

Quantitative characters I: polygenes and environment

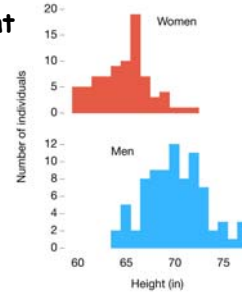
Most ecologically important quantitative traits (QTs) *vary*.

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*.



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

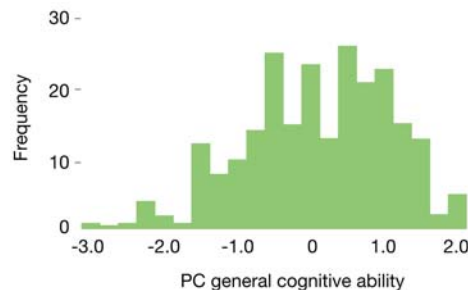
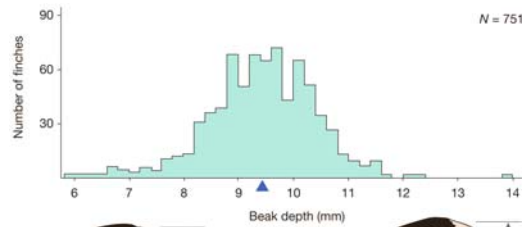
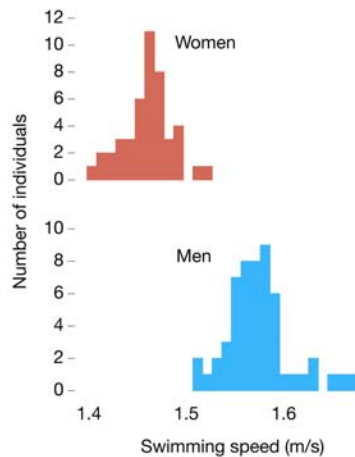
Some examples:

Morphology (size, shape)

Physiology (pressure, temp., rate)

Performance (speed, puzzle-solving)

Fitness! (seeds, surviving offspring)

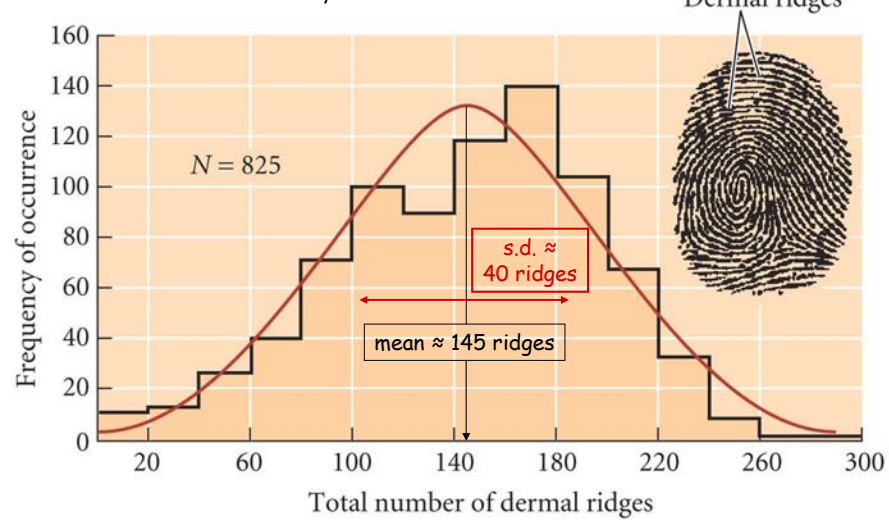


Most quantitative traits are distributed approximately *normally*.

