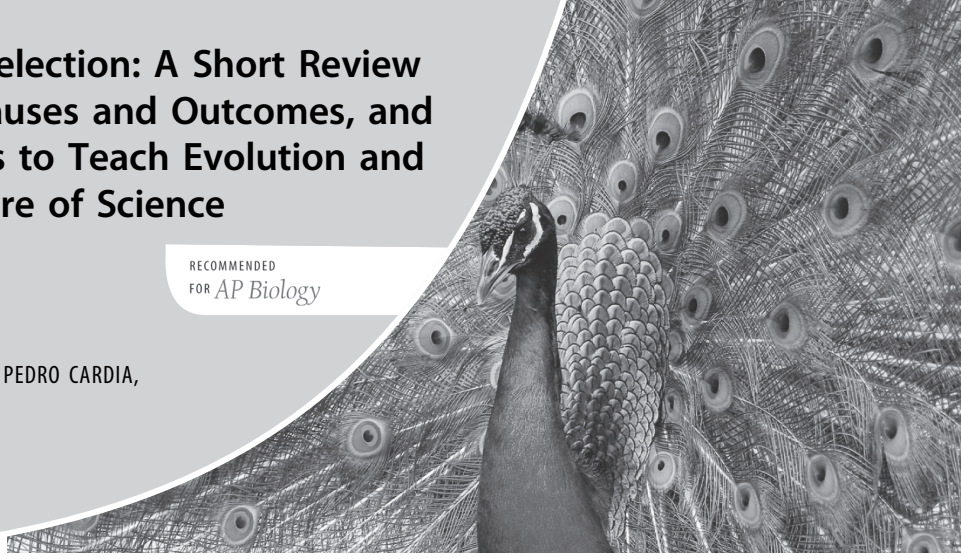


Sexual Selection: A Short Review on Its Causes and Outcomes, and Activities to Teach Evolution and the Nature of Science

RECOMMENDED
FOR AP Biology

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ABSTRACT

Sexual selection plays an important role in species evolution and speciation, and is fundamental to understanding of biological evolution. In the last decades, research on sexual selection helped understand its causes and impacts in species evolution, sexual dimorphism, and speciation. It also provided interesting examples that can be used to engage students in learning about evolution. Here we review the latest sexual selection research and propose two activities that model evolution by sexual selection. The engaging nature of these activities makes them useful to promote active learning about evolution, the nature of science, and methods used to construct scientific knowledge. Importantly, we address several performance expectations suggested by the Next Generation Science Standards.

Key Words: sexual selection; sexual dimorphism; mate choice; mate competition; scientific inquiry; scientific models; educational resources.

○ Sexual Selection: A Brief Review

Why do males and females of several species differ in so many features? And why do these features sometimes compromise individuals' survival? Darwin proposed a mechanism that could explain these observations (Darwin, 1858), which he later named sexual selection (Darwin, 1859). Since then, the importance of sexual selection for species' evolution and speciation has been amply supported by theoretical models and empirical evidence. Sexual selection can act on morphological, physiological, and behavioral traits, and may cause the evolution of sexual dimorphism and complex signals and ornaments that can compromise individual's survival (reviewed in Andersson, 1994; Andersson & Simmons, 2006). Furthermore, it may play an important role in speciation processes, contributing to restrict gene flow between

Why do males and females of several species differ in so many features?

diverging taxa (Coyne & Orr, 2004; Ritchie, 2007). Besides being fundamental to a deeper understanding of species evolution, sexual selection is particularly important for the teaching of evolution because it emphasizes the most important trait determining the fitness of an individual: its reproductive output. In fact, students tend to believe that an individual's fitness is mostly determined by its ability to survive, its strength, or its intelligence (Gregory, 2009), but the number of offspring left over time is the real measure of fitness and what determines species evolution. Thus, sexual selection should be explored together with natural selection to deconstruct misconceptions. Accordingly, even though not explicitly mentioning sexual selection, several performance expectations suggested by Next Generation Science Standards (NGSS, 2013; NRC, 2012) for elementary, middle, and high schools allow (4-LS1-1, 4-LS1-2, MS-LS1-4, HS-LS4-3) or even require (3-LS4-2, MS-LS4-4, MS-LS4-6, HS-LS4-2) students to explore sexual selection (see Table 1 for suggestions of activities to explore each of these standard expectations).

