

# Evolution by Natural Selection in Oldfield Mice

by

Katherine S. LaCommare, Department of Natural Sciences, University of Michigan–Dearborn

Peter A. Van Zandt, Department of Biology, Birmingham–Southern College

## Introduction

Notable for their two-toned fur color, their ability to jump, and the fact that they have been “trapped in nearly every patch of North America” (Osgood, 1909), deer mice (*Peromyscus spp*) are a ubiquitous fixture throughout the United States (Bedford & Hoekstra, 2015). Known to live in nearly every type of habitat—old fields, wetlands, forests, mountains—ecologists have long observed that their coat color varies dramatically depending on the habitat in which they live. In the western United States, where they live on dark soils, their fur is nearly black. In the southeastern part of the country, where they live on beaches, their fur can be white (Figure 1). Their ecology varies in a myriad of other ways as well. They are omnivorous and are known to eat seeds, fruit, insects and even other small vertebrates. They have a wide variety of visually-oriented predators including owls, hawks, foxes and wild as well as domesticated cats.

Ecologists have been interested in the natural variation found in this genus since the turn of the twentieth century (Osgood, 1909). Francis Sumner, a mid-twentieth century natural historian, studied oldfield mice (*Peromyscus polionotus*) in the southeastern United States. Like deer mice in general, oldfield mice exhibit tremendous geographic variation in coat color (Sumner, 1929). The principal question that has interested Sumner and other ecologists is how natural selection may have influenced and may be influencing this variation. He, and more recently others, have investigated the adaptive nature of coat color (Kaufman, 1974; Vignieri, 2010). And, most recently, Hopi Hoekstra has been uncovering the role of genetics in this geographic variation.

One interesting feature of this story is that oldfield mice (*Peromyscus polionotus*) are known to inhabit barrier islands along the coast of the Gulf of Mexico and that the mice on these beaches have very blond, or white, fur. These islands were formed about 6,000 years ago and are an excellent natural laboratory for trying to understand how natural variation, selection, and genetics may have led to the evolution of exceptionally light fur (Figure 2).

In this case study, you will be working in groups to analyze graphs and data from decades of research on oldfield mice (*Peromyscus polionotus*). By examining data on phenotypic variation, genetics, inheritance patterns, and the potential selective advantage of fur color, you will be able to piece together how these beach mice have evolved through natural selection to have white or blond fur on the beaches along the coast of the Gulf of Mexico and the east coast of Florida.

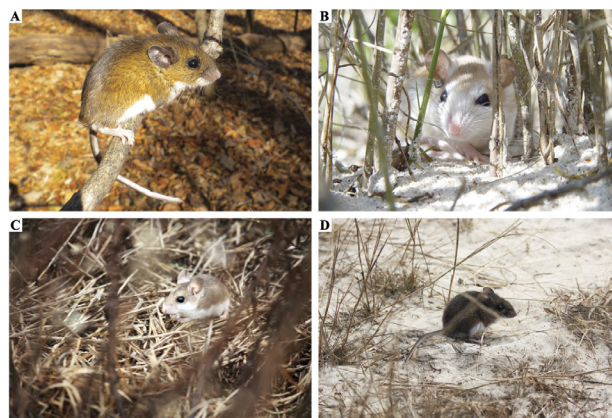


Figure 1. Mice in various habitats. Credits: A: Evan P. Kingsley; B: J.B. Miller; C, D: Nicole Bedford. <https://doi.org/10.7554/eLife.06813.005>. Source: Figure 3 in N.L Bedford, H.E. Hoekstra, 2015, CC BY 4.0.



Figure 2a: Barrier island along the Gulf coast.  
2b: Alabama beach mouse.

## Part I – Variation

### A. Predicting Variation

Natural selection cannot take place without the existence of phenotypic variation. Ecologists have been interested in the variation of fur color for nearly a century. Your first task is to consider what Francis Sumner may have found when he first started trapping mice 90 years ago.

Sumner (1929) collected samples of mice from several locations in Alabama and Florida (Figure 4). He scored the pelts (Figure 5) on a scale from 7 to 22, with higher numbers indicating darker mice.

