

An Introduction to Evolutionary Biology

Prof. Sutirth Dey

Biology Department, Population Biology Lab

Indian Institute of Science Education and Research (IISER) Pune

Week 7 Lecture 38

Sexual Selection: Part 2

Hi. So, in our last discussion on sexual selection, we looked at a bunch of cases where there was male-male competition for access. Towards the female or the females were choosing for reasons that were pretty obvious regarding the benefits the females were getting. And then we talked about a bunch of observations related to sexual selection, particularly those where Let us say the males were dancing or that they had some very showy organs with no apparent purpose. And in all those cases, it did not seem that those flashy organs or dances were providing any kind of benefit to the female. And therefore, the question was why exactly the females were choosing them, I mean, because we know that the choice is there, the females do prefer the showier options. Or you know the males with more showy organs, or more showy dances, and so on. So, the question was what exactly the female was trying to choose. Now, obviously, we said that there are no direct benefits.

So, that implies that there are probably some kinds of indirect benefits to female fitness. Because if there are no indirect benefits, it is very hard to see why the trait is still present in the population. And one kind of indirect benefit that can be present is in terms of improving the fitness of the offspring. But how exactly can that happen? What kind of mechanisms will lead to such a thing happening? So, it turns out that there are several hypotheses that have been proposed over time. Many of these hypotheses have empirical validation.

We are going to talk about many of those validations. But at the same time, there are many kinds of controversies that also exist in the context of many of those hypotheses. We would not really get into the controversies, but we are going to, you know, briefly just touch upon a few things that do not make sense in the context of some of those hypotheses. So, the first thing is that the first hypothesis or first possible mechanism can be in terms of the sensory bias of females.

So, what is it? This suggests that the females have certain physiological sensory biases. So, for example, let us say you know there is a female or females of a particular species that just love the color red. And that bias has come about because of some underlying physiological, neurological, and neural reasons. The males have then ended up evolving traits that match those sensory system biases. And that is what explains the entire process of sexual selection that we see.

So, do we have any evidence for this? So, here is a study on male guppies from Trinidad. If you are a cricket fan in Trinidad and Tobago, you must know where it is. These are parts of the Caribbean islands. So, on these islands, you have the streams, and in these streams, you have a very famous fish known as the guppy. So, the male guppies often have these orange spots that you can see over here, right? Now, these orange spots are preferred by the females, and generally, the females end up preferring the males that have the biggest orange patches. Now, very interestingly, in the natural habitat of these animals, there are bright orange fruits that continuously fall into these streams from the trees. The guppies also tend to eat these bright orange fruits a lot; both the males and the females eat them. So, just to see if there is a preference for color or not. What Rod et al. did was take discs of different colors and toss them into fish tanks containing these guppies. And what they found was that both the males and the female guppy, they were pecking a lot more at the orange-colored discs than they were pecking at any other colored discs. In other words, they had a preference for the color orange. Interestingly, this was true for both males and females. Remember, the females are not orange-colored; they do not have the orange spots; it is only the males who have them.

So, both the males and the females are responding to the orange color. Which essentially means that they are not really mistaking the disc for mates, right? Because if that were the case, the males would not have responded, but here both sexes are responding. Then what they did was, Rod et al. ended up looking at multiple guppy populations. and tried to quantify the amount of preference they had for these orange discs.

And it turns out that the average amount of attraction for the orange discs varied across the populations. So, some populations had a greater preference for the orange discs, while other populations had a lower preference for the orange discs. Then what they did was quantify how strongly the females are attracted to the orange patches. And that is what we are showing you here. On the x-axis, you have the normalized data which is why you are getting both (-) and (+) on the x-axis as well as the y-axis. So, on the x-axis, they are showing you the number of pecks that the females made on orange discs. So, as you go from left to right, there is a greater preference for orange disks. And on the y-axis, they are showing you the strength of the female preference for the orange color. And you can see right away that there is a strong positive correlation between how much preference the female has.