○ What Are the Causes of Sexual Selection?

Like natural selection, sexual selection also results from competition for scarce and limited resources. In sexual selection, it is access to mates that determines fitness (Andersson & Iwasa, 1996). Accordingly, the effects of this selection will more strongly affect the sex that is non-limiting for reproduction. But then, what determines which sex is limiting for reproduction and the intensity of sexual selection? Several non-mutually exclusive hypotheses were put forward to answer this question, including sex differences in parental investment, mating systems, and biased sex ratios or operational sex ratios.

Table 1. Performance expectations suggested by the Next Generation Science Standards (NGSS Lead States, 2013) that require (in bold) or allow (not bold) exploring sexual selection and suggestions to explore these expectations in the classroom.

School level	Expectation	Expectation description	Examples of resources that can be used in the classroom	Suggestions to explore the Nature of Science expectations
Elementary schools	3-LS4-2	Use evidence to construct an explanation for how the variations in characteristics among individuals of the same species may provide advantages in surviving, finding mates, and reproducing.	<p>Explore this expectation with the activities presented in this paper.</p> <p>Explore the Birds-of-Paradise Project website for additional information on individual traits that may provide advantages in reproduction.</p>	<p><i>Scientific investigations use a variety of methods, tools, and techniques to produce and revise scientific knowledge.</i></p> <p>Explore the activities proposed in this paper and in Lawson (2003) as examples of models similar (although simpler) to those used by researchers to simulate and study evolution, and contrast this research methodology with those presented in the Birds-of-Paradise Project, Human Endeavor, Methods & Technology.</p>
Elementary schools	4-LS1-1	Construct an argument that plants and animals have internal and external structures that function to support survival, growth, behavior, and reproduction.	Birds-of-paradise have feathers with distinct functions: flying, protection from the environment, and attracting mates. Discuss with your students what could be the function of these distinct feathers using the resources available on the Birds-of-Paradise Project website.	<p><i>Scientific findings are based on the recognition of patterns.</i></p> <p>Discuss with your students how patterns of feather coloration, size, position, and structure may help scientists to construct hypotheses regarding the function and origin of a particular feather.</p>
Elementary schools	4-LS1-2	Use a model to describe that animals receive different types of information through their senses, process the information in their brain, and respond to the information in different ways.	Use the variety of traits and displays of birds-of-paradise to explore this expectation. Resources are available at the Birds-of-Paradise Project website.	<p><i>Men and women from all cultures and backgrounds choose careers as scientists . . . Most scientists and engineers work in teams. Creativity and imagination are important to science.</i></p> <p>Use information about how scientists from distinct cultures and backgrounds work in teams and use their imaginations to gather information about birds-of-paradise, available on the Birds-of-Paradise Project website (Human Endeavor). Use also Lesson 1 from Fee and Alfano (2013).</p>

