Evolution through natural selection

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The Open University, Walton Hall, Milton Keynes MK7 6AA

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Introduction

In this , we describe the theory of evolution by natural selection as proposed by Charles Darwin in his book, first published in 1859, *On The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. We will look at natural selection as Darwin did, taking inheritance for granted, but ignoring the mechanisms underlying it.

This OpenLearn course provides a sample of level 1 study in Science

Learning Outcomes

After studying this course, you should be able to:

- understand that by biological evolution we mean that many of the organisms that inhabit the Earth today are different from those that inhabited it in the past
- understand that natural selection is one of several processes that can bring about evolution, although it can also promote stability rather than change
- understand that the four propositions underlying Darwin's theory of evolution through natural selection are: (1) more individuals are produced than can survive; (2) there is therefore a struggle for existence; (3) individuals within a species show variation; and (4) offspring tend to inherit their parents’ characters
- understand that the three necessary and sufficient conditions for natural selection to occur are: (1) a struggle for existence; (2) variation; and (3) inheritance
- understand that Endler's experiment with guppies demonstrated that evolution through natural selection can occur in relatively few generations.

1 Charles Darwin

Charles Darwin (1809-1882) briefly studied medicine in Edinburgh before going to Cambridge intending to become an Anglican clergyman. Soon after the voyage of the *Beagle* (1831-1836), during which he was gentleman companion to Captain FitzRoy, Darwin became convinced that biological evolution had occurred *and* saw how it could have been brought about by natural selection. Despite having gathered massive amounts of supporting evidence, Darwin refrained from publishing his revolutionary ideas on evolution for about 20 years until he was almost 'scooped' in 1858 by Alfred Russel Wallace (1823-1913). Darwin continued to live quietly in the country, 'enjoying' ill-health and working on a wide variety of biological problems, as the rest of the world struggled to come to terms with the implications of evolution.

Figure 1 Charles Darwin (1809-1882)

The word 'evolution' means 'change over time' and it can be used in relation to anything that has a history; thus, we could describe the evolution of the motor car or of parliamentary democracy. Biological **evolution** refers to the fact that the many organisms that inhabit the Earth today are different from those that existed in the past. The processes that have brought about changes among living organisms are many and varied and one of them, but only one of them, is natural selection.

In this , we describe the theory of evolution by natural selection as proposed by Charles Darwin (Figure 1) in his book, first published in 1859, *On The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. Incidentally, the title of this book, which is generally abbreviated to *The Origin of Species*, is somewhat misleading, as Darwin wrote rather little about how new species are formed, but did write a great deal about adaptation. It is important to note that, at the time when Darwin was writing, there was no knowledge of the mechanism for a crucial aspect of his theory, the passing of characters from parents to offspring. Darwin was aware that inheritance is a fundamental feature of living things, but he had no knowledge of DNA or chromosomes. In this , we will look at natural selection as Darwin did, taking inheritance for granted, but ignoring the mechanisms underlying it.

You have almost certainly heard of natural selection before and probably have an idea of what it means. But the way that the term 'natural selection' is often used in newspapers and the like can be misleading. To clarify the scientific meaning, we will begin by describing the theory of natural selection as set out by Darwin, and then consider a specific example of evolution by natural selection.

2 Darwin and natural selection

While Darwin knew nothing about the mechanism of inheritance, he was very aware of many other aspects of living organisms. Among these, three are particularly emphasized in his theory:

- The species that inhabit the Earth today are not the same species that existed in the past, although they do resemble them. This aspect of evolution was very apparent to Darwin from the fossil record.
- Each species possesses a number of characters that adapt individuals within that species to their way of life and their particular environment. Much of *The Origin of Species* is devoted to detailed descriptions of the adaptations of individual species, for example the various beak shapes of finches on the Galapagos Islands.
- Selective breeding of domestic species can produce characters in a diversity of forms. For example, dog breeders have produced numerous breeds that differ in characters such as ear length, stature and behaviour: different breeds have different forms of a character.

