I. Introduction
   A. Classification of traits
      1. Discontinuous traits: Traits that have only a few distinct phenotypes.
      2. Continuous traits: Traits that have an apparent continuous distributions of phenotypes.
   B. Quantitative genetics is the study of the inheritance of continuous traits.
   C. Why some traits have continuous phenotypes:
      1. Numerous genes affect the expression of the trait. The number of genotypes and, thus, the number of phenotypes is large and appears continuous.
      2. Environmental factors affect the expression of the trait. When environmental factors influence the expression of a trait, each genotype is capable of producing a range of phenotypes known as the norm of the reaction.
   D. Questions addressed:
      1. What proportion of the differences in phenotypes of a trait result from differences in genotypes and what proportion is due to differences in environment? Nature vs. nurture
      2. What are the norms of reactions for genotypes that influence a trait?
      3. How many genes influence a trait and are the contributions of each trait equal?
      4. How rapidly does selection for a continuous trait occur?
      5. Is there non-nuclear inheritance?
   E. Mendelian/Pop vs. Quant = Look at (1) the size of the phenotypic differences BETWEEN genotypes compared with (2) the individual differences WITHIN genotypes.
      → If 1 > 2, it is Mendelian; if 2 > 1, it is quantitative.

II. Statistical background
   A. Distribution = Description of a population in terms of the number of individuals that fall within a certain range of phenotypes.

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B. Mode = most frequent class in a frequency histogram

C. Mean = the arithmetic average of a population
   \[ \text{Mean} = \bar{x} = \frac{x_1 + x_2 + x_3 + \ldots + x_N}{N} = \frac{1}{N} \sum_{i=1}^{N} x_i \]

D. Variance = average squared deviation of the observed from the mean
   (measure of how much individual measurements spread out around the mean or the width of a distribution around its central class)
   \[ \text{Variance} = s^2 = \frac{(x_1 - \bar{x})^2 + (x_2 - \bar{x})^2 + \ldots + (x_N - \bar{x})^2}{N} = \frac{1}{N} \sum_{i=1}^{N} (x_i - \bar{x})^2 \]
   Standard deviation = \[ s = (s^2)^{1/2} \]

E. Correlation = the association of two or more traits (x and y)
   Measured by the correlation coefficient \[ (r_{xy}) = \frac{\text{cov}_{xy}}{(s_x s_y)} \]
   Where \[ \text{cov}_{xy} = \frac{(x_1 - \bar{x})(y_1 - \bar{y}) + \ldots + (x_N - \bar{x})(y_N - \bar{y})}{N} \]
   \[ = \frac{1}{N} \sum_{i=1}^{N} (x_i - \bar{x})(y_i - \bar{y}) \]
   \[ = \frac{1}{N} \sum_{i=1}^{N} x_i y_i - \bar{x} \bar{y} \]

   The correlation coefficient \( (r_{xy}) \) tells the strength of the correlation between two variables but not the precise relationship. Also, note that correlation does NOT = numerical identity.

   ![Strong correlation](image1)
   ![No correlation](image2)

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F. Regression
1. Used to calculate the precise mathematical relationships between variables that covary. Regression analysis can predict the average y for a given x.
2. \( y = bx + a \)
   where \( b = \frac{\text{cov}_{xy}}{s_x^2} \)
   \( b = \) how much an increase in y is associated with a change in x

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III. Norm of reaction
The norm of reaction refers to the array of phenotypes that result from one given genotype. The norms of reaction shows that heritability measurements only apply to the environment in which they are measured.

Norm of reaction curves are generated by plotting the phenotype of one genotype in each environment. The norm of reaction curve can then be used to determine the phenotypic distribution of a trait that we see over a wide range of environments.

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IV. Heritability
A. General definition = the proportion of a population's phenotypic variation that is attributable to genetic variation.
B. General assessment
1. Measure phenotypic variation in a trait
   (Phenotypic variance = \( s_p^2 = v_p = v_g + v_e + Cov_{ge} + v_{gxe} \))
2. Partition the phenotypic variance into components:
   a) Genetic: \( s_g^2 = v_g = v_a + v_d + v_i \)
      (1) \( v_a \) = additive genetic variance = each allele contributes to the genotype
      (2) \( v_d \) = dominance variance = takes into account that heterozygotes are frequently NOT intermediate in phenotype but show dominant phenotype (each allele is NOT equal)
      (3) \( v_i \) = interaction variance = takes into account epistatic interactions
   b) Environmental: \( s_e^2 = v_e = v_{eg} + v_{es} + v_{em} \)
      (1) \( v_{eg} \) = environmental variance due to general effects
      (2) \( v_{es} \) = environmental variance due to special, reversible effects
      (3) \( v_{em} \) = environmental variance due to maternal effects
   c) \( Cov_{ge} \) = covariance between an environment and a genotype
   d) \( v_{gxe} \) = genetic-environment interaction
3. Heritability determination can be based on:
   a) Phenotypic similarities between relatives
   b) Marker gene segregation
C. Broad sense heritability
   The proportion of a population's phenotypic variation that is attributable to genetic variation
   \[ h_B^2 = H^2 = \frac{v_g}{v_p} \]
   1. Calculations from genetically identical lines
      a) Make homozygous lines from a diverse population \( \rightarrow \) cross to get various heterozygotes that are genetically identical \( (v_g = 0) \)
      b) Since \( v_p = v_g + v_e \) and \( v_g = 0 \) \( \rightarrow \)
         \( v_p = v_e \) for this genetically identical population
      c) Now calculate
         \( v_g = v_p \) (observed from original population before they were made identical) - \( v_e \) (from part b)
2. Calculation from the differences in genetic correlations between different types of related individuals
   a) Two assumptions
      (1) the closer the relationship, the greater the genetic correlation = the greater the heritability
      (2) the environments are similar and thus cancel out of the equations
   b) Example (see handout)

3. If $H^2 > 0$, then genetic differences influence phenotypic variation.
4. If $H^2 = 0$, then in the population studied and in the environment studied, there is no effect of genetic variation of phenotypic variation.

D. Narrow sense heritability
   The proportion of a population's phenotypic variation that is attributable to additive genetic variation.
   
   \[ h_{N^2} = \frac{v_a}{v_p} \]

1. Calculated from parent-offspring regression plots where $y = bx + a$ and $b = h_{N^2}$

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If $b = 1$, then $v_a$ is the only component that influences variation.
If $b = 0.5$, then $v_a$ and other components influence variation.
If $b = 0$, then $v_a$ does not influence variation.
2. Important for breeding programs because calculation simply looks at likely 
hood of being able to select for an observable phenotype based on the phenotypes 
of the parents and the heritability of the trait.

Selection response = difference in trait between the selected individual’s progeny 
(average) and the average of the previous generation 
\[ = h_N^2 \times \text{selection differential} \]
\[ \text{(where selection differential = difference between } \]
\[ \text{selected parents and unselected mean)} \]

3. When selection is imposed upon a phenotype, the phenotype will change from 
one generation to the next provided that there is still genetic variation in the 
population that affects the trait of interest.