CURRICULUM ARTICLE

Selection and Evolution with a Deck of Cards

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Abstract Imparting a basic understanding of evolutionary principles to students in an active, engaging fashion can be troublesome because the logistics involved in designing experiments where students pose their own questions and use the data to test alternative hypotheses often outstrip time and financial constraints. In recent years, educators have begun publishing exercises that teach evolution using innovative, in-class experiments. This article adds to this growing forum by describing a classroom exercise that introduces the concept of evolution by natural selection in a hypothesis-driven, experimental fashion, using a deck of cards. Our standard exercise is suitable for upper-level high school and introductory biology students at the college level. In this paper, we discuss the exercise in detail and give several examples that illustrate how our games provide accessible bridges to the primary literature. Finally, we discuss how extensions of our basic exercise can be used to effectively teach advanced evolutionary concepts.

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Introduction

In a classic and often-cited essay, "Nothing in biology makes sense except in the light of evolution," Theodosius Dobzhansky (1973) convincingly illustrated how evolutionary theory unifies all biological disciplines and why evolutionary biology should be at the center of undergraduate biology curricula. Three decades later, the academic community is still wrestling with how best to effectively integrate evolutionary concepts into introductory biology programs. As Alters and Nelson (2002) eloquently discuss, conceptual misunderstandings of basic evolutionary concepts are rampant throughout all educational levels of our society, and these misconceptions rigidly persist because students have great difficulty displacing preconceived models that explain natural phenomena (Committee on Undergraduate Science Education 1997, p. 28). To facilitate the conceptual change required to promote evolutionary literacy, a number of authors have recommended a "constructivist" approach to teaching evolution (Lawson 1994; Tobin et al. 1994) whereby students are given an opportunity to pose questions, test their predictions through the acquisition of real data, and revise their mental models through analyzing and discussing their results with their peers (Good 1992; Scharmann 1993; Linhart 1997; Alters and Nelson 2002). In addition, many authors have focused on identifying common misunderstandings of evolutionary biology and devising strategies to correct them (Anderson et al. 2002; Tanner and Allen 2005; Meir et al. 2007; Nehm and Reilly 2007; Robbins and Roy 2007).

Recently, a number of educators have developed and published exercises designed to convey evolutionary principles in an active, engaged fashion. These exercises are fantastically well-designed, memorable experiences for students and cover a range of issues such as: using toilet paper to depict evolutionary time (O'Brien 2000), investigating the processes of natural selection (Lauer 2000) and genetic drift (Staub 2002) with candies, the evolution of complex adaptations (Dickenson 1998), development of virtual laboratories (Abraham et al. 2009), and the molecular evidence for evolution (Moss 1999). This article adds to this forum by describing a classroom exercise that effectively teaches the basic principles of quantitative genetics to students, allowing them to directly test the theory of evolution by natural selection using a standard deck of playing cards. Importantly, this exercise becomes a personal experience for students; in addition to generating predictions and collecting data to assess the validity of evolutionary theory, students actively participate as the subjects upon which the data are collected. As will be discussed later, it is this personal experience that more than anything else drives home the concepts of evolution, selection, and the interface between the two. Over the past decade, we have used variations of this exercise across the biology curriculum at three institutions, from a non-majors introductory course to a senior-level seminar in population biology. In our experience, introductory students have little difficulty with these basic concepts and exercises that follow and come to appreciate the richness of evolutionary theory; likewise, more advanced undergraduates appreciate the illustrative modifications that we have designed to teach difficult concepts.

