INQUIRY & INVESTIGATION

Population Evolution: The Pollination Game

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Abstract

To teach the most central concepts in evolutionary biology, we present an activity in pollination biology. Students play the role of either pollinator or flower and work through a set of scenarios to maximize plant fitness. This "Pollination Game" facilitates critical and inquiry-based thinking, and we accompany each round of the exercise with a set of discussion questions and answers. We have piloted and fine tuned this exercise with high school students, and improved the exercise with the input of high school teachers at a teaching conference. The activity could easily be adapted for freshman undergraduate students.

Key Words: *Natural selection; fitness; gene flow; indirect selection; adaptation; inbreeding; inbreeding depression; resource allocation.*

○ Introduction

Evolution is the single unifying theory in biology, and a solid understanding of how evolution occurs in nature is essential. Comprehension of evolutionary theory is often difficult for students, especially because many of the underlying concepts, such as selection and gene flow, are abstract. Participatory games are very useful for teaching abstract concepts because a personal experience of the simulated phenomena makes them much more tangible, relatable, and comprehensible (as emphasized by Hassard & Dias, 2009). Student experience of the evolutionary process at the population level through an interactive game can serve as a highly effective tool for teaching evolutionary concepts.

Plant pollination mechanisms are particularly amenable for teaching evolutionary concepts through games. Plant–pollinator interactions are a classic case of an ecological mutualism, with plants benefiting by obtaining reproductive services and pollinators benefiting by rewards of pollen or nectar. Plant pollination mechanisms have evolved through natural selection, the phenomenon whereby some individuals in a population have traits, or fitness components, that enable them to survive and reproduce more than other individuals in the population. These successful individuals have higher evolutionary fitness than other individuals and are more likely to pass on their genes. Therefore, genes and traits that help individual survival and reproduction will increase in prevalence in the population. For example, in the context of plant pollination, a plant with flowers full of nectar will be more likely to reproduce and have higher fitness than plants with a smaller nectar supply because it is more likely to be visited by a pollinator (for definitions of key terms, see Table 1). Like other ecological interactions, including competition and predation, mutualisms between plants and pollinators can result in evolution. In fact, the concordant evolutionary relationships between butterflies and their pollinators formed one of the earliest and most well-known examples of coevolution, or reciprocal evolution between two species (Ehrlich & Raven, 1964).

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Evolution can occur through plant–pollinator interactions in a variety of ways that can be demonstrated through the activities described below. In particular, this exercise promotes scientific learning that allows students to critically think as evolutionary biologists. Leonard (2010) emphasized this style of learning at the college level, and we applied that concept in this pollination exercise for high school students to approach evolution from the plant perspective. These activities have been field tested in classroom settings and are particularly appropriate for students in grades 8–12. Further development of the exercises for the college level could add in the perspective of evolution from the pollinator perspective to increase the level of complexity.

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Table 1. Explanation of key concepts presented throughout the Pollination Game. All definitions are acquired and adapted from Futuyma (2013), except *resource allocation* (from Krebs & Davies, 1993) and *sessile* (for which we give a commonly used definition).

Term	Definition
Evolution	A change over time in the proportions of individual organisms differing genetically in one or more traits.
Population	A group of conspecific organisms that occupy a geographic region and exhibit reproductive continuity from generation to generation.
Fitness	The success of an entity in reproducing; the average contribution of an allele or genotype to the next generation.
Natural selection	The differential survival and/or reproduction of classes of entities that differ in one or more characteristics. To constitute natural selection, the difference in survival and/or reproduction cannot be due to chance and it must have the potential consequence of altering the proportions of the different entities.
Gene flow	The incorporation of genes into the gene pool of one population from one or more other populations.
Migration	Used as a synonym for gene flow among populations.
Adaptation	A process of genetic change in a population whereby, as a result of natural selection, the average state of a character becomes improved with reference to a specific function, or whereby a population is thought to have become better suited to some feature of its environment.
Inbreeding	Mating between relatives that occurs more frequently than if mates were chosen at random from a population.
Inbreeding depression	Reduction, in inbred individuals, of the mean value of a character (usually one correlated with fitness).
Gene	The functional unit of heredity.
Indirect selection	To constitute indirect selection, the difference in the proportion of surviving and/or reproducing entities that differ in one or more characteristics must be in the absence of direct fitness effects on the individual (see *natural selection* for comparison).
Genetic variation	Within a population, genetic variation constitutes the extent of variation in alleles of genes of a gene pool. Alleles are forms of the same gene.
Resource allocation	The proportion of an organism's energy budget allocated to reproductive resources at a given time. Also known as "reproductive allocation" in the context of the Pollination Game.
Sessile	Fixed in place, immobile.

