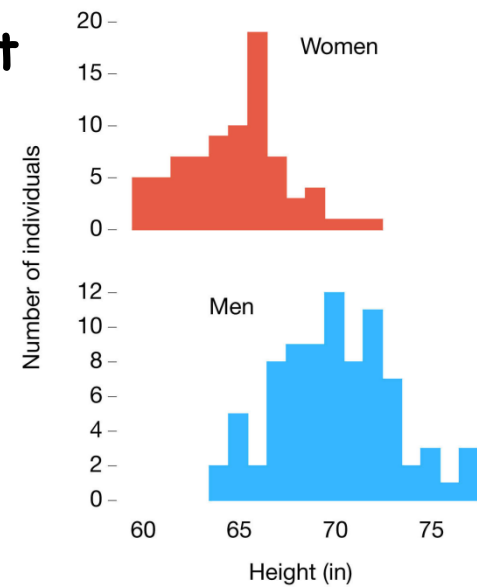
Most ecologically important quantitative traits (QTs) vary.

Distributions are often *unimodal* and approximately *normal*.

Offspring and parents are *correlated*.

What's the explanation?

Independent contributions by genotypes at *many loci*, and by *random environmental influences*.



XV.—The Correlation between Relatives on the Supposition of Mendelian Inheritance. By R. A. Fisher, B.A. Communicated by Professor J. ARTHUR THOMSON. (With Four Figures in Text.)

(MS. received June 15, 1918. Read July 8, 1918. Issued separately October 1, 1918.)

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Several attempts have already been made to interpret the well-established results of biometry in accordance with the Mendelian scheme of inheritance. It is here attempted to ascertain the biometrical properties of a population of a more general type than has hitherto been examined, inheritance in which follows this scheme. It is hoped that in this way it will be possible to make a more exact analysis of the causes of human variability. The great body of available statistics show us that the deviations of a human measurement from its mean follow very closely the Normal Law of Errors, and, therefore, that the variability may be uniformly measured by the standard deviation corresponding to the square root of the mean square error. When there are two independent causes of variability capable of producing in an otherwise uniform population distributions with standard deviations σ_1 and σ_2 , it is found that the distribution, when both causes act together, has a standard deviation $\sqrt{\sigma_1^2 + \sigma_2^2}$. It is therefore desirable in analysing the causes of variability to deal with the square of the standard deviation as the measure of variability. We shall term this quantity the Variance of the normal population to which it refers, and we may now ascribe to the constituent causes fractions or percentages of the total variance which they together produce. It is desirable on the one hand that the elementary ideas at the basis of the calculus of correlations should be clearly understood, and easily expressed in ordinary language, and on the other that loose phrases about the "percentage of causation,"

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Gillespie's colorless but personal example, with correlation

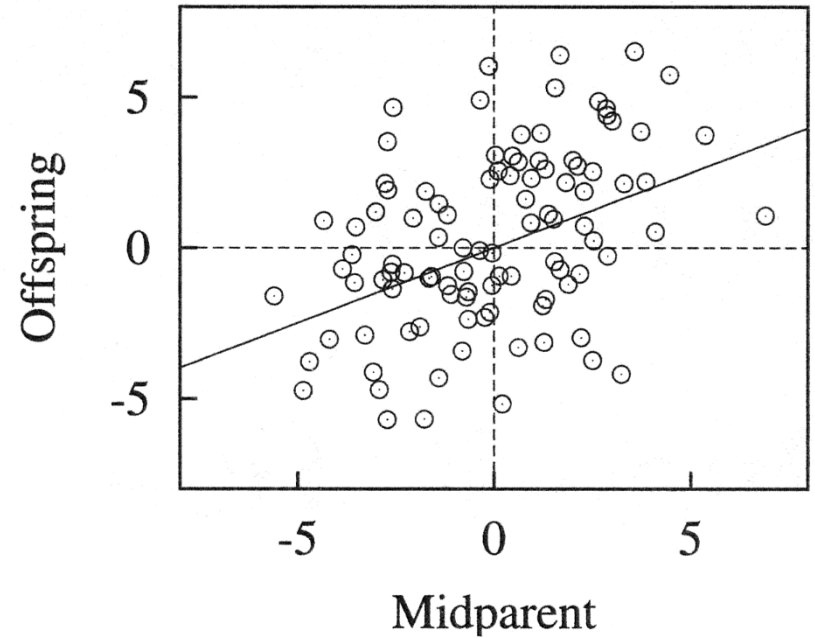
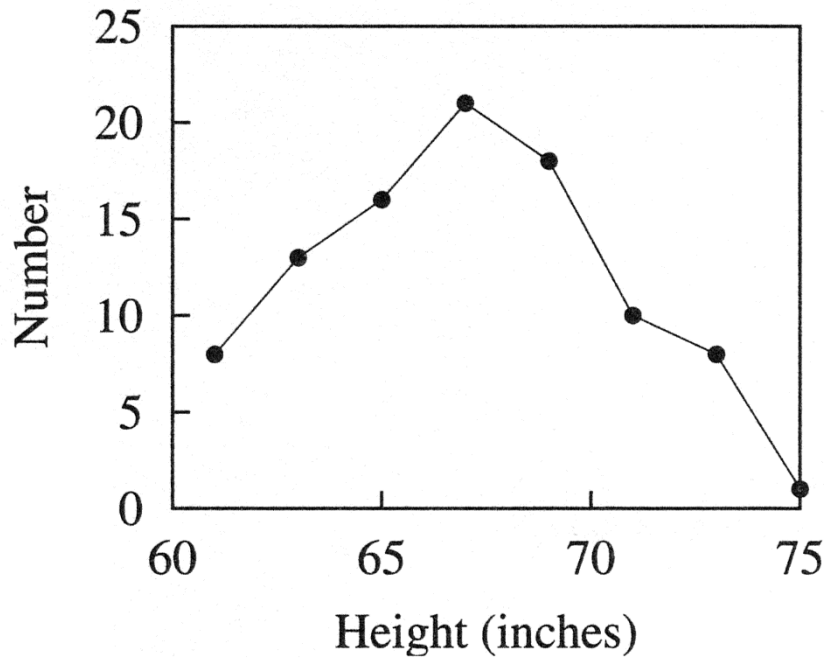


Figure 6.1: The left-hand figure is a histogram of the number of students of a particular height in an evolution class at UC Davis. The right-hand figure graphs the deviation of a student's height from the population mean against the deviation of the student's parents' average height from the population mean. The correlation coefficient is 0.476.

