

An Introduction to Evolutionary Biology

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Features of selection: Insights from experiments

As promised in the previous discussion, we are going to look at some features of selection from a more experimental point of view. Also, much of the stuff that we discussed in the last two or three discussions. They were related to what is happening at the level of the allele: the allele frequency. For this particular discussion, we are going to focus more on things that are happening at the level of the traits. In other words, we will focus more on what is happening at the trait distribution level. So, the first feature of selection that one really needs to keep in mind is that selection acts on individuals, although the effects of selection are visible at the population level. So, think about the Darwin's finches cases for which you saw that HHMI video. The individual finches, when under drought conditions, are either surviving or dying. which are either reproducing or not reproducing, and so on and so forth.

And yet, if you study what is happening in terms of evolution and also natural selection, we are essentially looking at The trait distribution at the parent generation is compared with the trait distribution at the offspring generation. In other words, both of which are population-level stuff, right? And this, of course, boils down to what we have already discussed: that the effect of evolution is always seen. Only at the population level, not at the individual level. Individuals will live and die; they do not have temporal continuity. It is only the population that has temporal continuity, and therefore the effect of selection

also needs to be seen at that level.

A very simple point, but very often people end up, you know, missing this concept, which leads to all kinds of issues. Second point, the effect of selection will partly, not entirely, depend on the shape of the fitness function. Now, what do I mean by the fitness function? The fitness function is a quantitative description of how some measure of fitness can be anything. It can be survivorship, it can be fecundity, it can be stress resistance—whatever. But how some measure of fitness will vary with the trait under consideration under the given circumstances.

This is very important under the given environmental context, and I will show you what I mean by that. So, for example, going back to the Darwin finches example for which you saw the video, When the drought, etc., was happening, the way the survivorship of the birds changed. With the depth of the bill, the size of the beak basically looked like this. And this thing that you are seeing over here, this quantitative relationship between the survival rate, And the bill depth is the fitness function in this situation.

What do I mean by that? What I mean is that this was true when the 1977 drought hit Daphne Major. And when the seeds became very, very, you know, the small seeds, the soft seeds, they became very, very rare. However, after some time, there was a very rainy season, and when that rainy season came, the entire situation essentially changed. Now, it was those birds that had smaller beaks; they were the ones who were finding more food, and therefore, they were the ones. who had greater survivorship, and therefore the entire form of the fitness function changed with the You know, there is a change in the seed availability.

So, that is what I mean by saying that the fitness function is always context-dependent. It is not a constant for a species or anything else. It depends on which environmental scenario the organism is found in. This needs to be kept in mind again. Now, with this concept of the fitness function before us, we will talk about three major kinds of selection.

The so-called directional selection, stabilizing selection, and disruptive selection. What do I mean by this? This is a slightly busy panel, but I will walk you through it. So, if you look at the first row, all you see is some kind of distribution of some trait. It does not matter what trait it is; it can be, you know, beak length, or it can be body size, or whatever. And as you can see in all three cases, the distributions are actually very, very similar to each other, I mean they are the same distribution. Now, the important thing is what you find in the middle panel. The middle panel shows you the fitness function for that particular trait under whatever environment it may be. Now, look at this one, the first one. What do you find? You find that as you go from a lower value of the trait to a higher value, the fitness continuously increases.

So, this is one fitness function. What do you find here? In this case, you find that the maximum fitness is for intermediate values of the trait. Whereas when you go towards either extreme, the fitness goes down quite a bit, right? So, this is the situation in which the intermediate value of the trait leads to the maximum fitness. And this is just the opposite of it. Here, the intermediate values of the trait have the lowest fitness whereas as you move away from the intermediate values, the fitness goes up, right? So, you can think of this conceptually as similar to the underdominance case. And conceptually, this is similar to the overdominance case. But the difference is that in the case of underdominance and overdominance, the x-axis is the three genotypes, right? Homozygote, heterozygote, homozygote. Whereas in this particular case, what you have on the x-axis are the trait distributions. That is the critical thing; nothing else.

