Cambridge University Press
978-0-521-02211-8 - Animal Traditions: Behavioural Inheritance in Evolution
Eytan Avital and Eva Jablonka
Excerpt
More information

1 New rules for old games

If you ask a biologist to explain the evolution of the elaborate morning song of a great tit, the subtle food preferences of a domestic mouse, or the efficient hunting techniques of a pack of wolves, what sort of explanation will you get? The chances are you will be told that this type of behaviour can readily be explained by the conventional theory of natural selection acting on genetic differences between individuals. Ever since Darwin, the theory of natural selection has been applied to all sorts of biological problems, from the origin of life to the origin of language, and for most of this century it has been assumed that genetic differences between individuals underlie the variation on which natural selection acts. It is not surprising, therefore, that behavioural evolution is also seen as the outcome of the selection of genetic variations. But is this view correct? In this book we are going to argue that when applied to the behaviour of higher animals, conventional evolutionary theory is rarely adequate and is often misleading. Natural selection acting on genetic differences between individuals is not a sufficient explanation for the evolution of the behaviour of the great tit, the mouse or the wolf.

To understand why we are not satisfied with the current application of Darwin's theory to behaviour, we need to go back to basics. Darwin's theory depends on some fundamental properties of biological entities: on their ability to reproduce, on the differences between individuals and on the heritable nature of some of these differences. In situations in which resources are limited, the interaction of these properties leads to natural selection: heritable variations that increase the chances that the individuals carrying them survive and reproduce will, in time, become more frequent. Eventually, the cumulative effects of selection lead to evolutionary adaptations – to the wing of the swallow, the song of the nightingale, the dam of the beaver. In this general formulation, the theory is comprehensive and powerful, and can bear upon evolutionary processes of all kinds and at all levels. Like most biologists, we accept that Darwinian natural selection is of central importance in the evolution of behaviour. What we are dissatisfied with is not Darwinism, but the currently fashionable version of Darwinism, which we will refer to as 'genic' Darwinism. Many of the assumptions made by the proponents of the genic version of Darwinism seem to us to be oversimplified and restrictive. We are therefore going to look again at some basic questions that are relevant to the application of Darwinian evolutionary theory to behaviour. We want to ask: what is the nature of the raw material of behavioural evolution? What is the origin of heritable variation? How are variations transmitted? How does behavioural evolution by natural selection work?

These questions may sound strange, even if not downright silly and unnecessary. After a century of genetics and over half a century of molecular biology, many people feel that they know the answers: the hereditary variations are variations in genes, in DNA base sequences. New variants arise through random changes in these DNA sequences, and are transmitted when DNA is replicated. The processes that lead to changes in genes are 'blind', so the new variants are not adaptive responses to the life experiences of the organisms that produce them, and do not anticipate the needs of the offspring that inherit them. The effects that these random changes in DNA have on the characteristics of organisms lead to differences in their ability to survive and their success in producing offspring. Over time, genes with effects that improve an individual's chances of leaving descendants – that increase fitness – become more frequent in the population.[1] Natural selection is basically gene selection.

What is wrong with these gene-centred answers to our questions? We are certainly not going to deny the fundamental importance of genetic variation in the evolution of behaviour. What we are going to maintain, however, is that explaining the evolution of animal behaviour in terms of gene selection alone is a mistake. Gene selection alone cannot account for a lot of the behaviour seen in higher animals, including the song of the great tit, the behaviour of the wolf pack and the food preferences of the mouse. These three examples were not chosen at random. What they have in common is that they all involve a special type of learning – social learning. With social learning, animals learn from others how to behave. Generally, in discussions of the evolution of behaviour, social learning is treated merely as a product of gene selection, but social learning is more than this: social learning can be an important agent of evolutionary change. We therefore think that it should be given a more prominent place in evolutionary theory. Darwinian evolution depends on heritable differences between individuals, but not all heritable differences stem from genetic differences. The behavioural differences that are transmitted through social learning also provide the raw material on which natural selection acts.

To illustrate our point we want to carry out a thought experiment that will enable us to think about the evolution of behaviour without resorting to the selection of genes. Imagine a large population of small, brownish, omnivorous, rodent-like mammals, living in small family groups in a species-rich, semi-desert habitat. Call them 'tarbutniks'.[2] Each family consists of a pair of parents and young of various ages. All individuals in the population, indeed in the whole species, are genetically identical. Furthermore, not only are all the tarbutniks genetically identical, but their genes never mutate, so there is not even the possibility of genetic differences between them. However, they are not all identical in appearance and behaviour. Some are larger than others, there are slight differences in their coat colour, their calls are not identical, they produce different numbers of offspring, and there are various other small differences in their anatomy and the way they behave. But there is no correlation between parents and offspring in either appearance or behaviour: the tarbutnik-pups are no more similar to their parents than to any other individual in the population. The differences between individuals are the result of accidental events during their development, and these variations are not heritable. Consequently, although the population may increase or decrease in size, may fill the earth or go extinct, since the variations are not inherited, it does not evolve.