A QT is anything you can measure on a scale (with units of some kind).

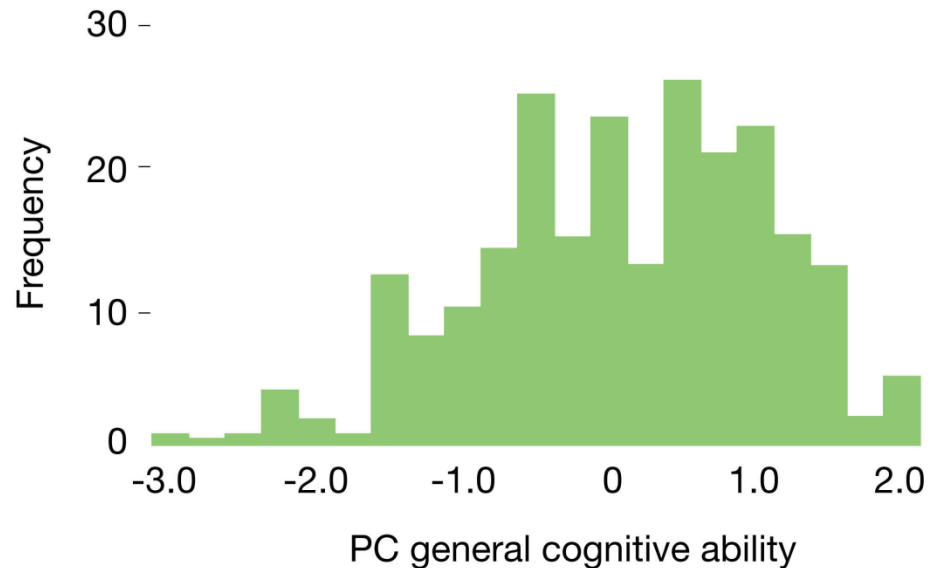
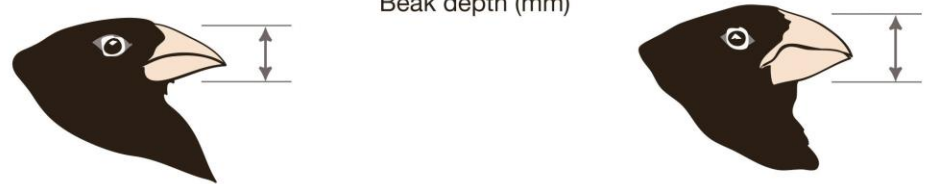
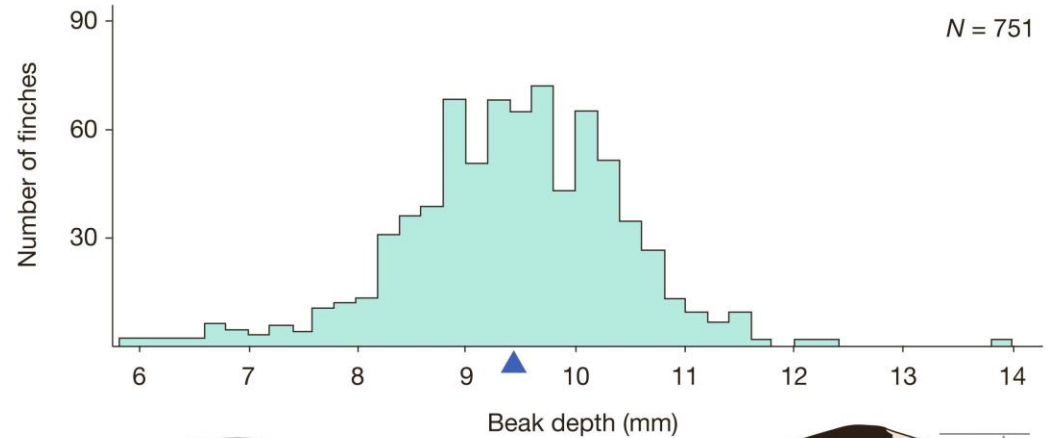
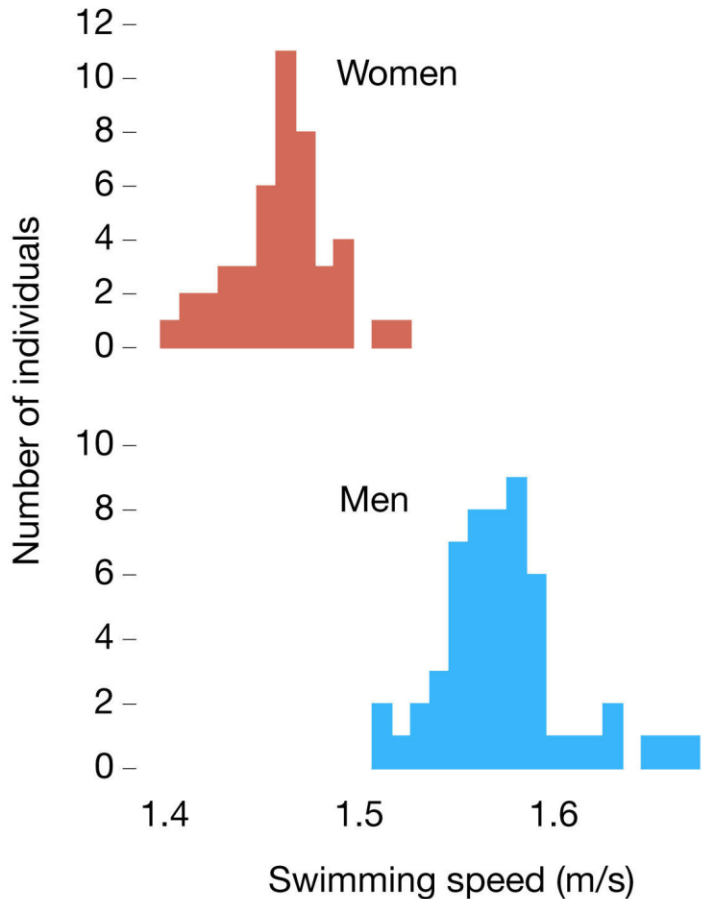
Some examples:

Morphology (size, shape)

Physiology (pressure, temp., rate)

Performance (speed, puzzle-solving)

Fitness! (seeds, surviving offspring)

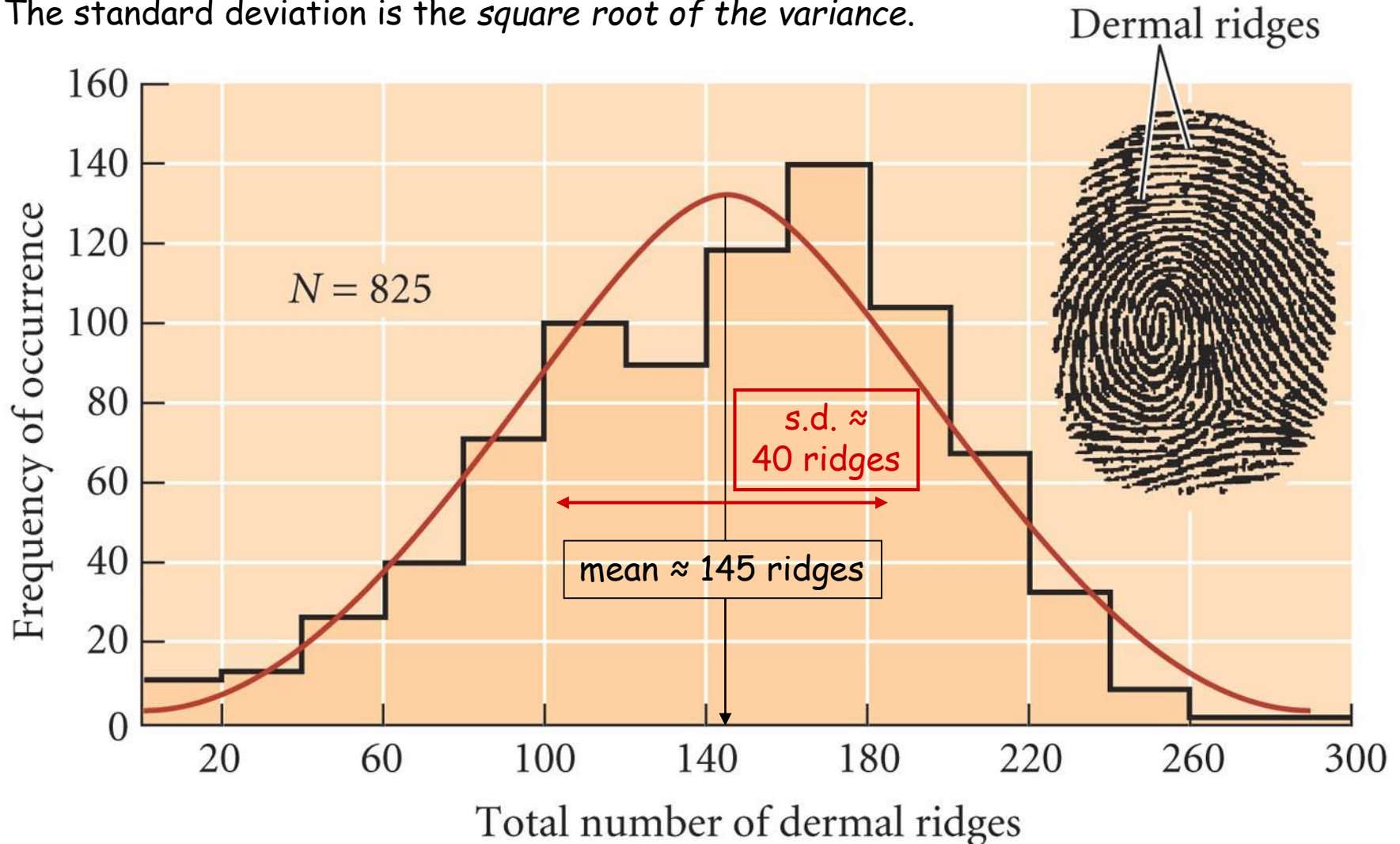


Most quantitative traits are distributed approximately normally.

A normal distribution is fully described by its *mean* and *variance* (or *standard deviation*).

The variance is the *average squared deviation from the mean*.