Darwin's theory of **natural selection** can be expressed as four propositions. These propositions are so important to an understanding of evolution through natural selection that you should try to remember them, although not necessarily word-for-word.

Darwin's four propositions

- Within a given species, more individuals are produced by reproduction than can survive within the constraints (e.g. food supply) imposed by the species' environment.
- Consequently, there is a **struggle for existence**, because of the disparity between the number of individuals produced by reproduction and the number that can survive.
- Individuals within a species show **variation**; no two individuals are exactly alike (not even those we call 'identical' twins). Those with advantageous characters have a greater probability of survival, and therefore of reproducing, in the struggle for existence.
- Individuals produce offspring that tend to resemble their parents (the principle of **inheritance**). Provided that the advantageous characters that promote survival are inherited by offspring, individuals possessing those characters will become more common in the population over successive generations because they are more likely than individuals not possessing those characters to survive and produce offspring in the next generation.

The essence of Darwin's theory is that natural selection will occur if three conditions are met. These conditions, highlighted in bold above, are a struggle for existence, variation and inheritance. These are said to be the *necessary and sufficient* conditions for natural selection to occur. To say that the three conditions are *necessary* means that, unless all three conditions are met, natural selection will not occur. Thus, it will not occur if reproduction does not produce more progeny than can survive, it will not occur if a character does not show variation, and it will not occur if variation does not have a heritable basis. To say that the three conditions are *sufficient* means that, if all three conditions are met, natural selection will inevitably occur and this *can* lead to change in the characters of a population from one generation to the next.

Darwin was concerned with evolution, i.e. change over time, and he proposed a process, natural selection, that could bring about such change. Evolution through natural selection is our main focus here. However, it is important to bear in mind that natural selection is also a process that can *prevent* change, i.e. promote stability. In other words, natural selection can occur *without* evolution. Furthermore, there are factors other than natural selection that affect evolution (some of which are considered in Section 3). The three conditions listed above are necessary and sufficient for natural selection to occur, rather than for evolution to occur. Nevertheless, the vast majority of biologists accept that *natural selection is the most important process by which evolution is brought about*.

Let us look a little more closely at the three necessary and sufficient conditions and consider how likely it is that they will be met. The first, a struggle for existence, is probably almost always met, because living organisms produce more progeny than are required to replace their parents when they die. The second condition, variation, is often but not always met. Some characters show virtually no variation between members of a species, whilst other characters show considerable variation. The third condition, inheritance, is only sometimes met; not all variation has a heritable basis. For example, toads vary in size. The two factors which make the largest contribution to variation in the body size of toads are variation in age (toads continue to grow throughout their lives) and variation in their environment (e.g. a good food supply). These are both external causes (i.e. body size is not a result of particular characters possessed by the toad). So body size in toads is not primarily an inherited character.

This last point brings us to an important aspect of natural selection, which was much discussed when Darwin first proposed his theory. This debate concerns the possible *inheritance of acquired characters*. As well as growing, individual organisms may develop particular skills or physical characters during the course of their lives as a result of differences in the way they live. Consider the human practices of ear-piercing, circumcision and decorative body scars. These characters, which are acquired deliberately during the course of an individual's life, are not inherited by that individual's offspring even though the practice may have been carried out for hundreds of generations. Likewise, a plant that has grown particularly large in a patch of good ground, or a toad that has grown very big because it lives in a garden full of food, will not pass their large size on to their progeny. So, inheritance of *acquired* characters does not occur.

Inheritance of a character occurs only if that character is passed from one generation to the next during reproduction. In other words, it is reproduction that is the crucial factor in natural selection. In a nutshell, natural selection is about the reproduction - rather than survival - of the fittest. (The term 'fitness' has a very particular meaning in biology.

