Genes and the Phenotype: The Heritability Concept

Eth. & Behav. Ecol.
Biology 287
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I. Introduction:

A. These notes deals with the general question of how we quantify the action of genes on the phenotype. We observe the phenotype directly and we can easily measure various aspects of it. We also come to believe (perhaps mistakenly) that hereditary factors are involved in the phenotype when we observe that offspring resemble their parents. And even though it is, in principle, possible to know an animal's entire genotype, the fact is that we have no way of directly relating this to most phenotypic traits due to their highly polygenic nature.

B. We have also already seen that there is a polarizing debate and rather meaningless debate about whether behavior is "genetic" or "environmental", plastic and non-plastic, instinctual or learned. In fact these couplets are often synonyms for each other. One feature that is often introduced into these debates, especially when humans are involved is heritability. Most people use this concept in attempt to be more sophisticated in their understanding of the determination of the phenotype. However, all too often, heritability turns into a formula for determining the extent to which a trait is "genetic" vs. "environmental". We will learn what heritability actually is, what its limitations are, and where it is useful. Everyone in this class should come to have a good understanding of heritability.

C. Beyond the implications for humans, we need to have a more general understanding of heritability because its real use has to do with understanding how susceptible the frequency of a trait in a population can be influenced by natural selection (or for that matter, to genetic drift).

D. The guiding features of our discussion will be the following principles:

1. **This is a discussion of populations not individuals**. Heritability and evolution have nothing to do *per se* with individuals; they are population phenomena.

2. Populations may be variable with respect to any feature of the phenotype.

3. Individuals (or genes) are the targets of selection (but populations evolve).

4. Evolution (OF A POPULATION) can only occur to the extent that the variation in behavior is tied to variation in genotype -- differences in behavior due to differences in environmental influences can matter very much in selection but not in evolution

II. How do we measure phenotypic variation?

A. Variability is a fundamental property of all living populations. No two individuals are exactly alike in their phenotype. This variability is of great importance since differences between individuals often translate into relative advantages or disadvantages. To the extent that these differences are based on heredity, these can serve as the raw stuff for evolution.

B. We often display data dealing with variation in the form of a histogram. Please see the appendix if you do not recall what histograms are; we will use them extensively in this course.

C. How do we characterize a distribution? There are really two important measurements.

      1. **A measure of the average**. This is quite easy to find in a normal distribution since the most commonly occurring types is the mean. Thus, the **mean** (average) is the peak on the histogram. This is because normal distributions are defined as being symmetrical about the mean. In other words, just as many observations occur above as below the mean and furthermore, the number of observations above the mean by some amount exactly equals the number below the mean by the same amount.

      2. **A measure of variation**. How much variation is there in the phenotype? There are two common ways to measure variation.

        (a) A common but not particularly satisfactory measurement is **range**. The range is simply the greatest and least values or their difference. The problem with the range is that it tells us nothing about how variation is distributed within the range. The illustration below illustrates this point. In it are two histograms, both with the same mean and the same range of values. Yet one clearly more variable than the other in the sense that there is a greater chance that an individual will have a value that differs considerably from the mean:

Histograms of Two Populations with Different Degree of Variation and the Same Means
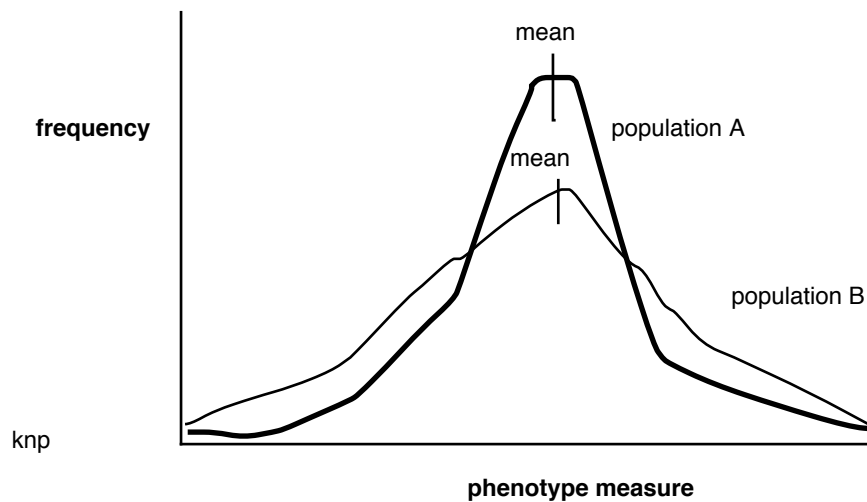
While both populations have the same mean, clearly Population B is more variable since a smaller percentage of individuals of the central type are found.

      (b) To get around this problem, we commonly use a measure called the **VARIANCE** (or its closely related measure, the standard deviation).

        (i) The <u>variance is the average square of the difference between each member of a sample or population and the mean</u>.

        (2) Here is how it is calculated.

(i) Recall that a histogram shows the frequency of each "degree" or extent of the phenotype in some population.

