

Beads and Dice in a Genetic Drift Exercise

Claudia A. M. Russo · Carolina M. Voloch

Published online: 29 August 2012
© Springer Science+Business Media, LLC 2012

Abstract Natural selection driving adaptive changes is a powerful and intuitive explanation for the evolution of the living world around us. Evolution at the molecular level, however, is chiefly ruled by random genetic drift. The idea that an advantageous allele may be lost by chance in a natural population is rather difficult to explore in the classroom. Low-cost and hands-on educational resources are needed to make genetic drift more intuitive among students. In this exercise, we use colored beads and the roll of a die to simulate drift and selection jointly affecting the fate of the genetic variants in an evolving population. Our aim is to teach students that natural selection does not determine but simply influences the fate of advantageous alleles because random genetic drift is always present. We have been using this exercise successfully for over a decade for the Biological Sciences students at the Federal University of Rio de Janeiro.

Keywords Education · Evolution · Randomness · Adaptation · Fitness · Probability of survival

Introduction

The evolutionary theory is the unifying principle in biology. Hence, the concept that evolution involves changes in the genetic composition of a population through time is extremely important. Charles Darwin's brilliant insights on evolution by natural selection have not been overlooked. Today, natural selection is one of the most influential and pervasive concepts in the biological sciences (Besterman and Baggott 2007). Professional biologists are eager to dazzle students by

explaining the wonderful adaptations that made a particular species possible, starting with the classics: the giraffe's neck and *Biston betularia* (Lauer 2000; Scott 2004).

Many decades after the publication of *The Origin of Species*, however, Motoo Kimura sketched a different portrait of the pace of evolution at the molecular level (Kimura 1954, 1968). Random genetic drift was not only important; it was the chief force governing molecular evolutionary change. The intuitively appealing force of Darwinian selection was to be viewed as an exception at the molecular level (Kimura 1985; Ohta 1992).

Despite its importance, however, genetic drift is constantly neglected and often dismissed as an evolutionary force in general biology textbooks (Hammersmith and Mertens 1990; Linhart 1997) and even by professionals in the field (Staub 2002; Nelson 2007). There are many reasons for this recurring neglect. First, when addressing topics related to evolution, the teacher is bound to face some antagonism and hostility in the classroom (Alters and Nelson 2002; Johnson et al. 2012). Second, although many beautifully detailed examples are available to illustrate natural selection (Darwin 1859; Lauer 2000), genetic drift is abstract by nature and is not directly observed. Third, theoretical foundations that support neutralist expectations have a deep mathematical basis that makes genetic drift conceptually even more difficult to grasp (Lenormand et al. 2008). Finally, the idea that the genetic drift (i.e., chance) may overcome the directional force of natural selection is counterintuitive and is thus difficult to explore in the classroom.

Several educational resources have been developed to demonstrate the significance of genetic drift or natural selection (see McComas 1998; Staub 2002; Heim 2002; Young and Young 2003). Most of these hands-on exercises, though, focus on a single evolutionary force, neglecting the interaction between selection and drift that is usually explored in computer simulations (Populus, Alstad 2007; PopG, Felsenstein 2008). Computer simulations, however, still require an abstractly oriented mind since results are depicted in theoretical graphs. Furthermore, computer-based resources

C. A. M. Russo · C. M. Voloch (✉)
Departamento de Genética, Laboratório de Biologia Evolutiva
Teórica e Aplicada, Universidade Federal do Rio de Janeiro,
Instituto de Biologia,
Av. Prof. Rodolpho Paulo Rocco s/n CCS, Bloco A, A2-097,
Ilha do Fundão, Rio de Janeiro 21941-617, Brazil
e-mail: carolina@biologia.ufrj.br

may not be available for students in most high schools or even in many undergraduate courses. Low-cost and hands-on resources are the key to make abstract concepts, such as genetic drift, more intuitive to the student (Colburn 1994; Brewer and Zabinski 1999).