Now, what will happen if you have these three different kinds of fitness functions in the trait distribution? After selection has happened, let us say one or multiple times. So, in this particular case, what is happening? The higher values of the trait are preferred. In other words, the frequency of these individuals will be great. is going to go up, and because of that, the mean of the trait value will shift in this direction. The reason it is shifting in this direction is that the higher fitness is in this direction.

If the trait function had looked like this, where the higher fitness was in the lower direction, It would have shifted in the other direction, but here, that is not what we are showing. So, in this particular case, where the highest fitness values are for those individuals who are on one side of the distribution, The kind of selection that you have is known as directional selection. And this generally leads to an increase or decrease in the mean trait value in one direction. How it affects the variation depends on what kind of genetics is present. But typically, we know it by the change in the mean value.

Now, what happens here? In this particular case, those individuals who are in the center of the trait distribution, these guys, They are the ones who have the highest fitness, and all the others have lower fitness on both sides. And therefore, what will happen is that these individuals. they are going to leave behind less offspring, these individuals will leave behind less offspring. And hence, the frequency of these central ones will go up. The frequency of these on the two sides will go down.

In other words, the total variation that exists in the population of which variance is a statistical measure. So, that variation or its measure of variance, whatever you talk about, is going to go down. In other words, the spread of the distribution that you are seeing over here is actually reducing, right? This is what is known as stabilizing selection. Now, what is happening in the third case is disruptive selection. In disruptive selection, these individuals have higher fitness; therefore, their frequency is going to increase.

These guys have lower fitness, so their frequency—I'm sorry—their frequency is going to go down. So, these guys have a lower frequency, so their frequency is going to go down and therefore, You can see that this is going to lead to an increase in the spread. In other words, the variance of the population is going to increase. So, I will give you, you know, specific empirical examples of each one of them. So, the first example is of, you know, directional selection.

This is a very, very famous example. This is the famous Illinois Long-Term Selection Experiment on maize. So, what they did was that they wanted to improve the oil content

and the protein content of the kernels of maize or corn. So, every generation, they took those individuals who had the higher oil content or those individuals which had the higher protein content in its cobs and only allowed those seeds to be planted for the next generation.

So, this experiment was initiated in 1896, which means that. Right now, this is a 100-plus, 129, close-to-130-years-old experiment; it is still going on. So, it was initiated by a person named Cyril Hopkins, and it has continued ever since, except for about four years. During World War II, they had to stop, but they maintained the lines. They did not do the selection, and after World War II, they started all over again.

Now, what you can see over here is the oil content graph, and what you can see is that Over 100 generations, the oil content increased by 4.5 times, so this data is a little old. and the protein content increased by approximately three times. So, this is one of the greatest examples of how much the selection can change a particular phenotype and to what extent. And frankly speaking, when they started this experiment, This was an experiment to figure out how to improve the oil content and the protein content.

However, at some point, they changed the goal of the experiment, and right now, The goal of the experiment is to see how long one can push this, what the limit of selection is, so to speak. So, this is one of the, you know, very, very famous textbook examples of what directional selection can do to a trait. We will come back to this in a few minutes. This is an example of stabilizing selection. So, you know that the weight of human babies at birth is a very important trait, and their survival depends on it.

So, it turns out that if you have babies who are very underweight, their survivorship is actually very low. On the other hand, if you have babies that are greatly overweight, their survivorship also goes down. It is the intermediate level of body weight at which the babies have the maximum survivorship. You can also see something similar in terms of height. So, people who are very, very short, we have already discussed the example of Peter Dinklage and achondroplasia, those people they have all kinds of you know

physiological problems. Similarly, people who are extremely tall, you know, the world record holders and all the 7 feet 6 inches and 8 feet, Many of those people have very high levels of physiological issues. It is the intermediate height people who actually have relatively fewer physiological problems related to height. So, that is another example of stabilizing selection for height in humans. What I am showing you is stabilizing selection for birth weight in humans.

