Explore Frequency Dependent Selection

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#### Abstract

The term frequency dependence describes scenarios in which the likelihood of an event occurring is strongly tied to how common a particular trait is. Understanding frequency dependence is key to understanding numerous biological processes relevant to evolution by natural selection, such as predation, mimicry, disease, and effective vaccinations. We use dodgeball to demonstrate frequency dependent selection in a hypothetical predator-prey community, and provide possible extensions into other topics. This activity can be used with biology students in high school through upper-level undergraduate courses.


Key Words: Dodgeball; evolution; frequency dependence; predation; active learning; natural selection.

## Introduction

Many scientific bodies have suggested that one of the key concepts students need to understand in order to be scientifically literate is evolution (e.g., AAAS, 2011). Further, the Next Generation Science Standards (NGSS Lead States, 2013) feature evolution as a unifying concept and natural selection as a disciplinary core idea. However, evolution by natural selection can be a particularly difficult topic for students to understand. This is not only due to its highly integrative nature and widespread societal misconceptions (Andrews et al., 2012; Foster, 2012), but also because understanding selection often involves mathematical constructs. Topics taught using mathematical formulas are often seen as less accessible by students, despite the widespread use of mathematics across the sciences (Betz, 1978; Metz, 2008). Mathematical anxiety also may make higher-order functions such as generalization and adapting to novel uses more difficult (Cates \& Rhymer, 2003), which contributes to the difficulty in understanding evolution by natural selection.

> One aspect of selection that is critical to evolution and that has a mathematical basis is frequency dependent selection.

One aspect of selection that is critical to evolution and that has a mathematical basis is frequency dependent selection. The term frequency dependence describes scenarios in which the probability of an event occurring is strongly tied to how common a particular trait is. For example, the fitness of a particular phenotype is often dependent on its frequency within a population. In positive fre-quency-dependent selection, a phenotype's fitness increases as it becomes more common. For example, toxic species may advertise their danger to predators using conspicuous coloration (a phenomenon known as aposematism; see Figure 1 and header image above). Predators may need to sample individuals to learn to recognize an aposematic appearance; therefore, when aposematic species are more abundant, there is a decreased likelihood that any one individual will be attacked by predators. In contrast, in negative frequency dependent selection, a phenotype's fitness decreases as it becomes more common. For example, when a particular type of edible prey is common, predators acquire a search image for that prey through repeated exposure. This search image increases the predator's foraging efficiency for that prey's appearance. In both scenarios, frequency dependent selection can produce change over time (i.e., evolution) in the appearance of prey.

When a topic is presented mathematically it may cause anxiety in students who perceive themselves to have poor math skills (Betz, 1978). These students may disengage before attempting to engage with the material. However, students use the rationale behind frequency dependence theory in their everyday lives, even if they don't realize it. Presenting the intuitive theoretical framework behind the theory and giving common examples can help students understand the phenomenon. Despite this possibility, there is a paucity of published lessons using active-learning techniques to teach frequency dependence. One published problem-based activity includes frequency dependent selection but is largely focused on other concepts and requires more background knowledge than

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Figure 1. Ameerega cainarachi, a poison frog endemic to Peru that demonstrates aposematism - the combination of bright warning coloration and a secondary defense (here, toxicity). Photo by A.M.M.S.
many high school students and some early undergraduates possess (Preszler, 2009).

Here, we describe an active-learning approach to illustrate frequency dependence in high school classrooms or smaller undergraduate courses in an intuitive manner. Class discussion revolves around a popular frequency dependent activity, the lottery. Discussion is followed by a game of dodgeball to simulate frequency dependence in the context of predator-prey interactions. These activities can be used to teach frequency dependence or, with minor modifications, extended into other examples of frequency dependence such as mimicry or herd immunity from vaccines. Table 1 lists the materials needed.

## ○ Class Discussion

Assign each student a random number, select a random number, and inform the class of the winner (perhaps for a small reward, such as extra credit). Then discuss the exercise and try to naturally direct the conversation toward the lottery. By the end, make sure students are aware that the odds of winning the lottery are dependent on the total number of people playing the lottery (therefore, students in a small class have a higher chance of winning than those in a large class). Exploration of this idea is a natural transition to discussing frequency dependence.

## O Dodgeball

This exercise will follow the rules of dodgeball, with a few modifications. An outline of rules for dodgeball can be found on the International Dodgeball Association's website (http://playdodgeball.org/ easy-dodgeball-rules/), but we will present them here in brief. A space is set up with borders. Each team occupies one half of the field of play, and players who step out of their half are out. To start, the balls are placed on the center line that divides the two halves. The game begins when the two teams, one starting from each end of the court, "rush" forward to pick up the balls. The players then

Table 1. Materials and numbers needed for dodgeball.

| Materials Needed | Number Needed |
| :--- | :--- |
| Randomly assigned numbers | One per student |
| Lottery method of choosing <br> random numbers | One |
| Area with open floor space | One |
| Dodgeballs/foam balls, <br> depending on size of space to <br> be used | $5+$ |
| Group indicators (e.g., vests of <br> two different colors) | One per student, split <br> into two groups |

throw the balls at the opposing players. Players are out if they are hit by a thrown ball or if a ball they threw is caught by another player. Balls are considered "dead" as soon as they hit the floor. Thrown balls may be blocked with a held ball, but the thrown ball may not touch any part of the body, and the held ball may not be dropped.