3 Natural selection in the guppy

3.1 Introduction

The purpose of this section is to consolidate your understanding of the theory of evolution through natural selection by looking at a specific example. The guppy (*Poecilia reticulata*) is a small fish whose natural habitat is small streams in northern Trinidad, but it is also a popular aquarium fish. Male and female guppies are very different in appearance (Figure 2); they are said to show sexual dimorphism as male guppies are very much more brightly coloured than females. We will consider how natural selection influences bright coloration in male guppies, and we will do so by considering each of Darwin's four propositions in turn.

Figure 2 A variety of guppies produced by selective breeding by aquarists. The two females in the foreground are relatively plain. The four brightly coloured males show variation in the number, size and colour of the spots on their bodies.

3.2 Number of progeny

Female guppies begin to breed as soon as they become mature at about three months old; they then produce clutches of eggs, most of which become fertilized, at roughly one-month intervals until they die or become too old. Clutches vary in size from one to 40 eggs; the average clutch contains about 10 eggs. Thus, female guppies produce a large number of offspring during their lives, far more than can survive to maturity.

Question 1

Suppose that, in a particular stream, the size of a population of guppies stays more or less stable over several years. How many of a given female's offspring, on average, must survive to reproductive age in such a population?

Two: one that 'replaces' her in the population when she dies and one that 'replaces' one of the males with whom she has mated during her life. If any more than two survive on average, then the population will increase.

Given the large number of fertilized eggs produced by female guppies, and the fact that, on average, only two survive to reproduce, it is clear that there is very high mortality among young organisms in this species. This obviously meets the first of Darwin's propositions. Guppies are fairly typical organisms and illustrate that mortality in nature is typically very high. This mortality provides the background against which natural selection acts.

3.3 The struggle for existence

During their lives, guppies face a variety of environmental hazards which cause mortality. They must find food and, if food supply is limited, some will die through starvation. Heavy rain periodically causes floods which may wash a large part of a population out to sea; occasional droughts cause populations to perish when streams dry out. Like all organisms, guppies are attacked by a rich variety of parasites and diseases. Of most interest to us in this discussion is that guppies are preyed upon by larger, predatory fishes. Of importance to what follows is the fact that, in their natural habitat, some streams contain many predatory fish, others contain few or none. There is thus variation in the level of predation to which wild populations of guppies are subjected.

3.4 Variation

Guppies vary in a number of characters; in particular, male guppies vary in the number, size and brightness of the coloured spots that decorate their bodies (Figure 2). This variation can be detected within a single population in a given stretch of stream, but is much more obvious when different populations, from different streams, are compared. Biologists working in Trinidad have shown that this variation is related to the presence of predatory fish. Male guppies from streams where predators are absent are much more brightly coloured than those from streams that contain predators.

Figure 2 A variety of guppies produced by selective breeding by aquarists. The two females in the foreground are relatively plain. The four brightly coloured males show variation in the number, size and colour of the spots on their bodies.

Question 2

Suggest an explanation, in terms of adaptation, for the relationship between the presence or absence of predatory fish in streams and the brightness of male guppies.?

Bright colouration makes male guppies more conspicuous to predators. Thus, where predators are present, it will be the less colourful males that tend to survive and reproduce. Putting it another way, in streams where predators are present, males have evolved less bright coloration, an adaptation that reduces their risk of being eaten.

As we shall see shortly, the explanation given in the answer to Question 2 is supported by other observations. But it does beg an important question: 'why are male guppies brightly coloured at all?' It is quite common among animals that males are more brightly coloured than females (an example of sexual dimorphism;). The explanation for this is quite complex, but can be summarized briefly. In the majority of animal species, males are the more active partner in initiating mating behaviour and they perform a variety of behaviour patterns to attract the attention of, and stimulate, females. Commonly, females are more effectively attracted and stimulated by the most brightly coloured males, giving such males an advantage in terms of enjoying a higher mating success. For example, peacocks with the greatest number of 'eyespots' in their tails mate with more females than those with fewer eyespots. Likewise, male guppies with more brightly coloured spots are more attractive to females than are those with fewer spots.