Normally Distributed Variation

number or frequency

mean

range of phenotypic expression
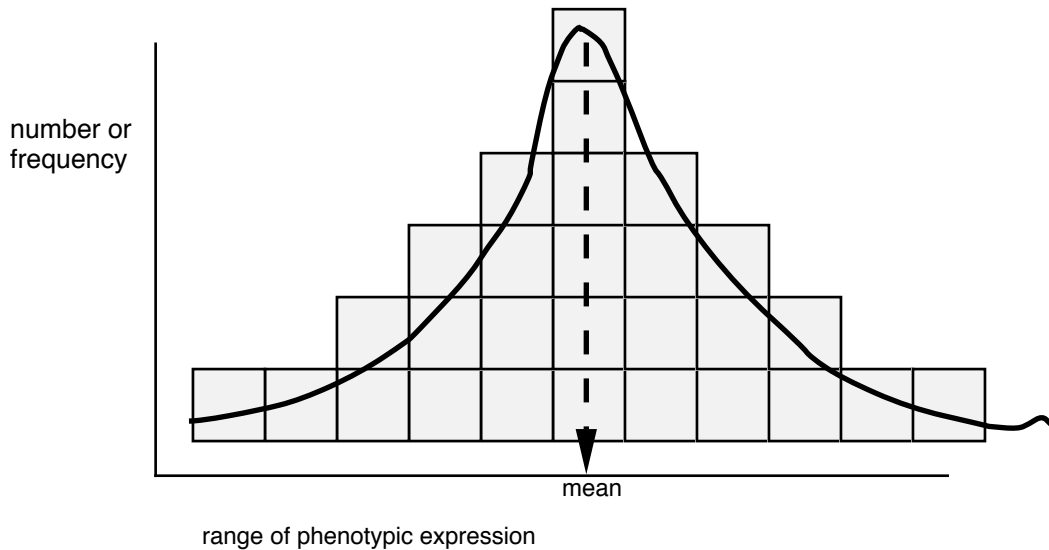
Each individual's phenotype is represented by a box; the line shows approximatley how it fits to a normal distribution and the dotted line with an arrow shows the mean

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(See footnote (*) about normal distributions)

(ii) The difference between each individual value (for instance the smallest value) and the mean is called the **deviation score**. For example, in the graph above, the deviation score for the phenotype with the "lowest value" is 5 units below the mean. So it has a score of -5. The next lowest is -4. Then, there are two individuals with a score of -3, three with -2, and four with -1. Looking at the deviation scores above the mean, there are four with +1, three with +2, two with +3 and one each with +4 and + 5.

(iii) Now, if we were to sum all the deviation scores, they would cancel each other out (since some are positive and others are negative). To get around this problem, we square each deviation score first and then we sum them. The result is called the **sum of the squares** of all of the deviation scores.

(iv) Finally, we need a way to adjust for the sample size. Notice that for a given shape distribution of data, the more individuals that are measured, the greater the sum of squares. But we can remove the influence of sample size by dividing the sum of squares by the number of individuals. This step gives us the

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* An aside -- If the phenotype is normally distributed, the mean is the peak of the histogram, the two "tails" are symmetrical around the mean, and they meet a certain mathematical criterion that about 2/3rds of all the observations would fall in the area corresponding to one standard deviation above and below the mean and that about ±93% of all observations would be within 2 standard deviations of the mean.

average of the squared deviations (average sum of squares). Another term for this averaging is "**normalizing**".

Note: The variance is closely related to the standard deviation. The difference is that the standard deviation is the square root of the variance.
We tend to use variance in to measure variability because they can be added. The importance of this property will be obvious when we learn how to calculate heritability.

One final and very important emphasis: it is important to realize that <u>**variance is a population phenomenon**</u> -- it is not the trait of an individual. Variance is a devise to systematically describe the amount of variation in a population

III. The Components of total phenotypic variance, V_P

      A. The total variation in phenotype that we observe in a population is called the phenotypic variance, V_P. We have already seen that this variance arises from influences of genes and environment. Let's look at this in a bit more detail.

      B. <u>**Phenotypic variation due to genotypic variance, V_G**</u>. Thus, we will expect that some of the differences we see in phenotypes may be due to differences in individual's genotypes. There are a number of ways whereby genes interact with each other to produce a phenotypic trait. Here are the most important:

          1. **V_A:** Phenotypic variation that traces to variation in genes that have **additive effects** on the phenotype. Additive effects are an important aspect of what is termed <u>quantitative inheritance</u> (see last notes).

          (a) A common example of quantitative inheritance is where each allele of a certain type that an individual possesses adds a fixed amount to the expression of a phenotype.

          (b) For example assume that there are two copies of a locus that controls the duration of an individual's mating call. Assume that there are two different alleles, A_1 and A_2, that can occur at these two copies of the locus. Assume that the number of A_1 alleles will determine the average time that an individual uses in making a specific call. The more A_1 alleles that are present, the longer the call. Thus, A_2A_2 A_2A_2 individuals do not call, A_2A_2 A_2A_1 individuals call for 1 unit of time and $A_1A_1A_1A_1$ individuals call for four time units.

          (c) This mode of inheritance is very important not only because it is quite common, but also because it tends to result in offspring whose phenotypes are close to being intermediates of their parents, if their parents are homozygous strains. Likewise, if heterozygotes breed, their offspring will tend to show a normal distribution of phenotypes. More about V_A in a moment.

          2. <u>**Phenotypic variation due to variation at loci where there are dominance relations, V_D**</u>. In this case the offspring of homozygotes of two different alleles will not be intermediates -- they will probably all resemble the dominant parent. Obviously, if you think of different possible crosses where dominance exists, you tend to get rather skewed offspring phenotypes

          3. <u>**Phenotypic variation due to variation in interactions between different genes (e.g., epistasis, V_I.**</u> Many times alleles at different loci interact in

manners that produce unusual phenotypic ratios. These also are rather common. There are many possible ways they can occur and the distributions of phenotypes they produce will depend both on the parents' genotypes and the ways the alleles interact

Thus, $V_G = V_A + V_D + V_I$

There are two other components to phenotypic variance:
        B. **Phenotypic variance due to differences in environment, V_E.** We will return to a more detailed consideration of this a bit later.
        C. **Phenotypic variance due to differences between the interaction of different genotypes and different environments, V_{GE}.** Shown below is a graph of such an interaction -- notice that in different environments each genotype responds in a similar manner. However, one genotype, Aa, is much more sensitive to this environmental change than is the other (AA). The variance that results from the difference in these two responses is termed gene-environmental interaction variance.

