BORN TO *RUN*

EXPERIMENTAL EVOLUTION OF HIGH VOLUNTARY EXERCISE IN MICE

by Tricia Radojcic and Theodore Garland, Jr.

Evolution is a "unifying theory" of biology and a key component of the science curriculum in many states. However, teachers are challenged in how to teach this complex set of facts and concepts to the point of full student understanding when learning experiences are limited to the historical study of Darwin's voyage and his observations of the organisms in the Galapagos Islands and inferences drawn from them. Moreover, this type of instruction falls short of reaching the goals of an inquiry-based classroom, where in studying students would collect and analyze data to understand how organisms change in response to selection. Although a variety of simulations model the process and outcomes of natural selection, these can fail to engage students, as they are often disconnected from "reality."

The importance of an inquiry-based approach cannot be underestimated, given the demands of the *Common Core State Standards* (NGAC and CCSSO 2010), new assessment strategies, and the importance of science, technology, engineering, and math (STEM) instruction. The recent adoption of the *Next Generation Science Standards (NGSS)* (NGSS Lead States 2013)

puts additional demands on instructors of evolution. How can students explore evolutionary change in response to selection using real organisms rather than simulations?

In the lesson described here, students interface with research being conducted by scientists and design their own investigations using samples produced in a research laboratory. They develop their own hypotheses and measurement protocols, collect data, and have the opportunity to compare their results with those published in the scientific literature by the original researchers. In essence, this lesson develops complex thought, problem solving, and creativity in students, thus supporting *Common Core* standards while simultaneously addressing the *Next Generation Science Standards* (see sidebar).

The Born to Run activity is intended for use after students have been introduced to natural selection, and it presumes they have been assessed on these concepts prior to beginning the activity and that they have a basic understanding to use for the upcoming task.

Background

Evolutionary biologists use multiple strategies to study how the phenotypic characteristics of organisms (their behavior, morphology, and physiology) evolve over time (across generations). These include phylogenetic comparative approaches that infer changes that have occurred in the past (Rezende and Diniz-Filho 2012), as well as studies of the variations that occur in existing populations in the wild (Linnen and Hoekstra 2009). An additional strategy uses artificial selection experiments to model natural selection in a controlled and reproducible environment (Garland and Rose 2009).

The second author, Theodore Garland Jr., and colleagues have developed four replicate lines of mice that have been selectively bred for a particular behavior: high levels of voluntary wheel running (Swallow, Carter, and Garland 1998; Swallow et al. 1999; Careau et al. 2013). As wheel running has increased across many generations of mice, the structural and physiological changes that co-occur with the selected behavior are being studied. The results of selection experiments like this can be adapted for inquiry-based instruction in the classroom (a direct application of *NGSS* life-science disciplinary core idea MS-LS4-5 showing that artificial selection can influence the characteristics of organisms [NGSS Lead States 2013]). In the present case, we have created a database containing digital photographs of the femurs (thigh bones) of mice from both selectively bred and nonselected control lines. These photographs can be easily measured by students, either from printed hard copies or as digital images using ImageJ, a measurement tool developed by the National Institutes of Health, which can be downloaded free of charge (see Resources). Using this flexible resource in conjunction with a spreadsheet program, students are able to collect and analyze the data graphically (or with statistical procedures) and test a variety of hypotheses, while simultaneously strengthening their skills in data analysis and graph interpretation.