The possibility that bright coloration makes male guppies more conspicuous to predators, and the observation that such males are more attractive to females, suggests that the evolution of coloration in male guppies must be seen as an example of a trade-off. In other words, there is a balance between the advantage that the more brightly coloured males experience in terms of enhanced mating success and the disadvantage they suffer in terms of increased predation risk. Moreover, the point of balance in this trade-off is likely to differ between streams or to shift over time in any one stream, depending on the presence or absence of predators. This example illustrates an important point about trying to explain specific characters of organisms in terms of adaptation. It is not sufficient to explain adaptations just in terms of their apparent advantages. Characters typically also involve costs of some kind and so the actual form of a particular character is the result of a trade-off between costs and benefits.

3.5 Inheritance

The adaptive explanation for bright coloration in male guppies given above can only be correct, and can only have evolved by natural selection, if male coloration has a heritable basis. Direct evidence that it is a heritable character is of two kinds. First, a wide variety of decorative guppies have been bred for sale on the aquarium market. Such forms could not have been produced if male coloration were not heritable. Second, if samples of guppies are taken from different Trinidadian streams and bred in the laboratory, they yield male offspring that resemble their fathers; stocks derived from predator-free streams are more brightly coloured than those from predator-rich streams.

Our discussion so far of the biology of guppies has concentrated on whether the necessary and sufficient conditions for natural selection exist in this species. The fact that they do strongly supports the hypothesis that male coloration has evolved by natural selection. However, this does not constitute a direct, rigorous test of the hypothesis. A series of experiments carried out during the 1970s by the American zoologist John Endler did put the hypothesis to such a test.

In one of his experiments, Endler built several artificial ponds and stocked each with a population of guppies derived from several different localities in Trinidad. At this stage, guppies were the only fish in the ponds. There was considerable variation among males in the number of their spots, but the mean number of spots per male across all the populations at the start of the experiment (time=0 months) was 10 (Figure 3). He left the ponds alone for six months, then sampled the populations in each of the ponds and counted the number of spots on the male guppies. He found that the mean number of spots per male had increased to 11.8 (Figure 3).