For the orange color and how much preference it has for the orange colors in the males in terms of sexual selection. And you can see straight away that they are very strongly correlated. So, this suggests that the guppy's attraction to the orange fruit. May have driven the evolution of a sensory bias in both males and females. But then the males ended up exploiting it.

When I say males ended up exploiting this, I do not mean that they made a conscious decision to exploit it. All that might have happened is that different males would have had orange patches of varying sizes. The males that had larger orange patches ended up getting more matings, and therefore, More reproductive success and, therefore, increased fitness; that is how the trait ended up spreading in the population. So, in other words, in this particular case, the female preference is being directly driven by a simple food preference. which in turn is coming from, you know, the environment in which the

females ended up growing.

So, this is one way in which sexual selection could have arisen: indirect benefits. Then, you have what is known as the good genes hypothesis. What does it say? It says that whenever a male is showing off by having some bright color or some, you know, large oversized organ or something, Then, essentially, that is indicating that it has genes which are going to increase its fitness. So, in what ways? So, in terms of efficient metabolism or in terms of how good the condition of the body is, or its ability to resist parasites, diseases, and so on. So, in those cases, the female actually does not know anything about the male.

But it is simply taking those flashy organs, those dance moves, or whatever as an indicator of the quality of the male. So, just to give you an empirical validation of this. So, this is work done on a three-spined stickleback fish, and in this particular fish, The males have red-colored bellies, and the females end up preferring the brighter red colors in the males. So, what is shown here is the redness of the father. So, you can see the red color over there.

So, how bright and how big the red patch is, and that is what is going on the x-axis from left to right. And there were two different populations, and in both of these populations, what the researchers did was take The offspring from the various males ended up asking how resistant they are to tapeworms. So, here you have the percentage of offspring infected by tapeworms on the y-axis. So, obviously the greater the percentage the lower the resistance and vice versa. And what you can see is a clear negative correlation for both ponds, which suggests that the offspring of fathers Whose feathers were, or you know, offspring of fathers whose scales were bright red, are.

Much more resistant to parasites compared to those offspring whose fathers had less-bright red bodies. So, this suggests to you that in this particular case, the female can be using the redness of the father. As an indicator of how resistant it is, or as an indicator of the genes that it has to resist tapeworm infection. And of course, tapeworm infection

has all kinds of implications for the fetus. But in order for this entire thing to work, the signal that is being given here in red color in this particular case, The signal has to be true; in other words, what is known in the literature is that it has to be an honest signal.

What do I mean by that? Now suppose in this particular population of fish that there are some fish which end up evolving the red color. but that red color is not backed up by genes that provide it resistance to tapeworm infection. What will happen? The female is only looking for the red color; it is not looking for anything else. Therefore, in that case, the female is still going to prefer the red color. And yet, the ability to resist the tapeworm infection is not going to be present in the offspring, correct? So, if there is a cheater in the population that ends up giving the signal, but not paying the cost in terms of having those traits for which the signal is supposed to be an indicator then there is nothing evolutionarily speaking which will prevent the spread of such a cheating phenotype. So, how exactly can the signals be maintained, to be honest? That is a huge question. And one answer to this comes from the Israeli biologist Amotz Zahavi's so-called handicap principle. So, what Zahabi says is that all these secondary sexual traits— you know, all these feathers, colors, etc. These are known as secondary sexual traits; all of these are costly handicaps which means that they end up reducing the fitness of the males who possess them. And the fact that they are costly indicates that the males have high quality. Because otherwise, they could not have possessed them. In other words, if there is a very fit male who has a costly handicap, then that costly handicap is lowering its fitness. That is fine, but even then it still has a lot of fitness to spare; it still has a high fitness.