Variance Due to Gene- Environment Interaction

response

A graph showing the variance due to gene-environment interactio, Vge. Note that in one environment, Aa produces a larger phenotype while in another, AA does.

genotype Aa

genotype AA

environmental factor   knp
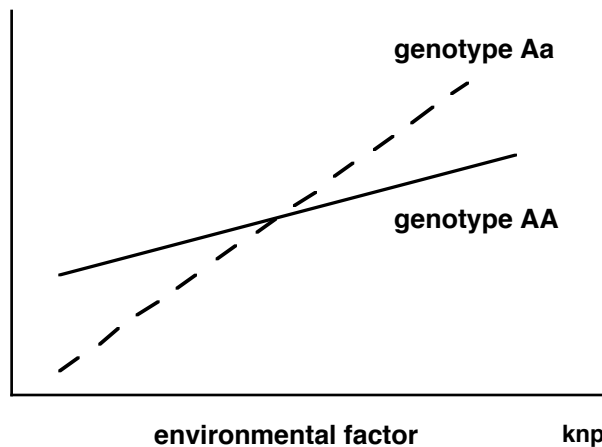
Do not confuse this gene-environmental interaction with the overall idea of gene environmental interaction. This source of variation is applied to a relatively small number of the genes that are responsible for producing the overall phenotype that we are studying. We have already seen that gene environmental interaction is the fundamental feature that allows the creation of the phenotype (see notes on genetics and behavior). V_{GE} is a very specific type of interaction that relates to very specific but different response patterns to environmental variance by certain alleles at a particular locus (see previous graph).
        D. Thus, we can say that **the total phenotypic variance**, V_P (sometimes also given as V_T) must equal the sum of all of these individual variances:

$$V_P = V_G + V_E + V_{GE}$$
$$= (V_A + V_D + V_I) + V_E + V_{GE}$$

Which of the terms in the equation given above can be measured directly for a population? (Hint: only one can be so measured)

IV. The <u>HERITABILITY</u> Concept
  A. Heritability defined: an attempt to describe how much of the phenotypic variance, V_P, is due to variance in genotype, V_G. Note that since variance is involved, it is a population not individual phenomenon and thus has no meaning in describing the extent to which a trait in an individual is genetic as compared to environmental.

> Keep Dawkins' cake analogy in mind -- an individual's phenotype is no more determined mainly by genes or mainly by environment anymore than a cake is determined by either recipe or ingredients.

There are two types and it is very important that you understand each:

  1. **BROAD SENSE HERITABILITY**, **H²**. This is the <u>proportion of the total phenotypic variance that can attributed to genotypic variance (i.e. to differences within the population in genotype).</u> Mathematically:

$$H^2 = \frac{V_G}{V_P}$$

  2. We are often more interested in <u>variance from additive genes</u>, since genes that show additive inheritance tend to show more intermediate forms for selection to operate on (and thus greater phenotypic variability). When examining the heritability of such genes the measure we use is called **NARROW SENSE HERITABILITY**, *h²*. Mathematically it is calculated as:

$$h^2 = \frac{V_A}{V_P}$$

  3. What do the calculated values mean?
   (a) If H^2 or h^2 equal 1.0 it means that all the variation of some trait that exists in a population is ascribable to genotypic variation in the population.
   (b) If the value is 0 it means that none of the variation is ascribable to genotypic variation. It does not mean that genes have nothing to do with the characteristic under study -- just that differences in genes are not causing differences in phenotype.
   (c) A value in between (the most common one) means that some percentage of the variation in phenotype e is due to variation in genotypes and the rest in differences that trace to inhomogeneities in the environment.
  B. Methods used to calculate heritability. Please note that this list is far from exhaustive and, believe it or not, the methods presented here are not very sophisticated. But they are understandable and they nicely illustrate what heritability is.
   1. The central problem in measuring heritability is estimating the proportion of phenotypic variation that is attributable to genotypic variation. Unlike total phenotypic variation, V_G is not something that can be measured directly -- it must be

estimated. That is what the methods below are all about although we will see that they do not directly estimate V_G but they do it in the process of finding an estimate of heritability. Hopefully with some experience this will make more sense.

2. **Regression of Phenotypes Among Relatives**: This method requires that the phenotypes of parents and offspring be plotted against each other.

(a) Again, keep in mind that we are talking only about one trait -- so when we say average phenotype, we mean the average measure of some specific phenotypic characteristic in a population

(b) It is easiest to understand the use of this technique in the calculation of narrow-sense heritability, h^2:

(i) In this case, the *average phenotype of the offspring* is plotted against the *average phenotype of the two parents*.

(ii) A least-squares linear regression is obtained. This is an equation in the form $Y = b*X + i$ where Y and X are the phenotypic values for the offspring and parents, i is the y-intercept and b is the slope of the line. It is calculated simply by finding a line that minimizes the total of the squared difference between the line and each point (note that this is similar to the sum of squares we talked about with variance).