The third kind of selection that we talked about is so-called disruptive selection and This example that I am giving you is from toads known as spadefoot toads or *Spea multiplicata*. So, these toads, depending on the environment they face, will end up becoming either an omnivore like this or a carnivore like this. So, there are two different morphologies. Now, very interestingly, either morphology or body size is relatively high, and in this particular case, body size is a measure of fitness. Because body size tells you the amount of resources that it has and is positively correlated with a bunch of other traits.

So, it turns out that if you are an omnivore or if you are a carnivore, then in either case your body size is large. and therefore, you are going to have reasonable fitness, good fitness. However, if you are an intermediate generalist, you know somewhere between the two, omnivore and carnivore morphology. Then actually, your body size becomes much, much lower and therefore, the fitness of this morph is much lower compared to the two other morphs. So, again, this is an example of disruptive selection where the intermediate form has low fitness and the two extreme forms have higher fitness. Okay, so that was number two. The third and very important thing is that selection can take the trait values between the starting range of phenotypic values. Now, why am I saying this? If you remember, Darwin started by saying that variation exists already. Selection operates on pre-existing variation, right? But if that is the case, then the corollary to that is that Then selection will never be able to take a trait in a population to a value that did not exist in the original population.

However, if you remember just a few minutes ago, we saw the example of the increase in

oil content in the Illinois experiment. Now, in this particular case, if you paid close attention, This red thing that is shown over here shows you the range of variation in the starting population. And yet, very obviously, the population has gone way past that starting range, right? So, if that is the case, obviously new phenotypic variation has come. Where is this variation coming from? Now, there are two major sources of this variation. One, of course, as we have already dealt with, is mutation. And mutation is a very, very important source. The only problem is that mutation is, in general, as we saw is a somewhat slow force. The rate of mutation is not so high that you will end up getting Too much of it very fast, and so on and so forth, particularly if your population size is small. So, the other source of variation that is very important for sexually reproducing organisms is recombination. Now, what exactly is happening? Suppose you have certain alleles. Remember, we are talking about traits that are dependent on multiple alleles here.

Now, suppose some of these alleles individually can lead to a slight increase in the trait value. Say oil content in this case, but it is relatively rare in the population. Because they are relatively rare in the population, their chances of coming together are very, very low. Now, what is happening? Selection is happening. Because of selection, These alleles, which individually also lead to a slight increase in the oil content, are being selected.

When they are selected, their frequency in the population is increasing. When their frequency in the population is increasing, Their chances of coming together into the same organism through the process of recombination are increasing. And once they end up coming together, they will obviously lead to a major increase. or if they lead to a major increase, then the chances of their getting selected increase, And therefore, the chances of their frequency in the population go up even further. In other words, what recombination does is create these new combinations, which selection can then act on.

Now, obviously, recombination is a double-edged sword, right? Remember, recombination can create new combinations; recombination can also break existing combinations, right? So, what is happening over here is that as the allele frequencies, you know, the frequencies of those alleles which will lead to these major increases, as those

frequencies go up, even if recombination is breaking the combination, It will also again, with some probability, bring them together. So, overall, as the frequencies of these favorable alleles keep going up, Recombination will end up bringing them together again and again. And each time they come together, there is going to be selection happening on those allele combinations. So, in other words, at least for sexually reproducing organisms, Recombination itself acts as a major source of variation on which selection can act.

Okay, now this is the interesting part. Selection for a particular trait often leads to changes in other traits, something that is known as a correlated response. So, if you remember when we were talking, I told you about a particular experiment. That we have been doing in our lab, where we are selecting for increased dispersal in *Drosophila*. And I said that when the whole thing started, the ancestral populations had about a 4-meter average, you know, dispersal ability. And we started with a 2-meter-long setup, which over time we have now gone to a 104-meter-long setup, right? Now, because of this selection, which again represents a huge amount of change in how much they can move, Because of this selection, these flies have now become champion dispersers, the distance that they can move is obviously very large. However, along with that, some other stuff has ended up happening in these flies for which we had not done any selection. So, to tell you what these are, it turns out that these flies' behaviors have been modified drastically. The selected flies have become more exploratory. So, they tend to move away, you know, from their natal habitat a lot more, and they also have greater aggressiveness.