Table 1. Continued

School level	Expectation	Expectation description	Examples of resources that can be used in the classroom	Suggestions to explore the Nature of Science expectations
Middle school	MS-LS1-4	Use argument based on empirical evidence and scientific reasoning to support an explanation for how characteristic animal behaviors and specialized plant structures affect the probability of successful reproduction of animals and plants, respectively.	Start exploring sexual selection by presenting students with species having distinct degrees of sexual dimorphism and providing information about their ecology, sex ratios, and mating systems. With this, motivate your students to use evidence to construct hypotheses and scientific arguments. Use the activities described in this paper to test your student's hypothesis.	<i>Science depends on evaluating proposed explanations.</i> Use the activities proposed in this paper as evolution simulators to gather empirical evidence to evaluate students' hypotheses to explain patterns of sexual dimorphism. Highlight this evaluation process.
Middle school	MS-LS4-4	Construct an evidence-based explanation that describes how genetic variations of traits in a population increase some individuals' probability of surviving and reproducing in a specific environment.	Explore this expectation with the mate choice activity presented in this paper. Perform the activity under distinct sex ratios and/or mating systems, allowing students to explore the evolutionary outcomes under these social environments. Further, use the example of lizards, <i>Uta stansburiana</i> , to highlight the importance of social context in evolutionary outcomes (Sinervo & Lively, 2006).	<i>Scientific knowledge is constrained by human capacity, technology, and materials.</i> Discuss with students the similarities and differences between their simulations of evolution based on this paper and evolution simulators used by researchers to test their hypotheses and predictions. Discuss how the advance of computational resources affected the use of evolution simulators to test hypotheses.
Middle school	MS-LS4-6	Use mathematical representations to support explanations of how natural selection may lead to increases and decreases of specific traits in populations over time.	Use the simulation proposed in Lawson (2003) to explore this expectation. Ask students to identify natural selection and sexual selection strengths, and to predict outcomes for scenarios with distinct relative strengths.	<i>Scientific explanations are subjected to revision and improvement in the light of new evidence.</i> <i>Science depends on evaluating proposed explanations.</i> Explore research projects that test whether giraffes' neck size evolved through natural or sexual selection (Simmons & Altwegg, 2010).
High school	HS-LS4-2	Construct an evidence-based explanation that the process of evolution primarily results from four factors: (1) the potential	Explore this expectation with the activities presented in Bouwma-Gearhart and Bouwama (2015) or with those presented in this	<i>Science distinguishes itself from other ways of knowing through the use of empirical standards, logic arguments, and skeptical review.</i>

Table 1. Continued

School level	Expectation	Expectation description	Examples of resources that can be used in the classroom	Suggestions to explore the Nature of Science expectations
		for a species to increase in number, (2) the heritable genetic variation of individuals in a species due to mutation and sexual reproduction, (3) competition for limited resources, and (4) the proliferation of those organisms that are better able to survive and reproduce in the environment.	paper. To contrast the effects of natural and sexual selection, you may compare the results obtained with the activities described in this paper with those described in Campos and Sá-Pinto (2013).	Explore this expectation with the activities presented in Bouwma-Gearhart and Bouwama (2015).
High school	HS-LS4-3	Apply concepts of statistics and probability to support explanations that the populations of organisms with an advantageous heritable trait tend to increase in proportion to organisms lacking this trait.	Explore this expectation with the mate choice activity presented in this paper. Perform the activity under distinct sex ratios and/or mating systems, and for each scenario, ask students to estimate the probability of each male to have offspring in the next generation, taking into account his traits. Discuss how this information helps you to predict the evolutionary outcomes under each scenario.	<i>Scientific investigations use diverse methods and do not always use the same set of procedures to obtain data.</i> Ask your students to make a list of the most common bird species around them and to gather data to test if sexual dimorphism tends to be more frequent in polygamous than monogamous species. Ask them to contrast their results with those obtained in the simulation.
High school	HS-LS2-8	Evaluate the evidence for the role of group behavior on individual's and species' chances to survive and reproduce.	Use the two distinct, colorful male types of the mate choice activity in this paper to discuss how the frequency of female preferences affects the male's chances to reproduce.	<i>New technologies advance scientific knowledge.</i> Discuss with your students how the evolution of genetic technologies allowed scientists to study female cryptic choice that occurs after copulation or spawning.

Parental Investment

In 1948, Bateman proposed that parental investment differentially limits the reproductive potential of each sex. Crossing male and female *Drosophila* flies with a given number of partners and tracking the number of progeny, Bateman observed that male reproductive success was mostly determined by mating frequency. Contrastingly, in females, after an initial increase, reproductive success rapidly became limited by factors other than mating frequency. He thus proposed that these limiting factors could include the costs associated with egg production, uterine nutrition, and in mammals, milk production. Although these results were probably biased by

methodological problems, several experiments have reported similar results in other species (see Gowaty et al., 2012, Collet et al., 2014, and references therein). However, the stronger correlation between mating and reproductive success in males than in females is far from being a universal pattern. In fact, several species show the opposite pattern and/or strong variability along the species range (reviewed in Brown et al., 2009). Trivers (1972) subsequently identified additional types of parental investment, such as feeding or protecting sexual partners and progeny, and defending a territory in which sexual partners can feed, lay eggs, or give birth and raise the progeny. He also proposed that the limiting resource