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

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

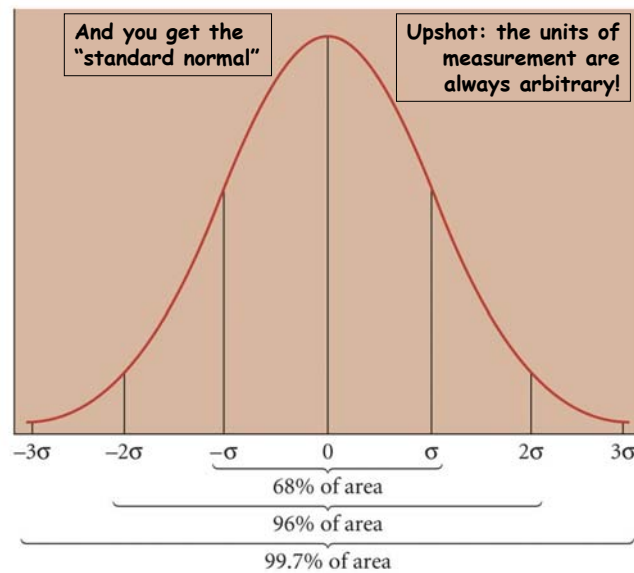
The standard deviation is the *square root of the variance*.



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

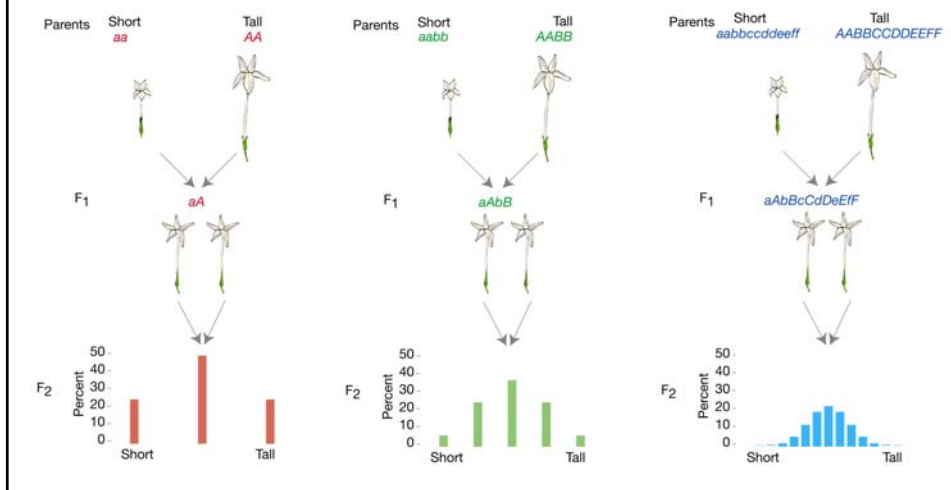
Just *subtract the mean* from every observation (so the mean becomes 0).

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



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

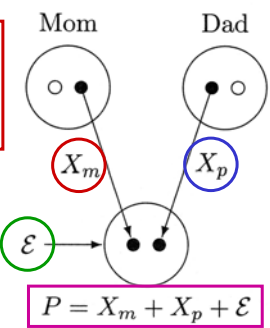
Assume each individual's trait value is the *sum* of its "+" alleles at all loci. That is, a "+" allele at locus A has the *same* effect as a "+" at locus B. Then with random mating and free recombination, we get *binomial* distributions. As the *number of loci* increases, these distributions become *smooth* and *normal*.



The general model: genomic and environmental "causes" add up

Mom makes a genomic contribution X_m . Its variance (over moms) is $V(X_m)$.

The environment makes a contribution \mathcal{E} . Its variance (over offspring) is $V(\mathcal{E})$.



Dad makes a genomic contribution X_p . Its variance (over dads) is $V(X_p)$.

$$P = X_m + X_p + \mathcal{E}$$

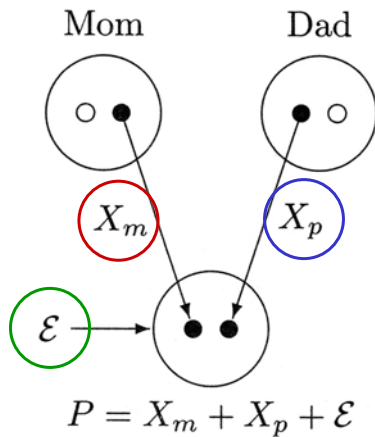
For any given offspring, its **phenotype** (quantitative character state) is the **sum** of these three contributions.