So, they are much better fighters, so to speak. Now, this thing, this stuff where changes are happening that you did not select for, These are what is known as correlated responses. Now, why exactly are these correlated responses happening? In this particular case, we know what has happened. So, it turns out that one of the important neuropeptides that allows for greater dispersal is octopamine. Now, octopamine is the analog for human adrenaline, right? So, because of dispersal, the octopamine level of these flies has gone up. Now, octopamine also ends up affecting other behavioral traits, for example, exploration and aggression, right? And because of that, the selection was on dispersal; as a result, octopamine levels went up.

And because octopamine levels went up, these other traits increased, right? So, this is an example of a correlated response in dispersal selection: a correlated response due to selection. Now, please appreciate one thing: in this particular case, Exploration going up or aggression going up, as far as we can make out, is not causing any trouble for the flies. They are not reducing the fitness of these flies in any way, as far as we can make out. However, that is not always the case. In many situations, the correlated responses are not good for selected populations.

And when that happens, we say that there is a trade-off. In other words, when, due to selection or whatever reason, one trait you know becomes better for the organism, But there are other traits that actually extract a cost for the organism; this phenomenon is what we call a trade-off, right? One goes up; the other goes down. So, to give you an example of a trade-off, remember we were talking about selection for faster pre-adult development in *Drosophila*? Now, remember I told you that those flies come out in about 6.33 weeks or so. Which is about 34 percent faster than the ancestral population.

They are the fastest-developing flies in the whole world. Great, but what is the cost of it? What is the toll that the ability to develop fast has taken on the flies? You can see that here. So, here we are showing you the males on this side and the females on this side. And these are the ancestral flies, and these are the selected flies. Can you see their body size? You can see that for both the male and the female, these flies have become much, much smaller. And this is after about 370 generations of selection, which you know in terms of evolution is actually not a very large number.

Now, what is the problem with reducing body size? The problem of reducing body size is that many other traits of an organism are typically strongly correlated with body size. So, for example, body size also reflects how many resources you have and how much resources you have. that then plays a role in terms of things like, you know, how many eggs you can lay as a fly. How much you can resist different stresses, and so on. And it turns out that with this reduction in body size, these faster-developing flies have actually

become absolutely, absolutely, How do I say "poor flies," in the sense that their body size has gone down and the amount of resources that they have? Has gone down; their fecundity, that is, how many eggs they lay, has gone down.

Their ability to do pretty much anything has gone down drastically; their activity levels are extremely poor. If you look at their body and their wings, which, obviously, if you are a fly, is a very important organ for you, The wings are totally deformed, so I am just showing you the deformities. So, all these arrows show you deformities. Look at this one; this wing is, you know, completely deformed and is useless for flying.

So, you know, basically, pretty much in any direction that you look. In terms of their life history, the flies have paid an enormous cost. They have become much worse along any axis. And yet, along the one axis that matters in this regime, which is developing quickly, these guys are the world champions. They develop faster than anybody else, right? So, this tells you something about the fitness of an organism. It is totally, totally dependent on the context, the environment in which that fitness is being expressed.

In this particular experiment, the faster-developing experiment, the fitness was entirely determined by how fast you could develop. Everything else was taken care of. Everything else didn't matter in some sense, right? But because of that, the flies ended up reducing their fitness without considering any other costs. They didn't have to think about any other costs because everything else was taken care of by the experimenters. The experimenters ensured that they got lots of food; they ensured that, however low their fecundity was, you know, All the eggs were taken care of, and they did not have to fight with any predators.

There was no disease, underlap condition, and so on and so forth. Now, because of this, the flies ended up becoming worse off in every other direction apart from That one along which the selection was being imposed. Now, this is something that we have to realize is a reality of fitness and selection. Selection is very focused on what exactly is being selected. You get precisely what you are selecting for, and the biggest example of that, for

instance, is us humans.

We humans obviously have a very, you know, inflated opinion of ourselves. We think we are great, and frankly speaking, if anybody looks at the Earth, they will say, "Yeah, humans are doing extremely well." There is no place in this world where humans have not gone. There is no environment that humans have left untouched. There is no resource that humans are not exploiting, and so on and so forth.

