A Role-Playing Exercise that Demonstrates the Process of Evolution by Natural Selection: Caching Squirrels in a World of Pilferers

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Published By: National Association of Biology Teachers
URL: http://www.bioone.org/doi/full/10.1525/abt.2011.73.4.4
ABSTRACT
We introduce a strategic role-playing exercise that is based on the fact that the strategies animals use in storing food for periods of famine differ in the degree to which the cache is successfully relocated and defended from pilferers. This highly engaging board game offers high school and college students a clear understanding of the process of natural selection.

Key Words: Evolution; quantifying natural selection; role-playing exercise; misconceptions.

The theory of evolution by natural selection provides a unifying framework for understanding and integrating the immense body of knowledge available on biological systems. Thus, the National Research Council (1996) recognized that our students should have a firm grasp of how natural selection functions both in maintaining traits and in leading to change in species over time. Yet this is a difficult concept for the instructor to convey, in particular because many students come in with alternative conceptions of the diversification of life. In fact, college entry tests indicate that the process of evolution by natural selection is misunderstood by the majority of students. Bishop and Anderson (2006), for instance, found that incoming students to a biology course for nonmajors understood only that evolution is a process that leads to gradual change of species over time in response to environmental conditions. A common misconception was the idea that evolution by natural selection is a need-driven adaptive process. Students further lacked understanding of the relationship between natural selection and both trait variation and differential reproductive success in populations. READINGS, LECTURES, FILM PRESENTATIONS OF EXAMPLES, DISCUSSIONS, AND EVEN DEBATES ABOUT EVOLUTION ARE IMPORTANT IN SETTING A FOUNDATION FOR THIS CONCEPT. THESE ARE FREQUENTLY USED TEACHING STRATEGIES IN HIGH SCHOOL AND COLLEGE BIOLOGY COURSES. HOWEVER, STUDENTS HAVE A MUCH HIGHER INVESTMENT IN LEARNING SOMETHING IN WHICH THEY ARE ACTIVELY ENGAGED. THE NATIONAL ACADEMY OF SCIENCES (NAS) RECOGNIZED THIS FACT IN THEIR 1998 GUIDE TO TEACHING ABOUT EVOLUTION. THE NAS CONCLUDED THAT ACTUALLY ACTING IN THE PLAY IS NECESSARY FOR STUDENTS TO DEVELOP A FIRM UNDERSTANDING OF THIS DIFFICULT TOPIC. IN A STUDY THAT COMPARED ROTE verses ACTIVE LEARNING OF EVOLUTIONARY CONCEPTS, NEHM AND REILLY (2007) FOUND THAT ACTIVE LEARNING SIGNIFICANTLY INCREASED UNDERSTANDING OF SUCH NATURAL-SELECTION CONCEPTS AS DIFFERENTIAL REPRODUCTIVE SUCCESS, PHENOTYPIC VARIATION, AND CHANGES IN THE DISTRIBUTIONS OF INDIVIDUALS THAT POSSESS HERITABLE TRAITS OVER GENERATIONS. HERE, WE INTRODUCE A ROLE-PLAYING EXERCISE IN WHICH STUDENTS ACT AS SQUIRRELS PROCURING FOOD FOR TIMES OF FAMINE, THUS GAINING A FIRM QUANTITATIVE CONCEPTION OF THE PROCESS OF NATURAL SELECTION AND ITS POTENTIAL TO LEAD TO TRAIT FREQUENCY CHANGES WITHIN POPULATIONS.

“Caching Food for Times of Famine” is an exercise presented under a behavior unit of the Biology in a Box project, which provides grade-level-appropriate exercises and permanent materials to school systems throughout Tennessee and, recently, in some school systems in neighboring states. Powerpoint and pdf versions of all exercises as well as materials lists and suggested readings are provided at the project’s website (http://biologyinabox.utk.edu). In collaboration with the National Institute for Mathematics and Biological Synthesis (NIMBioS), many of the exercises incorporate math, demonstrating the quantitative nature of biology.