Open-inquiry projects exploring this topic are easy to support; students already have prior knowledge of some of the physical characteristics of good runners (e.g., Olympic athletes, greyhounds versus other
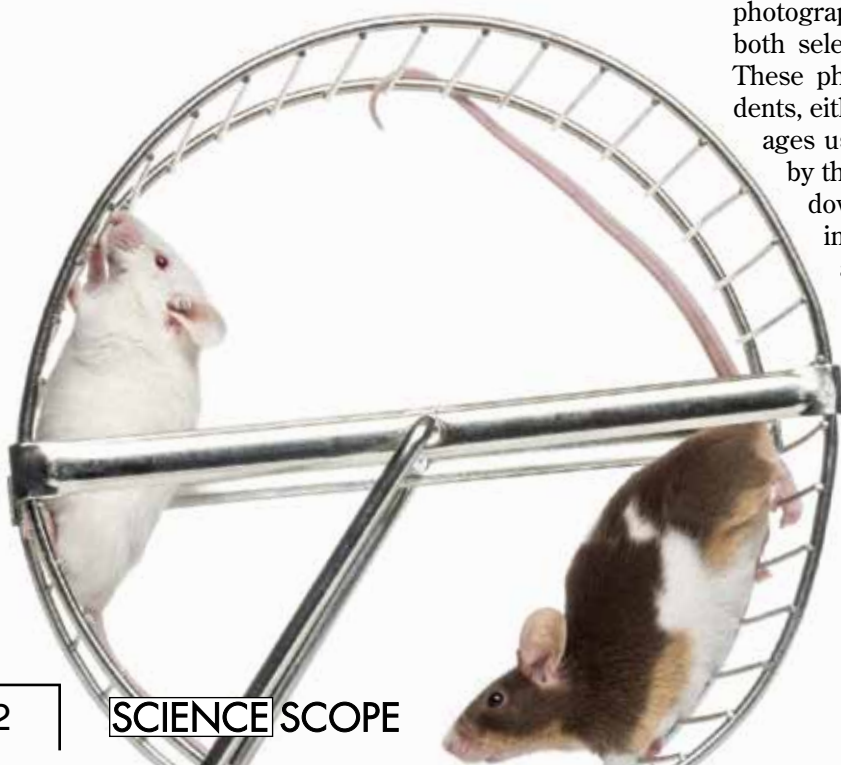
dogs) from which they can extrapolate and then test their predictions in the mouse model. However, an important learning outcome would be for students to realize that the changes in body structure in these lines of mice are the result of selection applied to a behavioral trait; hence the morphological changes epitomize correlated responses to selection, i.e., evolutionary changes that occur in traits that are not themselves necessarily subject to direct selection (Kelly et al. 2006; Middleton et al. 2008). Another important outcome would be instilling in students the fact that evolution can occur rapidly, not only in laboratory systems (Garland and Rose 2009; Barrett et al. 2010) but also in wild populations of plants and animals (Reznick et al. 2004; Herrel et al. 2008), not to mention such microorganisms as the viruses causing flu (see Resources). This dispels the common misconception that evolution is always slow and requires millions of years to effect observable changes in populations.

Developing a hypothesis

In the seventh-grade classroom of the first author, students are introduced to the project by viewing video clips of the selected "High Runner" mice (see Resources), followed by a discussion of the method that Garland's lab used to develop these lines of mice. Mice from the selected lines run more on the wheel because their populations have been selectively bred, not by nature but artificially by the researchers (Figure 1) (*NGSS* MS-LS4-5; NGSS Lead States 2013). Specifically, the mice that run the most over days 5 and 6 of a six-day period of wheel access are chosen to breed, while mice from the non-selected control lines are bred randomly with respect to how much they run. The behavior of daily amount of wheel running was heritable in the original starting population of mice (Swallow, Carter, and Garland 1998); parents that tended to run more than other mice had offspring that also tended to run more than the average of their generation. As the selection protocol was applied for many generations, offspring of the high-level runners tend to run more than their parents each generation, al-