The purpose of this activity is to simulate frequency dependence in the context of predator-prey interactions. Therefore, one team will be predators and the other team prey. Like normal prey communities, this activity's prey community is not a homogeneous group. Predators are naive with respect to the prey types present, as they would be in nature. This activity requires modification of the standard dodgeball rules as follows. Assign each student a role as either a predator (a quarter of the class) or prey (three quarters of the class). Ninety percent of the prey individuals should receive one group indicator (e.g., colored vest) while the other $10 \%$ should receive a different group indicator (e.g., differently colored vest). These group indicators represent two types of prey, edible ( $90 \%$ of prey) and inedible ( $10 \%$ of prey); instructors should not inform students of the meaning of these prey color designations (see Figure 2). Only the predators can throw the balls to get other students out. Prey may hold the balls for up to five seconds to block, but must roll them across to the predator side after five seconds. If a predator's ball strikes a student designated as edible prey, the prey individual is out and the predator remains in. However, if the predator's ball hits a student designated as inedible prey, then both the predator and prey individuals are out. Instructors should watch the game carefully, because the students are (intentionally) ignorant of the rules (like naive predators) and, therefore, instructors must inform students on a case-by-case basis when they must leave the game (without explaining why). Prey that successfully catch a thrown ball have escaped that predation attempt and are not out. However, unlike the normal rule of dodgeball in this situation, the thrower is not out because the predator would survive the predation attempt. Allow students to play for a set period (e.g., three minutes) or a set number of throws by predators.

After the first round of play, ask the students why they think certain predators had to leave the game. Try to elicit the idea that all the predators who struck prey with a particular color had to leave. Then attempt to engender ideas as to what characteristics of prey this specific group indicator might represent. After the idea of some prey


Figure 2. A mock-up of the dodgeball arena for a class of 20 students. Predators (daggers) are on the left half, and edible prey (" 1 ") are with the inedible prey (" 2 ") on the right. Circles represent the starting location of the dodgeballs at the center.
being inedible or dangerous has been discussed, describe the idea of aposematism to students, the phenomenon in which certain species possess a conspicuous warning appearance that is coupled with some sort of secondary defense. Inform students that predators in nature, like predators in the game, may be harmed by aposematic species and, hence, will learn to avoid them. Thus, these predators are "out" - they will no longer prey on the inedible prey species.

To extend the simulation, repeat the above game of dodgeball. This time, however, subdivide the prey into edible and inedible groups based on the ratio of edible to inedible prey left at the end of the previous round. For example, if 15 edible prey and 15 inedible prey were left at the end of the first round, then half of the prey in this second round would start off as edible and the other half of the prey would start off as inedible. Allow students to play for the same period of time or number of throws by predators as in the first game. If time allows, additional rounds can be included. The ratio of edible to inedible prey at the start of each round would again be based on the ending ratio of the previous round. This process mimics the survival of the prey population at the end of a generation, thereby simulating the effect that natural selection from frequency dependence, enforced by predators, would have on the population into the future.

After the conclusion of the dodgeball game, discuss what occurred during the game. Try to get students to explain that each dodgeball round can be an example of a generation of predators and prey, similar to what is seen in nature. Over the course of the discussion, students or the instructor should make the point that this game was an example of positive frequency dependence in which inedible individuals in the second and third rounds had a decreased likelihood that they would be attacked and killed.

## Reinforcement

The lottery and dodgeball activities illustrated here are only examples of what could be done using this framework. For example, this exercise could be extended to include negative frequency dependence in the context of Batesian mimicry (in which an edible species
mimics an inedible, aposematic species). In this variation on our game, a proportion of the "inedible" prey population would actually be "edible" and could be eliminated by predators without cost.

To assess student learning, instructors might assign a short essay on a novel scenario of frequency dependence. Requiring students to address a novel use of frequency dependence will test their ability to synthesize (a higher-order cognitive skill) the lessons learned through these exercises, rather than merely evaluating their comprehension (a lower-level cognitive skill) of frequency dependence in the original context. For example:


#### Abstract

Whooping cough is a highly contagious disease spread by bacteria. Many adults who get the disease do not exhibit symptoms and are thus unaware that they have contracted it. However, the disease can be deadly in infants. Therefore, adults may contract the disease and spread it to young children in ignorance, putting the lives of those children at risk. There are currently two vaccines available, both of which provide immunity and prevent an individual from being a host for the disease. Discuss the benefit of the use of these vaccines in the context of frequency dependence, even in individuals who are not likely to be in frequent close proximity to babies. Defend your arguments. Your response should focus on the relationship between disease spread and vaccines in regard to frequency dependent selection, not any controversy about vaccines.


## ○ Alternatives

If this activity is used in secondary education, students will first need to be introduced to the idea of evolution by natural selection, as well as the basics of predator-prey interactions. However, it is our experience that aposematic animals are so charismatic and captivating that even early primary-school students have a basic comprehension of the phenomenon of aposematism and why it works as an antipredator strategy. For students who lack this comprehension, there are many excellent resources that present interactive ways to teach about evolution, including BioInteractive (Howard Hughes Medical Institute, 2016) and the Understanding Evolution materials (Understanding Evolution, 2016). The level of prior knowledge necessary to complete this frequency dependence activity is also necessary to fulfill the Next Generation Science Standards (NGSS Lead States, 2013).

Dodgeball is a game played by all ages, including adults. If, however, dodgeball is not feasible for a given set of students, these same lessons could be covered by extending the lottery discussion with a lottery simulation. Another possibility is to simulate edible prey and inedible prey using colored pieces against a multicolored background and have students act as predators that select the first "prey" item they see. Class discussion and other means of assessment could easily tie these activities to student understanding of frequency dependent selection.

## ○ Summary

These activities are an effort to simplify the presentation of frequency dependence in the classroom. They make frequency dependence easily comprehensible for students while making the material fun and interactive. Frequency dependence is an important process across biological disciplines. Understanding the basic mechanisms
by which it functions is important not just for evolutionary biologists and ecologists, but also for medical doctors and the populace as a whole.

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