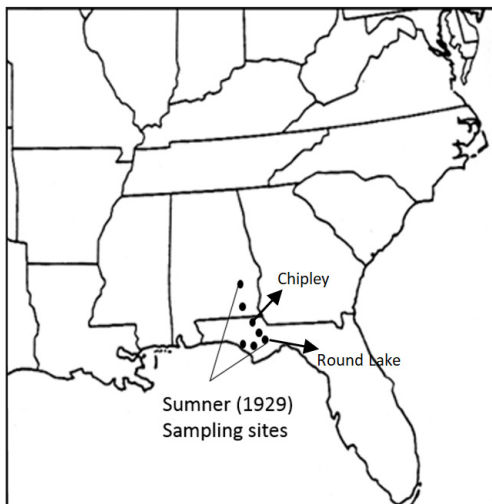


Figure 3. Francis Sumner's sampling sites in Alabama and Florida. Estimated from Sumner (1929). Credit: Katherine LaCommare and Peter Van Zandt.



Figure 4. Mouse pelts. Source: Figure 4 in Bedford & Hoekstra (2015).

### Question

1. Make a prediction. Given what you know about variation in natural populations, draw a histogram of mouse coat color for the sampling site called Chipley (see Figure 3). This population of mice is in a forested habitat. A histogram is a graph that shows the distribution of continuous data. The number of mice should be on the y-axis and color score on the x-axis and the bars should touch. Assume a sample size of 100 mice.

### B. Sumner's Results

In 1929, Sumner *et al.* published a paper detailing the phenotypic variation of oldfield mice in Alabama and Florida (Figure 5). In the previous exercise, you predicted variation for the Chipley Site. This figure shows data collected from a second location, Round Lake, which is also a forested habitat. The questions below ask you to consider these data. As you consider the characteristics of the populations, avoid making any inferences as to why the populations have specific characteristics and just describe the population.

#### Questions

2. Annotate the figures in a way that shows that you understand the data.
3. Do Sumner's figures resemble the histogram that you drew? Explain.

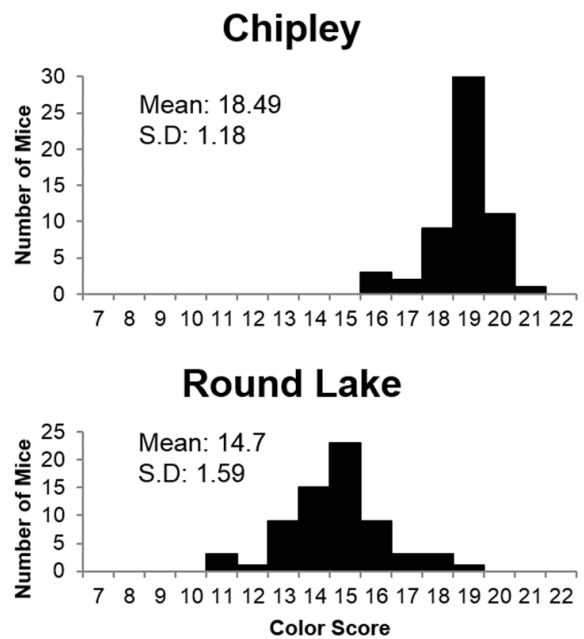


Figure 5. Number of mice with each coat color score at the Chipley and Round Lake sampling sites. Rescaled and redrawn from Sumner *et al.* (1929).

4. Redraw one of these histograms assuming that individuals within a population *do not* vary in their traits.
5. Examine Sumner's results above (Figure 5), thinking about both the variation among individuals within a population and variation among populations. Describe the data that you see in these two graphs. List at least two observations about the variation within a single population and two observations about the variation among populations.
6. Why do the data in Figure 5 look the way they do? Make a bulleted list of all of the factors that could influence the distribution (spread, mode, etc.) of coat color both within and among populations. What is the source of new alleles in a population (that is, where does genetic variation ultimately come from)?

