

An Introduction to Evolutionary Biology

Prof. Sutirth Dey

Biology Department, Population Biology Lab

Indian Institute of Science Education and Research (IISER) Pune

Week 5 Lecture 30

Migration: Interactions and examples

Hi, so in our last discussion, we looked at the evolutionary force of migration. And we quickly saw, you know, the very basic things that migration can do. And as I promised in this discussion, we are going to look at the ways migration interacts with other evolutionary forces. What are the major differences and what are the major points of similarity? And then we are going to look at a bunch of examples from real life to see how migration interacts with you know many things that lead to some very interesting outcomes. So, before that, we will quickly revise the two main observations that we made from the two-patch model during our last discussion. The first observation was that the overall allele frequency of the two populations would remain constant.

And as I said, that is not very surprising simply because all that is happening is that. The alleles are being redistributed due to migration across the populations. The much more interesting and important thing was that, for non-zero migration, the equilibrium is reached. When the allele frequencies become equal in both patches, it basically means that migration acts like a homogenizing force.

So, if you look at the evolutionary effects of migration, that is a homogenizing force; that part is the main thing over here. It tends to equalize the allele frequencies across the populations. And secondly, as I alluded to, it can introduce new alleles to a population. In that sense, it is kind of analogous to mutation, with a few differences. So, we will quickly compare the effects of migration with drift, and we will also compare the effects of

migration with mutation.

So, if you compare drift and migration in terms of the genetic variability across local populations, Drift tends to increase that variability. Why? Because you know you have a bunch of populations, drift is happening in all of them simultaneously, but it is a random thing. So, in some cases, the allele frequencies are going up; in other cases, they are going down. It is entirely possible that one allele gets fixed in the first population, while another gets fixed in the second population. So, if you look across populations, the genetic variability is going up.

On the other hand, migration, being a homogenizing force, actually ends up reducing the genetic variability across local populations. Now, if you look at genetic variability within a population, there are things that are slightly different. So, drift in general causes, you know, a decrease in the variability. This can happen either because a population, due to drifting, either fixes or loses an allele, or if you have a bottleneck effect. Or, you know, the founder effect, then you can end up having a loss or fixation again due to the same thing.

In the context of migration, it is actually a little more complicated. The genetic variability within a population can increase, for example, when immigration is happening, or it can even decrease. So, for example, there is an exit from a population, and it just so happens that all the individuals who had a certain trait, They were among the people who went out. So, obviously, in that case, the genetic variation can even decrease in the context of a population. So, the main point that you need to remember is that, in general, drift and migration tend to have opposing effects.

Now, if you look at the comparison between mutation and migration, things are a little more complex. So, both of them tend to introduce new alleles to a population, no issues over there, but the way they do it is slightly different. So, when it comes to mutation, as we have seen, mutation rates are generally low; therefore, At a given time, if there is a beneficial mutation that can arise in at most a few individuals. However, migration rates

can be either low or high; they can be pretty much anything, and therefore, the rate at which New alleles coming into the population can be much more diversified and varied when it comes to migration. And if you look at how many loci are affected in the context of a trait and in the context of mutation, Since the rates are low, you do not really expect too many loci to be affected at the same time.

So, that is why I have written it is typically one or at most a few. However, when migration is happening, you can have variation at multiple loci affected simultaneously. Because it entirely depends on how many individuals are coming and what exactly they are bringing with them. Now, if you think about what mutation and migration are doing, The overall interaction, or the overall way in which they interact with the other forces, is also slightly different. So, I will give you a bunch of, you know, statements to make the case.

So, as we discussed when we were talking about the distribution of fitness effects, many new mutations, the ones that actually bring about a change in fitness, Most of them are actually deleterious, and most of them will initially occur as a single copy. Therefore, many of these are actually lost from the population very rapidly. And I am talking about real populations that are undergoing some amount of drift at least. In most cases, they are lost very rapidly. Now, even if you have a mutation that is beneficial, it will either require being of very large beneficial effects for which the probabilities, as I told you, are relatively small, or it will require quite a bit of time. Substantial time is needed to reach a reasonably high frequency. However, if you think about migration, the way migration introduces new variation is slightly different. Typically, the variation comes from another population, right? And in many cases, the variation has been present in that population for multiple generations. And therefore, that population, in some sense, has adapted a bit better to that mutation.