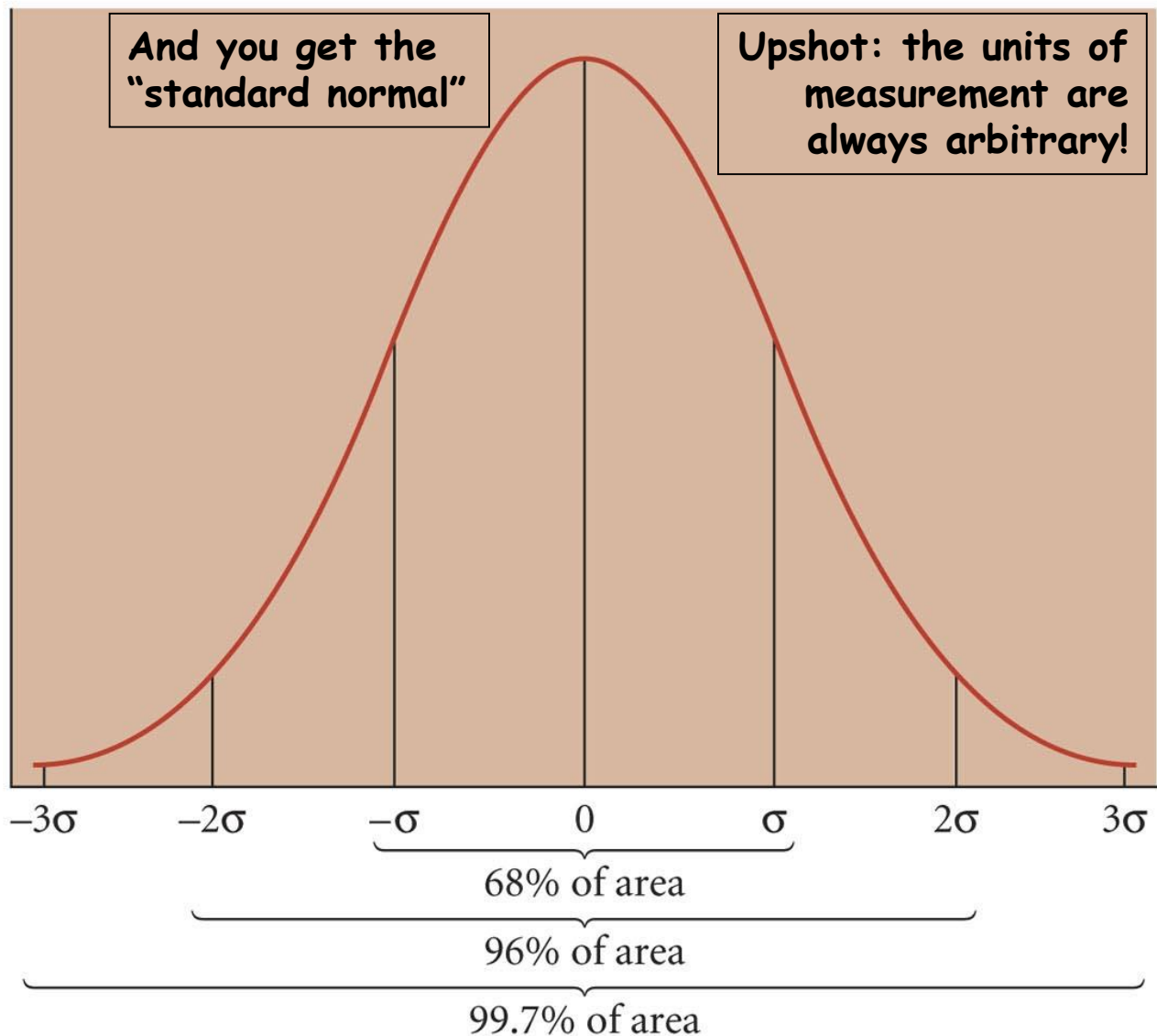
The standard deviation is the *square root of the variance*.

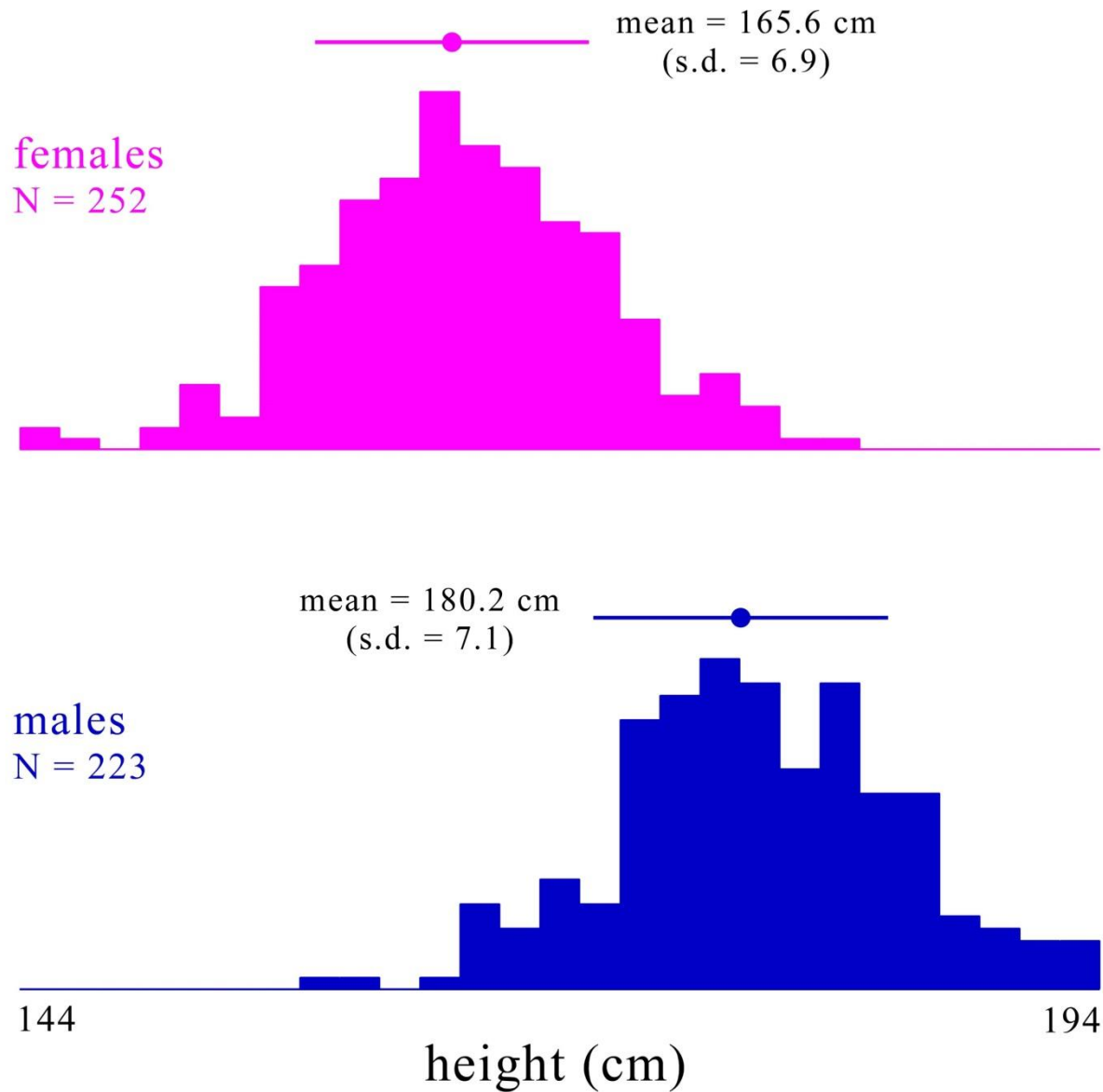


Normal distributions are natural and easy because they're all the same!