Basic Quantitative Genetics

We recognize that basic quantitative genetics is generally not taught at the introductory level, and although there are several accessible texts that discuss these techniques with varying degrees of difficulty (Ridley 1996, pp. 222–254; Falconer and Mackay 1996; Futuyma 1998, pp. 397–438; Freeman and Herron 2001, pp. 48–56, 224–234), we will cover them briefly here. We teach the theory of evolution by natural selection in the form of a syllogism (a logical argument consisting of a major premise, minor premise, and conclusion; for further discussion, see Haldane 1954; Lande and Arnold 1983):

- If trait variation within a population is due, in part, to differences among individuals in their genetic constitution [*heritability*], and
- If trait variation within a population is associated with the variation in survival or reproduction in the current environment [*selection*], then

- Over generational time, there will be an increase in the frequency of individuals having those trait values that confer a relative increase in reproductive success [*evolution*].

The first premise of the above syllogism is *heritability*, which is symbolized as h^2. Heritability is a measure that ranges between 0 and 1 and describes the proportion of variation present in a population for a particular trait that is due to the additive effects of alleles; it is the proportion of trait variation that can respond to natural selection. For example, if the heritability of beak size in a population of birds is 0.80, we can say that 80 percent of the observed variation for beak size in this population is because of differences among individuals in their allelic identity at loci that contribute to beak size. The other 20 percent of variation in beak size must be because of other factors, such as variation in maternal provisioning during development or the quality of food resources individuals consume. Although there are many ways to estimate heritability, the simplest is to calculate the slope of the best-fit line through a scatter plot of offspring vs. mid-parent (average of two parents) trait values. The second premise of the syllogism is *natural selection*—the association between variation in trait values and variation in reproductive success. When considering a single trait in a population and some selective "event" such as a drought, natural selection is most easily quantified using the *selection differential*, which is symbolized as S. The selection differential is calculated as the mean trait value in the population after selection subtracted from the mean trait value in the population before selection. For example, if the mean beak size in an adult population of birds was 10 centimeters before selection and 13 centimeters after selection (because individuals with smaller beaks could not successfully crack seeds to eat in the current environment and therefore died before mating), the selection differential would be +3 centimeters. In other words, there was selection for increased beak size in this population. If both premises of this syllogism are met in a population, there will be an *evolutionary response*—the average value of the trait in the population will change across generational time. The evolutionary response is symbolized as R, and is calculated as the average trait value in the current generation (offspring) subtracted from the average trait value in the previous generation (parents). In addition, if the heritability and selection differential for a given trait are known, the evolutionary response can be predicted using the simple equation $R = h^2 s$. Using our beak size example above, we would predict that the average beak size in the next generation of birds should be 2.4 centimeters larger than the parental generation. Thinking about evolution by natural selection in this manner illustrates how characteristics of populations can change through time.

Trait evolution will occur any time there is heritability and natural selection, provided that genetic drift is relatively weak in comparison to the strength of selection. In addition, it highlights how evolution is very different from natural selection—two concepts introductory students frequently view as synonymous.
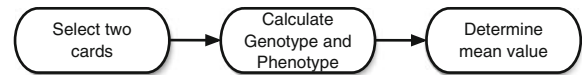
The Exercise

Conceptualizing the process of evolution by natural selection in the manner described above lends itself to hypothesis testing, data collection, and analysis in an interactive and engaging fashion. We have specifically designed this exercise to convey the following concepts:
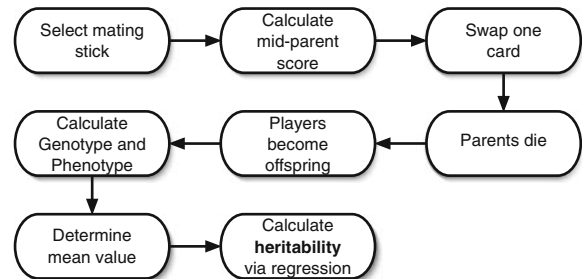
- For evolution to occur, some of the trait variation in a population must be due to differences among individuals in their genetic constitution [heritability].
- Natural selection is not the "survival of the fittest (best)."
- Natural selection is different from evolution.
- The process of evolution by natural selection can be quantified, and the validity of the theory can be rigorously tested experimentally.
- Natural selection operates on individuals; evolution is a population-level phenomenon.