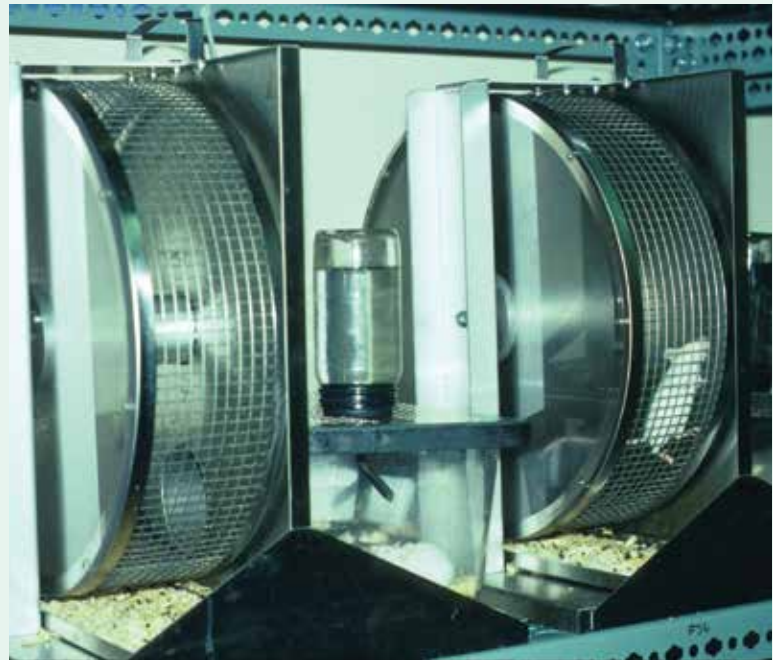| FIGURE 1 | Garland's laboratory mice in wheels attached to computers that collect data on the number of revolutions of the wheel during each minute over a six-day period |

PHOTO BY THEODORE GARLAND, JR.

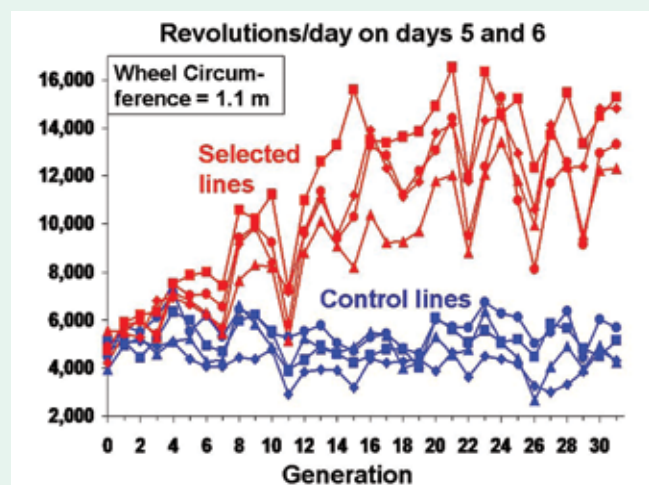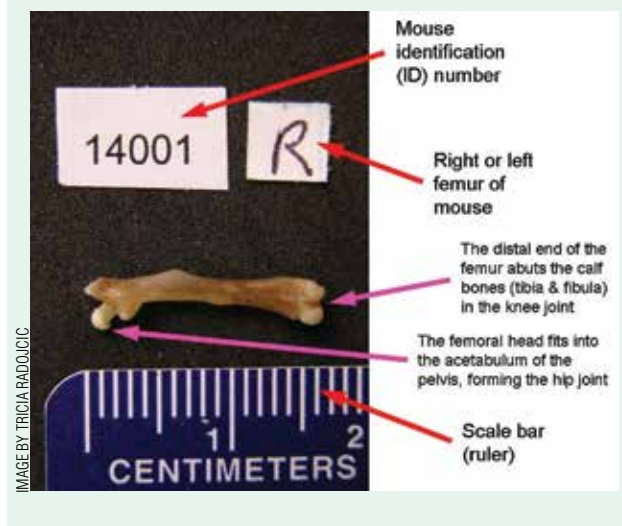| FIGURE 2 | Average value of wheel running for four selectively bred High Runner lines and four nonselected control lines across the first 31 generations of the experiment |

IMAGE BY THEODORE GARLAND, JR.

FIGURE 3	Image of a mouse femur, as would be provided to students for measurement

Mouse identification (ID) number

14001 R

Right or left femur of mouse

The distal end of the femur abuts the calf bones (tibia & fibula) in the knee joint

The femoral head fits into the acetabulum of the pelvis, forming the hip joint

Scale bar (ruler)

IMAGE BY TRICIA RADOJCIC

though a selection limit or plateau (Careau et al. 2013) was eventually reached in each selected line (Figure 2). Groups of students are then asked to list features they think are likely to distinguish "good runners" from average (or even poor) runners, and the teacher extends these ideas to changes that might occur in selected mice to enhance their motivation and/or ability for wheel running.