Just subtract the mean from every observation (so the mean becomes 0).

Then divide every observation by the standard deviation (so it and the variance become 1).





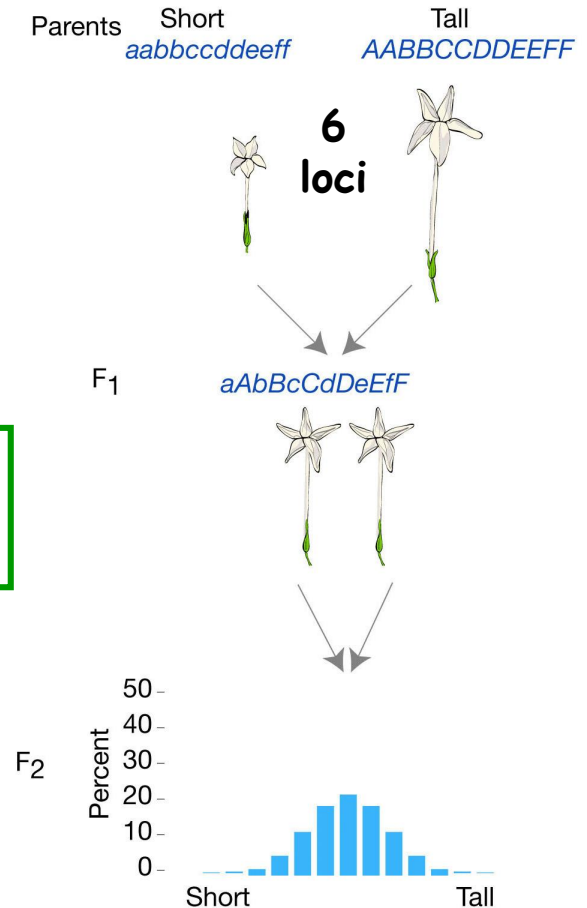
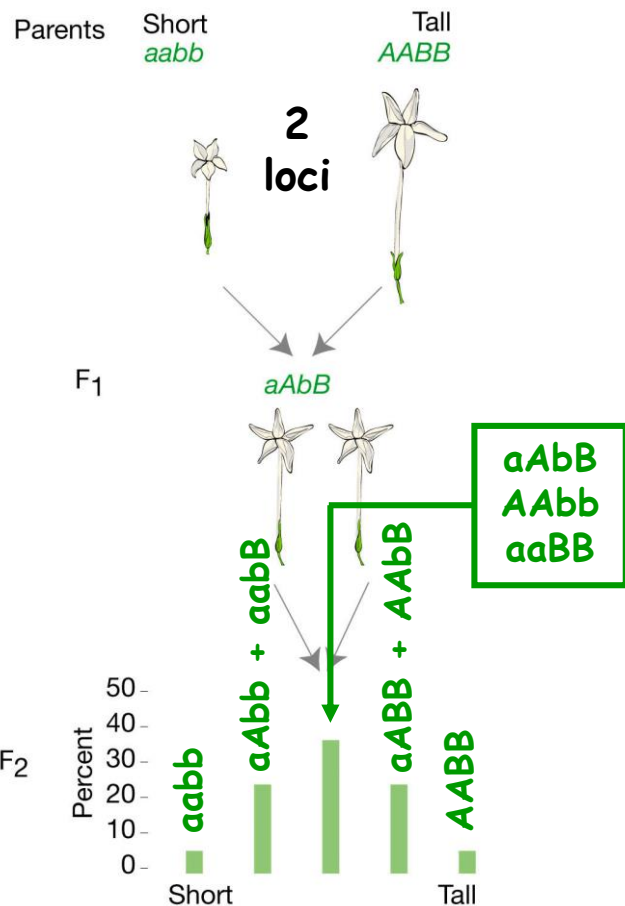
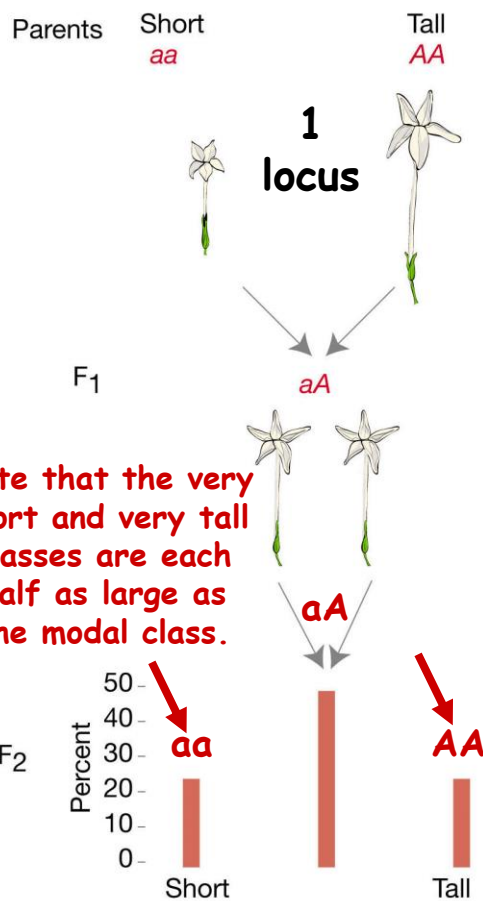
Distributions of height for individual adults participating in the Utah Genetic Reference Project (UGRP).

