101-NYA Class 17: Speciation

Marks

Group:

Total 0 /19

Part A: 25 Minutes

In the activity from the previous class (Class 17: Evolutionary Mechanisms) you were presented with genotype and phenotype data on rocket pocket mice sampled from separate populations in the Arizona Sonoran Desert. In this activity we will only consider two of these populations, one of which is based on rocky dark lava substrate, while the other lives on a light sandy and granite background. In each population, over 99% of the mice have fur colouration which matches the background substrate colour. These populations are separated by almost 10 Km, and are each over 20 Km away from their next nearest pocket mouse population. Thus, for all intents and purposes, these populations are physically isolated from one another, and gene flow is essentially non-existant.

Grading Explanation

From the very beginning of our examination of pocket mouse colouration, we have considered the dark and light mice to both be members of the same species. However, imagine that you were a biological researcher that was new to the area and was unfamiliar with the local mice. What pieces of evidence would you use to try and determine whether the mice from the two populations belonged to one or two species? Would any pieces of evidence suggest that they are actually separate species? In your answer to this question, define and make reference to any specific species concepts that could and would be useful towards making a decision.

/5

The morphological species concept is based on physical differences between species. An examination of the two groups of mice would indicate that they are mostly physically the same, but that they do have one very important and obvious difference, which is that one group is dark, while the other is light. Many separate species on the planet are distinguished only by colouration, so, from this perspective, it's very possible that the mice are different species. In contrast, the biological species concept is based on reproductive isolation. In other words, the dark and light mice would be considered different species if they were not able to interbreed. So, the first steps to determining whether the two types of mice are reproductively isolated would be to place them both together in a controlled environment and see if interbreeding occurs, but also to observe the two populations in the wild in an attempt to determine whether interbreeding occurs in a natural environment. If the mice are observed interbreeding, even if this is minimal, then the offspring need to be examined closely. If the offspring are not viable, meaning they are not able to survive and reproduce themselves, then you could consider the species as separate. However, if the offspring are viable, then a judgement decision must be made. If the offspring are viable, but are at a significant selective disadvantage for whatever reason, then this might suggest that the two groups are either separate species, or are in the process of becoming separate species. Similarly, if the two groups are only observed interbreeding in the lab, or the natural interbreeding rate is extremely low when the populations are in contact, then it could be possible to consider the species as separate or as becoming separate. The last, method for determing whether the species are separate is to examine the basic genetics of the two groups. Sequencing the genomes of a sample of mice from both groups can identify similarities and differences between them, and provide an indication of how much gene flow and hybridization occurs between the groups. If the hybridization rate is very low (<0.1%), and the two groups have significant differences in their genetic profiles, then this provides evidence that the groups are reproductively isolated. However, if the two groups are physically separated from each other and thus physically incapable of interbreeding, it's possible for these differences to develop even though the groups would not actually be reproductively isolated if they were in the same area.	1 mark for mention of morphological species concept, and 1 mark for appropriate description of how this would suggest they are two separate species. 1 mark for mention of biological species concept, and 1 mark for some form of description about this would be applied. Finally, 1 mark for mention of genetic comparison or some other method of assessing speciation. Part marks are possible, descriptions do not need to be anywhere near this elaborate, and no final decision is necessary (this is just here to help you make sense of things).

Ultimately, the decision as to whether two similar groups are one or two species is often subjective, and can change over time as environments change or new evidence emerges. In the case of the mice, we would almost certainly consider the mice as the same species, even though they look different. The reasons for this are that each population of mice contains a small percentage of the other colour (i.e., a few light mice in the dark environment, and vice versa), and these are able to interbreed. Plus, the mice have only been separated for about 1000 years, which is not actually that long in evolutionary and genetic terms. Thus, even though the two groups of mice are reproductively isolated, they are likely very similar from a genetic perspective (other than for the MC1R gene), which would suggest that they would still be able to interbreed, and are thus the same species.