And therefore, it is entirely possible that when that variation comes here to the focal population, Then the way it is established is much easier. Also, note that migration by its very nature can introduce multiple copies of the new variant. So, the problem of drift at

low frequency that we are talking about is much, much less over here. And therefore, there is a possibility that you can have a much larger influx of new genetic variability. Because it has undergone selection, etcetera, in the previous population, it is more likely to be beneficial.

Therefore, the ability of migration to drastically alter a gene pool, even in a short span of time, is much greater than that of mutation. Now, note that up to this point, whenever we have studied all these evolutionary forces, We have typically thought about it as, you know, one population in one place and, you know, experiencing one environment and so on. But in nature, in real life, we know that that is seldom the case. In nature, we know that populations are typically spread over space and at different locations. They are actually experiencing, in many cases, slightly different environments, and they are also drifting slightly differently.

And you know the different kinds of mutations can be favored in one place versus another. So, taken together, even if at a given time you know that a particular patch at a given spatial location has one genetic composition being favored. At a different genetic location, another spatial location and another genetic composition can be favored. And therefore, if you look at each population by itself, that population may or may not have access to the best genes. But once you have migration happening, then all these genetic things, you know, are getting shuffled around.

All the influx that is happening ends up becoming a very big source of high-quality genetic variation. on which then selection can act in your focal patch. So, in that sense, migration is actually, in the real world, a very, very potent force, and it is a force that can actually You know, act against the variation-reducing effects of selection, drift, and assortative mating, as we talked about. So, with this quick background, I am now going to give you a few examples of how migration has ended up affecting populations. So, the first example that I will take is of this species: these are grey wolves.

More specifically, these are the Scandinavian grey wolves; you know, the Scandinavian

populations. So, the gray wolves have been distributed over large parts of Europe for a long time, but they were also hunted rather ruthlessly. And in Scandinavia, which includes Norway, Finland, and Sweden, that part of northern Europe, basically. They were supposed to have gone extinct somewhere around the 1960s. However, in 1983 they discovered a breeding wolf pack about 900 kilometers from the nearest population.

How it reached there, nobody knows, but the pack was there, and genetic studies suggested. That this pack essentially started with just two individuals; that is it. So, basically, one male, one female, and that is it. Now this particular pack, the size in this, remained low, and it just remained as one pack. And you know, at best, the highest it reached was about 10 individuals in one breeding pack; that is it.

Now because the population size was so low, this pack actually suffered heavy amount of inbreeding and drift. We know this from genetic evidence that their allelic frequency and allelic variation were going down drastically. Although I am not aware of direct studies on the physiological effects that these populations were facing, It is known that other populations which have a similar level of inbreeding, you know. They were facing many physiological problems, including problems with blindness in the eyes. Now you can imagine if you are a wolf, and that too living, you know, in the wild having low eyesight is a very, very bad thing that can happen to you. So, obviously, this particular population was not doing very well, and then suddenly something happened. Around 1991, their population started increasing and actually increased pretty fast. So it turns out that around 1991 there was exactly one male wolf. which migrated to this population from the eastern populations of the gray wolves found in Finland and Russia.

And this particular male wolf, as luck would have it, had a disproportionate success in mating. Now, why it had that, we do not know; maybe it was very vigorous, or maybe, you know, those females over there really liked it. We do not know what exactly happened, but what we know is that of the 72 wolves that were born after 1993, 68 can trace at least part of its ancestry to this one immigrant male of 1991. And once this happened, the arrival of this wolf actually had a massive effect in terms of Increasing the

genetic and allelic diversity of the Scandinavian wolf population. And this thing actually coincided very nicely with a rapid increase in the population size. Today, in 2023-24, the last census data I could find shows that the population size has actually gone up to over 400. And there are multiple breeding packs in that area, and by and large, the population is actually doing very well. So, this is one example of how you know inbreeding depression is coming due to drift. Or you know, the founder effect and all that gets taken care of because you have a migrant. Now, why exactly is this happening? If you remember, we discussed this when we were talking about inbreeding.

We said that inbreeding and drift, along with all these factors, increase the homozygosity of the population. And when the homozygosity of the population goes up, then what happens? You know, rare recessive alleles, which have bad effects, start coming into the homozygous form. And when those alleles come into the homozygous form, all these diseases start getting expressed. Which is why typically inbreeding and inbreeding-like effects due to drift, assortative mating, etc. all that leads to a reduction in the overall fitness.