**Evolutionary Framework: Caching Food for Times of Famine**
This exercise is based on the fact that animals such as birds and squirrels experience a feast-or-famine existence: a relatively short period of food abundance is followed by a long period of food scarcity. Many animal species solve this problem by caching food items that are not prone to decay (Figure 1; Smith & Reichman, 1984; Balda & Kamil, 1989, 1992; Hadjichik et al., 1996; Leaver & Daly, 2001; Pravosudov & Clayton, 2002; DeKort & Clayton, 2006; Vander Wall, 2010).
Before engaging in this role-playing exercise, it is important that the students understand fitness and its relationship to natural selection. Thus, we introduce them to the concept of fitness and the various ways in which it is quantitatively expressed (e.g., absolute vs. relative). They will work problem sets to ensure that they understand how the relevant parameters combine in estimating these forms of fitness. For example, the absolute fitness \( w_{abs} \) of a particular trait is shown to be equal to the ratio of the number of individuals with that phenotype (trait value) after selection to the number of individuals possessing the phenotype before selection \( \frac{N_2}{N_1} \).

In this equation, \( N_2 \) is calculated as the product of (1) the number of individuals of a particular phenotype that survive selection and (2) the average number of offspring that individuals of this phenotype produce. Below is an example of a question on absolute fitness that we ask the students to complete (here, the answers are provided in parentheses).

**Question:** Compare absolute fitness for phenotypes A and B, where individuals that possess trait A have a probability of surviving to reproduction of three-quarters and survivors contribute an average of 6 viable offspring to the next generation \( w_{abs} = \frac{3}{4} \times 6 = 4.5 \); and individuals that possess trait B have a probability of surviving to reproduction of one half and surviving individuals contribute an average of 5 viable offspring to the next generation \( w_{abs} = \frac{1}{2} \times 5 = 2.5 \).

The students also learn how to graphically compare trait success over generations of selection. They use relative frequency or proportion in this comparison \( f = \frac{p}{1/N} \), calculated by dividing the number of individuals \( f \) that possess a particular trait by the total sum of individuals over all traits. They are shown a graph of some actual trait-success data over time (Figure 2) and asked to interpret these data. What are the relative frequencies of the three phenotypes at the end of the experiment, how many generations of selection were completed, which phenotype was preferred by the predators (students) in the experiment, and which phenotype had the greatest fitness? All answers to such questions are presented in an answer section at the end of the exercise.

Finally, the class is introduced to the topic of natural selection and its various forms: stabilizing, directional, and diversifying or disruptive. They are asked to interpret graphs that distinguish among these types of natural selection.

**Playing the Game**

The game itself involves squirrels (students) who cache acorns produced by oaks in their home ranges during the fall months. The squirrels revisit their caches to feed during the winter months when food is scarce. There are four caching strategies that animals are known to use, a single-cache strategy (easy to remember and relocate) and three multiple-cache strategies: reforage entire home range, (no memory), episodic memory (remember each caching trip in the order in which it occurred), and rules-based search (position caches under, or in set directions and distances from, signposts such as trees or rocks). Clearly, each of these caching strategies will have different associated costs and benefits, particularly when we consider the fact that there are two or three scroungers in each home range who will attempt to pilfer caches.

We assume that a given caching squirrel in a population does not vary its caching strategy over time: it has an underlying genetic basis and is heritable. Thus, caching strategies are subject to natural selection. The class is asked to discuss the relative costs and benefits of the four caching strategies in preparation for completing the game. From this discussion, they will establish a hypothesized ranking of the four strategies with respect to the fitness each confers to the squirrels that use it. This ranking will later be compared with that obtained from data collected during the course of the game.

**Figure 1.** Squirrel retrieving an acorn from one of its caches to eat in a safe place.

**Figure 2.** Change in the relative frequency of three colors (phenotypes) and, thus, flavors (underlying genotypes) of jelly beans under predation pressure by students in an animal behavior class. Briefly, this experiment involved an initial 15 jelly beans of each of the three colors shown here. Students interested in eating a jelly bean picked one of the color they preferred. Following this “foraging bout,” the jelly beans reproduced (i.e., we doubled the number of the remaining beans of each color). The process was repeated over three class periods, producing the changes in relative frequencies noted.
The game sequence and specifics of data collection are summarized in Table 1. Briefly, the data for the population (class) are collected for squirrels that possess home ranges (i.e., mats shown in Figure 3 placed on desk tops) within the woodlot (classroom). A team of three or four students work with a given home-range mat, as they are assumed to be foraging in the same area.