○ Pollination Biology as an Example

The evolution of plant reproductive systems has been of interest to scientists for quite some time (Darwin, 1876, 1877). This is not surprising given the enormous diversity exhibited in flowering plants. Plants are modular organisms, and thus male and female gametes are packaged in a wide array of spatial and temporal combinations at the flower, inflorescence, and plant levels. In fact, flowers, the reproductive unit of angiosperms, exhibit a stunning display of configurations and evolutionary strategies (Barrett, 2010).

One major reason for the evolution of floral diversity is that plants are sessile and therefore must rely on vectors – biotic or abiotic agents that transfer pollen between flowers – for cross-fertilization. Pollination vectors are a strong selective force leading to the evolution of pollination syndromes, suites of floral characteristics that enable abiotic pollination or appeal to specific pollinating animals (e.g., Schemske & Bradshaw, 1999).

Pollinators are essential for reproduction in the majority of flowering plants (Ollerton et al., 2011). By facilitating sexual reproduction, pollinators promote genetic variation in plants. In turn, genetic variation aids adaptation in new and variable environments and is strongly correlated with plant reproductive success (Charlesworth, 1993; Leimu et al., 2006). This classroom exercise utilizes the example of plant–pollinator systems to demonstrate the relation of plant fitness to natural selection. Participating students will meet performance expectations for communicating evolutionary concepts detailed in the *Next Generation Science Standards* (HS-LS4-2, HS-LS4-4). Students will also understand how fitness is related to gene flow, indirect selection, and inbreeding. Pollination biology provides a charismatic and approachable topic for exploring evolution.

○ Game Goals & Objectives

This is a game with three rounds for 15–20 students, designed to illustrate concepts in evolutionary biology. Students will learn central evolutionary themes, including natural selection, gene flow, indirect selection, and inbreeding depression. Pollinators facilitate the plant's male fitness component by donating pollen grains, while flowers represent the plant's female fitness component by gaining pollen grains to fertilize ovules. Each of the three rounds demonstrates a different concept. There is ample possibility for this game to be modified to illustrate additional concepts in ecology and evolution, particularly incorporating the fitness effects on pollinators (see Table 1 for key concepts and definitions).

The students will play a series of rounds in a "Pollination Game" with the goal of optimizing plant fitness in each round. Students in the flower group aim to receive as many pollen grains as possible, and students in the pollinator group aim to give away all their pollen grains.

○ Game Setup

Inform the students of the game goals, and then split them into two approximately equal groups and assign them roles as either "flowers" or "pollinators." Students in the flower group carry a sign with a picture of a flower (Figure 1A). Pollinators are each given five yellow circles that represent pollen grains, and an assigned pollinator type (e.g., hummingbird, bee, bat; Figure 1B). Discussion questions and answers for each round of the game are provided at the end of each round.

○ Materials

- Flower signs for approximately half the students (Figure 1A; flowers can be printed in the number or color equivalent to the number of types of candy used [see below] or colored in class, before Round 3)
- Pollen grains and pollinator type (e.g, hummingbird, bee, bat; Figure 1B)
- Candy of at least two or three different color varieties
- Score cards for each student (Figure 2).

○ The Pollination Game

Round 1: How Do Plants Achieve Fitness in Nature?

- **Setup.** Flowers are asked to pick a spot in the room and remain stationary.
- **Action.** Pollinators are given a short time (30 seconds to 1 minute) to visit flowers. On each visit a pollinator can give only *one* pollen grain to an individual flower.
- **Tally the score.** Each flower and pollinator marks on their score sheet how many pollen grains they received or gave. (*Note:* It is possible for flowers to acquire more than five pollen grains.) On their score cards, students record the class average for pollen grains received or donated.