But if you have low-quality individuals, when they are trying to get that, you know, costly handicap, they cannot afford it. And that is why the presence of that signal itself guarantees the presence of a costly signal, which guarantees reliability. Now, in some sense, this is analogous to a phenomenon which in economics is known as conspicuous consumption. So, you know that many people go for luxurious goods, very, very expensive handbags, or very, very expensive designer clothes, etc. Where it is very clear that the cost you pay for that particular object does not reflect the manufacturing cost of that object yet people buy that to show off. People buy that to signal to other people that,

hey, I have this many, you know. extra amounts of money to spend on these fancy clothes, these fancy accessories, and so on. So, in other words, this is essentially wasting resources to prove that I have a sufficient amount so that I can afford to waste. And this handicap is what guarantees that the signal that the possessor of that particular thing is giving is real. Now, this is a somewhat controversial theory, and people have written both for and against it.

We are not going to go into the depth of the controversy at all, but the most important thing. What I want to tell you is that this is not something that people have totally accepted in the field. But at the same time, it is reasonably famous such that most textbooks on sexual selection.

Our evolution is actually going to talk about this theory, which is why I am, you know, mentioning it in this course. Now, contrast this with another scenario that was propounded by Ronald Fisher, which actually says that it does not really matter what the benefit of the trait is. So suppose there is a sexually selected trait. A preference for that trait assumes that both of these things are genetically coded and genetically linked.

So they go hand in hand. So if that is the case, then Fisher suggests that these two are going to reinforce each other which will lead to a rapid exaggeration of the trait. The canonical example of that is the tail of the peacock, and this particular hypothesis is also known as the sexy son hypothesis. Now, how exactly does it work? I mean, as I told you, there has to be a preference; there has to be a trait that is being selected. And they have to be somehow related to each other, but then how does the entire thing work? So, we will take the example of the peacock's tail, and we will try to explain it in terms of the mechanisms and the underlying mechanism.

So, the way it works is as follows. So, assume that somehow in the population there is a preference for females to choose long-tailed males as mates. So, this is right at the beginning when this thing is evolving, right? At that point, let us assume that somehow the females, let us say, through some kind of sensory bias or whatever. They have a

preference for the slightly longer tails. Now, if that is the case, assuming that both the preference and the long tails are genetically inherited, Then the offspring that come from such matings will inherit genes for both, right? Now, when that happens, what is happening in the context of the male? Of course, for the males, the longer-tailed males have more matings, so there is positive selection. So obviously, the number of individuals who have longer and longer tails is going to keep increasing in the population.

So these are will keep on having mating advantages and that is where the sexy son comes in. You know the sons become sexier and sexier, which means they end up getting more and more mating advantages. But what is happening to the female? Think about it. If the sons of the females are getting a greater mating advantage, then that is also beneficial for the female itself, right? And therefore, all those females who have a preference for the showy phenotype, the sexy sons, you know. They are also going to benefit because their grandsons and great-grandsons are getting more and more matings.

So, over time, the stronger preference becomes even stronger. There is a selection for strong preference in females. So, what is happening? The male's long tail is getting selected. The female's ability or choice for that long tail, or the preference for the long tail, is also being selected. So, both the cause and the effect are being selected in the same direction.

And as a result of that, there is, you know, an intensification of selection on both components. And because this happens, you have what is known as runaway evolution. Which basically means that the thing just keeps increasing in one direction without any checks. Now, obviously, if all these things are happening, the population's overall fitness is decreasing. Why is that so? Because, remember, the male is paying a cost for having that long tail.

That cost is getting offset because it is having more mating; that is a different ball game, but overall its fitness is actually going down. And because its fitness is going down, Then, in the case where the females did not have such a preference, its fitness is down.

But because the female has a preference, the male does not have an option. It has to have the long tail because otherwise its fitness is 0 or very low. So, that is why here is a situation where selection is making something increase continuously.