## Part II – Heritability

### A. Determining Heritability

As a biologist, you are very intrigued by the geographic variation in phenotype that you have noticed in these mice. You know that natural selection can only act on traits that display phenotypic variation within a population. You have also found it interesting that different geographic locations have different coat colors. For example, you noticed that Round Lake has lighter mice than Chipley. Why? You also know that phenotypic variation must be linked to genetics and heritability for natural selection to take place. You are eager to investigate the heritability of fur color.

#### Questions

1. In your own words, what does heritability mean?

Recall that many quantitative traits are heritable and this can be suggested by a parent-offspring regression. For example, a graph illustrating the heritability of human height would look like the figure on the right (Figure 6).

2. Redraw this graph in a way that suggests heritability in the coat color of oldfield mice.

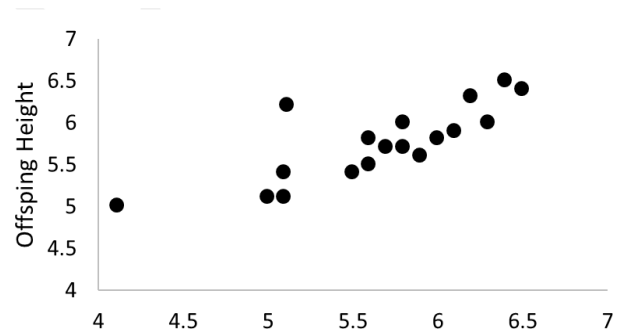


Figure 6. Height (in feet) of parents and their offspring.

3. Create a second graph that assumes there is no genetic component or heritability to fur color.

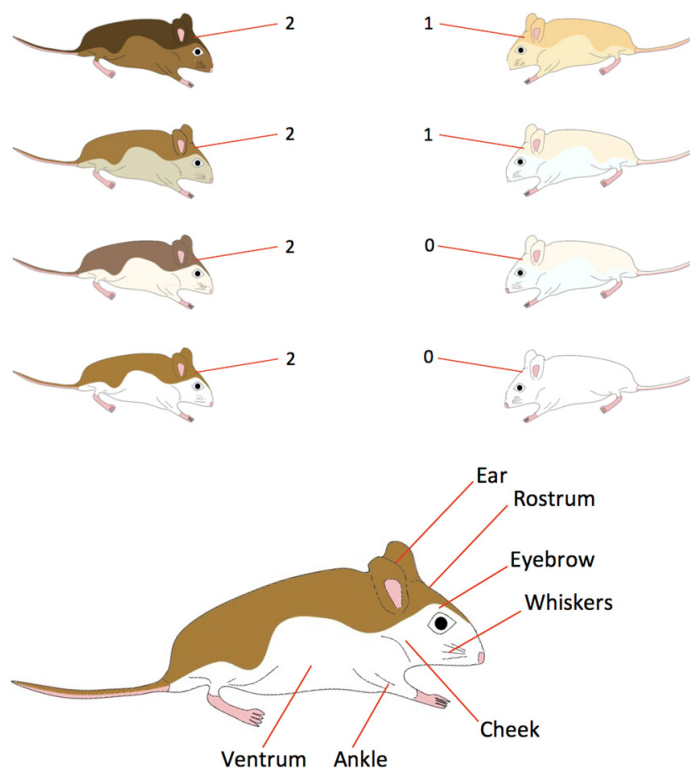
## B. Heritability and Genetics

Heritability is the link that allows biologists to estimate how much population-level phenotypic variation is linked to individual genetic variation. Like geographic variation, biologists have been interested in this link for centuries. Understanding the origins of genetic and organismal diversity requires understanding how genes influence traits in the organism (Hoekstra, 2006). Hopi Hoekstra and others have been working recently to understand how specific genes influence coat color in mice and other mammals. One of those is the *Mc1r* gene, which has two alleles (light and dark). A second gene is called *Agouti*. She and her team have also identified a third gene known as *Corin* (Pennisi, 2009).

The *Mc1r* gene and its alleles is the best understood. The *Mc1r* gene influences the color of mouse hair via the production of pigment. Dark hair is produced by high levels of pigment called eumelanin. Hair with lower levels of eumelanin appears lighter. *Mc1r* has at least two known alleles: the typical, or “wild-type” version (referred to as the  $M^R$  allele) produces regular levels of eumelanin. The mutated version (called the  $M^C$  allele) dampens pigment production and leads to lighter hair color.