(iii) Here are some examples:

Regression of Offspring on Parental Phenotype to Determine h^2
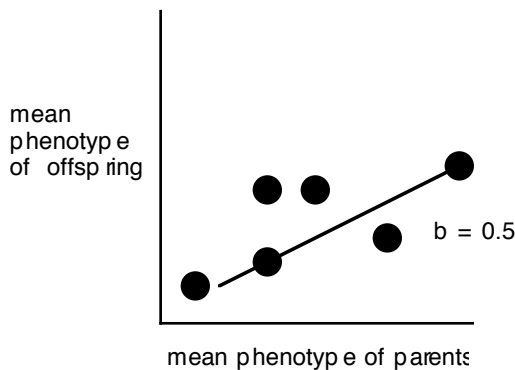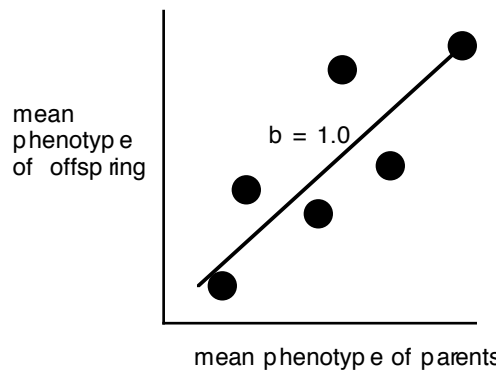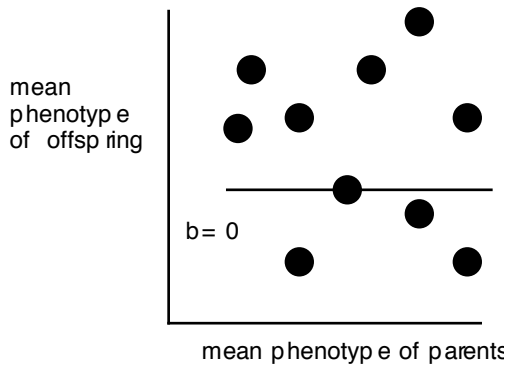
The heritability of the trait under study is equal to the value of the regression coefficient (slope) of each line. Thus, the variation in the figure at upper left can all be ascribed to variance in the environment, variation in the upper right comes from genetic variance and in the lower left about 0.5 of the variance in phenotype is explainable as due to environmental variation.

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? Why should the slope give the narrow sense heritability? Suppose we have the following parents $A_1A_1 * A_2A_2$, $A_1A_2 * A_1A_2$, $A_1A_2 * A_2A_2$, $A_2A_2 * A_2A_2$ and $A_1A_1 * A_1A_1$. Suppose this locus involves additive effects where the presence of each A_2 allele adds one unit to the phenotype.

Thus, for the first cross: $A_1A_1 * A_2A_2$
is phenotypically a cross of minimum phenotype * +2 phenotype
The average is therefore **+1 phenotype**

The possible offspring are all A_1A_2; therefore all offspring will have the **phenotype +1** (since each has one A_2)

Now, for $A_1A_2 * A_1A_2$
the average parental phenotype is $(+1 +1)/2 = $ **+1**
The following offspring will occur in the following numbers:

1 A_1A_1: 2 A_1A_2: 1 A_2A_2 for phenotypes of one +0, two +1, and one +2
where the average phenotype is $(0+2*1 + 1*2)/(1+2+1) = 4/4 = $ **+1.0**

For $A_1A_2 * A_2A_2$

we get an average parental phenotype of $(+1+2)/2 = 1.5$ and the following types and ratios of offspring: 1 A_1A_2, and 1 A_2A_2 for an average phenotype of $(+1 +2)/2 = 1.5$

and for $A_2A_2 * A_2A_2$ the average phenotype of both parents and offspring is +2; for $A_1A_1 * A_1A_1$ the averages are + 0 for both. Here is the plot
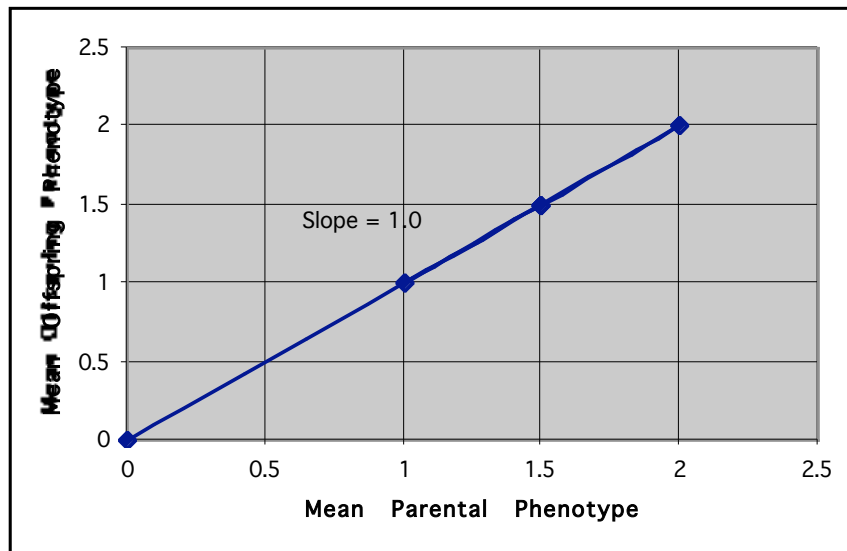
Now, what happens if the difference in genotype has nothing to do with differences in phenotype? In this case, suppose that we still use parents with the same phenotypes as above. So our crosses are now:

+0 * +2 (mean = +1); +1 * +1 (mean = +1); +1 * +2 (mean = +1.5); +2 * +2 (mean = +2); +0 * +0 (mean = +0). Since with our supreme powers we have said that genotypic

variation has no effect on this trait in this population, then the average phenotype of the offspring of each cross is totally random. Here is one possible result of a cross:
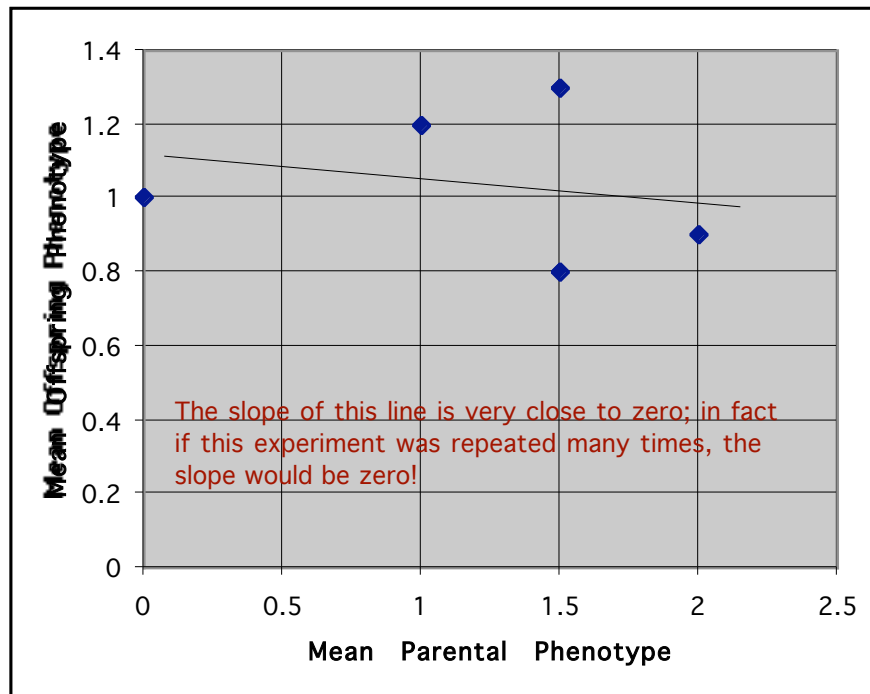
The exact graph will not always be the same but the effect will be -- no correlation between parents and offspring should give a line with a slope equal to or very close to zero.
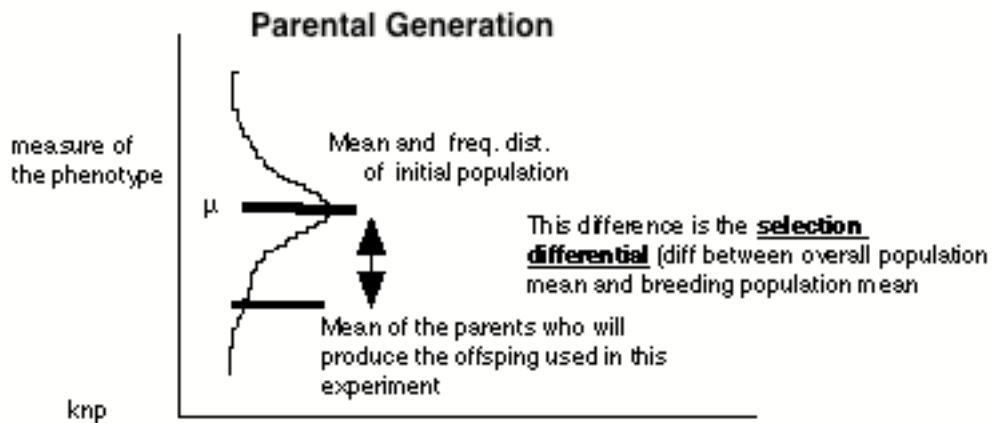
? Wouldn't it be important that I controlled the environment in these experiments? Explain. What does controlling the environment mean? Do all individuals have to experience identical environments to have an effective control?

? Why does a slope less than 1.0 indicate a lower heritability?

2. Determination of h^2 by Using the Response to Selection.

a. One way to measure narrow-sense heritability is to see how a population responds to selection. Selection is the process of allowing some phenotypes to out-reproduce others. In these experiments, selection involves picking a particular phenotype and usually crossing these individuals with each other (example: the fastest at solving mazes crossed with other similarly "fast" individuals).

b. Here are the two most important measurements used in one of these experiments:

i. **Selection differential** = the <u>difference </u>between the <u>mean population phenotype and the selected phenotype</u> (the one that is allowed to reproduce).

Parental Generation

measure of
the phenotype

μ

Mean and freq. dist.
of initial population

This difference is the **selection differential** (diff between overall population mean and breeding population mean

Mean of the parents who will
produce the offsping used in this
experiment

knp

        ii. Selection response = difference between the mean phenotypes of the F_1 and Parental generations (**Important note**: the parental generation in this case refers to all of the F_1 and all of the "parental generation" including those that were not allowed to reproduce. See the next illustration).