There are trials within rounds that constitute generations of selection. The number of trials completed for a generation of the selection study will be determined by team size, as each student should have the opportunity to be a caching squirrel in a round while the other team members serve as scroungers. A preliminary table will be compiled on the board at the front of the room to keep track of the individual trials within a round (see Table 2). The reproductive success of each caching squirrel in a trial (numbers of acorn chips recovered) is recorded with respect to caching strategy used. We have found that students take their roles as caching squirrels more seriously if their reproductive successes are listed under their names in this table. Note also that there is a column in Table 2 labeled “Trees.” Oak-tree fitness is increased by caching animals that fail to find all of their acorn caches. We have included the tree column so that the class might discuss the community consequences of animal caching strategies. Acorns are too heavy for wind dispersal. Rather, oaks and other nut-bearing trees depend (1) on mammals and birds to move the seeds from under the shade of the mother tree into a suitable location for germination and/or (2) on their failure to relocate all of the cached seeds (Vander Wall, 2010).

At the completion of a given round of the game, the class will use the data compiled in Table 2 in preparing a summary of the results for that generation by filling in the cells in Table 3. We assume that a caching squirrel produces one offspring for every acorn chip (cache) that it recovers and that offspring inherit the parents’ caching tactic because genes (genotypes) underlie caching strategies (phenotypes). From this second table, students can identify those caching strategies that produce the greatest individual fitness. Students can also obtain a quantitative picture of the change in strategy representation over each period of natural selection (generation/round of the game) from the data compiled in Table 3. Finally, they will use the relative frequency
scores presented in column F of Table 3 in determining the distribution of the four caching strategies used in the next round of the game.

Much insight into the process of natural selection can be gained from completing just one round of the game. This will demonstrate the relative fitness achieved by each of the four strategies that were equally represented at the start of the game. For instance, if rules-based search has a higher frequency of representation in the offspring produced by caching squirrels of generation 0 than the 0.25 it started out with (see Table 3), it would be a strategy favored by natural selection.

However, we recommend that three rounds of the caching squirrel game be completed over a number of days. This is because it provides another layer of understanding of evolutionary process. Over several rounds of the game, students are able to track how the relative frequency of a strategy affects its subsequent success. Thus, if rules-based search becomes the predominant caching strategy, scroungers may learn it and become more successful at finding these caches. Such ploy and counterploy tactics can lead to cyclic changes in strategy representation and are one reason why multiple strategies are maintained in populations.

### Conclusions

“Caching Food for Times of Famine” not only demonstrates core concepts of evolution by natural selection but also allows the students to explore evolutionary processes for themselves. In doing so, they can address the misconceptions they might have in their understanding of the concept of evolution by natural selection, such as the idea that evolutionary change is directive and purposeful (Moore et al., 2002). Including the mathematics that underlie the biology in this exercise illustrates the inherent quantitative nature of biology and allows students to make connections between concepts taught in biology and mathematics courses. We suggest that encouraging students to participate in their education is not only intellectually stimulating for them but also lead to a better understanding about the nature of science and, in this case, evolution by natural selection.

### Follow-up Exercises

Following the completion of the exercise, the class first reviews their results in terms of the predictions they have made concerning selection pressures and the types of natural selection they have observed. They are then asked to apply what they have learned to address additional problems in a brainstorming session. For example, could squirrel population size potentially influence strategy representation in the population? If not, why not? If so, under what conditions could this happen and what would be the consequences? This might bring them to a discussion of carrying capacity, differential dispersal of squirrels exhibiting less successful strategies, genetic drift or founder effects, and so on.

### Acknowledgments

We are grateful for the financial support offered by NIMBioS to Rachel Leander, Suzanne Lenhart, and the Biology in a Box project.
References


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