This exercise involves four basic steps (Fig. 1). In the first step, students haphazardly select two cards, which represent their allelic identity at a particular locus and therefore determine their genotype and phenotype (value of the trait expressed); they then "mate" with one another to create the next generation, and they use these data to determine the proportion of trait variation in the population that can be explained by genetic variation (heritability). In the third step, we artificially select against a portion of the class and the students calculate the selection differential. At this point, students make a quantitative prediction about what the average trait value should be in the next generation according to the theory of evolution by natural selection. The survivors then "mate" in step four, and we observe whether or not the class average in the next generation is similar to what was predicted. Through minor changes in the protocol, we have successfully used this exercise to illustrate how random environmental effects on the phenotype, dominance, and epistasis affect the evolutionary process. The specifics concerning the implementation of this exercise can be readily amended to the availability of materials and instructor preference. Below, we describe in detail how we use this exercise in our courses, and for illustrative purposes we draw from a year in which we had 32 students. Larger or smaller class sizes can be easily accommodated by modifying the number of decks (or cards) used and the number of "sticks" made.
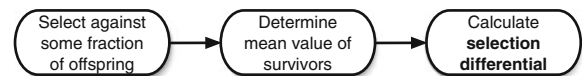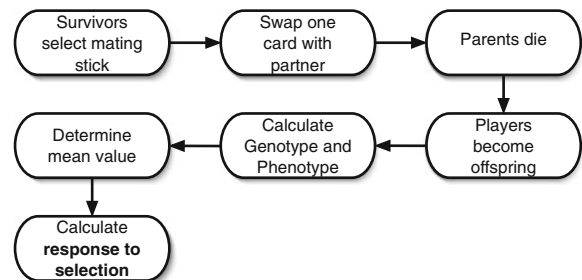

Fig. 1 A flowchart describing the four steps of our exercise

Prior to class, we prepared the following materials: two standard decks of playing cards with the same backing and with the jokers removed, a set of 32 "pre-selection" sticks numbered in pairs from one to 16 (i.e., two #1 sticks, two #2 sticks, etc.), and a set of 24 "post-selection" sticks numbered in pairs from one to 12. Normally, we use plastic plant identification sticks that are commonly available in greenhouses, but other materials could be used as well (poker chips, notecards, etc.). Having presented the theory of evolution by natural selection as a syllogism in previous meetings, we introduced this exercise to our students in the form of a challenge: the theoretical ideas outlined in class would be subject to experimental scrutiny, and we would determine whether the data support or reject the process of evolution by natural selection. We emphasized that we were directly testing the theory and that we were not presenting it as dogma. We have found that the students respond very positively to testing the ideas with the possibility of rejection, and that many strenuously object to bombardment with "facts of evolution." As such, most of our exercises

have been developed as fair tests, involving active participation of students rather than demonstrations.

To begin, our class became a closed population of 32 individuals (no immigration to or emigration from other classrooms), which we assumed to be at carrying capacity. Each student haphazardly selected two playing cards from the deck to determine their genetic constitution and a "pre-selection" stick that identified their mating partner. These two cards represented their allelic identity at the locus we were following, and were purely additive with respect to their effect on the phenotype. Students calculated their genotypic scores by summing allelic values according to the following rules: aces=1, face cards=12, all other cards= their face value. For example, 9♥ and 4♣ would equal a genotypic score of 13, and K♥ and A♣ would also equal a genotypic score of 13. We choose to let the face cards all have the same allelic value so the students could test the theory in a population where alleles were not equally represented. We explained to the students that, in this first exercise, we were considering a situation where the expression of a trait was only influenced by the identity of allelic values at a single locus and not influenced by environmental effects. Therefore, the phenotypic scores were identical to the genotypic scores. At this point, we sometimes ask students to brainstorm traits that are not influenced by environmental variation and those that are. After recording everyone's genotype and phenotype scores, we calculated the average genotypic and phenotypic values in our population and the variance associated with each. An Excel® spreadsheet to facilitate this and all other calculations is available from the authors. At this point, we asked the students:

- What proportion of the phenotypic variation in our population is due to genetic variation?
- What do you predict the heritability of our trait should be?