measure of
the phenotype

μ

Mean of Overall
Parental
Population

**Selection
Response**

Mean of
F_1 Population

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Parental
Generation

F_1 Generation
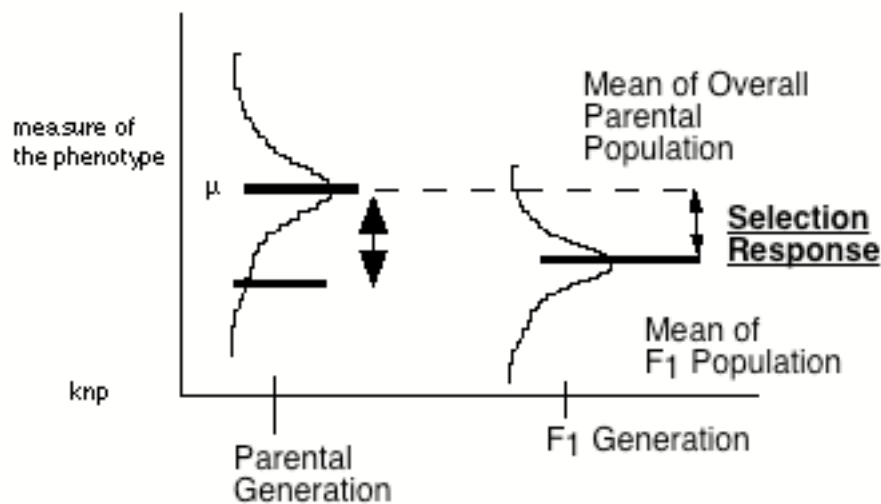
        c. The calculation: If something has a heritability of 1.0, it means that there should be a perfect correlation between differences in genotype and variation in phenotype (see last example) because environmental variation has nothing to do with phenotypic variation. Thus, in a selection response experiment, the greater the difference between the selected parents and the overall population (selection differential), the greater the difference between their offspring and the original population (selection response). Thus:

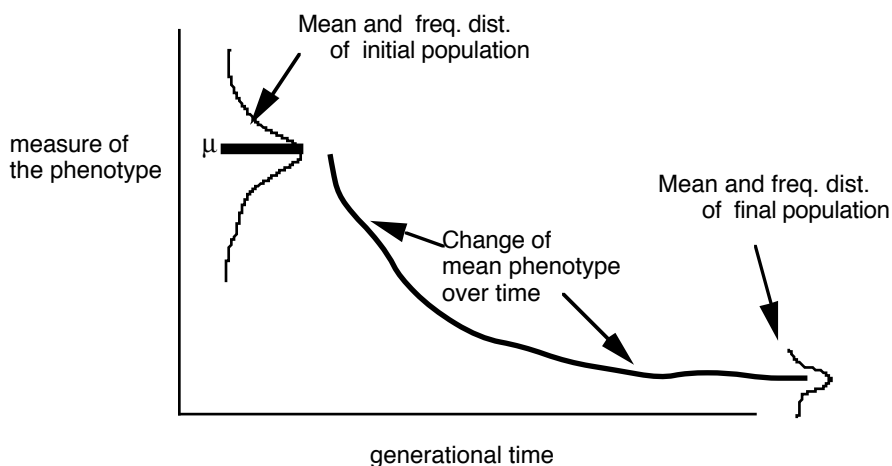   **selection response = h^2 * selection differential**
or

$$h^2 = \frac{\text{selection response}}{\text{selection differential}}$$

Notice that as the heritability decreases (as environment matters more), then we expect that the offspring will come to resemble their parents less and less

        d. A typical selection differential experiment: where the individuals with an extreme phenotype (for example, the least time needed to solve a maze) are breed with each other generation after generation:

An Illustration of the Change in a Population's Phenotype
Due to Selection When a Trait is Inherited Quantiatively

measure of the phenotype

Mean and freq. dist. of initial population

μ

Mean and freq. dist. of final population

Change of mean phenotype over time

generational time

knp

Notice that over time there is less and less change. Why is this?
        i. If a trait is quantitatively inherited and if there is plenty of initial genetically based variation, selection favoring one phenotype can potentially result in rapid changes in the phenotype of the population (if heritability is high and selection is rigorous). Eventually the change slows down or an equilibrium is reached for two reasons:
        1. The ***population has become largely homozygous*** with respect to the trait. Homozygous means that most of the genes with respect to this trait are the same. Things have gotten this way because genes that produced phenotypes that were not favored have been prevented from reproducing and only the genes that were "selected for" remain. Thus, eventually there is no more genetic variation for the selection to operate on and so the population stops evolving. Notice that **when this happens the heritability of this trait in this population will decrease!**
        2. It is also possible that the genes responsible for the trait have pleiotropic effects. Some of these effects may well be deleterious. As a population becomes more homozygous, the deleterious effects increase and impose a counter selection not seen at the start of the experiment. The result is counter-selection that tends to keep the population heterozygous and stops the response to selection. In other cases, as pleiotropy involving other genes breaks down, the expression of trait itself may

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suddenly be altered. Remember, few "macro" phenotypic traits are really determined by just a small number of loci.

3. Determination of H^2 and h^2 Using Studies of Mono- and Di-zygotic Twins

a. In both human and animal studies it is often possible to try to estimate heritability by using phenotypic variation in mono- (identical) and di- ("fraternal") zygotic twins. Since in humans the problem of FAMILIAL traits often looms large (these are traits whose expression is strongly affected by the very similar environments of family members), the preferred procedure is to use twins that were **raised separately.**

b. The method is based on the following assumptions:

1. Identical twins share 100% of their genes in common; therefore any variation in their phenotypes is assumed to be due to differences in the environments in which they were raised. Therefore:

$$V_{T(MZ)} = \textbf{environment only, } = V_E$$

2. On the other hand, dizygotic twins **on the average share only 0.5 of their genes** (some share more, some less). Thus, the variation that is seen in their phenotypes is due to proportion of genes that they do not share in common and also the environment. (Incidentally, dizygotics need to be of the same sex for obvious reasons if they are to be compared with monozygotic twins).