Even though on an absolute scale the fitness is going down, this is happening because on the relative scale, The males that have longer tails have greater fitness. So, here I said that there is going to be runaway selection, right? In other words, the cause and the effect will keep reinforcing each other; therefore, Both the preference and the length of the tail will continue to increase. Now, obviously, it cannot go up forever, because at some point or another, it is going to hit some kind of, you know, roadblock. What kind of roadblock is it going to face? When there are physiological or evolutionary limits that will be reached. If there is a balance between the gain of fitness due to sexual selection and the loss of fitness due to other reasons, like predation.

So, what do I mean by physiological limits? Of course, you know there is only a hard limit on how long a tail can be, right? Because at some point, the feather, if they are too tall, is going to become brittle, and they are going to break, or the amount of weight that the muscles of the bird can handle. A male bird can carry, but there will also be an upper limit on it at some point. So, those are what I mean by physiological limits. What do I mean by evolutionary limits? In terms of the genes, How long can you have variation at the genetic level to get longer and longer tails? So, those are the physiological and evolutionary limits, and of course, as I said.

The balance between the gain of fitness due to sexual selection and the loss of fitness due to other reasons. Now, has that kind of balance been reached at least under some situations? So, here is an empirical example to show that such a balance has indeed been reached In the context of this particular bird, known as the long-tailed widowbird. So, as you can see, this is the male; it has a very, very long tail. I also appreciate that when it is flying and making this display, it is creating a lot of drag. And it is kind of dragging down the flight of this particular bird.

Now, what was done here is that in this particular bird, the tails are often extremely long. You know more than half a meter, greater than 20; you know about 20 inches or so. So what the researchers did was create four groups. So this is an absolute textbook example of high-quality experimental design.

So in one case, what they did was cut the tails off the birds. So the tails are artificially shortened. In the other case, what they did was lengthen the tails by taking these cut pieces and attaching them to other birds. So these treatment B are birds whose tails are much longer than what you normally find in nature, supra long. And in this case, since you are cutting the tail, it is entirely possible that whatever results you are going to get is Because of the fact that you have injured the bird in some way, or you have, you know, somehow ended up mangling the bird. So, in order to control for that, what they did was cut the tails and attach them to the same bird.

So, if there is some effect of just the cutting itself, then these birds should have lower fitness compared to the others. and of course they had the control which was absolutely no manipulation. So, in this particular case, there are two controls: one is a no-manipulation control and the other is the cutting frequency control. Now the first thing they are trying to see is whether you have a greater tail length or a shorter tail length. Whether that ends up having a role in terms of being chosen by the females or not.

Now the first thing is that the results from the two controls were not significantly different from each other. So, they have been placed together in this particular graph. So this is data from Anderson 1982, sorry, not et al. Anderson 1982. And the first thing that this sees is that when the tail is artificially shortened.

Then the mean number of nests per male is significantly lower compared to the controls. This is absolutely fine because remember, there is sexual selection here. The females prefer males with longer tails. So obviously, if you have cut down the number and cut down the length of the tail, the females do not prefer those birds.

But what is more interesting is this case. So here you have tails that are much longer than those found naturally. And in this particular case, you can see that the females have a much, much greater preference for This particular, you know, supra-long, super-normally long-tailed birds. So this suggests that the females' preference for this, you know, longer and longer tails still exists. Yet the male bird is no longer able to evolve tails.

So the male bird has kind of stopped over here simply because. Some kind of balance has been reached between sexual selection and natural selection. Now, whether this balance is due to predation pressure. or whether this balance is due to the fact that genetic variation no longer exists, we do not know that part. But what we really know is that if the females are presented with even longer tails, They will be happier to mate with them, suggesting that an equilibrium has been reached. So the main point with runaway selection is that, although the explanatory power of this is very good, Unfortunately, nobody has really observed a runaway selection because it is a co-evolutionary process.