Our tarbutniks start their lives as helpless young, sucking their mother's milk; they grow rapidly, and are soon foraging with their parents for anything that is edible. They are extremely curious, and can learn about their environment through individual trial and error. By trying again and again, they eventually discover a good way of opening nuts and getting at the seeds. After some bitter experiences, they learn that black-and-red striped bugs are best avoided. This ability to learn is important: they possess an excellent memory, so they usually benefit greatly from their past experiences. But they cannot learn from the experience of other individuals, and can never be influenced by anyone else's behaviour. Whatever experience an individual has accumulated, whatever useful information it has acquired about its surroundings, this knowledge is never shared. Each young tarbutnik has to find out about the world through his or her own trial-and-error learning.

Now let us change just one single factor in our imaginary world: let us add to tarbutnik life social learning. By social learning we mean that individuals can learn not just from their own experience, but also from the experience of others. Since age groups overlap, information is transmitted between, as well as within, the generations. A mother can transmit information to her young, young can learn from their fathers and from neighbours, peers can learn from each other. Gradually, patterns of behaviour spread among individuals. What is more, the socially transmitted behaviour patterns can change progressively. An individual tarbutnik that somehow discovers or learns by trial and error something new and useful, such as an additional type of food, can transmit this knowledge to its offspring. Thanks to its new food source, this tarbutnik may be more successful than others in producing and rearing pups. Its lineage will thrive. Even if the better-informed individual does not have more biological offspring, it may have more 'students' ('cultural offspring') who learn its new and useful pattern of behaviour. The new behaviour may thus spread in the population. The addition of social learning to a social organisation in which young and adult individuals regularly interact has introduced the possibility that behaviour patterns can be transferred from one generation to the next. Since some variations in behaviour are now heritable, Darwinian evolution is possible!

It is easy to imagine how new and useful learnt behaviours in our tarbutnik population can accumulate and become perfected by natural selection, so that a complex behavioural adaptation, such as constructing and using a burrow, can evolve. First, a tarbutnik may discover by chance, or through individual trial-and-error learning, or perhaps even by observing individuals of other species, that by occupying a simple hole in the ground they and their offspring are better hidden from predators. The offspring do not have to reinvent or rediscover this: they, as well as other individuals in the group, learn this useful habit from experienced parents, and some may even elaborate on it. They may start extending existing holes by digging, and produce something resembling a short tunnel, which gives them even better protection, not only from predators but also from the extremities of the weather in their semi-desert habitat. By chance, some may dig a tunnel with an entrance and an exit. The tarbutniks who do this evade snake attacks and survive better than others, so the habit spreads. Some tarbutnik mothers produce their young in the burrow they dig, and this habit, which protects both mother and young, also spreads. The individually acquired inventions may be combined and accumulate, producing traditions that change the life style of the animals.

The evolution of traditions, which involves the modification and selection of behaviours learnt from family and neighbours, can lead to more than artefacts like burrows. Foraging traditions, traditions of parental care or traditions of mate choice may also evolve through the selective accumulation of individual variations in behaviour. The way tarbutniks communicate with each other may also be influenced by such evolved traditions. Imagine that a parent discovers that in dense cover, but not in the open, its young respond more readily to an alarm call of a particular frequency. The use of this dense-cover call will probably spread, because the young are less likely to get lost or be eaten by predators, and when they themselves become parents they will use, and hence transmit, the alarm call they learnt. Similarly, think of what might happen if a male discovers that females who are given their favourite food, red berries, are more willing to accept his advances. Thanks to this discovery, he fathers more young than his rivals. His observant sons and their young male friends soon learn and repeat this behaviour. The habit spreads.

But we can go even further. Imagine that the original large tarbutnik population becomes fragmented – massive flooding makes a river change its course and splits the original population into two groups, unable to contact each other. The individuals in one group may, in time, become so different in habits and preferences from members of the other group that, even if they had the chance, they would never, or seldom, communicate with, mate with or learn from members of the other group. One group's courtship offering is red berries, but the other uses nuts, which berry-preferrers have no idea how to deal with. Males offering nuts to berry-preferring females are rejected, and nut-preferring females do not accept berry-offering males. An effective reproductive barrier has been established. Behavioural speciation has occurred,[3] and may lead to the groups diverging even more. Remember that no genetic change is possible in our tarbutniks, so all of their evolution is through the transmission of behaviours. What we see is cultural evolution.

Now let us return to the real world. Unlike our tarbutniks, real organisms are not immune to genetic changes. There is an almost unlimited supply of genetic variation in real animals, which makes it impossible to focus exclusively on cultural evolution. But this is not a good reason for ignoring the role of the cultural inheritance of habits. To do so, leaves too much unexplained. For example, how can we explain differences, such as the different song dialects of family groups of sperm whales, which cannot be attributed to differences in genes? It seems that these dialects are not related to gene differences, but are determined by evolving local traditions, passed on by vocal imitation. In a case like this, we can focus on the transmission of behavioural variations through social learning while ignoring, for the time being, the effects of any gene differences. Of course this does not mean that genes are unnecessary and dispensable. What it does mean is that differences in genes may be irrelevant for some variation in heritable behaviour, at least for a while. So, when we talk about behavioural transmission, we mean that the transmitted differences in behaviour do not depend on genetic differences, but we do not mean that behaviour is devoid of a genetic basis, that it is gene-free!