$$V_{T(DZ, \text{ same sex})} = V_E + 0.5*V_G$$

c. To calculate broad-sense heritability, H^2, we need to know V_G. It should be evident that the difference between the phenotypic variance in dizygotic single sex twins vs. monozygotics will give us V_G:

$$V_{T(DZ, \text{ same sex})} - V_{T(MZ)} = (V_E + 0.5*V_G) - V_E$$
$$= 0.5*V_G$$

or

$$V_G = 2 * (V_{T(DZ, \text{ same sex})} - V_{T(MZ)})$$

Thus, heritability can be calculated:

$$H^2 = \frac{V_G}{V_P}$$

$$= \frac{2 * (V_{T(DZ, \text{ same sex})} - V_{T(MZ)})}{V_P}$$

In some cases, it is not easy to estimate V_P. In these cases a different equation can be used with twin studies to obtain H^2 or h^2:

$$H^2 = \frac{(V_{DZ} - V_{MZ})}{V_{DZ}}$$

Here is a list of the heritabilities for some human traits calculated using the above method:

Trait	H^2
Height	0.81
Weight	0.78
Binet IQ	0.68
Otis IQ	0.80
Verbal Aptitude	0.68
Arithmetic Aptitude	0.12
Aptitude for Science	0.34
Aptitude for History and literature	0.45
Spelling Ability	0.53
Foot-tapping speed	0.50
Source: Jenkins, JB <u>Human Genetics,</u> 2nd ed. 1990 Harper& Row	

V. Limitations and Warnings About the Heritability Concept:

1. The most fundamental rule to keep in mind is that ***all traits, whether they have high or low heritabilities, are both "genetic" and "environmental".*** As was stressed in class two, ***the phenotype is the result of an interaction between the two; it is not possible to produce to produce a phenotype without both.*** As Dawkins put it -- it is no more appropriate to ask whether the taste and texture of a cake is due to its recipe or its ingredients as it is to ask whether an organism's phenotype is determined by genes or environment. It is simply a meaningless question

2. With this in mind, let's look at several important aspects of heritability:

(a) **Heritability does not show the extent to which a trait is "genetic"**, as was indicated by the passage above. This is the most common mistake people make when talking about heritability. Here is an example:

Let's speculate about knowledge about some particular human activity, let's say women's field hockey at Holy Cross. Is knowledge of scores genetic or environmental? Again, this is a ridiculous question since it is due to both. A nervous system is required to have any knowledge at all and such a system is produced in large part by genes. Someone with a profound environmentally (for instance, an injury) or genetically caused defect (any number of inherited neural disorders) would simply not be able to learn about field hockey. On the other hand, of the normal individuals, some will be very knowledgeable while others will not be.

If we measured heritability of this trait in Holy Cross students we would find it to be very low -- near zero -- but that does not mean that genes are not involved. If we were to, on the other hand, construct a population of Holy Cross students plus profoundly retarded individuals we would get a much higher heritability.

(b) *Corollary:* <u>**Heritability does not indicate the proportion of an individual's phenotype that is genetic**</u>-- *individuals do not have variance* -- it is a population parameter.

(c) HERITABILITY IS NOT A FIXED CHARACTERISTIC OF A SPECIES -- IT IS <u>ONLY RELEVANT TO A PARTICULAR POPULATION OR ENVIRONMENT</u>. Here's an example taken from Russell's *Genetics* text: Let's look at the heritability of height. In the first comparison, we use two different populations -- one a small, typical New England town and the other is San Francisco. If h^2 for height is measured in both cases, we would expect to find the larger value in SF -- why? -- Because in both places the diet etc (important environmental influences) are probably similar, but the small town is probably more genetically homogeneous than is SF. Thus, the genetic variation compared to proportion of the total variation in height $(V_G + V_E)$ is greater in SF and as a result h^2 is more.

By contrast, if we compare SF with a third-world city of similar size and of similar genetic makeup (if that were possible, but assume that it is), it is likely now that differences in diet will become very significant. There is generally a greater disparity in nutrition in third world cities as compared to those of the economically developed world, especially those with good social welfare systems. It would be found that h^2 would be higher in the developed world city (even though V_G is about the same in both cases) since V_E is much larger (and therefore V_P is larger) in the third-world city.

Thus, individual measures of heritability are always dependent and only useful for a particular genetic population in a particular environment. As you can see, it would not be valid to generalize h^2 measured in the small New England village to the rest of the world.

(d) As an extension of the last argument, if H^2 or h^2 for two different populations differs greatly, even if the values are large, one can still not assume that the populations are different genetically. There is a tendency when high values of H^2 or h^2 are found in two different populations but where there is a difference in phenotype that the difference must be due to a difference in genetic structure of the two populations. Once again, an example:

Assume that we have **<u>two populations of study animals</u>** where the animals in each group are **<u>variable genetically</u>** but the two groups themselves are identical to each other -- the mean and variance are the same for each group. We could accomplish this by taking one large group of animals and subdividing it by randomly assigning all individuals into one of two subgroups.

In one group we feed all the animals a rich diet and otherwise keep the environment as similar as possible for each animal. When you measure h^2 you get a high value. This is not surprising since the environment is very constant and therefore the only variation is from the genetic differences between the animals.

Now we take the other group (genetically identical) and rear them on a poor diet but otherwise in an identical environment to group #1. As a rule, they are nearly all quite small. If we measure h^2 we will also get a large number (since once again there was little variance in their environment but there was genetic variance. None of this should be very surprising.