The simplest QT model: independent loci with "+" and "-" alleles

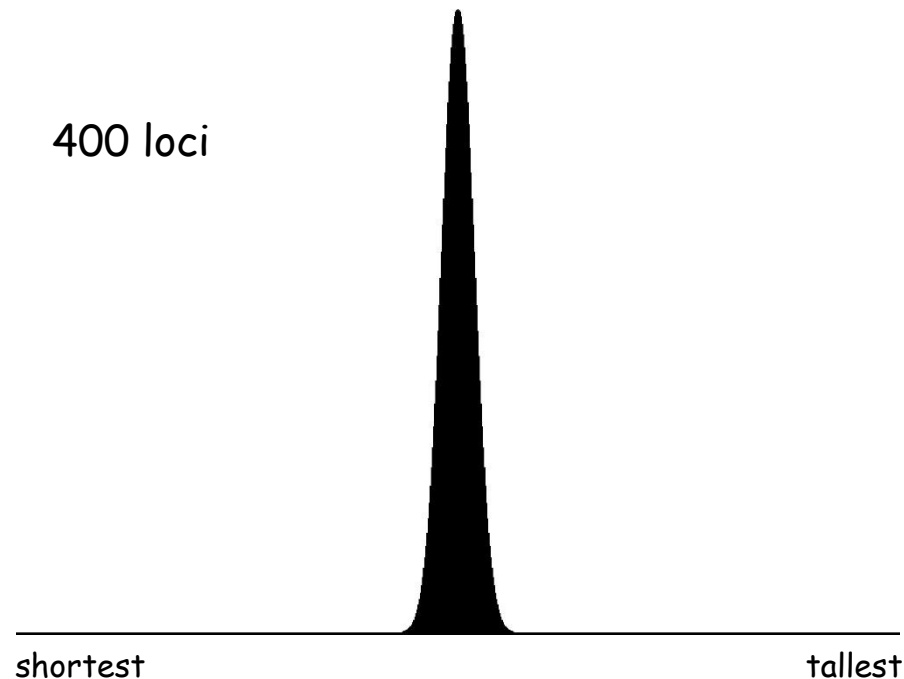
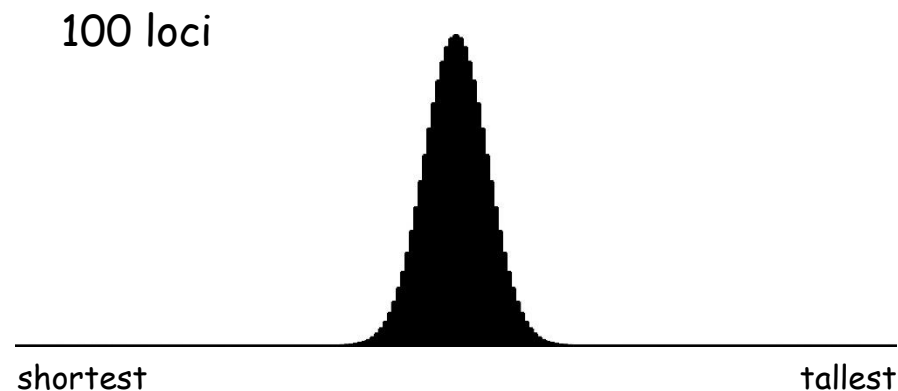
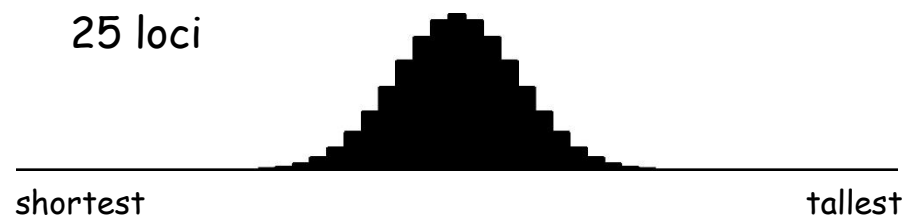
Assume each individual's trait value is the *sum* of its "+" alleles at *all* loci.

That is, a "+" allele at locus *A* has the **same effect** as a "+" at locus *B*.

Then with random mating, we get *quasi-binomial* distributions of the number of "+".
As the number of loci increases, these distributions become *smooth and normal*.



In general, as the number of loci affecting the trait *increases* ...



... the *variance* of trait values *decreases*
(relative to their potential range).

This principle has interesting implications (to be considered later) for the evolution of quantitative traits.

The general formal model: genomic and environmental “causes” add up

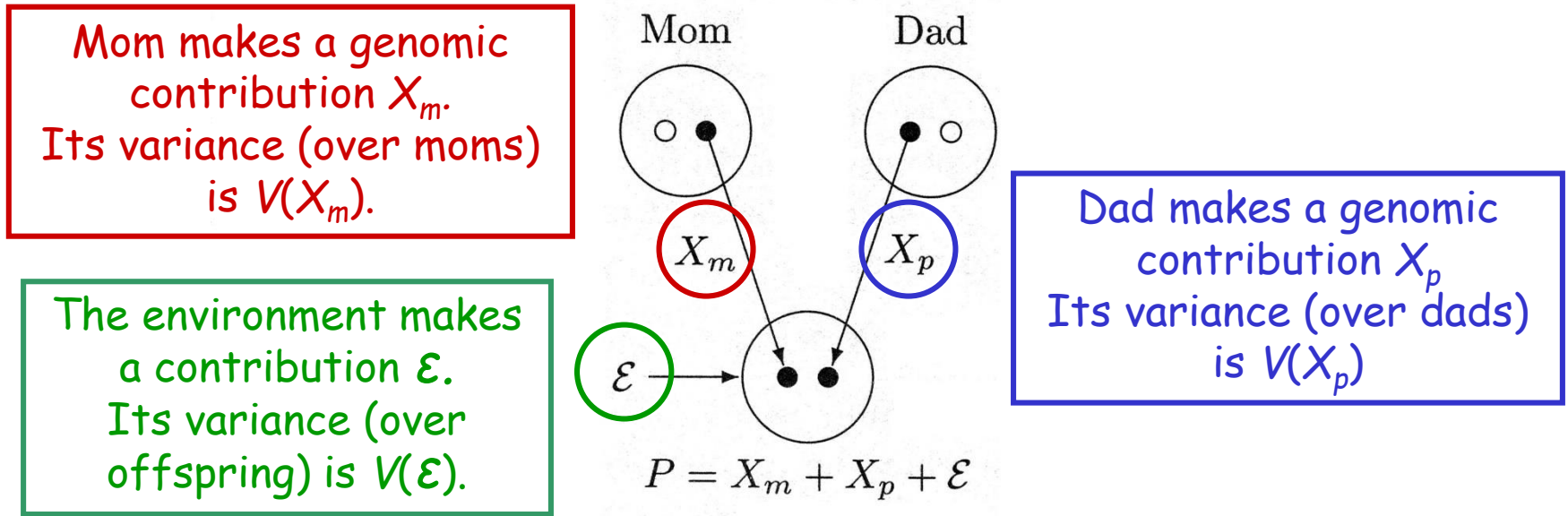


Figure 6.2: The additive model of inheritance for parents and offspring.