In an attempt to better understand the genetic connection between genes like *Mc1r* and coat color, Hopi Hoekstra *et al.* (2006) did a controlled cross between dark colored mice ( $M^R M^R$ ) and blond mice ( $M^C M^C$ ) to produce first generation hybrids ( $M^R M^C$ ), and these F1s were crossed to produce second generation hybrids (F2s). There were a total of 459 F2 offspring.

Individual mice in the F2 generation were then scored for their phenotypes. The categorical scores were based on the pigmentation pattern of individual hairs on the rostrum and back. Each mouse was scored as follows: 0, unpigmented hair; 1, partially pigmented hair; and 2, fully pigmented hair (Figure 7, top). She was also able to determine the genotype for each mouse. Data from Hoekstra *et al.* (2006) are also shown in Figure 7 (bottom). The total number of F2s with each phenotypic score is partitioned by *Mc1r* genotype for the rostrum.  $M^R M^R$  is homozygous for the dark *Mc1r* allele,  $M^R M^C$  is heterozygous, and  $M^C M^C$  is homozygous for the light *Mc1r* allele.



Trait	<i>Mc1r</i> genotype	Phenotypic Score		
		0	1	2
Rostrum	RR	0	0	126
	RC	0	40	175
	CC	49	42	27

Figure 7. Fur scoring system. Number of mice whose rostrum scored 0, 1, or 2 given the individual's genotype. Image Credit: EvoEd Cases for Evolution Education. <http://www.evo-ed.com/Pages/Mice/index.html>

### Questions

4. Transform these data into a bar graph. Put genotype on the x-axis and the proportion of F2s with each phenotype on the y-axis. Note any questions that arise.

5. Does the *Mclr* gene appear to follow a dominance/recessive inheritance pattern? Why or why not?
6. What role does the *Mclr* gene play in mouse fur color? Are there other genetic or environmental factors that might also influence fur color? If so, what are they?
7. Discuss the role of genetics for the evolution of fur color by natural selection in these mice.
8. Given the above information and the proportion of individual mice with light, medium and dark fur in the Round Lake population predict the proportion of each allele ( $M^R$  and  $M^C$ ) in this population. Remember: your graphs are just estimates and your estimates don't need to be perfect.

## Part III – Selection

### A. Clay Mice

One question remains: does the fur color of mice confer a selective advantage? In a 2010 paper, Vignieri *et al.* (2010) made models of mice out of dark and light colors of clay, and placed them in two separate habitats that had different colored soils. When they collected the models, they recorded the number of tooth and bill imprints made by visually oriented predators like birds and mammals.

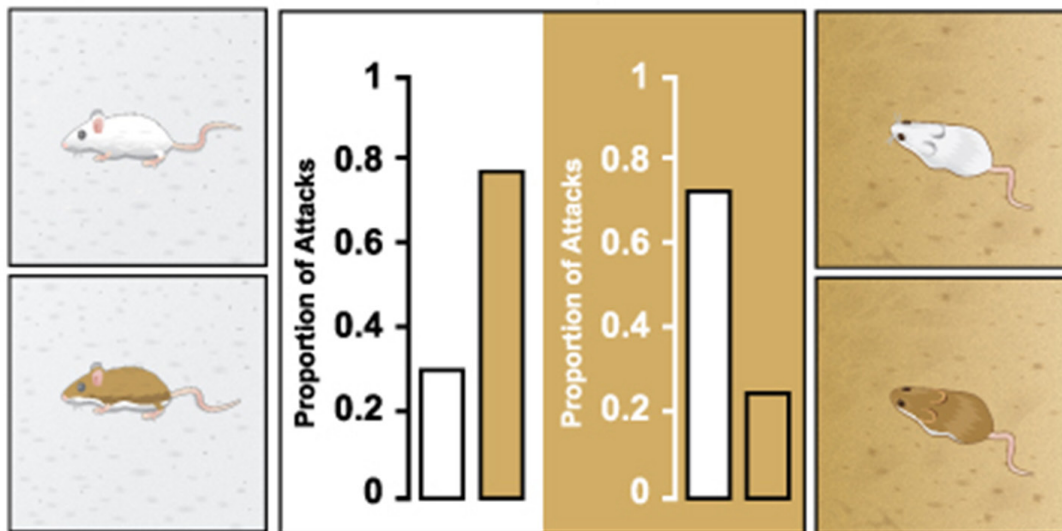


Figure 8. Redrawn from Vignieri, Larson, & Hoekstra (2010).