So in order to show that it is happening, You need to be able to observe the entire sequence in front of your own eyes, and that is very, very difficult. So while this is, you know, in terms of the theory, it is perfectly fine. In principle, it can explain many cases, such as the peacock's tail, the widowbird's tail, and many other things. We really do not have conclusive evidence showing that it is runaway selection that has done this. Now, until this point, whatever we were talking about was in terms of getting access to mates and pre-mating stuff.

But that does not mean that sexual selection stops at the pre-mating stage. Sexual selection can very interestingly happen during the post-mating stage. Now, how does that happen? Now remember, in many cases, the females are actually mating with multiple males, right? Therefore, in the reproductive tract of the females, you very often have sperm from multiple males. and the moment you have sperm from multiple males in the reproductive tracts There can be many ways in which there can be a competition between these sperm to fertilize the eggs. Remember, at the end of the day, one sperm is going to fertilize the egg, right? So, if there are many, many sperm, there is going to be a lot of

competition between the sperm themselves.

And this competition is what is known as sperm competition. So there are multiple ways in which sperm competition can take place. So I will show you four major examples and discuss what exactly happens in them. So the first example that we have is the phenomenon of sperm scoping. So what I am showing you here are damselflies. So this black thing over here is the male, and the golden thing over here is the female.

So this is a particular species known as copper demoiselles, and you can see the copper-colored wings of the female. So in this case, what happens is that multiple matings are possible. So the male on its penis has these horn-shaped structures; these are known as lateral horns. And when the male mates, as it is doing over here, what it does is use these horns to first scoop out the sperm that have been deposited by the previous male and then injects its own, you know sperms into the female tract.

Obviously, this thereby increases the chances of, you know, its sperm fertilizing the female or fertilizing the egg. The second example is what is known as a mating plug. So here we have something known as Richardson's ground squirrels. These are very large squirrels you typically find in North America. And in this species, once the male has mated with the female, what it does is actually insert a glue-like object that seals the vaginal opening of the female.

So, I do not know if you can see it over here, but there is a glue-like, you know, plug over here; that is the stuff we are talking about. Now, of course, this is not a permanent sealing. The female can expel this plug after a little time; otherwise, she would not be able to mate ever again.

That does not happen. The female can expel it after some time. But the point is that while the plug is on, another mating will not occur. And therefore, the sperm of this male are going to get a head start. In terms of traveling down the reproductive tract of the female and fertilizing the egg. So that head start is all that matters; therefore, this is a direct

benefit that the male gets by simply gluing shut the female's vaginal opening. The third example, sorry, this particular phenomenon that I talked about is not limited only to the ground squirrel. It is actually pretty prevalent in multiple species of mammals, reptiles, insects, spiders, etc. The third phenomenon is what is known as mate guarding. Female wants to mate with multiple males, I mate, I guard my female, I make sure that you know the female is not able to mate with anyone else.

So, what I am showing you over here is this phenomenon in these insects known as darters. So, this is a particular, you know, red-veined darter; this is the scientific name. So, this is the male, this is the female, mating has happened, and after mating has occurred, the male is not letting the female go. It is simply clasping the female behind its neck and forcing her not to mate with other females or other males. Now, again, this particular phenomenon of mate guarding is extremely common.

And you find it across species in insects, fish, lizards, birds, and of course, primates. The fourth example that we have is a very interesting example. So, until now, what we saw was essentially a lot of conflict happening at the level of the organism itself. So, now we are talking about the fact that the sperm compete directly with each other. Now, one thing I forgot to mention here is that when a male copulates with a female, in many species there are all kinds of chemicals that it injects along with the sperm, and these chemicals can do all kinds of things to the female.

So, for example, it can make the female recalcitrant to further mating. It will increase its refractory period to mate again, or it can cause several other kinds of damage. But what I am going to talk about here is a fascinating example. Where there is cooperation between sperm in this species known as the eastern deer mouse. So, this is a highly promiscuous species, with lots of matings happening, and in this species, it is known that when the sperm are swimming in the female's reproductive tract, if they swim singly, then they can go slow.

