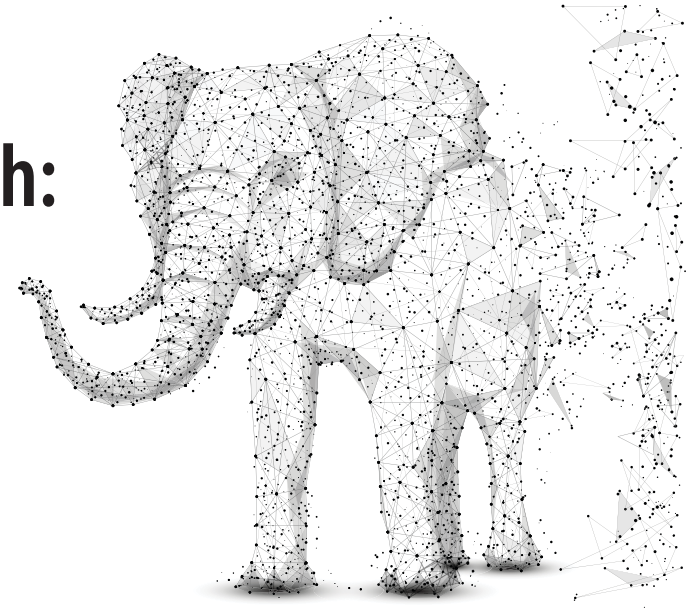
NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

No Longer Long in the Tooth:

Tusklessness in African Elephants



by

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Part I – Big Teeth Have Big Benefits

Mark and Bethany are game design majors working in the computer lab on a safari adventure game for one of their classes. In the process of designing the game, they want to recreate the African wildlife as realistically as possible.

"What animal should we add first?" Mark asked.

"Elephants! We have to have African elephants. They're the first animals I think about on a safari," replied Bethany.

"Well, they're the largest land mammals in the world. There are probably millions of them. That sounds like a good animal to start with," said Mark.

"We want our game to be realistic. Let's watch some YouTube videos on elephants so we can get their anatomy and movements right. I've never drawn trunks or tusks before," suggested Bethany.

"I'm all for that; watching elephant videos as 'research' sounds good to me," said Mark.

Before continuing, watch the following video to learn more about African elephants: <https://youtu.be/K8EVQdIUWBE>

"Wow, there's a lot to unpack there. Elephant populations have really declined. I knew elephant tusks were valuable and that elephants are killed for their ivory, but I didn't realize that poaching is actually changing the way elephants look. Tuskless African elephants? I had no idea!" said Bethany.

Questions

1. Elephants are a keystone species because they have a large influence on their communities relative to their own abundance. Specifically, as ecosystem engineers, elephants influence their communities through changes they make to the structure of their habitats. Describe how elephants act as ecosystem engineers. How might other species be affected by an increase in tuskless African elephants?

2. In the absence of poaching, what are the benefits of elephant tusks? Specifically, pick two of the uses of elephant tusks described in the video and explain how each increases an elephant's evolutionary fitness. *Hint:* remember that evolutionary fitness depends on an individual's reproductive output.

3. African elephants in Gorongosa National Park have undergone a genetic bottleneck. A bottleneck occurs when natural disaster, disease, or human influence creates a dramatic decrease in a population. When such a decrease is followed by a population increase, the rebounding population typically has reduced genetic diversity. Explain the cause of the bottleneck in the Mozambican African elephant population. Why were the elephants targeted?

4. African elephants have one of the longest gestation periods in the world. They are pregnant for nearly two years and do not reach sexual maturity until they are around 14–17 years old. Explain how these life history traits would affect the recovery of African elephants from a population bottleneck.

5. The video mentions that tusklessness normally occurs in about 2–6% of elephants and is only observed in females. Considering this is a genetic trait, what must have happened at the molecular level to cause the tuskless allele?

6. After the Mozambique Civil War, about 50% of older females were tuskless and about 33% of females born after the war were tuskless. How would poaching cause an increase in tuskless females?

Part II – Tusk and Tooth Formation

"Oh, those poor elephants! It makes me sick to think of so many being killed simply for their tusks. At least they were able to adapt and cause a mutation to make them tuskless," said Bethany.