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

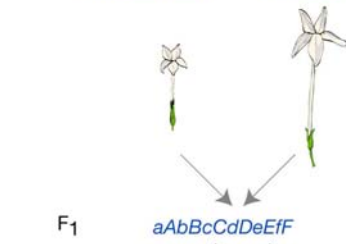
$$V(P) = V(X_m) + V(X_p) + V(\mathcal{E}) = V_G + V_E$$

(This assumes that the parents are uncorrelated with each other, and with the environment, which is often *roughly* true).

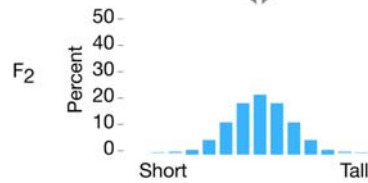
QTs are normally distributed because each of the three contributions is *itself* the sum of many independent genetic or environmental causes.



Parents Short *aabbccddeeff* Tall *AABBCCDDEEFF*



Offspring are *correlated* with their parents (and siblings) because their genes are *half identical* to those of each parent.



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.

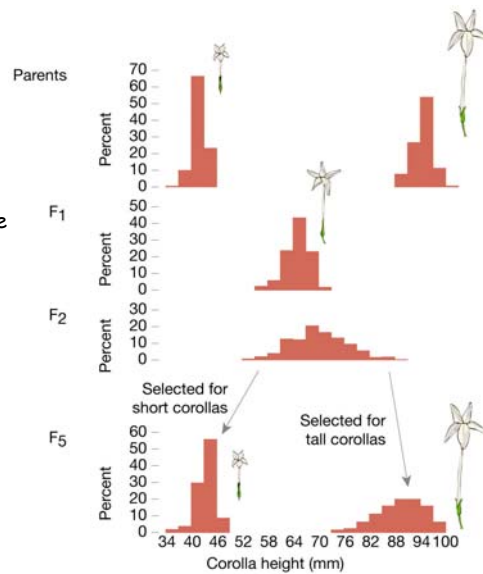
The F2s were also intermediate, but more variable.

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*.

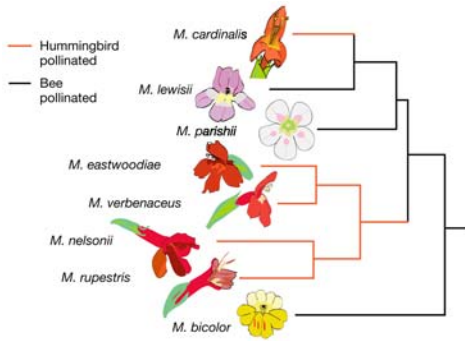
And there is *environmentally induced variation* even among the genetically identical parental plants.



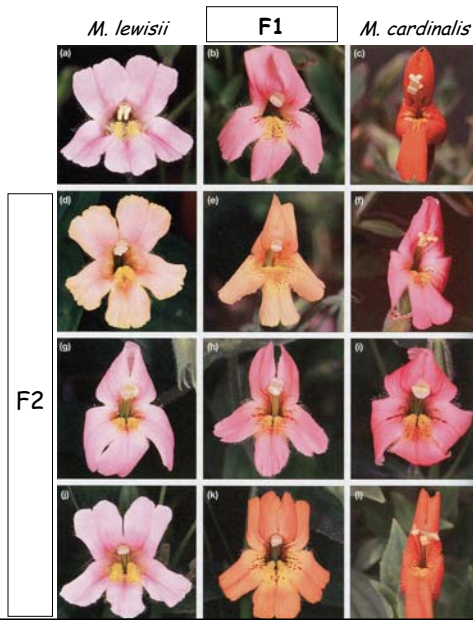
Nice theory. Is it true? (Modern test: QTL mapping)

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.