for reproduction would be the sex that invests more in the offspring; that is, sexual selection will more strongly affect the sex that invests less. In most species, males invest less in the offspring than females (Kokko & Jennions, 2008), which become the limiting sex, imposing stronger sexual selection on males. However, in species with higher paternal investment, we would expect the opposite pattern. This is the case of species characterized by “male pregnancy” such as seahorses, sea dragons, and pipefishes (Jones & Ratterman, 2009). As expected, in some of these species females are more conspicuous, display and initiate the courtship, and compete for males, who choose among females (e.g., Monteiro et al., 2002). Also, in some of these species, Bateman’s gradient seems to be reversed, with stronger and steeper correlation found between mating frequency and reproductive success in females than in males (Jones et al., 2000).

Sex Ratio and Operational Sex Ratio

To explain why competition for mates tends to be stronger in males than in females, Darwin (1871) hypothesized that natural populations would be male-biased. This hypothesis may explain the strong sexual dimorphism observed in species with male-biased sex ratios such as mallards and other duck species (Owen & Dix, 1986), but it is not supported by the evidence Darwin collected at that time nor by evidence collected more recently (Donald, 2007).

In 1977, Emlen and Oring proposed that it was the ratio of sexually active males and females—the operational sex ratio (OSR)—and not the overall population sex ratio that determines the intensity of sexual selection. The OSR is influenced by species’ life history traits such as sex-specific mortality rates, age of sexual maturity, and reproductive sexual synchrony. It is also affected by sex-specific parental investment, as the time invested in parental care limits the time individuals are available to reproduce (reviewed in Andersson, 1994). In species with an even adult sex ratio but whose males only invest in gamete production and mating, while females alone incubate, protect, feed, and teach the young (e.g., peacocks, pheasants, chickens), the OSR becomes male-biased and females are the limiting sex. By contrast, in sex-role-reversed species, such as pipefishes, the OSR may become female-biased because after mating males incubate the eggs and are unavailable to mate again (Monteiro et al., 2013).

Mating Systems

Darwin (1871) suggested that the strength of sexual selection would depend on the mating system. When some males mate with more than one female, many males cannot mate at all and sexual selection on males may become exaggerated. In fact, several studies suggest there is a tendency for monogamous species to be less sexually dimorphic than polygamous species, but there are numerous exceptions to this rule (reviewed in Isaac, 2005). Possible explanations for these exceptions may include strong genetic correlations between sexes in the selected traits, sexual dimorphism being caused or prevented by natural selection, uneven sex ratios, or geographic and seasonal variations in species’ mating systems (Andersson, 1994). For example, white-faced saki monkeys (*Pithecia pithecia*), a sexually dimorphic species, exhibit both a monogamous and a polygamous behavior (Thompson, 2013).

How Sexual Selection Operates and Which Traits Are Targeted

Sexual selection can operate at various stages of sexual reproduction, favoring traits that help individuals of the non-limiting sex win contests that maximize their access to mates. These contests may be about: (1) velocity and/or prospecting: the first one who finds a mate wins; (2) fighting: individuals that are better at keeping rivals away from the opposite sex win; (3) endurance: individuals that are reproductively active for a longer period win; (4) productivity: individuals that produce more gametes win; and (5) charm: individuals that are better at attracting the other sex win. Although sexual selection is usually associated with phenotypic characters evaluated before copulation, strong sexual selection can still occur after copulation or spawning (Pizzari & Parker, 2009). For examples of sexual selection to use in classroom, see our presentations “How sexual selection operates and which traits are targeted—Some examples” (Sá-Pinto et al., 2016a) and “Why do males and females of several species differ in so many features?” (Sá-Pinto et al., 2016b).

○ Introducing Activities to Explore Sexual Selection

The activities described below simulate mate choice and mate competitions, and allow testing hypotheses related to evolution by sexual selection (Figure 1).

