Tested Studies for Laboratory Teaching
Proceedings of the Association for Biology Laboratory Education
Vol. 33, 340–347, 2012

Runaway Sexual Selection Simulation Game

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Sexual selection was proposed by Charles Darwin as a special form of selection that could result from either competition between members of one sex for the opposite sex (typically male-male competition) or selective mate choice by one sex for the opposite sex (typically female choice). The process by which female choice may yield the elaborate modification of male traits, e.g. bright colors or large display morphology, that are attractive to females has appropriately been called *runaway selection*. Runaway selection occurs because female choice may induce rapid and extreme directional evolutionary change in male traits. We present an easily conducted simulation game that makes the dynamics of runaway selection clear and can improve student understanding of this important evolutionary process. The role of random mutation in the process of evolution by sexual selection and the factors that set limits on runaway selection also are introduced in the simulation.

Keywords: evolution game, sexual selection

Introduction

This simulation was originally developed as part of an invited workshop at the 2009 Annual Meeting of Animal Behavior Society on sexual selection. The idea for the simulation game came from Blumer and was implemented and presented by Zuk to an audience of faculty and graduate students with some background in animal behavior. Since then, the game was refined by Gray and tested in an upper-level undergraduate class by Blumer. Teaching the evolutionary process is always challenging since there are relatively few animal model systems in which students may induce and observe evolution by natural selection (an exception can be found in Blumer and Beck, 2010). Teaching the process of evolution by sexual selection is even more challenging because it is difficult to explain how traits such as ornamental tail feathers that appear to be detrimental to their bearer can evolve. Students often assume that the individual with a longer tail is somehow stronger, faster, or otherwise more fit than shorter-tailed individuals, but this need not be the case. Theory demonstrates that simply via a randomly-occurring preference for longer tails an ornamental trait can evolve to become more exaggerated. Illuminating the process of sexual selection in undergraduate courses may be facilitated by games that engage students in the process of evolutionary change. This was our motivation for developing this game.

Student Outline

Simulating Runaway Sexual Selection

Objective

Simulate three or more generations of sexual selection on tail feather length in a bird species, and describe, by means of frequency histograms, how tail length evolves.

Introduction

Sexual selection was proposed by Charles Darwin (1859) as a special form of selection that could result from either competition between members of one sex for the opposite sex (typically male-male competition) or selective mate choice by one sex for the opposite sex (typically female choice). The process by which female choice may yield the elaborate modification of male traits, such as bright male colors or large display morphology, that are attractive to females has appropriately been called **runaway selection** (Fisher 1958). Runaway selection occurs because female choice may induce rapid and extreme directional evolutionary change in male traits, regardless of any other advantage to the male with the ornamental trait. Each group of students will conduct a simulation game that makes the dynamics of runaway selection clearer. We will consider the evolutionary consequences of this process on the tail feather length of a bird species in which mating occurs in **leks**, aggregations of males that are visited by females exclusively for the purpose of choosing a mate (Bradbury and Gibson, 1983), and males are **polygynous** (a mating system in which one male mates with more than one female in a single breeding season). The population characteristics of males and females may not be the same, so each group will need to describe each sex separately. How may frequency histograms be used to describe the tail length of the bird population at different times? What role does random mutation play in the process of evolution by sexual selection? What factors could set limits on runaway selection in nature?

Simulation Process

Each group of 4-6 students will have two sets of cards, 50 male and 50 female, which constitute the Parental Generation of one population. Each card has an image, with the trait size indicated on it in arbitrary units (so you can see which is big and which is small without having to look back and forth at the cards). Each group also will have a set of mutation cards and some blank trait value cards for each sex.