Garland and his colleagues have prepared a set of skeletons from 133 individual mice from a particular generation of the experiment (11), including both selected and control lines, which have been used in a variety of studies to explore the skeletal changes that occur with the selection process. Right and left femurs from these skeletons have been digitally photographed along with accompanying scale bars and identification tags that indicate sex and whether the individual is from a selected or control line (Figure 3).

Students readily provide a variety of ideas and suggestions when they are asked to propose the ways that the legs might be different in individuals from lines bred for high levels of wheel running as compared with controls. However, they often need assistance in deciding how to connect their proposals to the femur images; guiding questions such as the following help students to arrive at their own testable hypothesis, for which they can then collect data: How would the femurs be different if the legs were stronger, longer, or more flexible? Which parts of the leg bones would be expected to be the most different in selected versus control animals? Would there be any differences in leg symmetry (e.g., relative length of right and left femurs)?

Data collection

The images of the femurs from selected and control mice offer great flexibility for data collection, either manually by direct measurement of the printed images or electronically using software such as ImageJ, which can be loaded onto school (or personal) computers. For schools with limited technological resources, the images of the bones can be printed and students can measure the photographs directly with a ruler, using the scale bar (Figure 3) to adjust for magnification. Cross-curricular reinforcement of scale and proportion in math skills becomes an added benefit using this technique, although students are much more motivated by using electronic measurement techniques. While several software options are available, we have had good success using ImageJ (see Resources). The images of the samples can be downloaded from the complete lesson, which is available for free online (see Resources). The images currently reside in folders that organize them into selected and control by sex; however, teachers may reorganize the images in ways that might help students extend their investigations, for example to explore other questions such as the degree of difference (asymmetry) in right versus left femurs in selected and control animals (Garland and Freeman 2005).

Once students have developed their hypotheses, they must decide how to make measurements of the photographs. Whether this is done electronically or directly on printouts, students will need to ensure that their measurements are consistent among students and from image to image, providing a concrete exemplar of one aspect of good experimental technique. Students can discover the importance of consistency when they compare the results of duplicate or triplicate measurements, or when they compare the measurements taken by two or more students on the same image. In addition, for students using ImageJ, a day spent practicing using the software increases the accuracy and consistency of their measurements. Students can be provided with a brief summary of the use of ImageJ (Figure 4) or a teacher-directed

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FIGURE 4	Student directions for using ImageJ to measure femur images from selected and control mice

1. Select "File" then select "Open" from the dropdown menu. Then select the image.
2. Select the line tool on the toolbar.
3. Draw a line on the ruler that is 10 mm (1 cm) long.
4. Select "Analyze" then select "Scale" from the dropdown menu.
5. Enter "10" in "Known scale" and "mm" in "Unit of length." You can also choose to display in centimeters and set the number of decimals of accuracy.
6. Click "Global." This will apply the scale measurement to each picture that you measure thereafter.
7. Draw a line at the dimension that will be measured. The scale bar will display the measurement as well as the angle of the line. This will disappear when you click the endpoint of the line.
8. Select "Analyze" then select "Measure" from the dropdown menu: A data table will appear with the first measurement.
9. Select "File" then select "Open next" from the dropdown menu: The next image to be measured will appear.
10. Draw a new line on the ruler in the new femur picture.
11. Select "Analyze" then select "Measure" from the dropdown menu: The next length will be displayed on the data table.
12. When your measurements are complete, select "Analyze" then select "Summarize" from the dropdown menu.
13. Record the average from the displayed information. You will be graphing these data later.
14. Repeat steps 1–13 for the control animals.

demonstration. Students often discover various shortcuts that they can use to increase speed of data collection, and this experience encourages independent and innovative thinking.

As the second author has begun implementing Born to Run in his college courses, he has also used a "hybrid" protocol in which students view each photograph on a computer monitor (or iPad) and then hold a ruler up to it to measure the scale bar and bone character of interest directly against the computer screen.