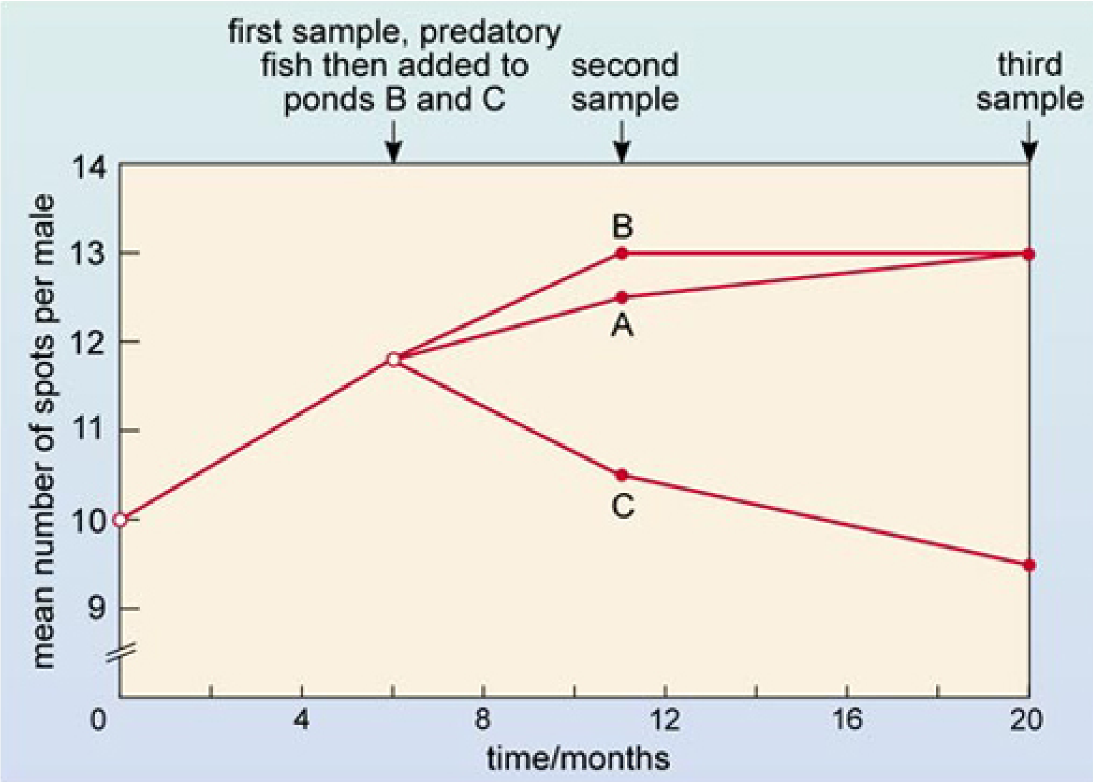

Figure 3 Results of Endler's experiment with artificial populations of guppies.

- What adaptive explanation can you suggest for this increase in male spot number?
- In the absence of any predatory fish, natural selection had favoured an increase in spot number. The more heavily spotted males had more offspring because they were more attractive to females.

Six months may well seem a remarkably short period of time for such a change to have come about. Indeed it is, although it is not the actual time that is important. The guppy is iteroparous, and over the course of six months, Endler's artificial populations were able to reproduce several times.

- Why is the number of breeding episodes more significant than the time in months?
- Because at each breeding episode females choose the most attractive males with which to mate. The more attractive males, i.e. those that have more spots, father more offspring and as spots are inherited, those offspring have more spots.

Having sampled his populations at six months, Endler divided them into three groups (A, B and C). He added to each group C pond one individual of a fish called *Crenicichla alta*, which is a particularly voracious predator of guppies. To each group B pond he added six individuals of another predatory fish called *Rivulus hartii*, which does not prey on guppies. No fish were added to the group A ponds. The ponds were then left alone for a further five months (time for guppies to breed several more times), at which point he sampled them again and counted the number of spots on the male guppies.

- From Figure 3, how did the mean number of spots per male differ between the time of the second sample (at 11 months) and the time of the first sample (at six months) for the three groups of ponds?

- The values for groups A and B had increased slightly from 11.8 to 12.5 and 13.0 spots, respectively. However, the value for group C had declined, from 11.8 to 10.5. The populations had therefore diverged in terms of mean male spot number.

In the final phase of his experiment, Endler left his populations for a further nine months (time for several more generations), after which he carried out a final analysis of male spot numbers. At 20 months, the populations had diverged even more than at the time of the second sample, with groups A and B now averaging 13.0 spots per fish and group C averaging 9.5 (Figure 3).

- Do the results summarized in Figure 3 support the hypothesis that, through natural selection, the presence of predatory fish affects the number of spots on male guppies?
- Yes, they do. Several guppy generations after the introduction of predators to some ponds, male guppies in those ponds that contained voracious predators had fewer spots than those in ponds that contained either no predators or predators that are innocuous to guppies.

Question 3

The purpose of the group C ponds was to see what the effect would be on the guppy populations of adding a voracious predator after several generations in which there had been no predation. What do you think was the purpose of the group A and B ponds?

The purpose of the group A ponds was to show what happened over the same period of time in the absence of predators. The change in the number of spots in the group C guppies might have taken place anyway, whether or not the predators had been introduced. The group A ponds allowed Endler to check on this possibility. {The group A ponds therefore served as 'controls' for the 'experimental' group C ponds. A 'control' is an important feature of scientific experimental procedure. It enables the investigator to be sure that any change taking place in the 'experimental' set-up is due to the factor that has been experimentally changed, and not to some other factor which has not been accounted for.} The group B ponds allowed Endler to check whether any change observed in the group C ponds could have been due, not so much to the addition of a fish that preys on guppies, but to the addition of *any* other species of fish or even *any* other species of predatory fish (whether it preyed on guppies or not). {So again, the group B ponds serve as 'controls' for the 'experimental' group C ponds.}

This example has illustrated four important points about natural selection. First, provided the three necessary and sufficient conditions listed in Section 1 are met, the form of a character can change from generation to generation. Second, the form of the character that results from natural selection represents a trade-off between the various ways in which that character affects the survival and reproduction of individuals. Third, natural selection can lead to a quite marked change in the form of a character in only a few generations. Finally, it shows that the theory of natural selection can be tested by carrying out experiments.