1. To start the game, shuffle **Parental Generation** cards. Randomly pull one male and one female card from the sets until 25 cards are pulled for each sex.
2. Plot the values separately for each sex (population trait frequency histograms) for the ancestral population (Generation 0).
3. Display all the male trait cards (that were pulled) face up on a table in 5 randomly assembled groups (leks).
4. Apply a female choice rule:

Taking a female card, “visit” one lek and choose the male with the longest tail in that lek by paper clipping the female card to the chosen male card or setting it on top of it. Each female must visit a different lek than the female before her and each female visits and chooses a mate at only one lek. However, more than one female may choose and mate with a given male in each lek.

5. Offspring production

Each chosen male produces male offspring 100% like dad and female offspring 100% like mom (print the trait size on color coded cards for each sex). Male offspring stay in the lek location of their father with cards face-up showing their trait. All adults, both males and females, die after offspring are produced. Males who were not chosen and did not reproduce also die. Only offspring get to reproduce in the next round of the simulation (i.e., the species is semelparous). The female offspring become the choosers in the next round of female choice.

6. Plot the frequency histograms for both sexes (Generation 1)

At least once each generation, in each population, a random mutation occurs in one male and one female that results in a trait change either positive or negative (select a card from the pack of mutation cards showing possible phenotypic consequences, then apply the mutation to one mated male and one female from your population, and apply that change to the offspring from those parents in that generation).

At least once each generation, in each population, predators remove a total of 5 offspring with a tail length longer than 4 units.

Repeat from step 4 to create Generation 2 and plot results.

Run the game for 3 or more generations.

Simulation Analysis and Discussion

Compare the starting Generation 0 phenotypes to those at the end of the game.

Discuss the runaway process and the cause for male phenotypic change.

What are we assuming about tail length in this simulation?
- Heritability is high
- Selection on tail length in males has no effect on tail length in females

What are we assuming about female choice?
- Choice is directional and consistent
- Choice is for the longest tail available among the males present

What is the role of mutation?

Are there limits to the runaway process?
- What sets those limits?
  - Predators in the game
  - Any causes for natural selection

Discuss examples of traits that may have resulted from a runaway sexual selection process. What are the alternative hypotheses? If a trait were the product of runaway selection, what predictions can we make that would permit us to identify that process as the cause for that trait elaboration?

Literature Cited

Bradbury, J.W. and R.M. Gibson. 1983. Leks and Mate Choice. Pages 109-138 *in Mate Choice* (P. Bateson, Editor). Cambridge University Press, NY, 462 pages.

Darwin, C. 1859. *The Origin of Species by Means of Natural Selection*, 7th ed. and *The Descent of Man and Selection in Relation to Sex*. Reprinted by The Modern Library, Random House, NY, 1000 pages.

Fisher, R.A. 1958. *The Genetical Theory of Natural Selection*. Dover Publications, NY, 291 pages.

Notes for the Instructor

In a 50-minute lecture format, the simulation may be modified to accommodate the limited time available. Provide a brief introduction to the subject of sexual selection (10-15 minutes maximum). Run the game for 30 minutes and plot only the change in male tail length in each generation including the ancestral generation. Reuse the female cards in each population (once the 25 females of the ancestral population have been created from the larger set of 50) since daughters will be identical to their mother. Apply a random mutation every generation but make the same change to both a male and female in a population. Use the blank trait cards to record each generation of male offspring and any changes in the female population. Students may reuse the blank trait cards by crossing through the previous tail length and writing the new tail length. Apply predation every generation but only to one of the five leks and only to the males with the longest tail. Run the game for 2-3 generations. Collect the histograms from each group in the final 5 minutes of class and prepare a single histogram for each population to show at the next class meeting to discuss. Alternatively, have each group prepare their results as a histogram in a single Powerpoint slide to present at the next class meeting for discussion.

It is important that students apply mutation and predation every generation in this game. The tail length may rapidly go to fixation at the longest tail length if mutation and predation are not applied in every generation. Fixation, the entire population having the same long tail phenotype, may make for a boring simulation, but could lead to an illuminating discussion on the roles of mutation and predation in the runaway process. Predation cards may be prepared to remind students to apply predation to each population, in each generation, immediately following offspring production.