Given that all of the phenotypic variation in our population was the result of differences among individuals in their allelic identity, we predicted that the heritability of our trait should be 1.0. To explicitly test this, students found their "pre-selection" stick partner (i.e., the other student with the same number) and calculated their average (mid-parent) phenotypic score. Then, they placed their cards face down and swapped one with their partner. Because our population was at carrying capacity to start, we assumed that parents died following reproduction, so that the students now became the offspring of the second generation. Again, we recorded everyone's genotypic and phenotypic scores and calculated trait averages and variances. Students then used these data to generate a scatter plot of offspring vs. mid-parent phenotype values and calculated the slope of the best-fit line through the data. This slope was the estimated heritability of our trait (Fig. 2a).
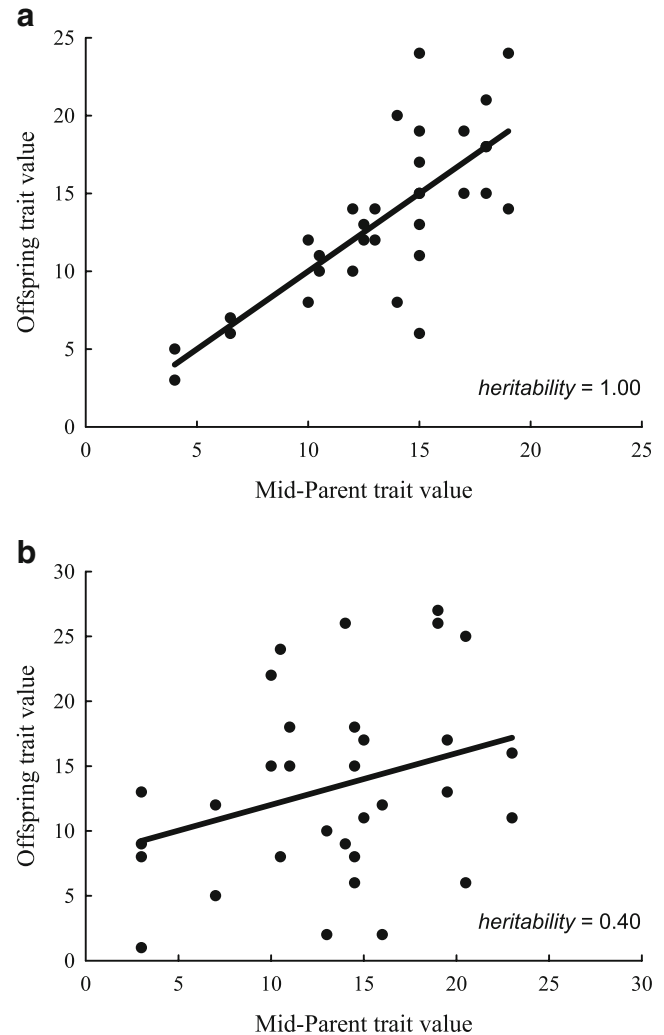
Fig. 2 Data figures used to calculate heritability in a class of 32 students. Both figures plot average trait value between the two parents (mid-parent trait value) and the trait values for each resulting offspring. The slope of the best-fit line through these points estimates heritability. The regular exercise resulted in a heritability of 1.0 (a). The inclusion of random environmental effects on the phenotype dramatically reduced the heritability (b)

Following this exercise, we selected against roughly one quarter of the class with either the highest or lowest phenotypic scores, taking care to leave an even number of students. After this selection event, students calculated the average phenotypic score in our population and the phenotypic variance. Here we asked:

- From these data, how could we calculate the selection differential?
- How should the average phenotype in the next generation compare with the mean phenotype in our population right now?
- Can you make a specific prediction about the magnitude of this evolutionary change?

