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.
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.

Dermal ridges

- mean $\approx 145$ ridges
- s.d. $\approx 40$ ridges

$N = 825$
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).

And you get the “standard normal”

Upshot: the units of measurement are always arbitrary!
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.
Also, as the number of loci affecting the trait *increases*...

...its *variance* relative to the potential range *decreases*.

This principle has interesting implications (to be considered later) for the evolution of quantitative traits.
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 $\varepsilon$. Its variance (over offspring) is $V(\varepsilon)$.

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

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:

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

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

Figure 6.2: The additive model of inheritance for parents and offspring.
QTs are normally distributed because each of the three contributions is itself the sum of many independent genetic or environmental causes.

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.

*MC* = *M. cardinalis* marker  
*ML* = *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 genetic contributions come from genotypes at several to very many loci.

Effects of the environment usually “blur” the effects of genotypes.