Cards needed for each student group (each independent population)

Clip art is **<long tail sunbird.gif>** from Arthur's All Types of Bird Clip Art **www.arthursclipart.org/birds/birds/page_06.htm** free clipart website.

Print male cards on a different color card stock than the female cards. Our prepared template cards are business card size, 2 x 3.5 inches.

The 50 male and 50 female cards are used to create the Parental (ancestral) Generation.

50 Male Cards:
- 5 – Tail length 1 unit
- 10 –Tail length 2 units
- 20 - Tail length 3 units
- 10 - Tail length 4 units
- 5 - Tail length 5 units

50 Female Cards:
- 5 – Tail length 1 unit
- 10 –Tail length 2 units
- 20 - Tail length 3 units
- 10 - Tail length 4 units
- 5 - Tail length 5 units

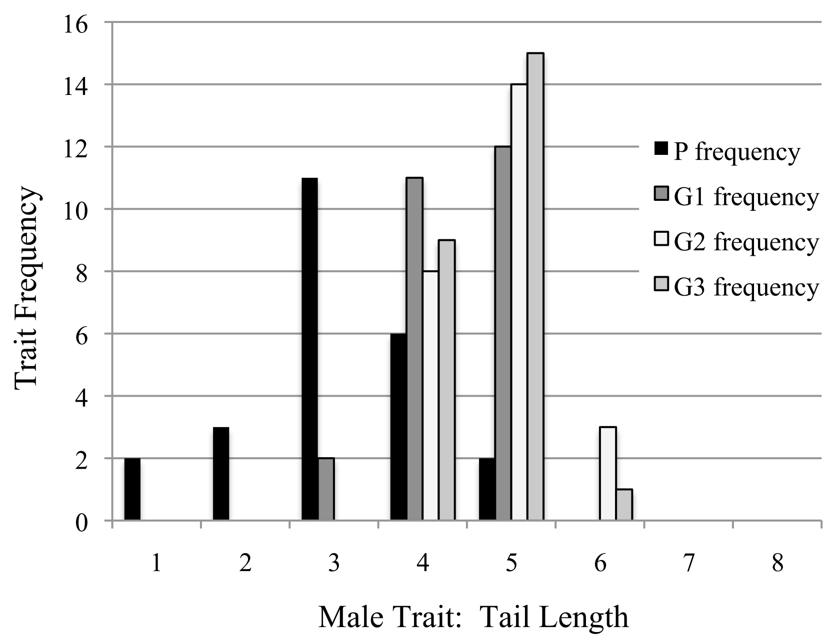


Figure 1. Results of sexual selection simulation. The male tail length frequency in four generations of the simulation game are shown, each in different color. Males in the parental generation (P) had a mean tail length of 3.1 units, generation 1 (G1) had a mean tail length of 4.4 units, G2 was 4.8 units, and G3 was 4.7 units. In this simplified simulation, the female population was not modified from one generation to the next.

Blank Trait cards:
- 25 - males (to be marked with the offspring tail length in each generation)
- 25 - females (since females produce daughters with the same tail length as themselves, these blank cards are not essential except to record changes due to mutation)

Mutation Cards:

These cards are not sex specific so they could be printed on white card stock.
- 10 - Random Mutation, Tail Length Increases 1 Unit
- 10 - Random Mutation, Tail Length Decreases 1 Unit

Predation Cards:

These are optional but may help remind students to apply predation every generation.

Need one card per group.

Sample Cards

Examples of cards, set-up in 2” x 3.5” format, are given in the Appendix.

Previous Results

Blumer conducted this game with upper-level undergraduate students in an ecology lecture course. Time was extremely limited and there was only 45 minutes available to actually conduct the game. Nonetheless, groups of 4-5 students performed three or four rounds of selection and prepared frequency histograms of their results in class. Blumer created PowerPoint slides of those data and discussed them with the entire class at the next class meeting.