The students then calculated the selection differential (S) as the average phenotypic score after selection subtracted from the average phenotypic score before selection, and predicted a specific evolutionary change equal to the product of our calculated heritability and selection differential. Following a brief discussion of these predictions, the "survivors" selected a "post-selection" mating stick, found their partner, and swapped alleles as before. Now they were the third generation of our experiment. We calculated the average phenotypic score and variance associated with it in this generation and determined the evolutionary response (R) to selection as the average trait value in the current generation subtracted from the average trait value in the previous generation prior to selection. These empirical results were compared to our predictions based on evolutionary theory, and we came to a class consensus as to the validity of the theory of evolution by natural selection (Table 1, "Standard exercise").

Random Environmental Effects

We have developed a suite of additional exercises that use this basic structure to illustrate additional concepts in evolutionary biology. Here we briefly discuss one of our favorites—the inclusion of random environmental effects. In the previous exercise, the evolutionary response to selection was equal to the selection differential because all of the trait variation in our population was due to differences among individuals in their allelic identity (h^2=1.0). Heritability can be thought of as a natural scaling factor; it scales the effect of selection in one generation on the distribution of phenotypes in the next generation. Anything that reduces heritability (e.g., random environmental effects, dominance, epistasis) will also reduce the evolutionary response to selection. For example, if the distribution of food sources that affect trait expression is patchy in a given environment and individuals encounter them haphazardly, some of the phenotypic variation for that trait will be due to variation among individuals in their food intake. As a result, selection will be less "effective" at

generating genetic change in the population over generational time.

To illustrate this concept, we prepared "environment before selection" and "environment after selection" sticks so that there would be one for every student in the population before and after selection, respectively (two sets of sticks are required because of the different numbers of students participating before and after selection). We labeled each set of sticks so that the average score in each set was 0, the variance about 20, and the range of individual stick values was between −9 and +9. Each time a student calculated their genotypic and phenotypic score, they haphazardly selected an environmental effect stick and added its score to their genotypic score to determine their phenotypic score. At the beginning of the exercise and after the first mating, students selected from the "environment before selection" sticks, and after the second mating they selected from the "environment after selection" sticks. For example, a student with a 10♥ and 9♣ for alleles that selected a +6 environmental stick would have a genotypic score of 19 and a phenotypic score of 25. If that same student with a 10♥ and 9♣ for alleles had selected a −9 environmental stick, they would have a genotypic score of 19 and a phenotypic score of 10. All other elements of the game remained the same (Fig. 1).

Performing the exercise with this additional tweak accomplishes several instructional goals. First, it becomes clear to the students that if random environmental effects contribute to trait values, the heritability of the phenotypic trait and the response to natural selection is reduced (Table 1, "With random environmental effects"; Fig. 2b). Second, this exercise shows in a very personal fashion how natural selection operates on phenotypes and is not the "survival of the fittest." By the time we do this second exercise, students assume that we are selecting the highest or lowest scores to make it to the final generation, and they want to make it to the end of the game. Often a student will pull two face cards thinking they've got it made, and then get hammered by a −9 environmental stick score (usually complaining that life is unfair…). Alternatively, a student will pull a low score from the deck (e.g., a 3♥ and 6♣), realize from the last exercise that their score is

Table 1 Summary statistics from class data for the standard exercise and the inclusion of random environmental effects. Data are from a class of 32 students

Gen 0 trait avg.	Gen 1 trait avg.	h^2	Gen 1 post-seln avg.	S	Gen 2 trait avg.	R
Standard exercise						
13.41	13.41	1.00[a]	11.08	−2.33	11.08	−2.33
With random environmental effects						
13.34	13.34	0.40[a]	16.21	2.86	14.67	1.33

[a] See Fig. 2a and b, respectively, for actual class data. Note that the inclusion of random environmental effects need not change the average trait value across generations; however, the heritability is drastically reduced leading to a dampened response to selection

unlikely to make it through to the end, and then pull a high environmental stick score and let out a small cheer. This personal experience reinforces that natural selection operates on *phenotypes* and that evolution is not "forward-looking." The inclusion of random environmental effects allows some low-scoring alleles to make it into the next generation and prevents some high-scoring alleles from being transmitted.