Why this is important however, is that it illustrates an important point -- **if the two groups were compared someone might conclude that there must have been a genetic difference between the two groups. They might base their conclusion on the high h^2 and difference in body size between the two groups. However, as you know that was not the case.** *Thus, heritability cannot be used to draw conclusions about the nature of population differences in the expression of some trait.*

(The examples above were generally borrowed from Russell, PJ, <u>Genetics</u> 2nd ed. Scott, Foresman & Co. Boston.)

Questions:
1. What is the relationship to the term "selection pressure" (generally used to describe the favored phenotype in a natural population) and selection differential?
2. How could one trait have decidedly different heritabilities over generational time in a largely isolated population of animals? Or could the heritability change in a such a case? Explain.
3. If selection is intense and maintained over time, it is not uncommon for heritability to drop or to change radically. How could this happen?
4. What is assumed to be the heritability of a traits commonly discussed in genetics classes (especially those where a particular phenotype is associated strongly with a particular genotype). Does the environment play any role in the production of such traits within an individual? How about in terms of variation within a population?

Appendix -- Histograms

Variation is often displayed visually in the form of a **HISTOGRAM.** Histograms are graphs of the number or frequency of something versus a measure of the phenotype. A common shape for a histogram is the so-called **NORMAL DISTRIBUTION**. This is a symmetrical curve with certain mathematical properties that we need not examine in this course:
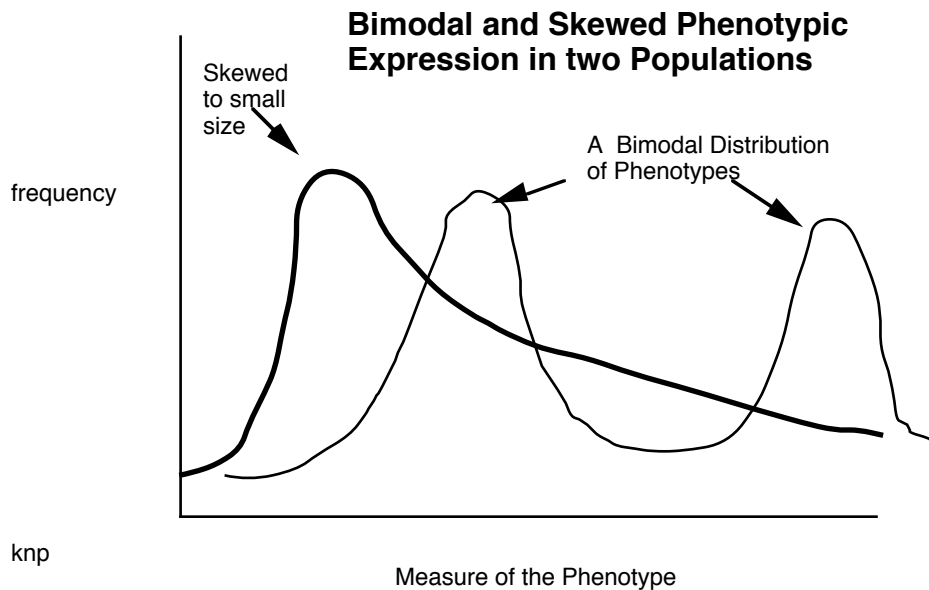
Normally Distributed Variation

mean

number or frequency

deviation of some individual from the mean

knp

range of phenotypic expression
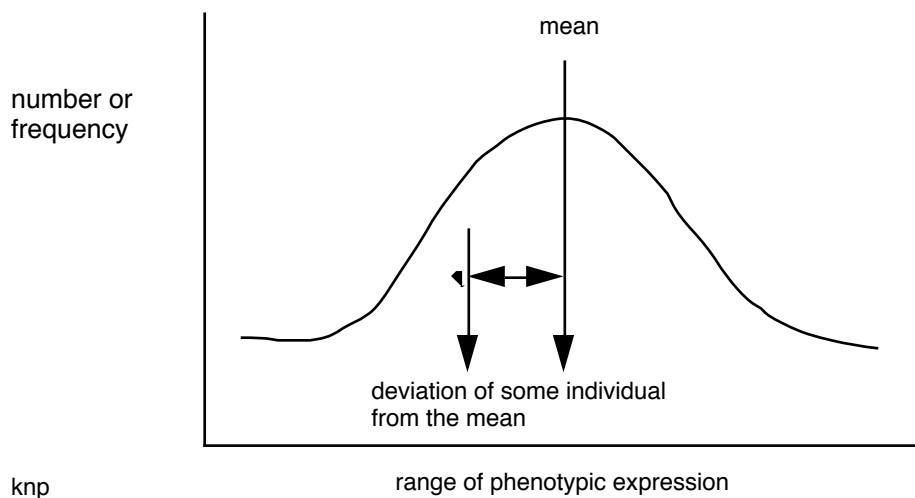
Common situations where normal distributions occur include:
(i) When a trait is <u>inherited quantitatively</u> (the effects of many genes add together to determine the degree of a trait's expression) and
(ii) Where there was <u>selection for some average type</u>.
(iii) Random differences in the environment acting on a population of individuals with the same genotype can also produce a normal distribution.
There are a number of <u>other distributions</u> that will be the result of different genetic, environmental, selection or chance factors. For instances, there may be more than one **<u>mode</u>** (phenotypic peak) or a population may be **<u>skewed</u>** (non-symmetrical about the mean and biased towards a certain range of phenotypes):

Bimodal and Skewed Phenotypic Expression in two Populations

frequency

Skewed to small size

A Bimodal Distribution of Phenotypes

knp

Measure of the Phenotype

We'll restrict our discussion to normal distributions since they are both common and the mathematics is relatively easy to understand.