This exercise uses the roll of a die to simulate drift and selection simultaneously affecting the fate of the genetic variants in an evolving population. The conventional argument is that because an individual with an advantageous allele will have a higher probability of survival and reproduction, this higher probability will tend to persist in the offspring that bear the allele. Here, we aim to teach the concept that *natural selection is the differential probability of the survival and the reproduction of variants* and other related concepts. Natural selection does not determine but simply influences the fate of advantageous alleles because random genetic drift is always present (Gregory and Ellis 2009). We have been using this exercise successfully for over a decade to make genetic drift more intuitive for the biological sciences students at the Federal University of Rio de Janeiro.

In this exercise, different selective pressures will be simulated by the different probabilities associated with the roll of a die. At the end of the exercise, we expect that the stochastic aspects that drive biological evolution will become clearer to students, who will tend to regard natural selection as the differential probabilities of survival and reproduction. This activity should be used in an evolutionary biology class or in an introductory biological sciences class with an evolutionary biology backbone.

Pre-Activity

Background

Basic concepts related to genetics, mutation, genetic variability, carrying capacity, competition, migration, natural selection, and random genetic drift should be introduced before the exercise starts. This activity will help further theoretical development of related themes on the neutral theory, molecular clocks, and conservation biology that will be easier to understand and to address in the classroom after the exercise.

Class Organization

The classroom must be organized into four-student groups so that all students participate in the exercise. One group member must be responsible for taking notes, another for rolling the die, a third member for selecting competition pairs, and the fourth for explaining results to the group. Each group should receive the necessary materials for the activity and may return them at the end of the exercise.

General Remarks

The teacher must gather and analyze the results and discuss the final conclusions with the students. The teacher must be aware that this simulation assumes a simple model in which haploid individuals compete in pairs, unlike the standard Wright–Fisher model. These remarks should be clear to the students before the activity begins, since natural populations do not organize in pairs to compete. In the next section, the exercise is described as it should be presented to the students. Following the exercise, we include directions to guide further theoretical discussion in the classroom.

Drift and Selection Exercise

In this exercise, you will observe how different characteristics may spread in natural populations through time by random genetic drift and natural selection.

Materials

1. A small cup with 60 flat beads. The beads should be flat so that they do not roll off the students' tables during the exercise. They must be of two different colors, e.g., 20 gray and 40 black beads. A small cup or bag to hold the beads is not crucial, but it will facilitate the exercise in the classroom. The beads may be easily replaced with corn kernels, beans, peas, or soybeans.
2. A six-sided die. (In all simulations, you may replace the roll of the die with a bag with the appropriate number of beads of each color representing the different selective pressures listed in the simulations. Nonetheless, we strongly encourage the use of the die-roll competition approach, even in the absence of selection simulation, to make matters simpler and more intuitive for the students. All materials are reusable.)

Exercise

First, let us imagine a natural population that presents genetic variability at a given locus. You have received beads that represent haploid individuals in a natural population. The bead colors mark variability for a particular character. For instance, black beads symbolize individuals with black body color. The simulations will explore different aspects of the interplay of selection and random drift in maintaining and eliminating genetic variation in natural populations.

The simulations begin in the first generation after a point mutation arises in the population. The population inhabits an environment that has a carrying capacity of ten

individuals, owing to resource limitation. At reproduction, individuals generate identical descendants and die immediately (This is a simplified model of asexual reproduction). Because the number of offspring produced at reproduction is larger than the carrying capacity of the environment, competition will occur. Only ten individuals will survive. You will determine the survivors to find the next generation by rolling the die according to the instructions in each simulation.

To select pairs for competition, place all offspring (beads) in the cup and randomly select competing pairs (by taking two beads at time) until all individuals are aligned for competition (see Fig. 1). You will need to roll the die only if a competing pair involves individuals of different colors. Otherwise, simply choose one individual to survive. In all cases, the result of the die roll will determine if the black or the gray individual survives the competition process. The outcome depends on the competitive skills of the color variants. These skills differ in each simulation. The survivors will constitute the next generation.