4 Other influences on evolution

One of the crucial conditions for natural selection to occur is that there must be variation. However, it is extremely important to appreciate that natural selection does not itself *cause* that variation; it simply acts on existing variation. The processes that do bring about variation are therefore major components of evolution. The most important of these processes, because it is really the ultimate source of all variation, is mutation. A **mutation** is an alteration in the genetic material which is copied from parent to offspring - the DNA in the cells of an organism. Such an alteration may be associated with a change in the appearance or behaviour of an individual carrying it. For example, there might be a mutant male guppy that has no spots at all, or one that has an unusually large number of spots.

Genetic drift is defined as chance variation in the genetic make-up of *a population* between one generation and the next. If, for a few years and purely by chance, the red-haired residents of Liverpool happened to have more children on average than the other residents did, then (as red hair is a heritable character) the proportion of red-haired people in the population of that city would increase. The change would be due to chance and not because red-haired people were better adapted than other people. Genetic drift would be responsible, not natural selection. In a large population, however, genetic drift is unlikely to have a great effect because chance differences in reproductive success between individuals will tend to even themselves out when a large number of individuals are involved. But in very small populations (say, fewer than 20 individuals) genetic drift can have a strong effect because if only one individual happens, purely by chance, to produce more offspring than the others, its characters will become more common in the next generation. Similarly, a particular character can easily disappear from a small population by genetic drift.

A somewhat different cause of variation between populations can be illustrated by the case of the Dunker sect. A number of small religious sects emigrated from Germany to the USA in the 18th century and have since married almost exclusively among their own numbers. The Dunkers are a sect that settled in Pennsylvania. The frequency of blood group A in the general population of Pennsylvania is 42%, and in Germany it is 45%. However, 60% of Dunkers are of blood group A.

- How would you account for the unusually high frequency of blood group A among the Dunkers?
- The small number of emigrants who established the Pennsylvania population in the 18th century must have included an unrepresentatively high number of people with blood group A.

For obvious reasons, this phenomenon is known as the **founder effect.** The frequency of a particular character in a particular population, in this case the frequency of blood group A in the Dunker population of Pennsylvania, may be due more to chance (the frequency of the character in the small founding population being different from that in the population from which it was derived) than to natural selection.

10.4 Summary

By biological evolution we mean that many of the organisms that inhabit the Earth today are different from those that inhabited it in the past.

Natural selection is one of several processes that can bring about evolution, although it can also promote stability rather than change. It follows that natural selection is not the same thing as evolution.

The four propositions underlying Darwin's theory of evolution through natural selection are: (1) more individuals are produced than can survive; (2) there is therefore a struggle for existence; (3) individuals within a species show variation; and (4) offspring tend to inherit their parents' characters.

The three necessary and sufficient conditions for natural selection to occur are: (1) a struggle for existence; (2) variation; and (3) inheritance.

Endler's experiment with guppies demonstrated that evolution through natural selection can occur in relatively few generations.

Mutation is the ultimate source of variation.

The frequency of a particular character in a particular population may be due to chance events (e.g. the founder effect and/or genetic drift) rather than to natural selection.

Conclusion

This free course provided an introduction to studying Science. It took you through a series of exercises designed to develop your approach to study and learning at a distance, and helped to improve your confidence as an independent learner.

Acknowledgements

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Figure 1 English Heritage Photo Library;

Figure 3 Endler, J. A. 1980, 'Natural selection on colour patterns in Poecilia reticulata', Evolution, 34(1), pp. 76-91, AllenPress, Inc.