A representative frequency histogram is shown in Fig. 1.

Acknowledgements

Blumer thanks his students in Ecology (BIO 320) Spring 2011, at Morehouse College, for enthusiastically testing this simulation. Zuk is grateful to the attendees at the workshop on sexual selection at the 2009 meeting of the Animal Behavior Society, as well as to Regina Macedo for the invitation to present the workshop.

Literature Cited

Blumer, L.S. and C.W. Beck. 2010. Inducing Evolution in Bean Beetles. Pages 25-35, in *Tested Studies for Laboratory Teaching, Volume 31* (K.L. Clase, Editor). Proceedings of the 31st Workshop/Conference of the Association for Biology Laboratory Education (ABLE), 534 pages.

About the Authors

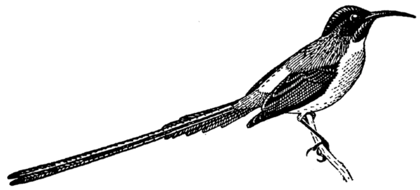
Marlene Zuk earned her Ph.D. from the University of Michigan in 1986 and she is Professor of Biology at the University of California, Riverside. Her research centers on sexual selection and the effects of parasites on mate choice and the evolution of secondary sex characters. She is also interested more generally in the influence of parasites on host ecology and evolution.

Larry Blumer earned his Ph.D. from the University of Michigan in 1982 and he is Professor of Biology and Director of Environmental Studies at Morehouse College. He teaches ecology, environmental biology, and introductory biology. His research interests are in the development of effective pedagogy in the sciences, and the evolutionary biology and social behavior of insects and fishes.

Brian Gray is a Ph.D. candidate at the University of California, Riverside, studying the consequences of a rapid evolutionary change in sexual signaling in field crickets. He has participated in a number of education initiatives designed to encourage participation by underrepresented groups in science.

Appendix

1



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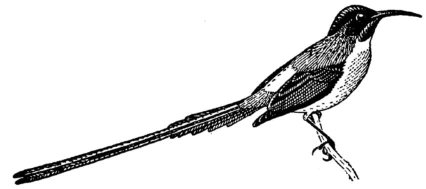

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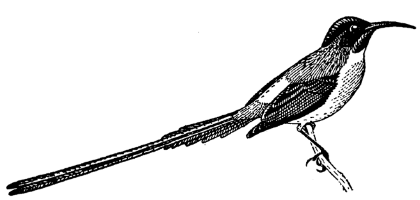

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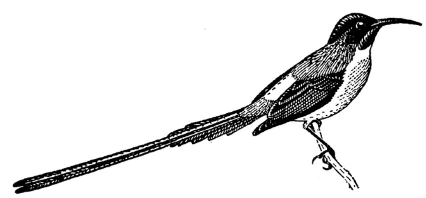

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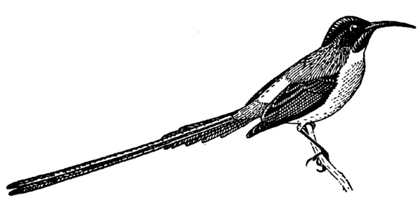

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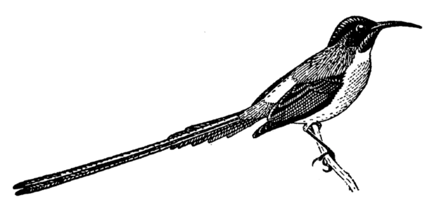

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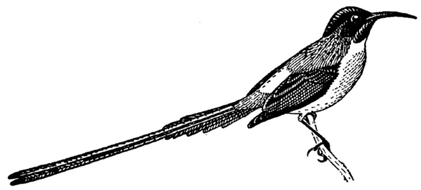