To use these activities to promote inquiry-based learning about evolution, we suggest a walk in a natural area or in a natural history museum with your students (Figure 1, “Observing the surrounding natural world”). Ask them to record the species and observe the morphology and behavior of individuals. Use field guides to identify species, to sex the individuals, and to obtain additional information (e.g., sex dimorphism, mating systems, sex ratios). Alternatively, or in complement, use images or videos of different species to illustrate patterns of sexual dimorphism (see examples in Sá-Pinto et al., 2016a, and Birds-of-Paradise Project, 2016). Then, ask students: (1) Why are sexes in some species markedly different morphologically and behaviorally, while in others sexes are indistinguishable by external features?, and (2) Why are males usually more conspicuous than females? (Figure 1, “Questioning” and “Hypothesis”; and NGSS, 2013, practices: asking questions, constructing explanations; NRC, 2012). Use the activities described below to test students’ hypotheses (NGSS, 2013, practices: planning and carrying out investigations; NRC, 2012). In both activities, discuss with the students whether the results support their hypotheses, or whether more data or different scenarios are necessary (NGSS, 2013, practices: obtaining, evaluating, and communicating information; analyzing and interpreting data; engaging in argument from evidence; NRC, 2012). Take the opportunity to explore scientific models, addressing both their potential and limitations (NGSS, 2013, practice: using and developing models; NRC, 2012). Finally, encourage your students to collect data from nature or public databases to further test their hypotheses (NGSS, 2013, practice: planning and carrying out investigations; obtaining, evaluating, and communicating information; analyzing and interpreting data; NRC, 2012).

Modeling Selection by Mate Choice

For this activity you need a set of masks with four distinct colors and color patterns (Figure 2).

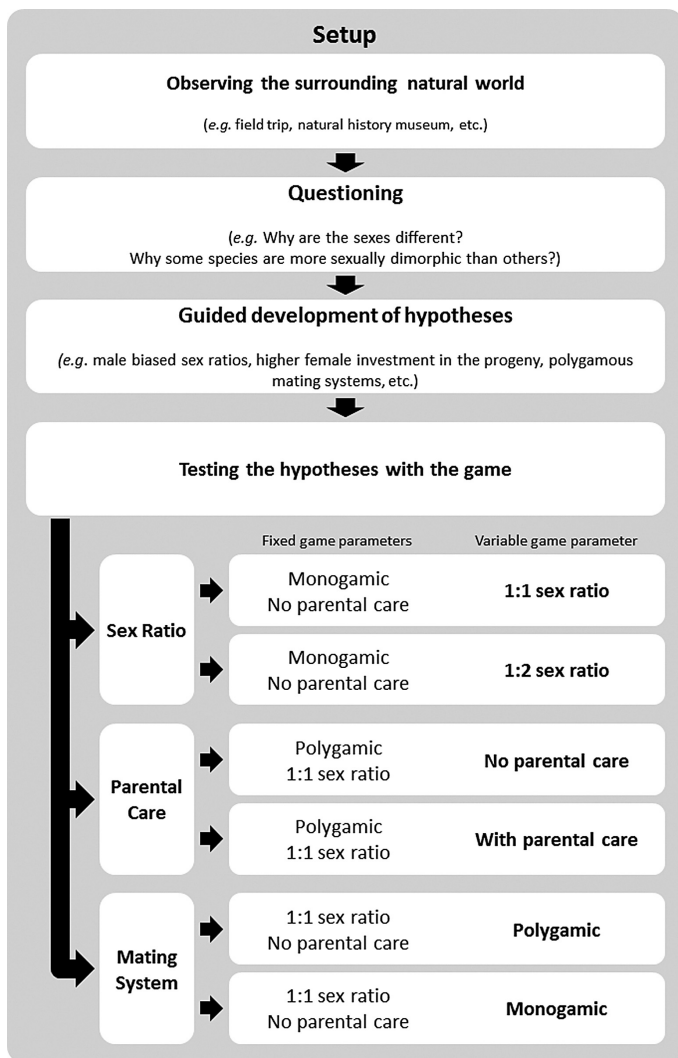


Figure 1. Diagram representing the different stages of the activities. To test students' hypotheses, you will need to contrast the results obtained by varying the parameter hypothesized to explain the observed patterns of sexual dimorphism while keeping other parameters constant.

Each mask represents one male, and each student represents one female. The number of masks and procedures for each scenario depend on the hypotheses being tested (Figure 1, "Testing the hypotheses with the game"); here we describe the basic activity for all simulated scenarios.