No matter which way students take measurements, their next step is to record their data in a spreadsheet (Figure 5) that summarizes other information about the selected and control individuals (provided with the online lesson plan; see Resources). This includes the identification number of the individual (which is also recorded on the image), the sex, and its body mass at death. Teachers can customize how the data are collected—students can record the measurements independently or in small groups (Figure 6). Using Google Drive (formerly Google Docs) applications to share the spreadsheet with a whole class makes it possible for students to work collaboratively on the same data set by adding the measurements taken from assigned photographs. This is one example of crowdsourcing of data collection, and instructors can easily assemble their own large, cumulative database of measurements taken by classes across different years. (When developing the spreadsheets, students should be sure to add a column used to indicate the person making the measurements.) A potential shortcoming of this technique is that all students have access to the data and may be able to (accidentally) make alterations to the measurements taken by other students. This issue can be ameliorated by having students create their own spreadsheets initially and then merge them at a later time, or through creation of a Google Form that students fill out and submit, and which then automatically enters the measurements into a spreadsheet that only the instructor can access.

Data analysis

Data analysis using a spreadsheet program affords an ideal math-science connection for students, allowing them to rapidly generate a variety of graphs of a data set and to use those graphs to reveal patterns that may or may not match their preconceived expectations (hypotheses). Students may complete this component either independently or collaboratively. For students examining the effect of selective breeding on femur length, it is interesting to note that the average femoral length of selected individuals is not statistically different

FIGURE 5	Excerpt from a student spreadsheet

In this example, students would be instructed to take each femur measurement three times then compute the mean for use in graphs. Repeated measurements of the same object are used to teach students about reproducibility and measurement error, as well as aid in detecting anomalous measurements.

ID	Sex	Body mass (g)	Measurement 1 (mm)	Measurement 2 (mm)	Measurement 3 (mm)	Average (mm)
14001	Female	37.68				
14004	Male	39.17				
14006	Female	36				
14007	Male	50				
14011	Female	41.98				
14018	Female	35.2				
14024	Male	44.46				
14027	Female	30.03				
14028	Male	40.4				
14029	Male	44.04				
14039	Female	41.17				
14043	Male	44.92				
14045	Male	46.47				
14047	Female	31.33				
14048	Female	38.86				
14056	Male	47.08				
14057	Male	48.13				

from those of controls, once variation in body mass has been considered (Figure 7; Garland and Freeman 2005).

Swallow et al. (1999) have found that body size is in fact smaller in mice from the selected lines, and this fact can be readily confirmed by students' graphs of the lab's data on body mass (e.g., see Figure 8). Scatter plots of average femur length versus body mass reveal that femur length increases with body size (Figure 7), and the overlap between selected and control animals indicates that there is no appreciable difference between the femoral length of control and selected animals, at comparable body size. This confirms the findings obtained for these animals by Garland and Freeman (2005), who used direct measurement of the bones with handheld calipers.

Class discussions can explore the questions that are generated by these data: Does it make sense that the smaller-bodied selected animals have shorter legs? Might there be an evolutionary advantage of a smaller body size to running? For the latter question, students might discuss the differences in the body size of Olympic marathoners as compared with other types of athletes.

Assessment

With the advent of *Common Core State Standards*, teachers must not only strive to develop critical-thinking skills in their students but also to infuse into their curricula more writing that supports language-arts standards. Using a lab report is an optimal strategy for assessing the depth of student understanding as well as supporting the writing component of the *Common Core* standards. A suggested rubric appears in Figure 9, or teachers may create their own. Student report handouts are available with the online version of the article. Scientific collaborative skills in investigating a scientific question (how might selecting for a behavior correlate with anatomical differences?) are developed as students share the results of their studies with each other. Student groups might be asked to

FIGURE 6 — Students working on data collection

PHOTO BY TRICIA RADOJCIC

interpret data from other groups by viewing either the raw data or the graphs (what do these data tell us about the legs of selected mice versus controls?).

Student presentations are an effective way to both assess student understanding and to develop students' communication skills. Teachers might consider incorporating student presentations as a culminating activity to this lab, especially for groups of students that have investigated diverse questions. Complex thinking skills are increased when students are exposed to a variety of approaches and the perspectives of their peers.