For any given offspring, its **phenotype** (quantitative character state) is the **sum** of these three contributions.

And over the *population* as a whole, the *variance* of the phenotypic values is the **sum of the variances** of the three contributions:

$$V(P) = V(X_m) + V(X_p) + V(\epsilon) = V_G + V_E$$

(This assumes that the parents are uncorrelated with each other, and with the environment - see Gillespie p. 198).

Nice theory. Is it true? (Classical test: breeding experiments)

Edward East (1916) crossed pure breeding (inbred) lines of tobacco (*Nicotiana longiflora*) that differed in corolla height.

The F1s were intermediate, but not significantly more variable than the parental lines.

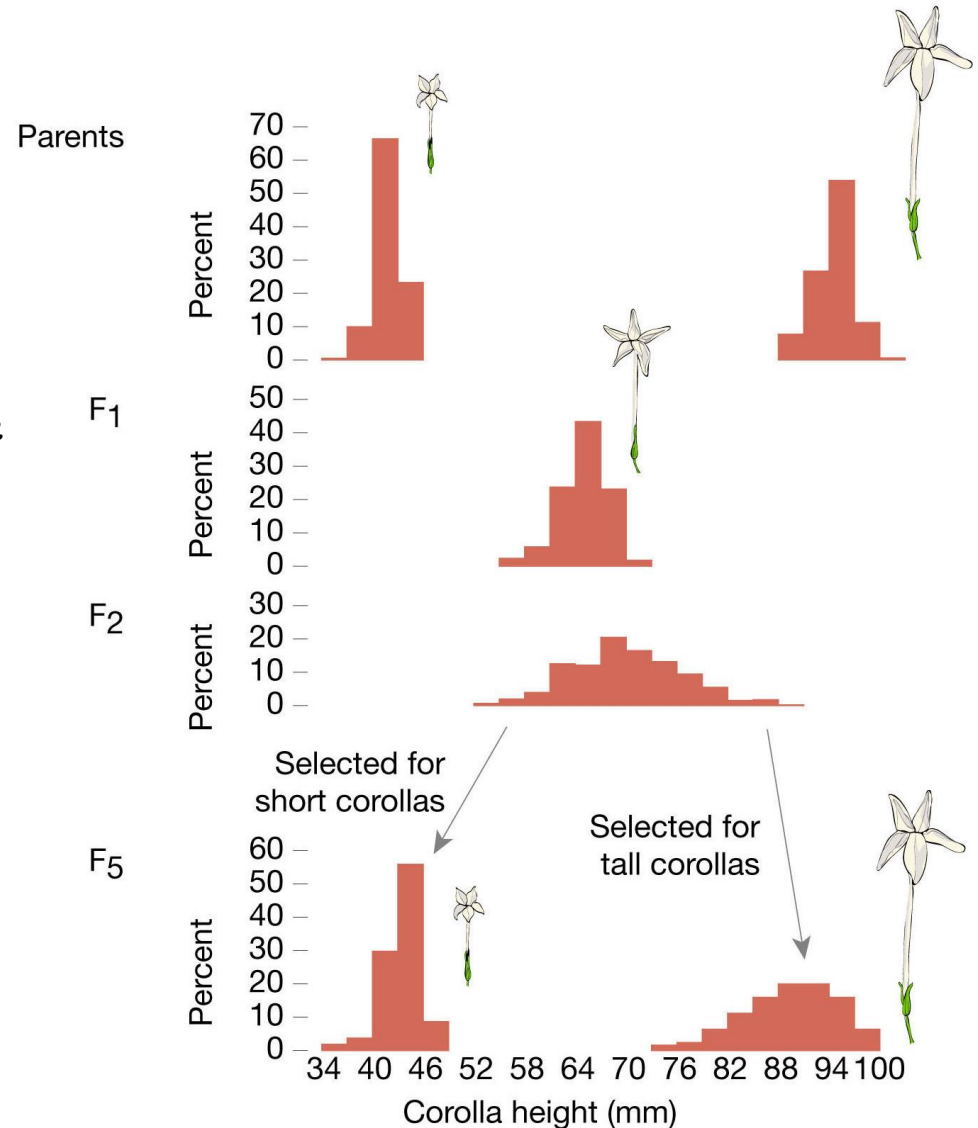
The F2s were also intermediate, but more variable.

By breeding selectively from the smallest-flowered and largest-flowered F2, F3, and F4 individuals, East was able to reconstitute lines nearly as different and uniform as his original parental lines.

Implications:

Many polymorphic loci contribute to corolla length in *N. longiflora*.

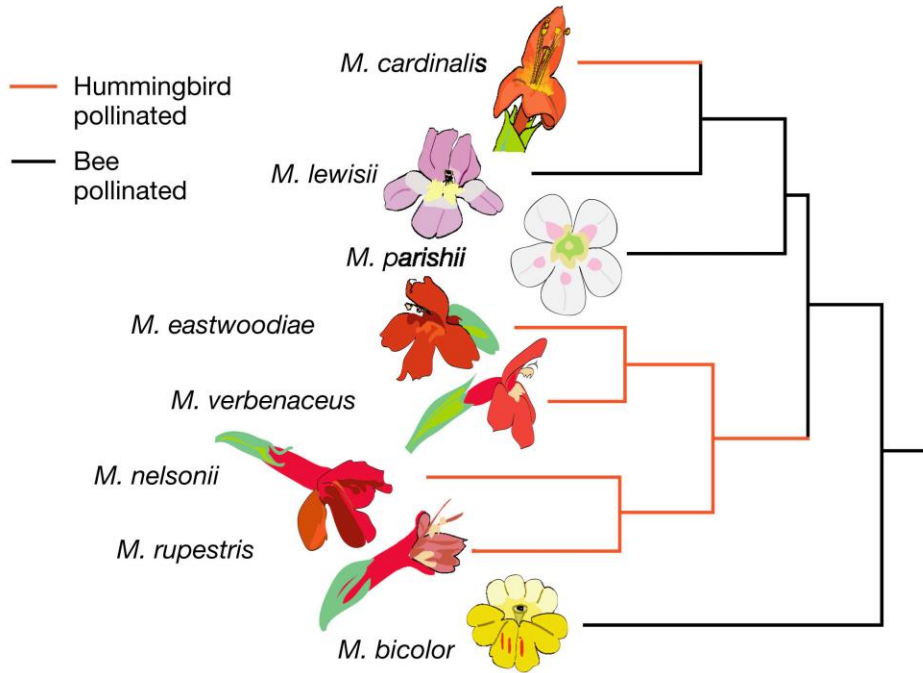
And there is *environmentally induced variation* even among the genetically identical parental plants.