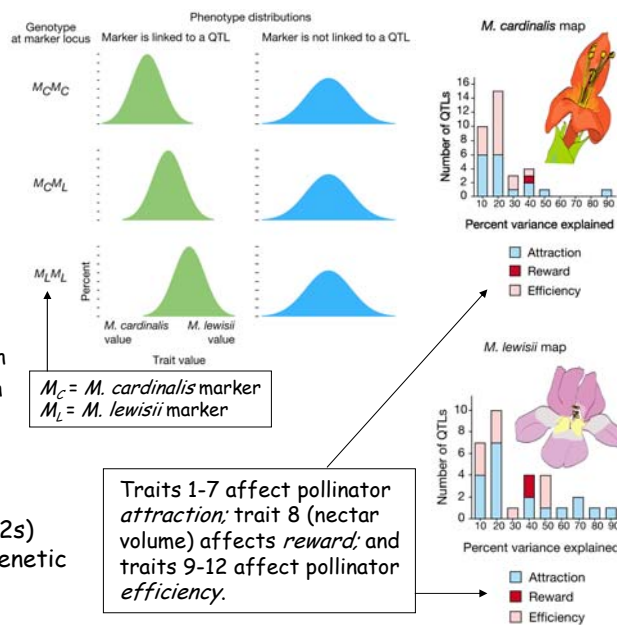


To locate QTLs, correlate linked marker genes with trait values

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.

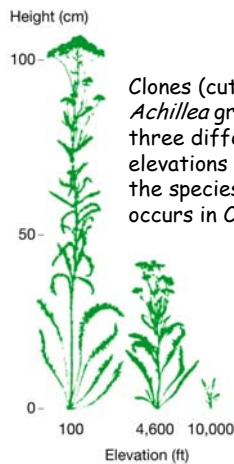


Quantitative trait loci (QTLs) are numerous *within* species, too

Almost any quantitative trait you care to define and study is affected by several to many QTLs.

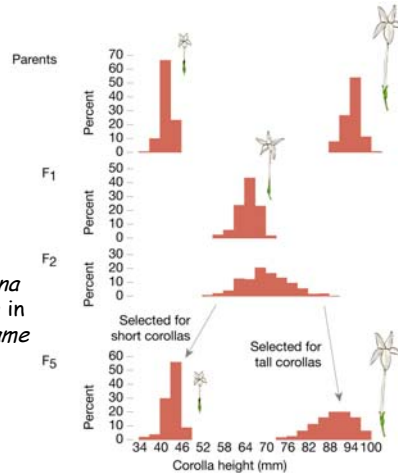
But what about variation induced by *environmental* factors?

After all, even *clones* and *identical twins* differ from each other!



Clones (cuttings) of *Achillea* grown at three different elevations where the species normally occurs in California

East's *Nicotiana* plants growing in exactly the *same* garden plots.



Total phenotypic variance = genetic variance + environmental variance

What you *see* is what you get from two distinct sources that can be separated.

1. *Genetic variance* is the variance among phenotypes caused by *genotypic* differences among individuals (holding their *environments* constant).
2. *Environmental variance* is the variance among *phenotypes* caused by differences in the *experiences* of individuals (holding *genotypes* constant).

Example: Suppose the *average* trait values of AA, Aa and aa individuals are -1, 0, and +1 units, and $p = q = 0.5$.

Then the *genetic variance* (average squared deviation from the population mean) is 0.5.

But suppose 25% of each genotype deviates one unit above or below its average trait value, because of the environment.

Then the *environmental variance* is also 0.5.

The resulting *phenotypic variance* is $0.5 + 0.5 = 1.0$.

In general, $V_p = V_G + V_E$.

This matters because a trait's *heritability* is the *fraction* of V_p that is *genetic* (actually, *additive genetic*, as we will see).