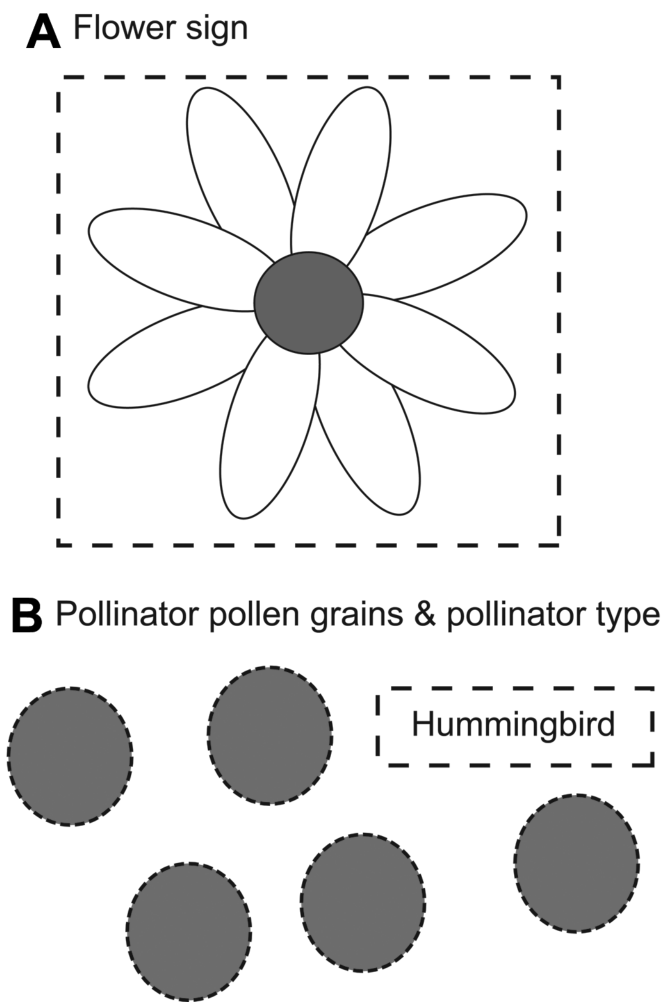

Figure 1. (A) Students in the "flower group" can wear or hold the flower sign. Students receive pollen grains. (B) Students in the "pollinator group" each get five cut-out pollen grains and a pollinator type. Students hand out one pollen grain during each round of the game.

Discussion Questions & Answers: Round 1

1. What component of the *plants' fitness* do the pollen grains represent, and what component do the flowers represent?
   Answer: The pollen grains represent the *male* fitness component of flowering plants in nature because pollinators transport the male reproductive unit, pollen; whereas the flower represents the *female* fitness component that receives the pollen. In nature, most flowering plants will optimize female and male fitness by both receiving and donating as many pollen grains as possible.
2. Plants that had flowers with the most pollen grains had the highest female fitness. Why?
   Answer: The more pollen grains a flower received, the more ovules that could be fertilized to make seeds. The plant with the most seeds will pass on its genes more and have high *fitness*.
3. Pollinators that gave away all their pollen grains had higher plant male fitness than those that did not give away all their pollen grains. Why?
   Answer: In this exercise, pollinators represent the male side of plant fitness, and plants that donate all their pollen grains to

A Flower

Round One	# of pollen grains received	Class average received

Round Two	# of pollen grains for TEAM	Class average for TEAMS

Round Three Color of reward: ____________________

	# of pollen grains received	Class avg received (for reward color)

Strategy notes (Round 2): ____________________

B Pollinator

Round One	# of pollen grains received	Class average received

Round Two	# of pollen grains for TEAM	Class average for TEAMS

Round Three Color of reward: ____________________

	# of pollen grains received	Class avg received (for reward color)

Strategy notes (Round 2): ____________________

Figure 2. Score card for keeping track of individual and population (classroom) fitness achieved during each round of the Pollination Game.

receptive flowers fertilize more ovules. They are more likely to pass their genes on through the seeds and therefore have higher fitness than those plants that do not donate all their pollen grains.

Reset the game. "Flowers" return pollen grains to "pollinators," so that each pollinator has five pollen grains.

Round 2: How Can a Flower Maximize Male *and* Female Fitness?