Great. But as animals, we are worthless. We are stupid. You put a human in a jungle, and until that human undergoes very, very strong training, the human will not be able to survive. The human will not be able to run, the human will not be able to catch a prey, The human doesn't have the teeth to kill the prey, it doesn't have the claws to do anything, and most of us humans are actually. So unable to take care of any disease, any pathogen, any predator, nothing. Look at our babies.

Our mothers, first of all, are stuck with the babies inside them for 9 months. And once the baby comes out, the baby is dependent on the mom and dad for how long? For like years and years, right? At least 5 to 6 years, if not more. And even then, after 5-6 years, the baby is probably just able to toddle around on its own. The baby, in order to become worthy of catching its own food, etc., never happens. So, the point I am trying to make here is, why has all this happened? That has happened because, in the context of humans, the focus of our selection has shifted entirely toward a cultural side.

Biologically, we have ended up escaping almost all the selection pressures, because of which, although culturally we are pretty decent, Although culturally we can accomplish a lot, from the biological side, we have ended up becoming worthless organisms. And this is true of pretty much all the cases where selection has happened, you know, strongly either in nature or in the lab. So, the main point I am trying to make here is that selection does not lead to perfection of any kind. Lots of people, many students have this trait; selection has perfected it over millions of years.

No, the selection has not done any such thing. Selection has simply and blindly kept on increasing the fitness along a particular axis on which the selection has been happening. Period, done. Whether it has led to perfection or not, selection does not matter. And as I showed you with the human example, in most cases, almost all cases, there is no concept of perfection. And because there is no concept of perfection, there is also no concept of a higher organism or a lower organism, right? Now, this is a term that we use all the time, right? This is a higher organism, and that is a lower organism.

Humans, dogs, and all mammals are higher organisms, and let us say bacteria and other things are lower organisms. Absolutely not. Each organism exists in a certain context, and the organism is trying to do well within that context. That is all selection is trying to make it do. You can talk about levels of complexity, more complex organisms, less complex organisms in terms of how many things, how many kinds of tissues, and so on and so forth.

You can talk in terms of the age of the organism; okay, this organism came into being so many millions of years ago. But that one came into being whatever 10 million years earlier. So, this is a more ancestral form; this is a more recent form. You can talk along those lines.

But talking about higher organisms or lower organisms makes zero sense. Simply because, as I showed you, there is no organism that is perfect. Selection never leads to perfection, right? And, of course, corollary to this is, I mean, there is no plan of nature either. Selection is a blind force, okay. Whichever way fitness increases, selection will take the organism that way. Period. Done. Over. Right? So, unfortunately, the terms "higher organism" and "lower organism" are very popular, and To be very honest, even I end up saying "higher organism" and "lower organism" now and then. But in the proper technical sense, these labels actually do not have any meaning. And, of course, there are all kinds of moral and ethical issues with that. You know, if you have no higher organism or no lower organism, then does a human being have the right to take an animal's life? Killing a human is almost universally a crime, but killing, let us say, a goat or killing, let

us say, a cat is not a crime.

Why not? We are higher; they are lower. But I just told you that there is no higher; there is no lower. So, in that case, how exactly do you justify taking any lives? If you are saying, let us say, moving versus non-moving, how do you justify, let us say, taking the life of a plant? Okay, you cannot because after all, the plant is also a living organism. It is doing extremely well in whatever niche it exists, under whatever conditions it exists. So, anyway, those are the kinds of debates that emanate from evolutionary thinking. We are not going to get into those kinds of debates in the context of this particular course, but there are lots of places where exactly are these kinds of debates conducted by people, and when do they look at evolution, you know? Tell them what the scientific basis of it is; all we tell them is, "Look," We do not think that there is a higher organism or a lower organism; all organisms are whatever they are; that is about it. Okay, so we are going to stop here, and in our next discussion, We are going to look at the other forces of evolution; you know, things like drift and inbreeding, etc. And we are also going to look at how some of them end up interacting with selection and these forces. Okay, see you in the next module. Bye.