Start the activity with a population of masks with similar color frequencies (e.g., for a population of 40 individuals, you should have 10 masks of each color or color pattern), and ask students to choose one male to mate. After all students have chosen their mates, discuss which males reproduced and the differences between these and the ones that weren't chosen by any female. Continue the activity simulating the next generation, taking into account mating pairs: for a given couple, sons (represented by the masks) are similar to their fathers, while daughters (represented by the students) are similar to their mothers (including their mate preferences). Parents die after reproduction and are not present in the next generation. Males that are not chosen die without leaving offspring. Depending on the simulated scenario, two to four generations are usually enough to

observe changes in color frequency and for mask frequencies to reflect female preferences. Discuss the significance of the frequency changes. Frequency changes will be faster in scenarios where sexual selection is stronger, that is, in polygamous systems and systems with strongly biased sex ratios.

With simple variations to this basic activity, it is possible to simulate distinct biological scenarios and test the effect of the sex ratio (or operational sex ratio) and mating system on male evolution and sexual dimorphism (Figure 1, "Testing the hypotheses with the game"). The number of both the masks and the offspring of each couple depend on the sex ratio that we want to simulate. To simulate unbiased sex ratios (Figure 1, "1:1 sex ratio"), the total number of masks must be equal to the number of participants (or only slightly higher), and each couple has one daughter (the students themselves) and one son. To simulate biased sex ratios (Figure 1, "1:2 sex ratio"), set the number of masks to be at least twice the number of students, and each couple has at least two sons and one daughter (the student). To simulate a polygamous system (Figure 1, "Polygamic"), students should choose their mate without taking the mask from the mating pool, so that each male can mate with multiple females (i.e., can be chosen by more than one student) in a given reproductive round. To simulate a monogamous mating system (Figure 1, "Monogamic"), each student should take their chosen mask from the mating pool and keep it until the end of each reproductive round, so that each male can mate with only one female.

Modeling Selection by Mate Competition

For this activity you need modeling balloons (or pool noodles of distinct sizes, if you have any students allergic to latex), an air pump, masks, and two opaque bags. Students play the role of reproductively active males; the balloons represent a feature (such as horns or jaws) with heritable size variability used by males to fight other males for females. The masks represent females, and the bags are used to randomly assign the balloons to students and to form random pairs. With the air pump, inflate the balloons to obtain two different sizes: long and very short (Figure 3).

To simulate a scenario of male-biased sex ratio (2 males: 1 female) in a monogamous species, the number of females should be half the number of students. Given the scarcity of females, males fight for the female: every two students should face each other and try to touch the opponent using the balloons; the male who first touches his opponent three times wins. Randomly distribute one balloon to each student, form random pairs, and let them fight for females. After the fights, ask students to record the number of males with long and short balloons that won the fights, and to estimate the frequency of each male phenotype in the next generation knowing that: (1) males who lose die without leaving offspring; and (2) each winning male mates with one female and has one daughter similar to the mother and two sons similar to the father (represented by the balloon size). Again, randomly distribute the balloons among the students and repeat these steps to simulate at least three generations; this should be enough to observe an increase in frequency of the longer balloon phenotype.

Final Remarks

As we highlight in this paper, sexual selection is an important evolutionary process with strong impacts on species features. These