But if they form aggregates, then these aggregates and clumps can actually swim faster.

So, there is sperm cooperation that happens so that the males The sperm end up clumping together, swimming faster, and once they reach there, they will fertilize. But now we have a problem. If you have only one male putting its sperm inside this female, then this is not an issue. Because all the sperm are, after all, from the same male, the sperm are cooperating, and therefore you know. After they reach there, anyone fertilizes the egg; it does not really matter; some sperm from that male has fertilized. But suppose, because this is a promiscuous species, there are sperm from multiple males inside the same female.

Then what will happen? So this is what was studied by Fisher and Hoekstra in 2010. So what they did was take sperm from two different males of the same species and then they just colored them. Using different colored dyes, they put them together and tried to see what happened, and this is what they found. So you remember I told you that the sperm aggregate so that they can swim faster.

So that is what you are seeing: aggregations. But look at what is happening. The red sperm, which are from one male, are all aggregating with each other. And the green sperms, which are from another male, are all aggregating with each other. In other words, the sperm from the same male They are preferentially aggregating rather than aggregating with sperm from a different male. So you have competition happening between two males in the form of their sperm aggregating with each other inside the reproductive tract of the deer mouse. This is absolutely mind-boggling, but this is one of the several other mind-boggling things that we could have talked about. So, before we finish this discussion, there is one remark that I need to make. You know what we talked about in the previous discussion, and this is very, very small. A portion of what is known and understood about sexual selection, its direct benefits, indirect benefits, etcetera, etcetera. We just dealt with four of the more well-known theories of, you know, sexual selection's indirect benefits, but, Trust me, there are many, many more.

The other thing that we absolutely did not look at is the math behind all that. So, I presented all these things as just, you know, stories, narratives, possibilities, but,

Remember, ecology and evolution are among the most highly formalized sub-disciplines of biology. And there is a lot of math behind each one of them. We haven't looked at any of it simply because this is an introductory course. But people who are more into the theory part of biology, I urge you to have a look at the theory behind these things.

They are often extremely, you know, interesting and give superb insights. There are several other topics that are typically considered in the context of sex. So, for example, the evolution of sex ratios. Why is it that sex ratios are typically 1:1 across most species of which we are aware? Then there is something known as intralocus conflict. Remember I told you that the same gene sometimes has to pass through the female body; sometimes it has to pass through the male's body and something that is good while it is a part of the male may not be good while the same gene is part of a female.

So, there is a conflict right at that level; that is what is known as intralocus conflict. We did not discuss that, and of course, you know fascinating stuff is about mating systems. There are some organisms that are polygamous, with multiple females, polyandrous, and with multiple males. So, why is it that all these various mating systems have evolved? What are the benefits of those things? None of this has been discussed by us.

That is primarily because, again, A. we lack time and B. this is an introductory course. Therefore, there are other interesting things to discuss. But all that I want to tell you is that sex is a seriously vast topic in evolutionary biology. And it ends up explaining an enormous number of observations. If you want to do full justice to it, you need to actually give a separate course on that topic. However, there are certain cases where the individuals, as far as we can see, are not even getting benefits related to reproduction.

They are not getting benefits directly; they are not getting any benefits in the context of reproduction either. So, that means there is no sexual selection happening. So, one such case, for example, is the behavior where bees go and sting intruders, and you know that. Whenever a bee stings an intruder, it leaves its sting inside the body of the intruder and, therefore, in the process, it dies. Why? Because when the bee flies away, the sting is

inside the intruder's body.

So, the sting is attached to the, you know, internal organs of the bee. So, when it flies away, it actually its entire belly is ripped off and that thing remains inside the body of the intruder. So, this bee is going to die anyway after a few minutes, right? So, it is basically committing suicide. So, this is not something that you can explain either by natural selection or by sexual selection. There is some other stuff that needs to be explained. And that other stuff is what we are going to explain or discuss in our next module. See you next week. Bye.