Another round of reproduction and competition will occur before the subsequent generation. The results for each generation must be recorded. If one of the alleles is fixed, i.e., the other allele is eliminated; the die is no longer rolled. No more evolution will occur until mutation or migration creates variation at the locus again. In this case, the results last obtained should be copied for all the subsequent generations until the tenth generation.

Simulation A—No Selection

The first generation starts after the occurrence of a point mutation and consists of nine gray individuals and the black mutant. Each individual will produce two identical offspring and die shortly after reproduction. Hence, 18 gray and two black individuals (beads) will be produced after the first generation finishes reproducing. Place all 20 individuals in the cup. You must arrange the individuals so that competition pairs are aligned from top to bottom (see Fig. 1) and roll the die if the colors differ. In this simulation, no selection is acting. The evolutionary force operating on this particular locus is random genetic drift.

Imagine that black and gray are markers for body colors, but the population lives in a completely dark cave so that body color bestows no selective advantage. Hence, the allelic frequencies for this marker will increase and decrease purely by random genetic drift. Black and gray are neutral characteristics that confer equal survival probabilities on the bearers. If the die-roll result is 1, 2, or 3, the gray survives competition. Alternatively, if the die roll is 4, 5, or 6, the black survives competition. Competition takes place among the 20, and only ten survive the process. These ten survivors will form the second generation. In turn, each survivor will produce two identical individuals that will compete for survival to represent the third generation. Record the number of individuals of each color that you observe in each generation until the tenth generation.