- **Setup.** Each flower now pairs up with a pollinator. (With an odd number of students, someone can become the observer.) While the flower will want to collect as many pollen grains as possible, the pollinator will have the goal of delivering all five pollen grains during the action phase. At the end of this round, the flower/pollinator team will get back together and combine tallies to determine the team score.
- **Action.** First, students are given a short time (2–5 minutes) to strategize ways to maximize fitness. They can add "flare" to flowers (e.g., nectar guides, frills to petals) to attract visitors and position themselves at a strategic part of the room to maximize pollen donation and receipt. The team should also think about the best way for the pollinator to deliver pollen grains efficiently. They should write short notes about their strategy on their scorecards. Once everyone is ready, pollinators are given about 2 minutes to visit flowers. On each visit, a pollinator can give only *one* pollen grain to an individual flower.
- **Tally the score.** Each flower and pollinator team gets back together and tallies their score on their score sheet. The class as a whole should calculate the average of all the team scores; this will serve as a comparison to the average score when accounting for only one component of fitness.

Discussion Questions & Answers: Round 2

1. Why did the flower and pollinator teams combine scores?
   Answer: This more accurately represents fitness in nature – the female component via seeds that will be formed after receiving pollen grains and the male component via pollen donation to sire seeds. Many flowering plants are actually hermaphroditic, and therefore individuals are capable of achieving fitness through male and female success. Many worms, mollusks, and fish are hermaphroditic as well (Barrett, 2010).
2. Did students optimize fitness by visiting (or being visited by) near neighbors, or did pollinators move around the room a lot? Why might this matter?
   Answer: In nature, near neighbors of sessile organisms are more likely to be related. By exchanging genetic material with neighbors, the chance of *inbreeding* is very high. Inbreeding has negative consequences due to *inbreeding depression*. With inbreeding, rare deleterious alleles can be expressed that have severe negative impacts on fitness.
3. Thinking about the last question: What could happen if a pollinator visited the flowers with pollen from a *completely different* population? Would this increase or decrease the fitness of the flowers that the pollinator visited?
   Answer: It could be either. Pollen from another population could introduce novel *genetic variation through gene flow* that would benefit the offspring of any seeds that it sires. On the other hand, pollen from another population may introduce genes that are *not adapted* to the conditions that this population is experiencing. (For example, the pollen could contain genes that are better adapted to cold conditions, and the present population may be in a warm environment.)
4. Now, all the *flowers* whose *team* has a high score (greater than the average score for the class) should raise their hands. What if all of the plants with these flowers also carried a gene that resulted in smaller leaves? What would the next generation look like, and what natural evolutionary concept does this exemplify?
5. **Answer:** The next generation would have a greater proportion of individuals with small leaves. This is an example of *indirect selection*, whereby the gene that changed in frequency *was not under direct selection* but increased in prevalence due to an association to a trait that was under direct selection.

Round 3: Survival of the Fittest!

- **Setup.** Flowers are asked to pick a spot in the room and remain stationary. A portion of the flowers (30–50% of students in the flower group) are given four pieces of candy of a certain variety based on their flower color (e.g., chocolate candy for red flowers, hard candy for yellow flowers). *After* the flowers are given candy, the pollinator types are each assigned a candy color preference. For example: bats prefer green, bees prefer yellow, and hummingbirds prefer red. *Just make sure each pollinator has a single color preference.*

- **Action.** Pollinators are given 2 minutes to visit flowers with a reward of their color preference. On each visit, a pollinator can give only *two* pollen grains to an individual flower. But in exchange for pollen grains, the flowers can give the pollinators one piece of candy per pollen grain.
- **Tally the score.** Each flower and pollinator marks on their score sheet how many pollen grains they received or gave. As a class, students calculate the average number of pollen grains received by color reward type and pollen grains donated by pollinator type.