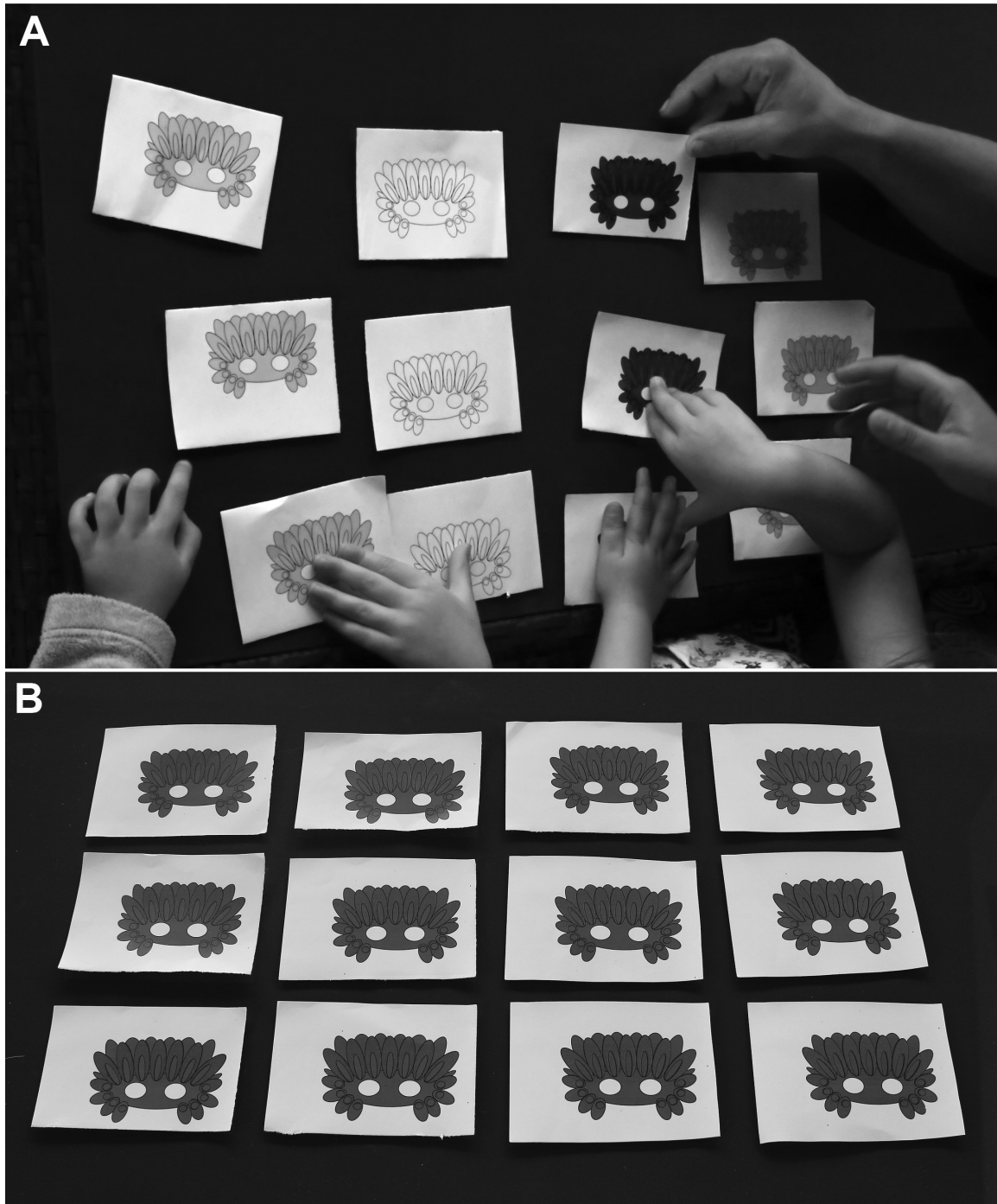


Figure 2. (A) Start the activity of mate choice with a population of masks with four equally frequent colors. Ask students to choose the mask they like the most to be their mate. (Masks are available at <https://goo.gl/bI0INU>.) (B) When participants represent the limiting sex, sexual selection will cause the increase in frequency of the preferred male phenotype through generations. Photo credits: Pedro Cardia.

exercises are designed to help students understand the most important factor driving evolution—the number of offspring left over time—and thus to help them overcome possible misconceptions about the origin and evolution of some traits, and to achieve some of the performance expectations suggested by NGSS (Table 1). Accordingly, we emphasize the importance of exploring sexual

selection across distinct school grades using examples and historic contexts, as well as the activities here detailed and other available resources, such as photos, videos (Birds-of-Paradise Project, 2016; Clark, n.d.) or activities to model and/or promote inquiry based learning about this evolutionary mechanism (Moore et al., 2012; Lawson, 2003; Bouwma-Gearhart & Bouwma, 2015).