"Wait, Bethany. I think you're confused about the nature of mutations. The trait for tusklessness was already present before the Mozambique Civil War. Remember, the video said that normally 2–6% of elephants are tuskless? It's just that those without tusks weren't killed so they were able to have more baby elephants and pass on the tuskless trait to their babies," clarified Mark.

"Oh, so the war or poaching didn't cause the mutation?"

"No, the frequency of the mutation increased in the population because of the war and poaching so it became more prevalent and you saw more elephants that were tuskless," explained Mark.

"Thanks for clearing that up. That video had so many interesting facts. Did you catch that tusks are really incisor teeth?" said Bethany.

"I know, right?! Imagine having to brush those two times a day."

Bethany paused a moment and said, "How do you think elephant teeth and tusks are made?"

"I don't know, but let's find out. I know that the outer coating on teeth is called enamel and it's the hardest substance found in any living organism. Let's start there," suggested Mark.

After a quick Google search, they found that enamel is made of 95% hydroxyapatite.

"Hydroxyapatite? What's that?" asked Bethany.

After reading a bit more, Mark replied, "Hydroxyapatite is just a fancy word for calcium phosphate, a mineral. Remember when your mom said to drink milk for healthy teeth and bones? Well, the calcium in milk is used to make the calcium phosphate or hydroxyapatite. It says here that hydroxyapatite is also used to make bones. Bone contains only about 60% hydroxyapatite so it isn't as hard as tooth enamel. Plus, bone can regenerate and repair itself, but teeth can't."

"Cool! I had no idea that we'd learn about teeth and bones when we decided to have elephants in our safari game. I'm curious, though. How does the hydroxyapatite get into our teeth?" asked Bethany.

"What do you mean?"

"Well, it's a mineral, right? How does that mineral become enamel?"

"Hmm…Google has gotten us this far. Let's see what else we can learn."

"Well," said Mark after a few more minutes of research, "this paper from Welborn (2020) that I found on Google Scholar says that hydroxyapatite forms crystals that have an elongated or rod-like shape. In order for the crystals to form though, they need a scaffold to grow on. A protein called amelogenin is used to make the scaffolding. Calcium and phosphate are seeded in the amelogenin scaffold and calcium phosphate (hydroxyapatite) crystals form and start to grow. As the crystals continue to grow they also harden until they form enamel rods. Once the hydroxyapatite forms the enamel rods, the amelogenin degrades, leaving behind only the crystals, which we see as solid tooth enamel (Welborn, 2020). This is why the tusks of elephants appear to have striations on them, since the enamel builds in layers on top of each other due to the rod structures growing towards each other."

Questions

1. Describe how amelogenin contributes to enamel formation.

2. Describe how a lack of amelogenin would affect tooth formation.

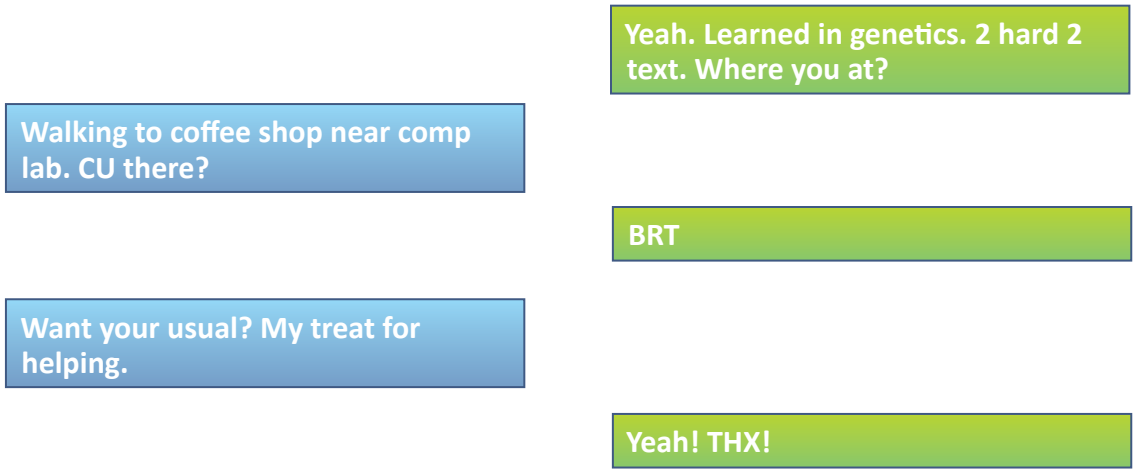
Part III – Tusklessness in Female African Elephants

"Cool, but how does this relate to tuskless elephants?" asked Bethany.