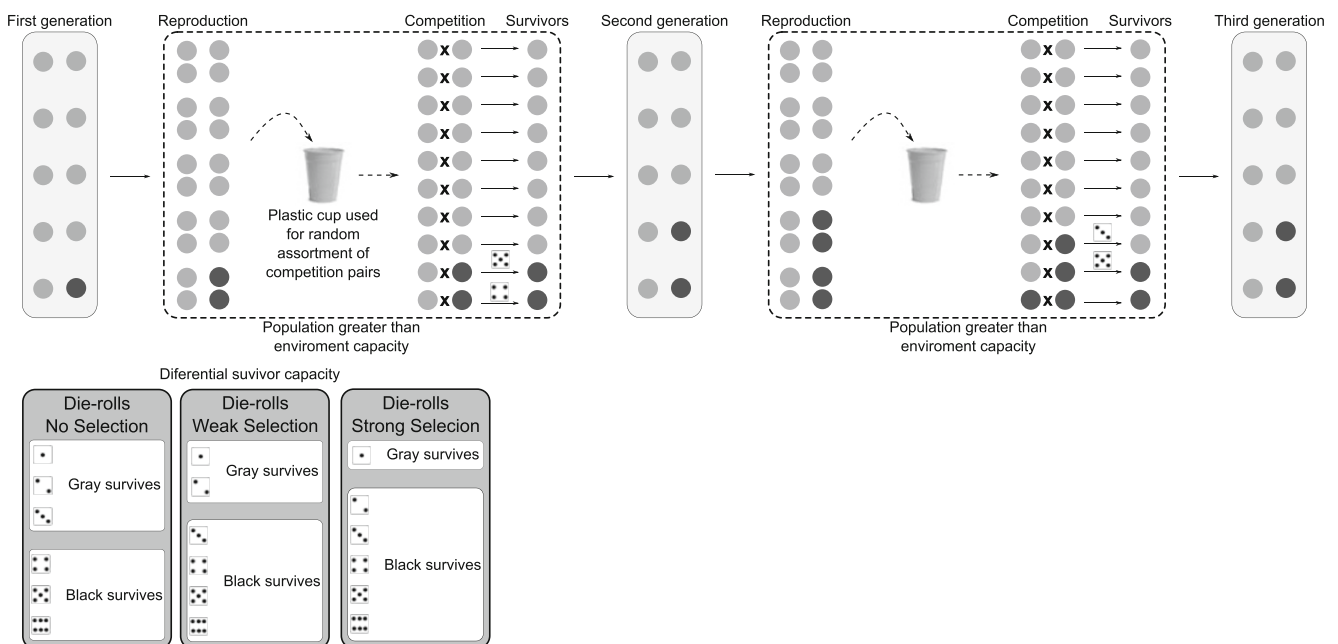


Fig. 1 General arrangement pattern for competing pairs. The difference in competitive skills increases the chances but do not determine the survival of the black variant. In the no selection model (simulation A), there is no selective pressure because each of the variants has a

50% chance of winning the competition event. The associated survival probabilities for weak and strong selection simulation patterns are also depicted (simulations B and C)

Simulation B—Weak Selection

In the second simulation, we will add the effect of natural selection. Imagine that there is a small amount of dim light coming into the cave. Here, body color will affect survival and competitive success because the cave floor is dark and black bodies are better camouflaged. We will simulate natural selection pressure by changing the probabilities of survival of the color variants in a competition event. In this simulation, if the die roll is 1 or 2, the gray wins the competition. If the roll is 3, 4, 5, or 6, the black wins (Fig. 1). You must notice that even though the black variant has a selective advantage over the gray, it is possible for the gray to win several competition events. If this occurs, the evolutionary change was driven not by the directional selective pressure but by random genetic drift acting even on this adaptive scenario. Natural selection was at play, influencing but not determining the survival of variants. It is even possible that the advantageous black will be completely eliminated by genetic drift, although this outcome is more likely in the early generations because the frequency of the advantageous black is initially small.

Simulation C—Strong Selection

In this third simulation, selection pressure will further increase. The body color now determines higher chances of survival because a strong beam of light enters the cave and the black allele is highly advantageous over the gray. Hence, if the die-roll result is 1, the gray wins, whereas if the result is 2, 3, 4, 5, or 6, the black wins the competition (Fig. 1). Here, the selective pressure is even stronger. Nevertheless, as before, selection does not determine the fate of the variants because random genetic drift is still at play. Only if the survival probability of a variant is null, i.e., lethality, will selection actually determine the genotypes of the next generation. Notice how rapidly an advantageous allele becomes fixed. Indeed, low variability is expected in an adaptive scenario because natural selection tends to eliminate other, less adaptive, alleles in only a few generations.

Simulation D—Changes in Environment

Let us imagine now that the environment is changing. At first, the population lives in a very dark cave, but light and visibility are increasing and produce an escalating advantage of the black allele over the gray. In this simulation, a neutral black allele becomes more and more adaptive through the generations. The first generation begins with nine gray individuals and a black mutant. At reproduction, each individual produces two offspring. The carrying capacity of the environment remains at ten individuals. In the first and second generations, the cave is very dark and selective pressure is absent (i.e., 1–3

means gray survives and 4–6 means black survives, Fig. 1). The brightness increases in the third, fourth, and fifth generations, and so does the selective advantage of the black (i.e., 1–2 means gray survives, 3–6 means black survives, Fig. 1). From the sixth generation on, luminosity increases even further, and selective pressure follows (i.e., 1 means gray survives, 2–6 means black survives).

Simulation E—Difference in Fertility

All of the simulations described above assumed that the variants produced the same number of offspring and that selective advantage was limited to competitive skills and success. Nevertheless, natural selection may act in different ways, such as fertility variation. We will explore differences in fertility in this simulation. Here, the black individuals hold no competitive advantage over the gray variants. Nevertheless, the black individuals produce four descendants during reproduction, whereas the grays produce two. This difference illustrates another mode of selective advantage. One important aspect of the simulation is that the carrying capacity of the environment does not change, so that more than one round of competition will take place between generations. The fixed carrying capacity ensures that only ten individuals will survive and constitute the subsequent generation (Fig. 2a).

