

Estimating the heritability of a quantitative trait

This tutorial challenges you to design and conduct experiments to estimate the heritability of a quantitative trait in a model population, and to predict the response to selection. The analytical tools you will need are described briefly here, and discussed in more detail in Chapter 8 of *Evolutionary Analysis*.

The organisms in the model population you will study are ladybugs. The trait you will analyze is number of spots. I must make a disclaimer at the outset: I don't know anything about the genetics of spot number in real ladybugs. For this simulation, I have assumed that spot number can vary from zero to fourteen and is under the combined influence of several genes of small effect plus a random environmental component.

The Bugsville application

To complete this tutorial, you will need the software application Bugsville. You can download Bugsville from Jon Herron's website at the following URL:

<http://faculty.washington.edu/~herronjc/>

Click on Software, then on Bugsville. There are versions of Bugsville for Windows, Mac OS Classic, and Mac OS X. Download the appropriate version to your computer and launch it.

The first window you will see is an ad for my book. Click on the Proceed button to dismiss it.

Next you'll see a small dialog box asking you to select a scenario from a popup menu. You can choose from among four scenarios:

1. The heritability of spot number is 0.9.
2. The heritability of spot number is 0.5.
3. The heritability of spot number is 0.1.
4. The heritability of spot number is chosen at random, and unknown to the user.

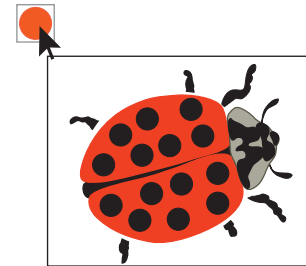
You may want to play with scenarios 1 through 3 as you practice the experiments and analyses required to estimate the heritability of spot number. Ultimately, however, your challenge will be to run scenario four and accurately estimate an unknown heritability.

After selecting a scenario, you will see Bugsville's main window (see next page). On the top are two large boxes, Left Field and Right Field. Left Field is full of ladybugs, represented by red dots. To get a better look at them, click on some of the bugs and hold the mouse button down (right). The smaller dots are larvae. The larger ones are adults.

Click the Run button at lower right. The ladybugs will move around. Sometimes when two bugs bump into each other, they mate and make larvae (watch closely!). Larvae take 50 days to turn into adults. After maturing, adults live another 150 days, then die. Click on the Pause button to suspend the simulation.

Note that while the simulation is paused you can move bugs around by pointing at them, holding the mouse button down, and dragging them to a new location. This gives you the ability to design and conduct your own experiments. For example:

- You can mate two ladybugs to see what their offspring look like. Drag two adults to one of the empty cages in the bottom half of the Bugsville window. Encourage them to mate by making sure they are touching. Run the simulation. Typically, the adults will make one or two offspring in short order. Pause the simulation to separate the offspring from the adults (so that you know who is who). Run the simulation until the babies grow up. Compare the offspring to the adults.
- You can do selective breeding experiments. From the Left Field population, pick out the ladybugs with the most—or the fewest—spots. Move them to Right Field. Place them near each other to encourage them to mate. Run the simulation for an entire generation (200 days), then compare the new generation to the original population you started with.



Estimating the heritability of a quantitative trait

The two large white boxes are fields that will support populations of 100 ladybugs each.

The five small white boxes are experimental cages that will support 25 ladybugs each. To move a bug from one place to another, click on the bug, hold the mouse button down, and drag the bug to its new location.

You can type labels here to keep track of your experiments.

The red dots represent ladybugs. Large dots are adults, small dots are larvae. To see what a larva or bug looks like, click on one and hold the mouse button down.

This button will empty the cage of bugs. You can get rid of a particular bug by simply dragging it out of the cage.

This button will run the simulation. Click on it to see the bugs run around and mate with each other.

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Under the tools menu you will find two items that will help you analyze your data. **Histogram** will graph the distribution of spot numbers in any of your populations, and calculate the average number of spots. **Scatterplot** will let you enter paired X and Y values, then plot them on a scatterplot.

If you need to reset your simulation, you can do so with the Reset command under the File menu. (Note, however, that if you reset scenario four Bugsville will pick a new heritability at random. This means that you will have to repeat your experiments to estimate the new value).

Your tasks in this tutorial are to:

1. Assess the variation in spot number in the Left Field population.
2. Estimate the heritability of spot number in the Left Field population.
3. Set up a selection experiment to select for high or low spot count, and calculate the selection differential.
4. Use the selection differential and your estimate of the heritability to predict the response to selection.
5. Run your selection experiment, and compare your prediction to the actual response.

If you have not already done so, use the Reset command under the File menu to reset your simulation with an unknown heritability. You are now ready to begin.