"Well," said Mark, "it gets really confusing here, something about sequencing, chromosomes, deletions, and gene dosage. I think I'm in over my head. My roommate Liam is a biology major. I'll text him and see if he can help us make sense of this."

"You know, we've been working on this for a while. Want to take a break and walk over to the coffee shop while we wait for Liam to reply?" asked Bethany.

On the walk over, Mark received a text reply from Liam:



Mark and Bethany got the drinks and sat down at a table to wait for Liam. He soon arrived and joined them.

"I'm really surprised you texted me about tuskless elephants. We just learned about that in genetics class last week. Did you guys know that tusks are really teeth?" Liam asked.

"Yeah, we watched a video and learned that. We think we have teeth formation figured out, but when we were trying to understand how tooth formation relates to tuskless elephants, we got lost. Too many big words!" replied Mark.

"Let me try to break it down for you," said Liam. "Tusklessness is a genetic trait. This means it's caused by a mutation in the DNA that can be passed down from parent to offspring. Mutations can be small changes, like the deletion or addition of a single nucleotide that affects a single gene. Or they can be large like a deletion or addition of a large section of the chromosome that can affect multiple genes. Scientists wanted to identify the genes and alleles that are likely responsible for the tuskless trait in elephants from Gorongosa National Park. They collected blood samples from elephants and sequenced their DNA. Tuskless individuals had an X chromosome with a large deletion comprising a region of 23 genes. Interestingly, one of the 23 deleted genes was a gene called *AMELX* that is responsible for making amelogenin. Without the gene *AMELX*, the amelogenin protein isn't made."

"Oh! We read about the importance of amelogenin in enamel formation! Amelogenin creates a scaffolding matrix that allows the hydroxyapatite crystals to form and grow enamel," said Bethany.

"So," asked Mark, "does that mean that the reason elephants are tuskless is because the mutation resulting in the deletion of the *AMELX* gene means that they can't make the amelogenin protein and don't form the matrix that allows the hydroxyapatite crystals to grow?"

"Yes, exactly!" replied Liam.

"Oh, poor elephants! Not only are they tuskless, but they don't have any teeth," exclaimed Bethany.

"Well, actually, they do have teeth in their mouth. The only 'teeth' that don't get made are their tusks," replied Liam.

"What?! How is that possible?" asked Mark. "I thought without *AMELX,* enamel wouldn't form."

"The answer to that question has to do with gene dosage, which is all about the number of copies of a gene in a genome that can affect how much of the protein that gene codes for gets made," replied Liam.

Questions

1. *AMELX* is on the X chromosome. Explain why the gene dosage for *AMELX* differs between males and females. For this question, assume that the *AMELX* gene is not affected by X-inactivation (Carrel & Willard, 2005).

2. Complete the table below connecting gene dosage to the genetic terms homozygous, heterozygous, and hemizygous to explain the genotypes of tusked and tuskless female and male elephants. (Hemizygous means that only one copy of the gene is present.)

Phenotype	*Homo/hemi/heterozygous for* AMELX *locus?*	*How many functional copies of* AMELX*?*	*How many* AMELX *deletions?*
Tusked females			
Tuskless females			
Tusked males			
Tuskless males			

3. How does gene dosage explain why female tuskless elephants make mouth teeth, but not tusks?

4. The tuskless trait is only found in female elephants. Propose a genetic hypothesis for why male elephants are not tuskless.

Part IV – Lethality of Tusklessness in Males

Bethany was beginning to understand, but she still had some questions. "Wow! So, gene dosage can be different between males and females for the genes present on the X chromosome. But that doesn't really explain tusked and tuskless males. If males have only one X chromosome with *AMELX,* shouldn't they make the same amount of amelogenin as heterozygous females? Wouldn't that make all males tuskless?"

"Well," began Liam, "it turns out that there's a gene on the Y chromosome called *AMELY* that also makes amelogenin. Males with tusks actually have two genes for making amelogenin. One is on the X chromosome and one is on the Y chromosome. Tusked males are able to make as much amelogenin as tusked females because of these two genes."