Nice theory. Is it true? (Modern test: QTL mapping)

Hummingbird pollination has evolved twice in the genus *Mimulus* (monkeyflowers).

How did a bee flower like that of *M. lewisii* turn into the h'bird flower of *M. cardinalis*?



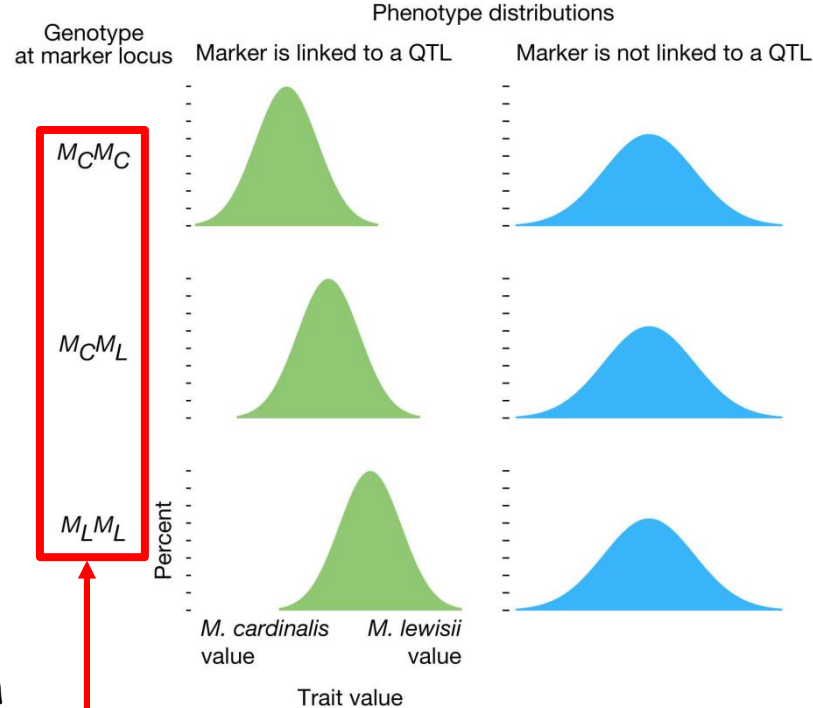
H.D. Bradshaw and colleagues crossed the two species and then made large numbers of F2 progeny from crosses among F1's.

To locate QTLs, correlate linked marker genes with trait values

Bradshaw and colleagues scored the F₂s on 12 different floral traits:

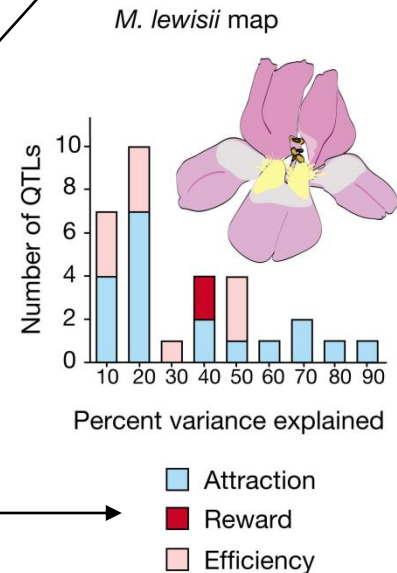
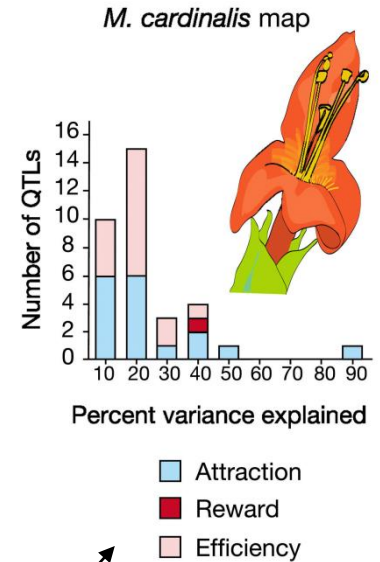
1. Purple pigment in petals
2. Yellow pigment in petals
3. Lateral petal width
4. Corolla width
5. Corolla area
6. Upper petal reflexing
7. Lateral petal reflexing
8. Nectar volume
9. Stamen (male part) length
10. Pistil (female part) length
11. Corolla aperture width
12. Corolla aperture height

Then they looked for associations (among the F₂s) between **parent-specific genetic markers** and trait values.



M_C = *M. cardinalis* marker
 M_L = *M. lewisii* marker

Traits 1-7 affect pollinator attraction; trait 8 (nectar volume) affects reward; and traits 9-12 affect pollinator efficiency.



Summary

All quantitative traits vary, and many are roughly normally distributed.

Offspring tend to resemble their parents.

This implies that some of the variation is genetic (hence "evolvable").

Breeding experiments and models suggest that the genetic contributions come from genotypes at several to very many loci.

Effects of the environment cause additional variation that in most cases will not be correlated with the genetically caused variation.

Beak depth in *Geospiza fortis*
(Darwin's medium ground finch) on Isla Daphne Major, before and after a severe drought.
Peter and Rosemary Grant and friends studied the population for 40 years.