Now, obviously, when you have new genes coming up, these genes, or you know, there is breeding with these new genes. Then many of these recessive alleles go back into a heterozygous form. And the moment they go back into the heterozygous form, the overall fitness goes up. So this is what is known in technical language as heterosis. When heterozygotes have much greater fitness than the corresponding homozygotes, it is called heterosis.

So it is thought that migration leads to heterosis, which in turn acts as an antidote against inbreeding or inbreeding-like effects. Just to give you one more example: this is the Arctic fox, *Vulpes lagopus*. As you can see, it is a very cute-looking animal. Its fur is, you know, also very, very expensive, and because of this fur, it has been hunted absolutely indiscriminately in Europe. So, although the population size used to be pretty high, in the tens of thousands, by the end of the 19th century, only a few hundred remained, you know individuals were left, and those were also not in one population;

they were fragmented across multiple populations. So obviously, an enormous amount of ingredients was happening, an enormous amount of drift was happening, and in the midst of all this. A particular Swedish population started with just 7 individuals, and after getting started, remember it was all fragmented. So this population ended up remaining isolated for 9 full years, leading to heavy levels of inbreeding. Due to the inbreeding depression, there were very low levels of both reproduction and juvenile survival.

And basically, this population was in trouble. However, something happened. What happened? So remember that this particular Arctic fox is very commercially important. So people were thinking about, you know, captive breeding programs, which basically means that they were breeding foxes in artificial enclosures and introducing these into the wild. So between 2010 and 2011, there was a Norwegian captive breeding program from which they ended up releasing three male foxes.

And these male foxes wandered around a bit in that area and finally immigrated into the Swedish population. And they started reproduction over there. It turns out that in the first generation, the offspring themselves that came out. There was 1.9 times higher juvenile survival and 1.3 times higher breeding success in the offspring of the immigrants. So, obviously this was absolutely great and 5 years after immigration, remember these are mammals, right. So, five years is not a very large time. Five years after immigration, the population had more than doubled in size, allelic richness. Had increased by 41 percent, and if you look at 2010, you know only 10 percent of the litters were offspring of the immigrants. In 2015, within 5 years, 89 percent of the litters were related to the 3 immigrants. which basically means that their offspring had a very high fitness under those circumstances. They were probably surviving more, and they were also reproducing more, as the figures suggest. So, this is again an example of how just three individuals are able to rescue a population in a very, very big way. Now, if this is the case, then does this imply that one should always introduce individuals from outside? To genetically rescue populations with low genetic diversity.

And although I would have loved to say that the answer is yes, unfortunately, that is not

the case. And the reason that is not the case is that just as you have inbreeding depression, you can also end up having something. Known as outbreeding depression, what is outbreeding depression? So outbreeding depression is a phenomenon of reduced fitness in offspring arising from mating between individuals. From very different populations. So remember what we have been saying until now is that if you have, let us say, two populations.

And you know drift might be happening in these two populations, or inbreeding depression might be occurring, and if you bring them together, heterosis will happen, and the hybrids will have high fitness. Now we are saying that the hybrids will have low fitness. How can this be? What can lead to this? So there are many ways in which this can happen. I will give you just two examples. So, for example, suppose each population has actually adapted very well to their respective habitat.

And when they have adapted very well to their respective habitats, now if you are, you know, bringing those genes. I mean "adapted very well" is in two different contexts. One is that they have adapted very well to the context of their respective environments. Also, the alleles that are responsible for that adaptation are very well suited to those given genetic backgrounds.

In other words, epistasis is happening. Now, if you suddenly make them hybrids, then what is happening? Alleles of one genetic background are now being expressed in another genetic background, and if that happens if the epistatic effects are not proper, then that can end up leading to reduced fitness. So, this is one way that it can happen. The other way is something that we have already talked about, which is underdominance. What is underdominance? Remember, underdominance is a situation where the heterozygotes have less fitness than the two homozygotes. So, if the genetics of these alleles are such that there is underdominance, then obviously the moment you breed them together, the hybrids are going to have lower fitness.

Now we have examples of such a scenario, outbreeding depression. It turns out that we

have quite a few examples in the literature. So I will just show you one or two. The first example is from this lovely fish known as rainbow trout. So these are fish that are, you know, eaten, and therefore they are of some commercial importance.