As in the previous simulations, the die must be rolled if different-colored individuals form a pair for competition. Consider that neither variant enjoys a competitive advantage and that if the result of the die roll is 1–3, the gray survives, whereas if it is 4–6, the black survives. For instance, suppose that the single black individual in the first generation produced four black individuals, whereas the nine gray individuals produced 18 gray offspring. The total offspring count is 22, but again only ten will survive. The first round of competition will reduce these 22 individuals to 11 individuals. From these 11 individuals, two (one pair) must be randomly chosen from the cup to compete again. The second round of competition will produce ten survivors. These survivors will establish the second generation, and the process will continue until the tenth generation.

Simulation F—Colonizing a New Environment

In this last simulation, we will consider a population colonizing a new environment. At this point, environmental carrying capacity is not a limiting factor owing to the small size of the colonizing population. This part of the exercise will simulate the effect of population size on selective pressure (Fig. 2b). If two individuals do compete, selection pressure is strong for the black (if the die-roll is 1, the gray survives; if 2–6, the black survives). In the first generations, however, very few competing pairs will actually form

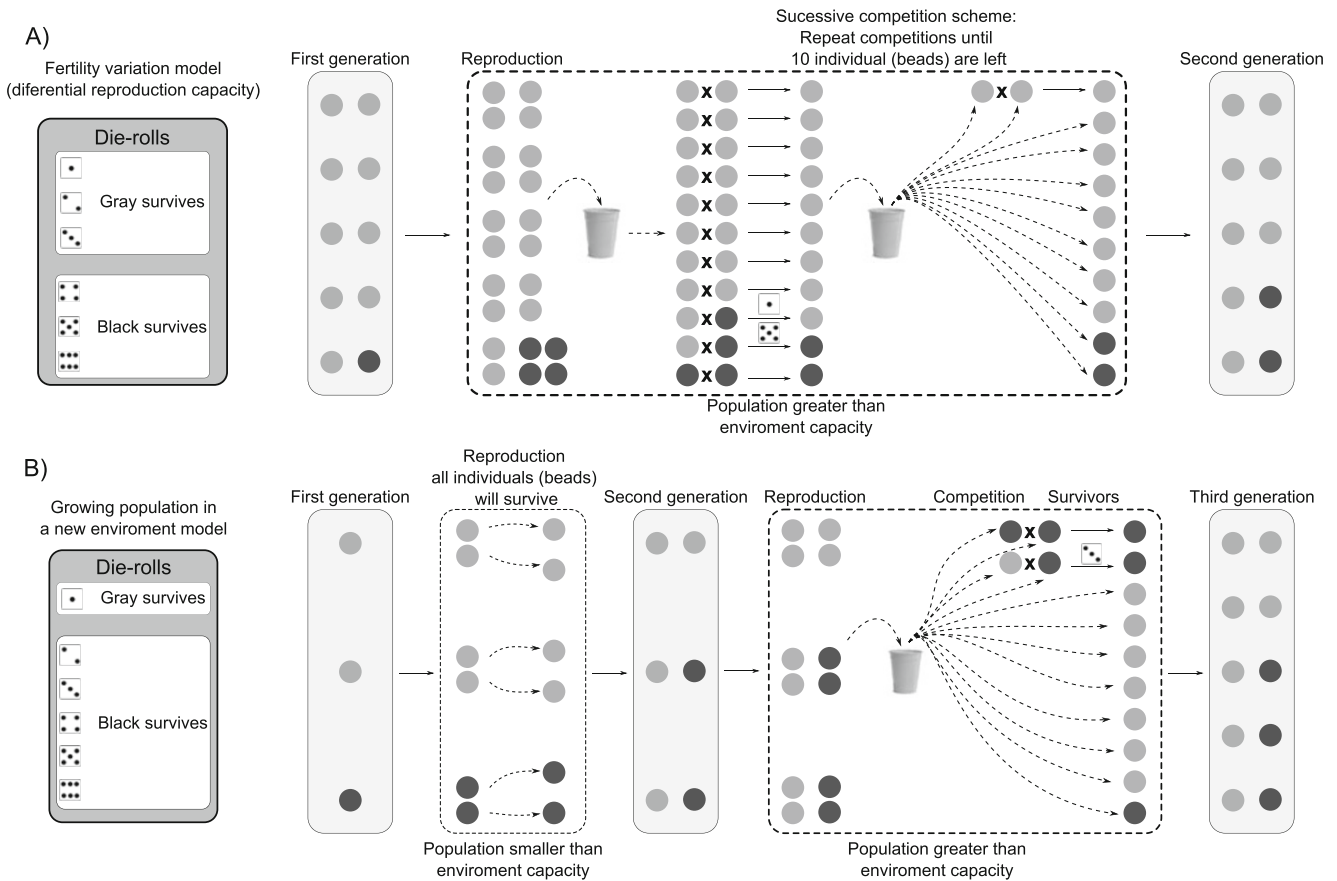


Fig. 2 a A difference in fertility rather than in competitive skills characterizes simulation E. The selective advantage of the black mutant occurs because it produces four offspring, in contrast to the two produced by gray. In this case, an extra round of competition will be necessary to determine the ten survivors for the next generation. **b** This

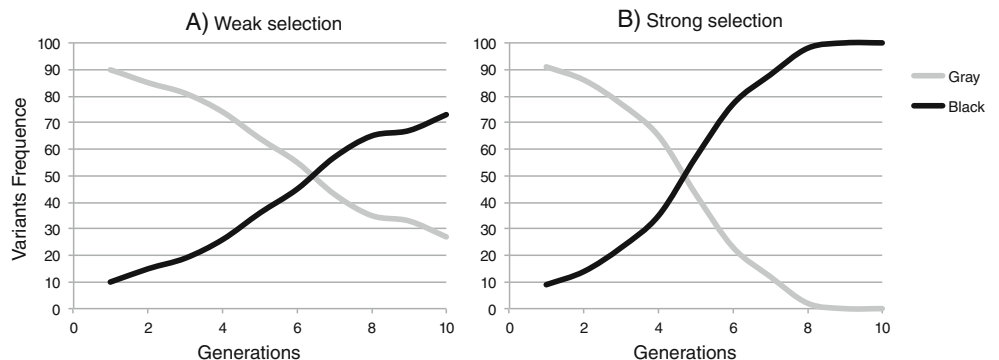