Imagine for a moment that the two populations of mice were in fact considered to belong to different species. In this hypothetical context, phylogenetic and genome analysis would no doubt indicate that the mice had shared a common ancestor in fairly recent history, as the lava flows which created the dark substrate are only about 1000 years old. Thus, in the intervening millenium, a group of dark mice would have established a population on the cooled lava flows, and would have become geographically isolated from other mouse populations. They then would have diverged sufficiently to be considered a separate species (this likely wouldn't be enough time for such divergence to take place, but this is a hypothetical example).

What mode of speciation is being described in this example? /1

Allopatric

1 mark for correct answer. No part marks.

The reality is that, while the two populations are geographically isolated and phenotypically different, it's unlikely that enough time has elapsed since the two populations were established for sufficient genetic variation to accumulate between the groups to lead to them being meaningfully reproductively isolated, and thus considered two separate species. Still, the mice are different, and there are no doubt potential fitness consequences for a camouflaged mouse that mates with another mouse whose colouration does not match the background, in that they might produce offspring that are not well camouflaged.

Imagine now that a freak seismic event brought both populations together, such that the dark population, still living on the dark lava rocks, was now immediately adjacent to the light population, which was still living on the sandy granite. In this scenario, mice living on the edges of their respective habitats could easily venture into the other habitat and back again, and matings between the two groups could be quite prevalent, especially for mice on the borders of the two habitats.

Based on the potential fitness consequences of mating with a different colour mouse, do you believe that reproductive isolation would arise between these two groups? If no, why not? If yes, why, and what mechanisms might evolve to prevent the mice from mating? /3

If the scenario above developed, the prediction would be that the two types of mice would eventually evolve barriers to reproduction, simply because of the fitness consequences of mating with the wrong mouse. How quickly these barriers evolve and how strong they are would depend directly on how strong the selection was against the wrong colour mouse. In other words, if a dark mouse in a light background had almost no chance of surviving to reproductive age, then the barriers would evolve fairly quickly, as there would be big fitness consequences for a light mouse that mated with a dark mouse. However, if most dark mice were able to survive almost as well as light mice on a light background, the barriers would only evolve over a very long period of time, and might not actually be in place before the environment 'changed' again.

The mechanism that could evolve most easily would be behavioural isolation, as this would only require a shift in female preference (dark mice prefer dark mice, light mice prefer light mice), or a change in mating behaviour. Alternatively, the mice could begin mating during slightly different times of the season (temporal isolation), or develop a preference for only mating on their preferred background (habitat isolation). Either way, pre-zygotic isolating mechanisms would almost certainly evolve before post-zygotic isolating mechanisms (other than the low hybrid adult viability described above, which is the driver for the development and reinforcement of pre-zygotic barriers).

1 mark for stating that isolation would arise, 1 mark for appropriate description of why this would occur, and 1 mark for mentioning and appropriately describing an isolating mechanism. Part marks are possible. 0.5 marks awarded for answering that isolation would not arise, and 1 mark awarded if a reasonable explanation is provided.

From the question above, if we assume that reproductive isolation was going to evolve, in which group do you believe these mechanisms might evolve first, and why?

/2

The mechanisms would likely evolve first in the light mice, as the consequences of mating with a dark mouse would be greater for them. The reason for this is related to the genetics of mouse colouration. Recall that the dark allele is dominant, so a light mouse would absolutely have the dd genotype. If this mouse mated with a dark mouse that had the DD genotype, then all of the babies would be dark. Otherwise, if the dd mouse mated with a Dd dark mouse, half the babies would be dark, while the other half would be light. Thus, for a light mouse, mating with a dark mouse on average means producing more dark babies than light babies. This same principle applies for a dark mouse, except, in this case, the skew towards dark mice is beneficial. Thus, natural selection would be stronger for light mice not to mate with dark ones, and therefore you would expect reproductive barriers to evolve in these mice first.

1 mark for answering light mice, 1 mark for explanation that relates in some way to phenotypic proportions in offspring from mixed matings.

Part marks for any answers that seem at least somewhat reasonable.

Part B: Extra (You should have time to do at least some of this, though)

Hawthorn trees (genus Crataegus) are native to North America, and grow throughout the continent. They produce a small fruit that ranges in size from 5mm to 20mm, with an average of 12.6mm. This fruit is eaten by larvae of the hawthorn maggot fly, Rhagoletis pomonella.