So this is an example from Canada where there are wild populations. And, you know, Vandersteen et al. also took individuals from a fishery. So it is well known that when fish are, you know, raised in a fishery generation after generation. Then, they adapt to the fishery conditions, which is basically how they become domesticated to the fishery conditions.

So what Van der Steen et al. did was take the wild fishes, take the domesticated fishes, and then basically create hybrids. And then they took these populations and released all three types. The wilds, the domesticated, and the hybrids were taken to two different natural lakes and their survivorship was studied. And what they found was that the hybrid had a survivorship that was intermediate between the two parents in one lake, but not in the other. And the main lesson from this is that outbreeding depression can be context-specific.

Now here I have to tell you one more thing: outbreeding depression can be context-specific, Outbreeding depression can also be definition-specific. So I will just tell you what I mean. So I defined outbreeding depression as when hybrids from two different populations have lower fitness. Now, when I am talking about it, I am thinking in terms of populations that are coming, I mean two populations of the same species. Now that is the context in which the term "outbreeding depression" is typically used.

But sometimes they also use the term "outbreeding depression" to mean When you have hybrids of two different species or hybrids of two different subspecies of the same species. Now, technically speaking, the entire biological species definition says that if you are calling two things as two different species, Then that automatically means that their hybrids are either not going to form, or if they do form, they are going to have low fitness. So, that kind of outbreeding depression, where you are talking about hybrids

between two species, you actually expect that, right? What is less expected is that you have the same species with two different populations, but the hybrids between them, them having a lower amount of fitness, and that is the kind of outbreeding depression that we are dealing with over here. So, this is the first example from rainbow trout.

The second example is from the world of plants. So, this is *Arabidopsis thaliana*, also known as thale cress. Most of you have probably heard this name. It is a very well-known model system extensively used by molecular biologists and botanists. So, what Oakley et al. did was take two independent population pairs, each from Italy and Sweden.

So, basically, they had two different locations in Italy and two different locations in Sweden. From each location, they ended up taking two different populations. So, two to four populations from Italy and two to four populations from Sweden paired them up, and then essentially compared the fitness of the hybrids against both parents. And in this particular case, they measured fitness by how many fruits were set, how many seeds were set, and in one pair between the Italy and Sweden pair, the hybrids had greater fitness than either parent, which I called heterosis. In the other pair, the hybrids had a 15 to 44 percent reduction in fitness, defined as fruit and seed production.

So, what this is telling you is that even if you have the same species, sometimes you will have heterosis and sometimes you won't. You will have outbreeding depression, which again boils down to the same thing: outbreeding depression is very, very context-specific. You know, it all depends on which species, which environment, under what conditions, and so on and so forth. So, what do we do? To outbreed or not to outbreed? That is the question. So, it turns out that there is a bit of controversy in the literature about this.

So, on one hand, you have people you know; for example, this is a review from 2007 which straight away says that the risk of outbreeding particularly in the second generation, the risks are on par with the risks of inbreeding, which basically means they are equally bad. So, you better not outbreed until and unless you are very very sure. However, at the same time, there is another review from 2015, and here what I am giving

you is the title of the review itself. Which simply says that genetic rescue of small, inbred populations, meta-analysis reveals large and Consistent benefits of gene flow, which basically means to outbreed.

So, the overall picture is that there is a bit of controversy. Lots of people, particularly you know, Frankham et al., believe that, by and large, you know inbreeding depression. Getting rid of it using migration is a very good idea, and they have actually suggested that. What are the conditions under which one expects outbreeding, and do you know how to take care of it? So, that is not a part of this course.

I want you to look at it and look it up in case you are interested. But the main point that I want to make here is that there is a debate, and the debate is still ongoing. We still do not know precisely what the answer is. So, what exactly have we learned till now? So, we started with the history of evolutionary thought in the first week, and Then we looked at various pieces of evidence which lead us to believe that evolution has indeed happened. And then we talked about the various mechanics, you know, various mechanisms or forces that lead to evolution. We talked about starting with the raw material, which was variation; then we discussed mutation.

We talked about selection, drift, assortative mating, inbreeding, and now we have spoken about migration. So, roughly speaking, these are the major forces responsible for microevolution. And now, with this background, we need to ask the question: what exactly is evolution explaining? What are the various patterns that you know one can think about that can be explained based on these forces? And that is what will be the focus of the next three or four weeks of discussion. See you then. Bye.