Possible extensions

The digital photographs have great flexibility as a resource for students to conduct open-ended inquiry projects and test a variety of student-generated hypotheses about the skeletal differences between selected and control animals. These may include differences in the femoral head, the knee joint, and other features of the femur that students observe on the photographs (Figure 3). Internet searches relating to bones, joints, and locomotion can lead students to a variety of questions testable with the bone images. Students can explore leg symmetry by comparing measurements of the right and the left femur and comparing their results to those obtained in the laboratory, which indicate that leg-length symmetry has increased in selected animals (Garland and Freeman 2005). Are other parts of the femur also more symmetrical in selected versus control animals?

Femur lengths and widths can be determined in a variety of ways, depending on how and where students choose to measure the photographs. Discussions about the procedures that will be used to measure the bones should emphasize the importance of consistency in experimental protocols, and the ability to describe the

FIGURE 7 — Sample of student-generated scatter plot of femoral length (mm) (student data, average of right and left) versus body mass (g) (body masses are provided to students) for male mice

This graph was produced with the graphing function of a spreadsheet program. Note that, as shown in a summarized fashion in Figure 8, males from the selected lines tend to be smaller than those from control lines. As would be expected, across all mice, femur length is positively correlated with body mass: Larger mice tend to have longer femurs. However, for a given body mass (e.g., at 40 grams or 50 grams), there is no general tendency for mice from selected lines to have femurs that differ in length from those of control lines.
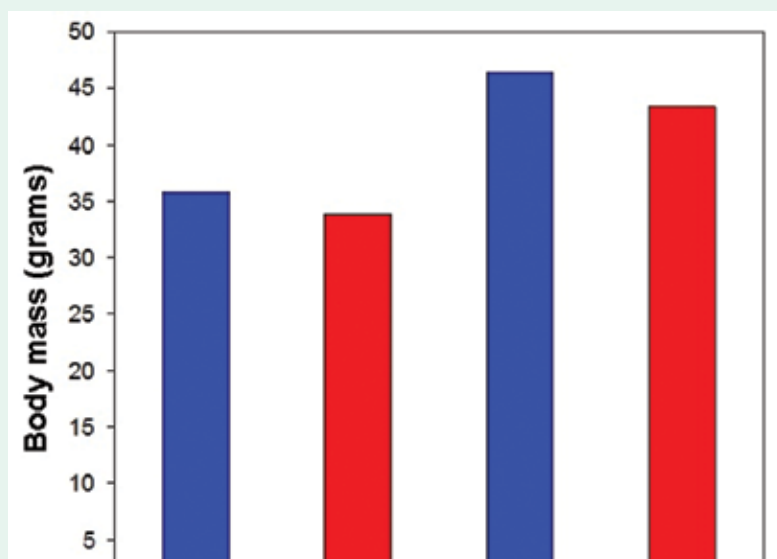
protocols in a written form so that other researchers could then duplicate the procedures (replicability of the scientific process). Is it important to measure the bones in the same way each time? Are the results obtained by the class consistent with the measurements obtained in the original research laboratory using a different way of measuring the bones? Which would be more likely to be accurate? Photographs of leg bones from later generations of mice can be obtained from Garland and could be used to explore whether any further changes have occurred with continued selective breeding.