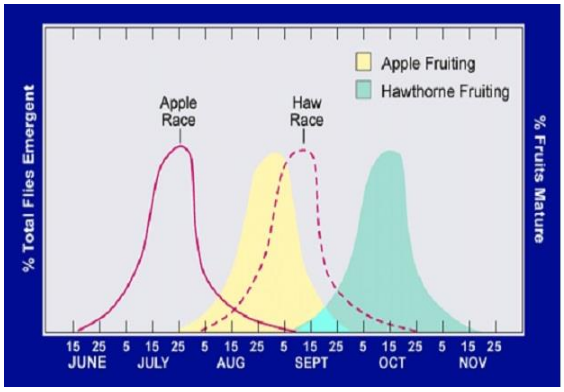
Apple trees (genus Malus), on the other hand, are not native to North America. They were introduced to North America by European settlers in the 1600s, but have since become the most widely grown fruit on the continent. In contrast to the small hawthorn fruit, a typical commercial apple has a diameter of 70mm. These fruit are also consumed by the larvae of fly pests called apple maggot flies. Despite the different name, though, these flies are actually currently considered the same species as the hawthorn maggot fly, i.e., Rhagoletis pomonella. It seems as though when apples were first introduced here, some Rhagoletis pomonella maggot flies began to shift their food source, and the first infestation was actually noted in 1864.

Rhagoletis pomonella has a fairly elaborate life cycle. Female flies first lay eggs in their fruit of choice (be it hawthorn or apple).

Maggot Differences

From a maggot's point of view, the large apple fruit provides 220 times more food than a hawthorn fruit. However, the nutritional quality of the hawthorn fruit is superior, as 52% of maggots that develop in hawthorn fruits survive, compared to only 27% for a similar measure in apples. The apple does provide more protection from parasitoid wasps, though, because apple maggots can burrow more deeply into the apple and avoid the wasp's stinger, which isn't possible in the hawthorn fruit. Thus, apple maggots carry significantly fewer parasitoid wasp eggs than hawthorn maggots do.

Today, there are farely distinct apple and hawthorn maggot flies. However, the distinction isn't morphological (appearance), as the two types of flies are physically indistinguishable. Furthermore, the flies are not geographically or physically separated, as apple and hawthorn trees often grow side by each in the same areas. Where the flies do differ is in their genetic profiles. In other words, a fly researcher could not tell two flies apart just from looking at them, but could tell them apart if they sequenced the flies' genomes, because the flies are genetically distinct. These genetic differences emerged because the flies tend to mate with their own kind: hawthorn maggot flies strongly prefer to mate on and lay fertilized eggs on hawthorn fruit, whereas the same can be said about apple maggot flies and apples. Ultimately, there is only 4%-6% hybridization rate between hawthorn and apple maggot flies. However, it's important to note that when the flies do hybridize, the hybrids are perfectly viable and fertile, meaning there are no post-zygotic barriers to reproduction.



The final important point to make about apple and maggot flies is that they are generally temporally isolated. In other words, apple and maggot flies don't tend to be flying around each other at the same time very often. The reason for this stems from the ripening time of their host fruit. As the graph to the right indicates, apples fruit earlier than hawthorns, and this leads to the apple maggot flies emerging earlier than the hawthorn maggot flies. There is a small period of overlap, where flies of both 'races' can be obeserved together. However, for the most part, apple and hawthorn flies live their adult lives during separate time windows.

Recap:

Hawthorns	Apples
Native	Introduced ~1600
Small Fruit	Big Fruit
More Nutritious	Less Nutritious
More Parasitoid Attacks	Less Parasitoid Attacks
Fruit Ripens Late	Fruit Ripens Early

Hawthorn Maggot Flies	Apple Maggot Flies
Flies Look the Same	
Flies Live in the Same Areas	
Flies Have Same Life Cycle	

Flies are Genetically Distinct	
Mate and Reproduce on Hawthorns	Mate and Reproduce on Apples
Mate and Reproduce Late	Mate and Reproduce Early
Only 5% Hybridization Rate, Hybrids are Viable and Fertile	

The apple maggot flies and hawthorn maggot flies have historically been considered to be part of the same species. Based on all of the information presented so far, do you believe that this characterization is correct, or do believe that these two types of flies should be grouped as separate species? In your answer, outline the evidence in favour of both sides, and make reference to the particular species concepts which could be used to justify either position.