simulation explores the colonization of a new environment (simulation F). The population size increases with time (generations). Once the population reaches the carrying capacity, the competition events begin. The competing pairs should be arranged as previously mentioned

due to the small size of the population. If there is food for everyone, even the individuals carrying deleterious (gray) alleles will be likely to find food and survive. As the population size approaches the carrying capacity, the selective pressure will be stronger and more die rolls will occur.

In this simulation, a small group of three individuals, two grays and one black, colonize the new environment and constitute the first generation. The carrying capacity remains at ten individuals. Despite the black advantage in competi-

tion, selective pressure on survival is absent in the first generation. All six offspring survive, bypassing competition. In the second generation, selective pressure increases because the population size is closer to carrying capacity. Of the 12 offspring produced, only two pairs will compete for resources. The remaining eight individuals will bypass competition. From the third generation on, selective pressure increases to a maximum because the population size equals the carrying capacity.

Fig. 3 The results from all student groups were gathered and are depicted in the graphs. **a** Weak selection (simulation B) and **b** strong selection (simulation C)



Final Remarks to the Teacher

After the students finish the simulations, it is important to gather the results and discuss the final conclusions in the classroom. The results from the application of this exercise (simulations B and C) conducted by 30 groups of four students at the Federal University of Rio de Janeiro are shown in Fig. 3. In practice, our results are similar to those from computational simulations (e.g., *Populus*). Even though no formal assessment has been implemented, this similarity indicates the mathematical rigor of the exercise.