Multiple opportunities for cross-curricular collaboration are inherent in this project. Successful interface with math, language-arts, and computer-essentials classes can be arranged within schools, achieving a high level of integration in students' science experiences. This strategy is a key feature that meets the demands of the *Common Core*, the *Next Generation Science Standards*, and also STEM approaches in general. Students' data can be used to illustrate concepts discussed in their math classes. For example, using direct measurements of the bones and calculating actual bone length with the scale provides an application of ratios and proportions, a critical area of focus for seventh-grade mathematics. (Separately from this, students can examine aspects of bone "shape" by computing such ratios as femur length/femur width.) In their computer classes, students can be instructed as to the use of Excel spreadsheets to analyze and graph their data. Their presentations and lab reports can be refined in language-arts classes, supporting *Common Core State Standards* in writing.
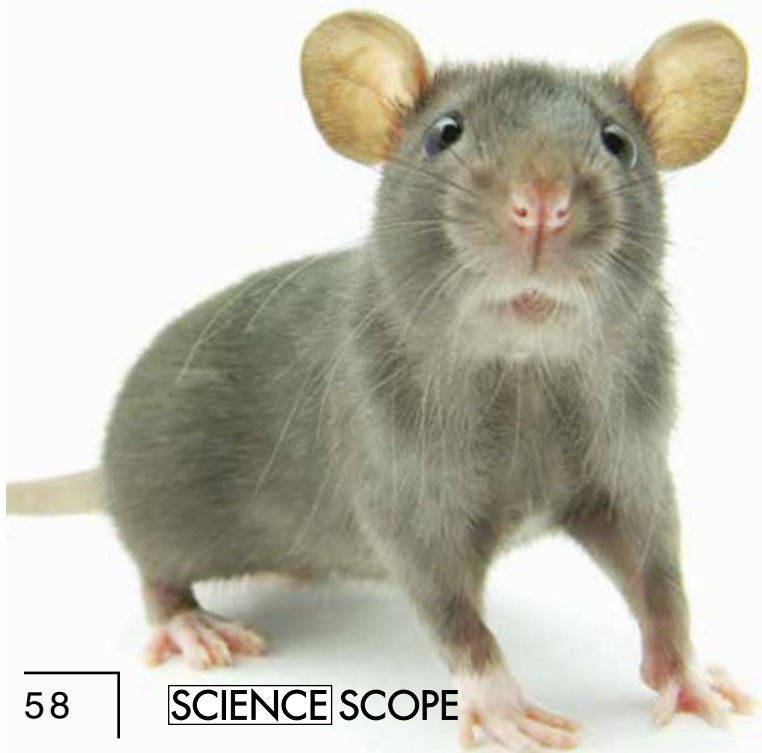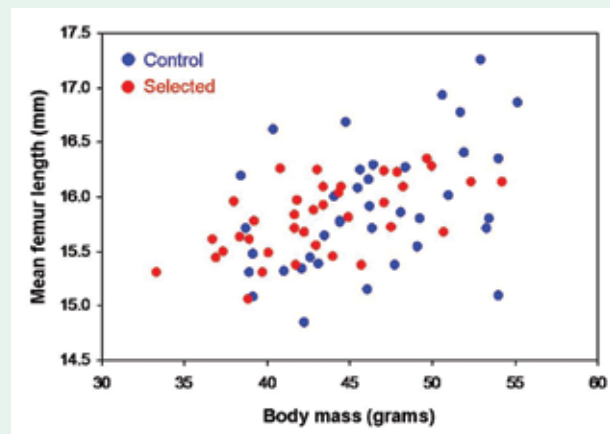
FIGURE 8	Sample graph of body mass (provided to students) in control versus selected animals

This graph was produced with the graphing function of a spreadsheet program. Note that, on average, male mice are larger than females, and those from the selectively bred High Runner lines are smaller than those from the nonselected control lines.

Conclusion

The ability to gather and interpret data is a vital skill for science students; however, the limitations of time and resources curtail practicing these skills in the context of many classrooms. This is especially true in the study of evolution, where the possibility for students to conduct experiments is virtually absent. Lesson plans based on the High Runner mice can meet this need, allowing students to develop their mathematical, investigation, reasoning, and experimentation skills within the context of the study of biological evolution.

A major consideration in the modern classroom is the need to develop students' technology skills. Using such programs as ImageJ to measure the femur images, as well as employing spreadsheets in a more sophisticated way to analyze the results and graph the data, has a substantial ability to address this need. However, as many school sites have limited availability of technological resources—especially student computers—flexibility is an important consideration in lesson design. Accordingly, teachers can easily tai-