### Questions

1. Examine and annotate the Figure 8.
2. Discuss the fitness consequences for mice that are mismatched for their environment.
3. Considering only the results of this one experiment, rank your level of confidence in the interpretation that mouse fur color has fitness consequences (use a scale of 1–5, where 5 is absolutely convinced, 3 is neutral, and 1 is unconvinced). Justify your choice.

### B. First Caught

Kaufman (1974) tested the nighttime hunting behaviors of barn and screech owls. He put equal numbers of both light and dark deer mice in both dark and light soil color enclosures. He then recorded which color of mouse was captured first by the owl.

In the dark soil treatment, owls caught the dark mouse first 37% of the time and caught the light mouse first 63% of the time. In the light soil treatment, owls caught the dark mouse first 64% of the time and caught the light mouse first 36% of the time (Figure 9).

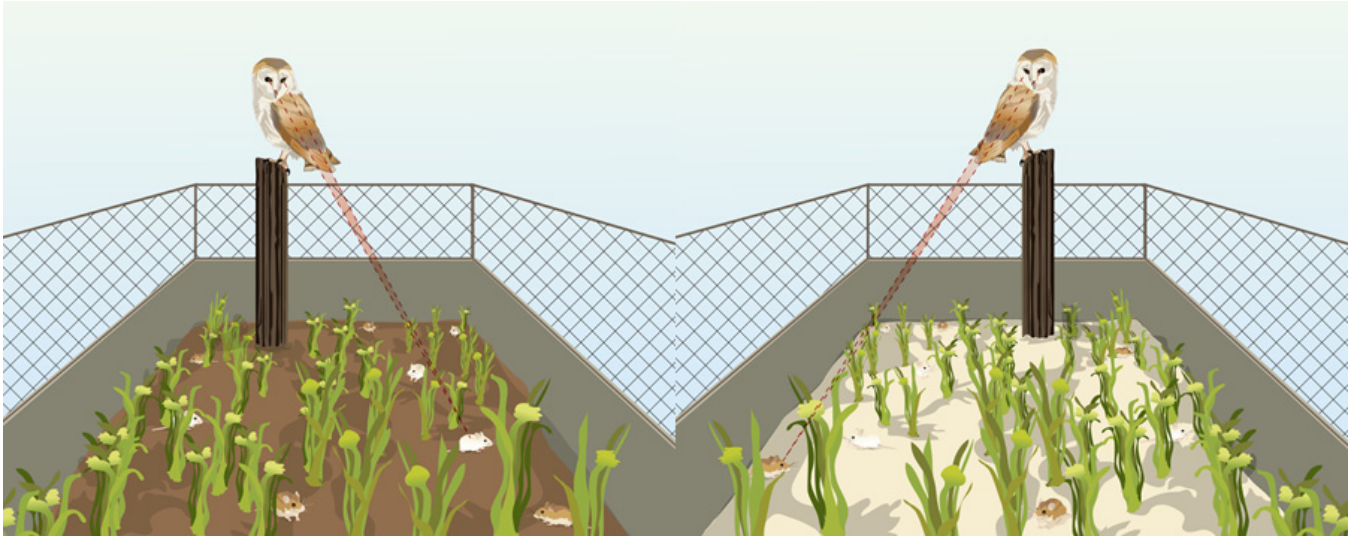


Figure 9. Kaufman placed light and dark mice in enclosures with either light or dark soil. Credit: EvoEd Cases for Evolution Education. <<http://www.evo-ed.com/Pages/Mice/index.html>>.