We believe that the influence of population size on genetic drift will become more intuitive if individual group results are compared with class results. If the results from the individual groups are combined, the effect of random genetic drift will be smoothed, and the class results will represent the behavior of a larger population. The advantageous mutant might be lost in one or two groups, but the directional tendency is for the fixation of the advantageous allele that will become an adaptation. This point will be clear from the class results.

An important concept to address at this point is the predictability associated with large populations. The chance of having a nonrepresentative sample of variants to found the next generation is much greater in a small population than in a large group. For this reason, genetic drift, i.e., the chance fluctuation of allele frequencies, is stronger in small populations. The outcome of a single event involving selective pressure is as unpredictable as the die roll because genetic drift is always at play on the random sampling of gametes (Wright 1931) and on the randomly fluctuating selection intensities (Kimura 1954), even in an adaptive scenario.

In the first four simulations of this exercise, the students are introduced to the most general aspects of natural selection and genetic drift. It is important to show the students that with no selection (simulation A), the probability that a neutral allele will be fixed in a population is proportional to its frequency (Hartl and Clark 2006). It should also be noted that when the selective pressure is weak (simulation B), the time until the fixation of the advantageous allele is greater than it would be in the case of a strong selection pressure (simulation C). It is important to explain that we expect low variability if one of the alleles has a selective advantage relative to the others. Because natural populations exhibit high variability, this argument strongly supports neutralist expectations (Kimura 1985).

Once variability is lost, the locus ceases to evolve. Only new mutation or migration events will restore variability and evolution at this locus. This finding has important conservation consequences because genetic variability, not population size, will ensure the survival and the viability of an endangered population (Rouzic and Calborg 2008). Also noteworthy to conservation issues is that if the environment

changes, a former neutral allele might become advantageous (simulation D). The presence of this newly advantageous allele might determine the difference between survival and extinction.

Another aspect of adaptive evolution is addressed in simulation E. In that case, increased fertility, rather than competitive skills, creates the selective advantage for the bearer. Leaving more descendants naturally increases the selective advantage even if no competitive advantage is present. Selective pressure is related to population size and the carrying capacity of the environment. Hence, if there is food for everyone, everyone is bound to survive (simulation F). If the population grows, it will reach a size closer to carrying capacity. Accordingly, the selective pressure is expected to grow.

After the exercise, students tend to recognize that environmental pressure and fertility, not outcomes, represent the evolutionary force of natural selection on natural populations. Alternative educational resources such as this exercise have the potential to complement existing approaches to science instruction by creating appropriate environments for the construction of student knowledge (Dede et al. 1994; Kolb 1984). We believe that by serving as direct agents of the phenomenon by rolling the die, learners gain direct experiential intuitions about the ways in which evolutionary forces operate and can accordingly make genetic drift more intuitive and concrete.

Directions to the Discussion

Simulation A: The probability that a neutral allele becomes fixed is proportional to the frequency of that allele in a population.

Simulations B and C: An advantageous allele may be lost by chance. This does not mean that natural selection was not acting. It means that natural selection is the differential probability of survival among variants, but chance may overcome the natural selection force. This is particularly true in a small population. If clustered, class results should reveal that in larger populations, the strength of the chance is weaker.

Simulation D: The advantage of an allele may change over time due to unpredictable environmental changes.

Simulations E and F: The advantage of an allele may result in more descendants compared to other variants. The strength of the competition between individuals is directly proportional to how close the population size is to the carrying capacity of the environment.

Acknowledgments The authors wish to thank Carlos G. Schrago for his support and insights on the theme and on previous versions of the manuscript. Financial support from FAPERJ (Rio de Janeiro State agency for research funding) and CNPq (Brazilian Federal Research funding) to C.A.M.R. are to be acknowledged for making this study possible.