FIGURE 9

FIGURE 9 — Sample rubric for evaluating student lab reports or presentations

	4	3	2	1
Hypothesis	1. Hypothesis is stated in "If... then..." format. 2. The measurement techniques are clearly connected with the question. 3. The reasoning is clearly explained.	1. Hypothesis is stated in "If... then..." format. 2. The measurement techniques are clearly connected with the question. 3. The explanation of the reasoning is unclear.	1. Hypothesis is stated in "If... then... " format. 2. The connection between the measurement techniques and the question is unclear. 3. The reasoning is unclear.	1. Hypothesis does not use "If... then... " format. 2. There is no connection between the question and the measurements made. 3. The reasoning is not explained.
Graphing	1. A bar graph is shown with labeled axes. 2. The measurement is shown on the *y*-axis, and the *x*-axis is labeled with "selected" and "control." 3. Measurements are shown in cm or mm and the values are rounded. 4. The scale selected clearly shows the differences (or lack thereof) in the measurements.	1. A bar graph is shown with partially labeled axes. 2. The measurement is shown on the *y*-axis, and the *x*-axis is labeled with "selected" and "control." 3. Measurements are shown in cm or mm and the values are rounded. 4. The scale selected clearly shows the differences (or lack thereof) in the measurements.	1. A bar graph is shown but the axes are not labeled. 2. The axes are reversed. 3. Measurements are shown in cm or mm but the values are not rounded. 4. The scale selected yields a misleading representation of the data.	1. The graph type is incorrect and unlabeled. 2. The axes are reversed. 3. Measurements are not shown in metric. 4. The scale is misleading or missing.
Presentation	1. Every person in the group speaks clearly and shows in-depth understanding of the results. 2. The results shown by the graph are clearly explained. 3. Group members are able to respond to questions.	1. Some people in the group show in-depth understanding of the results. 2. The results shown by the graph are clearly explained. 3. Group members are able to respond to some questions.	1. Group members are unclear in their understanding of the results. 2. The results shown by the graph are explained. 3. Group members are unable to respond to questions.	1. There is no evidence that group members have any understanding of the results. 2. There is no explanation of the results obtained. 3. Group members are unable to respond to questions.
Conclusion	1. All elements of the conclusion are included. 2. Reference is made to the data shown in the graph to support the conclusion. 3. Sources of error are clearly and completely explained and extend beyond human error. 4. Further analyses are suggested, and the reasoning behind these analyses is described.	1. All elements of the conclusion are included. 2. Reference is made to the data shown in the graph to support the conclusion. 3. Sources of error are lacking in depth. 4. Further analyses are suggested but reasoning is not explained.	1. Most elements of the conclusion are included. 2. Reference is made to the data shown in the graph to support the conclusion but the explanation is unclear. 3. Sources of error are restricted to human error. 4. There are no suggestions for further analyses.	1. Most elements of the conclusion are missing. 2. No reference is made to the data and the conclusion is not explained. 3. No reference is made to sources of error. 4. There are no suggestions for further analyses.

lor the Born to Run exercise to fit the resources they have at hand. Photographs can be downloaded and printed for students to measure by hand, and perhaps laminated to allow repeated use. Teachers can create and print a variety of graphs of the data and distribute them to student groups to interpret and present. The adaptability of this resource to classrooms with a wide spectrum of technological resources fosters accessibility and equity both within and among schools. ■

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Resources

Born to Run: Artificial selection lab—*www.indiana. edu/~ensiweb/lessons/BornToRun.html*

Evolution and the avian flu—*http://evolution.berkeley.edu/ evolibrary/news/051115_birdflu*

Garland lecture, "Born to Run"—*http://cnas.ucr.edu/ sciencelectures/garlandlecture.html*

ImageJ—*http://rsbweb.nih.gov/ij*

ImageJ basics—*http://rsbweb.nih.gov/ij/docs/pdfs/ImageJ. pdf*

Mice running on wheels—*www.youtube.com/ watch?v=RuqhC7g_XP0*

Publications on the High Runner lines of mice (with PDF files available for download)—*http://biology.ucr. edu/people/faculty/Garland/Experimental_Evolution_ Publications_by_Ted_Garland.html*

Swine flu is evolution in action—*www.livescience. com/7745-swine-flu-evolution-action.html*

Theodore Garland, Jr.—*www.biology.ucr.edu/people/faculty/ Garland.html*

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