Other Variations on the Game

This exercise can be easily modified to teach advanced evolutionary topics in upper-level courses. To illustrate how dominance affects the evolutionary process, simply create a rule for how the alleles interact to generate the phenotype. For example, black cards might be dominant to red cards. If students draw a red and black card, their genotype is twice the black card. To include epistasis, incorporate a second deck into the exercise and let the value of alleles at one locus (red-backed deck) affect the expression of alleles at the second locus (blue-backed deck). Experimental controls can also be incorporated without much work. For example, in the case of the epistasis exercise, students could keep track of two sets of scores for themselves—one the result of adding the four alleles across the two loci (control), the other the result of playing by the "epistasis rules." In the same exercise, heritabilities, selection differentials, and responses to selection can be calculated for each set of scores, and the results can be compared to one another. Correlated responses to selection and pleiotropy can be investigated by the inclusion of a third deck. To do this, have students keep track of two traits in the standard additive fashion with decks 1 and 2 contributing to the first trait, and decks 2 and 3 contributing to the second trait, and select on only one trait. Selection for increased values of the second trait will indirectly result in an increase in the first trait. Finally, there are many ways in which to modify the selection component of this exercise to simulate directional, or other modes of, selection. For example, students could halve their phenotypic score, round to the nearest integer, and flip a coin that number of times (e.g., scores of 13 and 14=seven flips, scores of 11 and 12=six flips). If they get "heads" at any point in their coin flips, they are selected for. In this case, there would be directional selection for larger trait values. Importantly, this modification illustrates how selection is a probabilistic phenomenon (larger trait values are more likely, but not guaranteed, to survive).

Topics for Discussion

This exercise works well when paired with a discussion of real-world examples where researchers have empirically estimated heritability and natural selection in the field and have obtained data to test evolutionary predictions. Although there are several possible examples that could be used, we briefly discuss two here. Peter and Rosemary Grant's long-term data set on several species of Galápagos finches are classic accompaniments to introductory and advanced biology courses. Although there are a number of publications on their work, we feel that Peter Grant's overview article in *Scientific American* (1991) on the evolution of beak size in *Geospiza fortis* is most suitable for introducing these concepts to upper-level high school and college-level introductory biology students. In addition to showing students the parallels between this exercise and experiments performed in nature, a discussion focused on experimental methods (e.g., what kinds of things would we have to do to measure the heritability of trait x in species y?) can help solidify these concepts in students' minds. As a follow-up assignment, we typically have students research a species whose members exhibit variation for a particular trait of interest, and have the students write a short "methods section" detailing how they would estimate heritability and selection following a "selective event" (e.g., a drought).

For more advanced courses, we recommend Peter and Rosemary Grant's paper in *Evolution* (1995) coupled with a discussion of how selection might be measured when there is no clear "selective event" (i.e., selection gradients instead of selection differentials). Alternatively, we recommend Candace Galen's work on flower size evolution in alpine skypilots (Galen 1989, 1996) to show how empirically derived estimates of heritability and selection generated through pollinator preferences can be combined into a testable prediction of evolutionary change.

Summary

These interactive exercises provide students with an opportunity to test predictions generated from evolutionary theory and to decide for themselves whether or not the data match the expectations. In its most basic form, this card game conveys the basic principles of evolution by natural selection, and through minor modifications in the structure of the game, advanced topics such as epistasis can be incorporated. Furthermore, this exercise provides accessible bridges to evolutionary studies covered in the primary literature by providing students with first-hand knowledge of how heritabilities, selection differentials, and responses to selection are calculated, and how researchers use these parameters to ascertain whether or not evolution may occur.

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