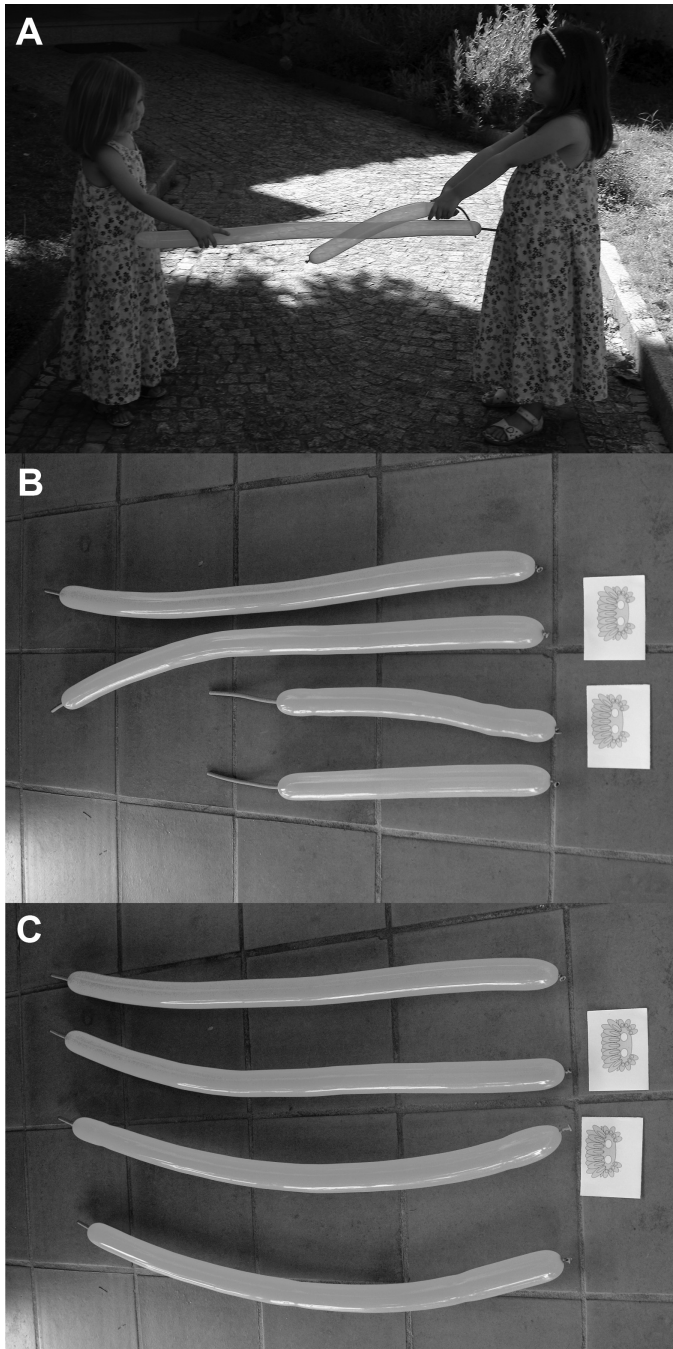


Figure 3. In the activity that models sexual selection by mate competitions, participants use balloons of two distinct sizes (A) to fight other participants for the opportunity to mate with individuals of the limiting sex (represented by the masks used in the mate choice activity; Figure 2). At the beginning of the activity the two balloon sizes are equally frequent (B). Sexual selection causes the increase in frequency of the longer balloon (C). Photo credits: Pedro Cardia.

○ Acknowledgments

We are grateful to Kristin Jenkins and Antigoni Kaliontzopoulou for reviewing this manuscript and activities and for their comments and suggestions that helped to improve it. This work was funded

by FEDER funds through the Program for Competitiveness Factors (COMPETE) and by national funds through FCT (*Foundation for Science and Technology*), under PTDC/BIA-BEC/105221/2008 and FCOMP-01-0124-FEDER-008967, and by *Ciência Viva*, within the scope of the Program “*Ciência Viva no Verão*.” X.S.P. and R.C. are supported by Programa Operacional Potencial Humano-Quadro de Referência Estratégico Nacional funds from the European Social Fund and Portuguese Ministério da Educação e Ciência (FCT; grants SFRH/BPD/103613/2014, SFRH/BPD/64365/2009 and SFRH/BPD/110348/2015, respectively). All authors contributed to and approved the final version of this manuscript.

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