"I understand that," replied Bethany, "but I still don't get why males aren't tuskless. If they have *AMELY* on the Y chromosome and the *AMELX* deletion on the X chromosome, shouldn't they make approximately the same amount of amelogenin as females heterozygous for the deletion? Wouldn't that cause tuskless males?"

Liam responded, "Remember when I told you that the deletion that causes tuskless females didn't just delete the *AMELX* gene, but also deleted 22 other genes? It turns out that one of those other deleted genes is called *HCCS* and it's right next to *AMELX* on the X chromosome. There's not a copy of *HCCS* on the Y chromosome. *HCCS* is necessary for an embryo to develop properly, so deletion of *HCCS* causes death in utero."

Bethany nodded her head with satisfaction. "Ahh, now I get it; *that's* why there aren't tuskless males."

Questions

1. Using genetic terms, explain why there are no tuskless males, but there are tuskless females.

2. If a wildtype male and a tuskless female elephant were to mate, what would be the phenotypic ratio of their offspring? How many offspring would survive to birth? Write out the cross and draw a Punnett square to answer this question.

Part V – It All Depends…

"Ok, Liam, you've convinced us that we need to add in some tuskless female elephants for the most accurate game experience. This has me thinking though; isn't it bad from an elephant's perspective to be tuskless?" asked Mark.

"That's right," replied Liam. "Tuskless female elephants have a harder time gathering food and water and defending their young from predators. Also 50% of their male embryos died in utero, so all of the energy and resources that they expend on those particular embryos doesn't actually contribute to their fitness. Definitely not good for the elephants!"

"If it's so bad to be tuskless, why did the number of tuskless females increase as a result of the Mozambique Civil War?" asked Mark, struggling to understand.

"That has to do with selection and evolution. Selection favors those with adaptations that increase the overall reproductive success of individuals, which is known as fitness."

"Right,"said Bethany, "so with all the benefits of tusks, shouldn't tusks always increase the fitness of female elephants?"

"That's where things get complicated," said Liam. "As my ecology professor always reminds us, which particular traits are the most beneficial for individuals in a population always depends on that population's environment. In an environment without poaching, absolutely, the presence of tusks should increase an elephant's fitness. But during the war, elephants were poached for the ivory in their tusks because revenue from ivory sales was used by both sides to fund the war. Elephants with tusks were very likely to be killed by humans, while elephants without tusks would not be targeted by humans. Poaching is such a strong selective force that even with all the disadvantages of not having tusks and losing half their male embryos, tuskless females will still have a higher reproductive output than tusked females who are killed for their tusks before they ever have an opportunity to reproduce. The intense selective pressure of poaching allowed the seemingly disadvantageous trait of tusklessness to spread in the Gorongosa population of African elephants because it increased the likelihood of surviving long enough to reproduce."

"Wow, the video was right," said Bethany. "Humans are *literally* changing the face of elephants!"

Questions

1. Liam emphasized that the fitness benefits of a trait depend on a population's environment. Apply this concept to the following scenario: field mustard (*Brassica rapa*) is an annual plant, meaning that it reproduces only once before dying. Individuals in a population of field mustard vary in how long they grow before reproducing. Individuals that grow for longer before reproducing reach a larger size and can produce more seeds than individuals that start reproducing sooner. However, individuals that grow for a longer time before reproducing run the risk of dying before they get to reproduce.
    a. Which strategy would result in the greatest fitness during a year in which steady rainfall enables high survival rates of field mustard individuals? Explain why.

    b. Which strategy would result in the greatest fitness during a year in which drought conditions result in high mortality rates of field mustard individuals? Explain why.

2. Compare the fitness drawbacks of being tuskless in any environment to the fitness drawbacks of being tusked in an environment with poaching. Based on this comparison, what conclusions can you draw about the strength of the selective force caused by poaching?

3. Consider that the average frequency of tuskless female elephants in the Gorongosa population went from 2–6% to 33% in one generation. This is an enormous frequency change for a trait in a single generation! Come up with at least two other examples of very rapid evolution caused by human behaviors.

4. Explain one way that we as humans could help increase the elephant population (beyond "don't kill elephants").

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