Discussion Questions & Answers: Round 3

1. Did some plants achieve much higher female fitness through the flowers in this round than in the other rounds? Why?
   Answer: Pollinators showed preference for certain flowers because they offered rewards. In this game, the candy is analogous to flowers that offer different kinds of nectar in nature. Flowers that offered no reward may not have been visited much or at all.
2. If flowers that offered one type of reward (e.g., red candy) had more pollen grains, what would the next generation (the offspring) of plants with those flowers be like?
   Answer: There would be a great proportion of flowers that offered that reward, because more of those *genes* were passed on to the offspring. Plants offering that reward would have much higher female fitness. Pollinator preference acts as a selective force for flowers with certain floral rewards.
3. What would happen if only one type of pollinator was present?
   Answer: If the pollinator had a strong preference (as in this exercise), the flowers with that type of reward would receive more pollen grains and those individuals would have greater female fitness.
4. If plants with flowers that have more rewards to offer can achieve high fitness, then why don't all flowers offer lots and lots of the best rewards?
   Answer: There is a resource trade-off between generating rewards like nectar and also having enough *resources* to produce viable seeds. This is known as *resource allocation*.

Round 3 Variations

- For higher-level classes like AP Biology courses or intro-level undergraduate courses, the instructor can introduce the added level of plant-mediated selection on pollinators and how floral rewards influence pollinators' behavior and, ultimately, their fitness. When setting up this added level of complexity, the instructor should carefully consider how individual pollinators can learn to associate floral rewards with specific floral traits versus the population of pollinators evolving in response to plant-mediated selection (e.g., floral rewards and scents). This scenario would provide an excellent opportunity to discuss the difference between learned and inherited traits in terms of pollinator evolution.
- Assign one pollinator as a "generalist" – this pollinator likes all types of rewards. This will likely result in this pollinator type easily donating lots of pollen grains. Discuss the trade-offs between generalizing or specializing from the plant perspective: Generalist pollinators are often less efficient pollinators than specialists, which can lead to the evolution of floral traits and rewards for specialist pollinators that thereby monopolize those rewards (Larsson, 2005).
- Give out candy to flowers again, but greatly skew the proportions of colors that are given to the students. Or give some flowers far more candy or multiple types of candy. All these setups will create scenarios in which the next generation will be influenced by the pollinator preference.

○ Additional Assignment after the Pollination Game: Develop Hypotheses for Optimized Flower & Pollinator Combinations

This exercise is best done in groups but will work for pairs or individuals as well. Students are asked to synthesize the concepts learned in the game to develop hypotheses on what combinations of flowers and their associated pollinator(s) would result in high fitness for the flowering-plant population. Students should consider resources needed to supply rewards or maintain showy, large flowers. For each flower, students should consider: How many ovules (seeds) can it produce? What is the habitat of the population? Are there other species competing for pollen or helping to attract pollinators? After creating the flower and pollinator combination, each group can present its rationale to the class. Students can then debate the pros and cons of each scenario and even run the exercise again to test these hypotheses the next week and collect data to present results on their hypotheses.

References

Barrett, S.C.H. (2010). Understanding plant reproductive diversity. *Philosophical Transactions of the Royal Society of London Series B, 365,* 99–109.

Charlesworth, B. (1993). The evolution of sex and recombination in a varying environment. *Journal of Heredity, 84,* 345–350.

Darwin, C. (1876). *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*. London: John Murray.

Darwin, C. (1877). *The Different Forms of Flowers on Plants of the Same Species*. London: John Murray.

Ehrlich, P.R. & Raven, P.H. (1964). Butterflies and plants: a study in coevolution. *Evolution, 18,* 586–608.

Futuyma, D.J. (2013). *Evolution, 3rd Ed.* Sunderland, MA: Sinauer Associates.

Hassard, J. & Dias, M. (2009). *The Art of Teaching Science: Inquiry and Innovation in Middle School and High School, 2nd Ed.* New York, NY: Routledge.

Krebs, J.R. & Davies, N.B. (1993). *An Introduction to Behavioural Ecology, 3rd Ed.* Oxford, UK: Blackwell Science.

Larsson, M. (2005). Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia, 146,* 394–403.

Leimu, R., Mutikainen, P., Koricheva, J. & Fischer, M. (2006). How general are positive relationships between plant population size, fitness and genetic variation?. *Journal of Ecology, 94,* 942–952.

Leonard, B. (2010). Encouraging new manuscripts in critical areas of biology education. *American Biology Teacher, 72,* 6.

Masel, J. (2011). Genetic drift. *Current Biology, 21,* R837–R838.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos, 120,* 321–326.

Schemske, D.W. & Bradshaw, H.D., Jr. (1999). Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences USA, 96,* 11910–11915.

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