/3

The two types of flies should be grouped as one species, because they are able to mate with each other in the wild. The biological species concept defines species as reproductively isolated groups of organisms, and, since these two groups do reproduce, they should be considered as one species. Furthermore, they look exactly alike, and so, based on the morphological species concept, they would also be considered as one species.

Two other species concepts not directly addressed in this class would actually group the flies as separate species, though. First, the phylogenetic species concept would classify the two as separate species because of their different genetic profiles. These profiles arise because of the lack of gene flow characteristic of two species. Here there still is gene flow (which is why we still consider the flies as one species), but it is very limited, which is what has led to the different genetic profiles. The other species concept in question is the ecological species concept. This looks at where and how the flies live. In this case, because the flies live on and in different fruit, and preferentially mate on these different fruit, they would be considered as separate species.

1 mark for stating that flies should be grouped as 1 species, 1 mark for identifying that they are not reproductively isolated. 1 mark for writing something which mentions that different genetic profiles and/or different living and mating conditions suggests that they are 2 species; not necessary to specifically mention the phylogenetic or ecological species concepts. Part marks possible.

0.5 marks for saying the flies should be 2 species, 1 mark for some form of reasonable explanation of why.

If the flies have recently become two separate species, or if they are in the process of becoming two separate species, what mode of speciation is taking or has taken place? Explain your answer.

/1

Sympatric speciation is occurring, because the flies share exactly the same habitat. It's true that the flies preferentially mate and reproduce on different types of trees, but, when they are not reproducing, they are all flying around in exactly the same area. Thus, they are not technically geographically isolated.

1 mark for correct explanation. No marks for correct answer, but this is necessary to have correct explanation. Part marks possible.

What specific reproductive isolating mechanisms are at play in the maggot fly study system? For each mechanism you define, identify whether this is pre- or post-zygotic.

/2

The reproductive isolating mechanisms at play are all pre-zygotic, as the flies are capable of reproducing viable and fertile offspring. These flies are mostly not reproducing because they do so on different plants (habitat isolation), and because they do so during different times of the season (temporal isolation).

0.5 marks per correct isolating mechanism, 0.5 marks for correctly identifying each as pre-zygotic. Only two possible answers.

Hawthorn and Apple maggot flies still hybridize, albeit rarely. Within what context do you believe the flies would eventually evolve to cease inter-breeding entirely? What mechanisms could theoretically evolve or develop to finally isolate these flies completely?

/2

At this point, it seems that the flies don't mate with each other simply because the situation doesn't arise where they would. Hawthorn flies try to mate on hawthorn fruit, while apple flies try to mate on apples, and so the two flies just don't end up trying to mate with each other. Plus, because of the different ripening times, the flies mostly aren't even trying to mate at the same time. However, the fact that they do still hybridize suggests that mistakes do occur, or that preferences for specific types of fruit aren't ironclad. If there is no cost to making these mistakes, in that the offspring produced have an average fitness equal to the fitness of either apple of hawthorn flies on their own, then the mistakes will continue happening, and these flies might only ever speciate through genetic drift (which means they might never fully become separate species). However, if there is even the slightest cost associated with making a mating mistake, in the form of hybrid offspring having slightly lower fitness, then, over evolutionary time, mechanisms will evolve to prevent the flies from mating. There are already habitat and temporal isolating mechanisms in place, but these are unlikely to change as they are based on the plants rather than the flies themselves. Thus, the most likely isolating mechanism that would evolve in this context would be some form of behavioural isolation, which could include some type of physical differentiation between the male flies which would keep females from mating with the wrong type of male.

1 mark for describing a viable scenario whereby the flies cease interbreeding, 1 mark for describing at least one mechanism which could lead to complete reproductive isolation. Several answers are possible. Part marks are possible. Answers do not need to be this elaborate.