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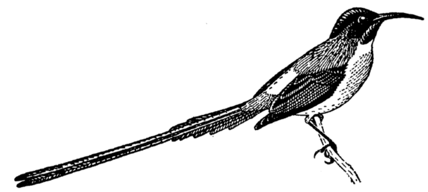

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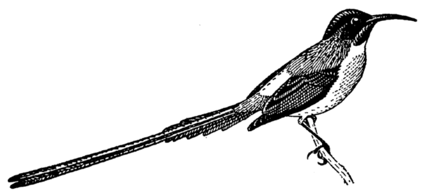

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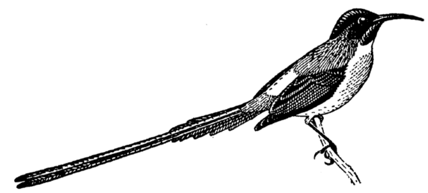
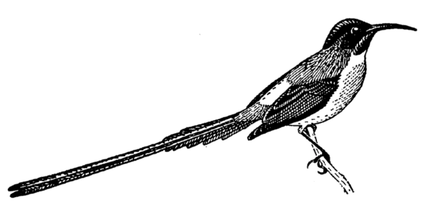


[ ] trait value



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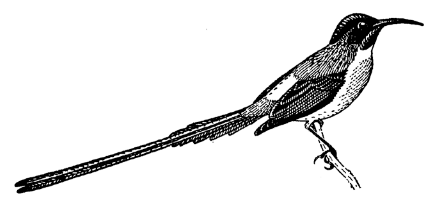
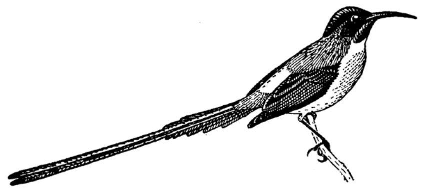
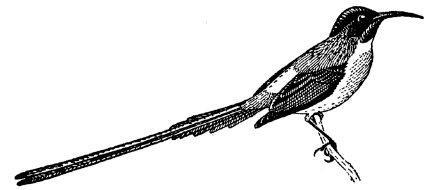


Random Mutation



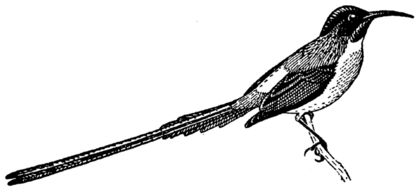
Tail Length Increases 1 unit

Random Mutation



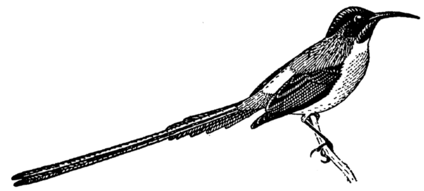
Tail Length Increases 1 unit

Random Mutation



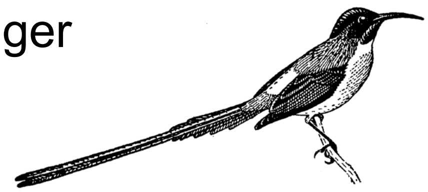
Tail Length Decreases 1 unit

Random Mutation



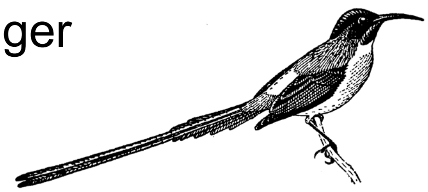
Tail Length Decreases 1 unit

Predation on birds with tails 4 and longer



Remove 5 offspring

Predation on birds with tails 4 and longer



Remove 5 offspring

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Citing This Article

Zuk, M., Blumer, L.S., and Gray, B. 2012. Runaway Sexual Selection Simulation Game. *Tested Studies for Laboratory Teaching,* Volume 33 (K. McMahon, Editor). Proceedings of the 33rd Conference of the Association for Biology Laboratory Educa-tion (ABLE), 390 pages. http://www.ableweb.org/volumes/vol-33/?art=40