Evolving Crickets - Understanding heritability and evolutionary responses

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Introduction

Humans have a long interest in understanding how populations will evolve in response to selection, not only for general evolutionary questions but also for the purposes of agriculture. Agriculture and domestication provide many of the clearest examples of evolution in action and many evolutionary biologists, including Charles Darwin, used domesticated species to better understand evolution. One very well studied mathematical approach to predicting evolutionary change is rooted in this framework: the Breeder's Equation:

$$\Delta\bar{z} = h^2 s$$

where $\Delta\bar{z}$ is the change in a population's mean for a trait after selection, h^2 is the "narrow-sense heritability" that we talked about in class, and s is the difference between the population's mean for a trait before selection and the mean for those individuals able to reproduce. The Breeder's Equation, and modifications of it have been used extensively by agronomists and animal scientists to increase agricultural yields for everything from corn yield to milk production.

In this exercise you'll first examine a common method to estimate heritability: parent-offspring regression and will then measure how selection acts on a single behavior.

Learning Goals

1. Understand the concept of heritability and its relation to genetic variance
2. Understand how selection is predicted to act on single traits

Learning Objectives

Part 1.

a. Understand the concept of genetic and environmental sources of variation in phenotype and its relation to heritability
b. Measure heritability using parent-offspring regression

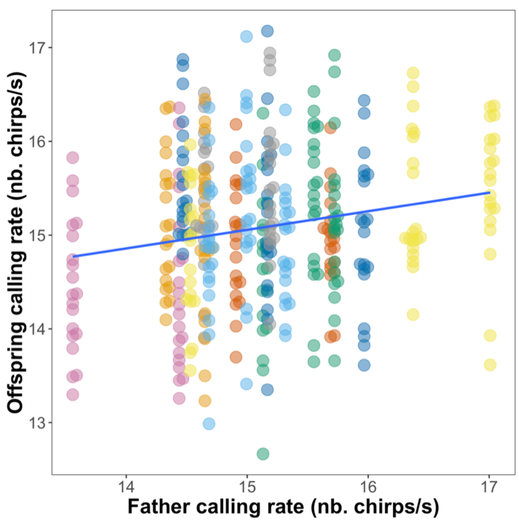
Part 2.

a. Apply the breeder's equation: Given selection, predict composition of population after selection. Extend over multiple generations.
b. Infer long-term effects of selection on populations
    i. Trait means
    ii. Genetic variation

Part I—Estimating Heritability with Parent-Offspring Regression

Because this equation might initially be somewhat intimidating, let's work through an example:

Scenario: A friend of yours is raising crickets in order to feed her pet lizards. Being a bit of a naturalist, she observed that some males never seem to attract any females despite high courtship effort, while others are more successful. After some more experiments she notices that males with higher chirp frequency (more chirps per second) are much more attractive to females. She would like to increase the success of her rearing by getting rid of the poorly performing males but is unsure of how to go about it. After some discussion, you suggest she could establish a breeding program so that she would only keep the best cricket callers. She would need to know if calling is heritable to determine if this trait can respond to selection and how fast it can evolve. Following your recommendations, she randomly selects 20 males and mate each male with 1 female at random (20 pairs total). She then selects 20 offspring of each pair at random and measure the call structure of father and male offspring. She comes back with the following results:



Intercept	Slope
12.05	0.20

Based on the above data, calculate the heritability based on the parent-offspring regression. Hint: Heritability is equal to 2 x the value of the slope for the single parent offspring regression.

Based on the calculated heritability, what portion of calling rate is under genetic control? What portion is driven by the environment?

Can a male with low calling rate produce sons with high calling rate? Explain your reasoning

To play a little further with different values of heritability, go to the following webpage: https://raphael-royaute.shinyapps.io/Evolving_crickets_h2/

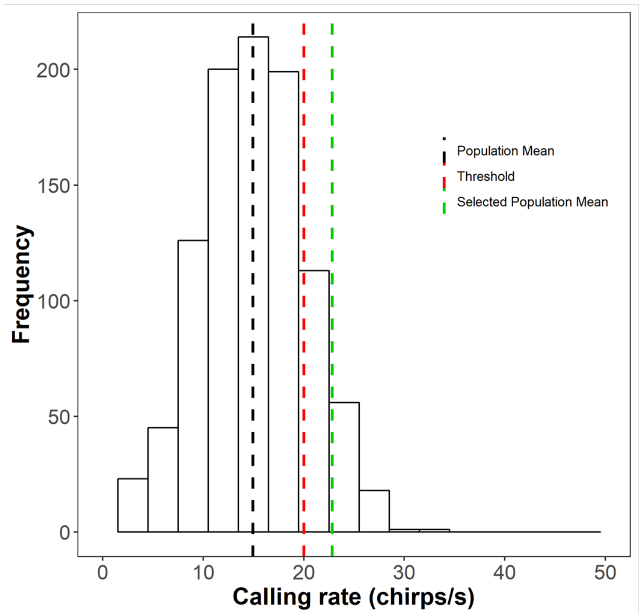
Set heritability to 0.9 and compare the offspring of the fathers with highest and lowest calling rates. Can an offspring from the best calling dad have a higher calling rate than the worst calling father? Where is that variation coming from? Explain your answer.

Now set heritability to 1. What happens to the variation in calling rate for offspring of the same father?

Set heritability to 0 and repeat the process. Do fathers with high calling rates have offspring with higher calling rate? Where does the variation in calling rate come from?

Part II—Estimating the Response to Selection using the Breeder's Equation

Having figured out that calling frequency is indeed heritable, you and your friend are now wondering by how much calling frequency will improve if she only allows high performing males to breed. Your friend has established that males with call frequencies above 20 chirps per second have a mating success of almost 100 % with females. However, these males only represent a small portion of her current population. The histogram below indicates the distribution of calling phenotype in the population:



Parameters	Values
Population Mean	14.9
Selection Threshold	20.0
Mean of Selected Population	22.8

What is the difference between the average call frequency in the population and the average calling rate of individual above the threshold (this is "*s*"):?

Based on the Breeder's Equation, calculate by how much call frequency will increase if your friend only allows the top males to reproduce (the males with calling rates above the threshold). Note that $\Delta\bar{z}$ is the *change* in population means. What would be the average call frequency observed in the next generation?

Would a biologist say that this population has evolved? Briefly explain your answer.
!

Go now to the following webpage:

https://raphael-royaute.shinyapps.io/Evolving_crickets_selection/

First keep the selection threshold fixed and modify the values of heritability. How does the offspring population after selection responds for low values of heritability. How does it respond to high values of heritability? Hint: put these results in the context of changes to $\Delta\bar{z}$

Calculate the values of $\Delta\bar{z}$ happens when $h^2 = 0$ and when $h^2 = 1$.

Now reset the value of heritability to 0.4 and modify the selection threshold. What happens at high threshold values? How does the selection threshold affect the response to selection $\Delta\bar{z}$?

What combination of values of h^2 and s are necessary to get the largest response to selection? Explain your answer.

Based on what you have learned today, would you say that if a population is under selection, this will always lead to evolutionary change (change in the mean phenotype over multiple generations). Explain your answer.