### Questions

- Imagine that the light soil treatment was replicated in an area the size of a football field with hundreds of mice and several owls. Make a figure that shows the phenotypic variation of the mice in the large area before, and then again after the owls have had several days to hunt in the arena. Along with your figure, give a brief written description of what would happen to the distribution of phenotypes of mice in these conditions.
- Given the results of both experiments in Part III, what are the fitness consequences for mice that are mismatched for their environment? Rank your level of confidence again, justifying your answer.



## Part IV – Results

Imagine you have a time machine and are able to go back in time to 6,000 years ago. You are standing on newly formed Santa Rosa Island, a barrier island off the coast of Florida that consists entirely of beach habitat. You see that a large and genetically diverse mainland population of oldfield mice have just colonized the island.

Using all of the information in this case study, answer the following questions and justify your answers with reasoning.

### Questions

1. Draw a histogram representing coat color for the initial colonists on the island. Write a brief statement justifying your graph. Describe the population in terms of the proportion of light, medium, and dark individuals.
2. Assuming that this population successfully colonizes the island and persists until the present, add a histogram of the 21<sup>st</sup> century island population to your figure (make sure that they can be easily compared to each other). Describe the population in terms of light, medium, and dark individuals. Write a brief statement justifying your graph and answer.
3. Draw two bar charts illustrating how you think the proportion of the *Mc1r* wild-type and mutant alleles ( $M^R$  and  $M^C$ ) changed over time.
4. (a) How would your answer to Question 1 and 2 change (if at all) if the initial colonizing mice were phenotypically and genetically uniform and the *Mc1r* gene never experienced any mutations in 6,000 years? (b) How would your answers to Question 1 and 2 change (if at all) if there is phenotypic and genetic variability, but no clear relationship between parents and offspring? Be sure to reference your graphs to justify your answer.
5. How would your answer to Question 1 and 2 change (if at all) if Santa Rosa Island only had predators like snakes that relied on olfactory cues and heat sensing when hunting as opposed to visual cues (movement, coloration, etc.) relied on by birds of prey? Provide both a written description as well as a figure.
6. Explain how evolution by natural selection changed the population from the one described by the histogram you drew for Question 1 to that described by the histogram you drew for Question 2. Your answer should describe the initial population, explain how the three conditions of evolution by natural selection acted on the population, and how the population changed in terms of proportions of phenotypes and genotypes between the two populations.

### Literature Cited

- Bedford, N.L. and H.E. Hoekstra. 2015. The natural history of model organisms: *Peromyscus* mice as a model for studying natural variation. *eLife* 2015; 4:e06813. DOI:10.7554/eLife.06813.
- Hoekstra, H.E., R.J. Hirschmann, R.A. Bunday, P.A. Insel, and J.P. Crossland. 2006. A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science* 313(5783): 101–4. DOI:10.1126/science.1126121.
- Hoekstra, H.E. 2006. Genetics, development and evolution of adaptive pigmentation in vertebrates. *Heredity* 97(3): 222–34.
- Kaufman, D.W. 1974. Adaptive coloration in *Peromyscus polionotus*: experimental selection by owls. *Journal of Mammalogy* 55(2): 271–83.
- Osgood, W.H. 1909. Revision of the mice of the American genus *Peromyscus*. *North American Fauna* 28: 1–285. DOI:10.3996/nafa.28.0001.
- Pennisi, E. 2009. How beach life favors blond mice. *Science* 325(5946): 1330–3. DOI:10.1126/science.325\_1330.
- Sumner, F.B. 1929. The analysis of a concrete case of intergradation between two subspecies. *Proceedings of the National Academy of Sciences of USA* 15(2): 110–20. DOI:10.1073/pnas.15.2.110.
- Vignieri, S.N., J.G. Larson, and H.E. Hoekstra. 2010. The selective advantage of crypsis in mice. *Evolution* 64(7): 2153–8. DOI:10.1111/j.1558-5646.2010.00976.x.



*Acknowledgements:* We would like to thank Eli Meir and John Roach for their feedback, support, and guidance on the case study. This work was supported through a workshop sponsored by SimBiotic Software and QUBES (<http://qubeshub.org>) and was built to accompany SimBio's Evolution for Ecology interactive chapter. It was supported in part by National Science Foundation grants DUE 1446269, DUE 1446258, and DUE 1446284. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.