References

- Alstad DN. *Populus* (<http://www.cbs.umn.edu/populus>). Copyright 2007 Alstad DN & University of Minnesota. 2007.
- Alters BJ, Nelson CE. Perspective: teaching evolution in higher education. *Evolution*. 2002;56:1891–901.
- Besterman H, Baggott L. Using human evolution to teach evolutionary theory. *J Biol Educ*. 2007;41:76–81.
- Brewer CA, Zabinski C. Simulating genetic change in a large lecture hall: the ultimate bean counting experience. *Am Biol Teach*. 1999;61:298–302.
- Colburn AI. Misconceptions in evolution education. In: McComas WF, editor. *Investigating evolutionary biology in the laboratory*. Virginia: National Association of Biology Teachers; 1994.
- Darwin C. *On the Origin of Species*. London: John Murray; 1859.
- Dede C, Loftin B, Salzman M, Calhoun C, Hoblit J, Regian W. The design of artificial realities to improve learning Newtonian mechanics. In: Brusilovsky P, editor. *Proceedings of the East–West International Conference on Multimedia, Hypermedia and Virtual Reality*. Moscow, Russia: International Centre for Scientific and Technical Information; 1994. p. 34–41.
- Felsenstein J. (2008) PopG (<http://evolution.gs.washington.edu/popgen/popg.html>). Copyright 1993–2008 University of Washington & Felsenstein J.
- Gregory TR, Ellis CAJ. Conceptions of evolution among science graduate students. *BioScience*. 2009;59:792–9.
- Hammersmith RL, Mertens TR. Teaching the concept of genetic drift using a simulation. *Am Biol Teach*. 1990;52:497–9.
- Hartl DL, Clark AG. *Principles of population genetics*. 4th ed. Sunderland: Sinauer Associates Inc.; 2006.
- Heim WG. Natural selection among playing cards. *Am Biol Teach*. 2002;64:276–8.
- Johnson NJ, Lang-Walker R, Fail JL, Champion T. A student activity that simulates evolution. *Am Biol Teach*. 2012;74:117–20.
- Kimura M. Process leading to quasi-fixation of genes in natural populations due to random fluctuation of selection intensities. *Genetics*. 1954;39:280–95.
- Kimura M. Evolutionary rate at the molecular level. *Nature*. 1968;217:624–6.
- Kimura M. *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press; 1985.
- Kolb DA (1984) *Experiential learning: experience as the source of learning and development*. www.learningfromexperience.com/images/uploads/process-of-experiential-learning.pdf. Accessed 27 Oct 2011.
- Lauer TE. Jelly belly jelly beans & evolutionary principles in the classroom: appealing to the students' stomachs. *Am Biol Teach*. 2000;62:42–5.
- Lenormand T, Roze D, Rousset F. Stochasticity in evolution. *Trends Ecol Evol*. 2008;24:157–65.
- Linhart YB. The teaching of evolution—we need to do better. *BioScience*. 1997;47:385–91.
- McComas WF. *The nature of science in science education: rationales and Strategies*. Norwell: Kluwer Academic; 1998.
- Nelson CE. Teaching evolution effectively: a central dilemma and alternative strategies. *McGill J Educ*. 2007;42:265–83.
- Ohta T. The nearly neutral theory of molecular evolution. *Annu Rev Ecol Syst*. 1992;23:263–86.
- Rouzic A, Carlborg Ö. Evolutionary potential of hidden genetic variation. *Trends Ecol Evol*. 2008;23:33–7.
- Scott EC (2004) *Evolution vs. creationism*. University of California Press: California
- Staub N. Teaching evolutionary mechanisms: genetic drift and M&M. *BioScience*. 2002;52:373–7.
- Young HJ, Young TP. A hands-on exercise to demonstrate evolution. *Am Biol Teach*. 2003;65:444–8.
- Wright S. Evolution in Mendelian populations. *Genetics*. 1931;16:97–159.