Assessing the variation in spot number

Take a minute to examine some of the lady bugs in the Left Field population. What is the highest spot count you can find? The lowest? What is a typical number of spots?

Now use the Histogram command under the Tools menu to plot a graph showing the distribution of spot number in the population. Note that the Histogram tool also reports the population average. Sketch the histogram in the space provided on the Bugsville Worksheet, and record the average number of spots.

Estimating the heritability of spot count

The **Heritability** of a trait is defined as that fraction of the variation among individuals that is due to differences in genes they inherited from their parents. If a trait is heritable, then parents and their offspring will resemble each other. You will use the resemblance between parents and offspring to estimate the heritability of spot number. Before proceeding, read about this technique on pages 303 to 308 in *Evolutionary Analysis*.

Set up a mating between a different pair of ladybugs in each of the small empty cages on the lower half of the Bugsville window. Before running the simulation count the spots on each parent, and record your data in the table provided on the Bugsville Worksheet. Also calculate the average spot number for each pair of parents, or midparent value. Now run the simulation until larvae appear in each cage, then pause. Separate the adults from the larvae (you can return the adults to Left Field if you like, or just throw them out), then run the simulation again

until the larvae grow up and pause again. Record the spot counts for the offspring in each family, and calculate the midoffspring value.

Continue to set up matings and examine offspring until you have data on at least 15 families. Then select the Scatterplot tool under the Tools menu. Enter your data in the table on the left side of the Scatterplot window. Each family gets its own row. Enter the average spot count for the parents as the X value, and the average spot count for offspring as the Y value. After entering all your data click on the graph button. You will get a scatterplot that will show you whether offspring resemble their parents. You will also get the best-fit line. The slope of this line is an estimate of the heritability of spot number.

How accurate is your estimate of the heritability? Set up more matings and gather more data until you feel your estimate is a good one. Are there particular matings you can set up to get the information you need more quickly? Before moving on, sketch the scatterplot on the Bugsville Worksheet and record your best estimate of the heritability.

Set up a selection experiment and calculate the selection differential

You can check the accuracy of your heritability estimate by doing a selection experiment. Before proceeding, read about measuring differences in survival and reproductive success on pages 308 to 313 in *Evolutionary Analysis*.

Decide whether you are going to select for high spot counts or low spot counts. Select from the Left Field population individual bugs with high (or low) spot counts and move them to Right Field. Use the histogram to plot the distribution of spot counts among your selected par-

Estimating the heritability of a quantitative trait

ents, and to get their mean spot count. Sketch the histogram and record the mean on the Bugsville Worksheet.

The **selection differential** is the difference between the average of the selected breeders and the average of the whole parental population (selected breeders plus nonbreeders). You recorded the average spot count for the whole Left Field population in question 1. Calculate and record the selection differential.

Predict the response to selection

The **response to selection** is the difference between average of the selected breeders' offspring and the average of the offspring of all the parents. Before proceeding, read about how to predict the response to selection on pages 313 to 314 in *Evolutionary Analysis*.

If you multiply the selection differential by the heritability, it should give you a reasonably accurate estimate of the response to selection.

Run your selection experiment and compare your predicted response to the actual response

Before proceeding, read about Candy Galen's selection experiment on pages 314 to 317 of *Evolutionary Analysis*.

Run your simulation for 200 days. This will give all the parents in your Right Field population time to complete their life spans, and thereby ensure that only their offspring remain. Now use the histogram tool to plot the distribution and determine the average spot count in

your Right Field population. Sketch the histogram and record the mean spot count on the Bugsville Worksheet.

Recall that the response to selection is the difference between the average of the offspring of the selected parents and the average of the offspring of all the parents. You don't know this second value. But you can use the mean of your starting Left Field population, from task #1, as a reasonable estimate. In other words, you can calculate the actual response to selection as the difference between the average of your present Right Field population (the offspring of the selected parents) and the average of the original Left Field population (the entire population before selection).

Compare the actual response to selection to your prediction. How closely do they match?

Learning the Truth

Because Bugsville is a simulation, it allows you to do something you cannot do in the real world. You can ask the application to tell you the Truth about the simulation you are running. Under the Tools menu, select Tell the truth. Enter the password 'Galton'. Then click Now tell me. Bugsville will reveal the true heritability of spot number in your population.

Did your experiments give you a reasonably accurate estimate? If not, try to figure out why. Design a new experiment that will give you a better estimate. Then run your new experiment and see how well it works.

Write a brief discussion, as might appear at the end of a lab report

Summarize your study:

What did you set out to determine?

What experiments did you perform?

What did you learn and on what evidence?

How well did your data match your predictions?

How might your study have been better designed?

What is the broader significance?