
Note: the same question is sometimes asked in slightly different ways.

How would you define “fitness” in a way that avoids the criticism that evolution by natural selection is an empty tautology (i.e., “Evolution by natural selection is the survivor of the survivors”)?

Write the equations for variance and covariance. Then write a sentence in English that defines variance and covariance. Compare the two. In what way can a variance be seen as the covariance of a thing with itself? Write the equation for the slope of a regression line. How is it related to variance and covariance?

Why did Francis Galton (Darwin’s cousin) reject Darwin’s view of evolution by natural selection? Why did he reject both gradualism and the provisional theory of pangenesis? How did he test the provisional theory?

What did Galton mean by “regression on mediocrity”?

In class we showed (assuming one locus with two alleles, and infinite population size) that

\[ \Delta p = \frac{pq[p(W_{11} - W_{12}) + q(W_{12} - W_{22})]}{W} \]

There are “trivial” equilibria at \( p=0, \) and \( p=1. \) Why are those called trivial equilibria? There is also an equilibrium at \( W_{11}=W_{12}=W_{22}. \) Why is that an equilibrium? This equilibrium is called the \__________ equilibrium (fill in the blank). If the population is perturbed away from the equilibrium, will the population return to the starting point? Why or why not?

Now suppose that there is variation in fitness, and that there is genetic variation. Solve for \( p \) at equilibrium (\( \hat{p} \)). Show the algebra.

For \( \hat{p} \) to be on the interval between zero and one requires that \( 1> \hat{p}>0. \) Show what this means algebraically with respect to your solution for \( p \) at equilibrium. What does it mean in words?
We also showed in class, using \( h \) as the coefficient of dominance and assuming weak selection (small \( s \)), that

\[
\Delta p \approx pqs[ph + q(1 - h)],
\]

Assuming

\[
\begin{align*}
W_{11} &= 1 \\
W_{12} &= 1 - hs \\
W_{22} &= 1 - s
\end{align*}
\]

If allele 1 is dominant, what is \( h \)? What is \( \Delta p \)?
If allele 1 is recessive, what is \( h \)? What is \( \Delta p \)?
If allele 1 is co-dominant, what is \( h \)? What is \( \Delta p \)?

Relatively speaking, compare the spread of allele 1 when rare for each of the three conditions above. Defend your reasoning (hint: your excel model should help here).

What are the consequences of assuming an infinite population size in the model with respect to the spread of a recessive beneficial allele? How might this be different in small populations? (note: the exercises using Allele1 should help here.)

What is meant by “mutation-selection” balance? In English words, what is going on at mutation selection balance? How would you explain it to your neighbor? (Note: the solution for \( \hat{q} \) is given on the course website.)

What is meant by “fixation” in population genetics?

What is the heritability of two ears in a population of mice, all having two ears?

Given our population genetic formulation to this point, what is the general long-term effect of directional selection on additive genetic variance?

Will natural selection always drive population mean fitness up? Why, or why not?

When will genetic drift over-ride natural selection? (we will cover this later.)

Can there be additive genetic variation in an asexual population composed of multiple, genetically different clones?

What is the difference between “dominance” and “dominance variation”?

Why was Darwin’s idea of gradual evolutionary change through the action of "natural selection" rejected by most of his contemporaries?
Is natural selection necessary and sufficient for evolutionary change? What is the difference between natural selection and evolution? Define both.

What is essentialism? What is typological thinking? How are these different from populational thinking?

What is meant by blending inheritance? Why was it thought to be a problem for natural selection?

Who were the Mendelians? Who were the Biostatisticians. What where the arguing about? Who won? Why?

More on Population Genetics:

What was Darwin's provisional theory of pangenesis?

Why did Huxley think that Darwin’s commitment to gradual change was an unnecessary burden?

For one locus with two alleles, write the equation for $\bar{W}$. What does it mean?

The equation for $p_{t+1}$ is: $p_{t+1} = p(pW_{11} + qW_{12})/\bar{W}$. Give an intuitive feeling for why this should be so. What is true at the equilibrium value for $p$?

Is $\bar{W}$ necessarily maximized by selection? Why or why not?

What is meant by mutation-selection balance?

What difference does it make if an allele is dominant or recessive on the spread of that allele when it confers a slight fitness advantage when expressed.

Remember that $\Delta p \approx pq^2s$ for a favored dominant and $\Delta p \approx p^2qs$ for a favored recessive. Give an intuitive feeling for why the equations are correct (or incorrect, if they seem wrong to you).

Quantitative Genetics:

Give an intuitive feeling for the equation: $R = h^2S$. How is $h^2$ related to Galton’s worry about regression on mediocrity?

What is the selection differential ($S$)? How is it similar/different to the selection gradient ($\beta_w$)? How is it different from the selection coefficient ($s$) in Population Genetics?

What is meant by additive genetic variance? Why is it so important? How is it affected by dominance? How is it affected by allele frequencies? How is it related to the rate of evolution?
Give an intuitive feeling for the equation: $h^2 = \frac{V_A}{V_P}$

$h^2 = \beta_{o,\bar{p}}$, where $\beta_{o,\bar{p}}$ is the regression coefficient for the regression of the mean of a brood for a quantitative trait against the mean of their parents (the mid-parent value) for the same trait. Why is $\beta_{o,\bar{p}} = \frac{\text{cov}(\bar{p}, o)}{\text{var}(\bar{p})}$? What does it mean, in words?

What is meant by $H^2$? This is the broad-sense heritability. How is it different from $h^2$? (I don’t remember if I explicitly covered this, but $H^2 = \frac{V_G}{V_P}$). In words, $H^2$ is the total genetic variance divided by the total phenotypic variance. So the numerators for $H^2$ and $h^2$ are different. Why would that matter?

"Unpack" $V_G$. Give graphical examples of Dominance, Additivity, and an interaction between two loci. Make a clear distinction between dominance and $V_D$.

Does complete dominance mean that there is no additive genetic variance? Does an interaction between loci imply that there is no additive genetic variance? Why or why not?

Give an intuitive feeling for why the additive genetic variance depends on allele frequencies. Connect your reasoning with the population genetic models.

Design a simple experiment to estimate the environmental variance, $V_E$.

Give an intuitive explanation (or graph) for why dominance might reduce the slope of the regression of offspring value on mid-parent value compared to the slope of the regression of the same slope under co-dominance.

Explain why heritability, $h^2$, is different from the probability of inheriting a trait. Design an undergraduate lab to get the difference across to the students.

What do you think the long-term effect of strong directional selection would be on $h^2$, $V_A$, and $V_P$.

What was the effect of the 1977 drought on Darwin’s medium ground finch?

What are breeding values? How are they involved in the calculation of Additive Genetic Variance? How are breeding values calculated?
Assuming we start with a rare, dominant mutation that is favored by natural selection. Why does the additive genetic variation change over time as the mutation spreads to fixation? Why does the dominance variation also change over time? Why does heritability change over time?

What is the fundamental theorem of natural selection? What does it mean?