It can be argued, of course, that, although cultural evolution can, in theory, lead to staggering diversity and spectacular adaptations, it is really a relatively minor and unimportant process, of no significance in the evolution of the basic patterns of behaviour in animals, or even in man. According to this line of argument, all the significant questions about the song of the great tit, the hunting of the wolves or the food preferences of mice, can be answered in terms of gene selection alone, without recourse to non-genetic transmission of behaviour. This gene-centred view is the prevalent view today, so we need to look at it more closely.

Why genes are not enough

The gene-centred view of behavioural evolution is the one offered by classical sociobiology theory. Through the publication of E. O. Wilson's milestone book *Sociobiology*, the grand ambition of sociobiology was clearly spelled out: to understand the social behaviour of animals, and even of man, in terms of gene selection. According to the sociobiologists, variations in genes determine heritable variations in social behaviour; some behaviours result in the production and survival of more offspring than others, so the genes responsible increase in frequency and the social behaviour of the population evolves. Psychology and sociology were to be incorporated into biology, since explanations of human behaviour would be found in the genes that have been selected during evolutionary history. This idea, and in particular its supposed implications for human freedom of action, was, and still is, hotly debated, and split the scientific community into excited supporters and scornful dismissers.

The case for a gene-centred view of evolution in general, and of the evolution of non-human behaviour in particular, was persuasively advocated by Richard Dawkins in books such as *The Selfish Gene* and *The Extended Phenotype*. In time, this once controversial view became the standard evolutionary wisdom. Dawkins argued that the most fruitful and economical way of interpreting adaptive evolution is to look at it through the lens of the gene: to consider the gene as the unit of variation and selection. The catch-phrase Dawkins coined, 'the selfish gene', in fact denotes the way copies of a gene spread through a population at the expense of other variants of the same gene. It is a different way of formulating the old view that evolution is a change in gene frequencies. Using ideas developed by William Hamilton and George Williams in the 1960s, Dawkins showed how many of the long-standing problems in evolutionary biology disappeared if the gene, rather than the individual, was made the principal level of analysis. In particular, the unselfish, altruistic acts of social animals made evolutionary sense when looked at from the selfish gene's point of view.

The selfish gene idea generated a lot of controversy. Some critics attacked it for being a restrictive view of evolution which, because it ignores other levels of selection and variation, leads to more or less (usually less) sophisticated versions of genetic determinism, of the notion that genes govern everything animals are and do.[4] However, most of the critics were less concerned about general issues, and far more worried about the implication of the gene-centred approach for interpreting human social behaviour. They ignored, or uncritically accepted, its implications for animal social evolution, but attacked its application to humans. These critics felt that something rather important – culture – had been left out. However, even in his first book, *The Selfish Gene*, Dawkins had suggested that something extra was involved in human evolution: he argued that cultural evolution proceeded through the selection of 'memes'. He defined memes as units of information (such as ideas) which reside in the brain and are transmitted from one person to another by behavioural means. He envisaged human cultural evolution as being dominated by the replication and selection of memes rather than genes.[5] Nevertheless, in spite of the meme idea, the majority of sociobiologists, who endorsed Dawkins' view of evolution, regarded human culture as an adaptive by-product of the selection of genes. The transmission of memes did not alter the basic rules of the evolutionary game. It was assumed that, since the ability to pass on ideas and behaviours is itself a result of gene-based selection, it is only the genetically determined ability to produce culture that is evolutionarily interesting. Culture is, in fact, still considered as a kind of 'icing on the cake', even when thinking about human evolution. It is usually excluded from the interpretations of the evolution of those fundamental species-specific human behaviours that have a significant 'innate' component. So cultural inheritance is deemed irrelevant to the evolution of the *ability* to acquire language, the *ability* to have complex and multiple social interactions, the *ability* to control muscles and emotions, and so on. Gene differences are so obviously involved in the evolution of 'innate' behaviours, that most evolutionary biologists automatically exclude any role for culture in their evolution.

It is important to clarify at this early point what we mean by 'innate'. 'Innate behaviour' is the term used for a pattern of behaviour whose development is not dependent (or is only slightly dependent) on a process of learning, and is not altered by variations in the environmental conditions that the animal experiences. This does not mean that environmental conditions and experience are unimportant; like any other trait, a pattern of behaviour is always the result of interactions between the animal and its environment. What it means is that most of the differences in individual experiences and conditions make no difference to the development of the mature, species-specific, behaviour. 'Innate' behaviour is relatively independent of learning. Most people think of 'innate' behaviour as 'genetically determined' behaviour, but, as we shall see in this and later chapters, there are problems with this view.

The relative contribution of culture and genes to the development of social behaviour is a complex issue and one that is often misunderstood. No biologist in his or her right mind would deny that there is a genetic basis for the ability to transmit cultural practices. Equally, even the most fanatical sociobiologist would happily admit that many behaviours are the result of the way genes are expressed in a particular environment, and that genetically identical organisms, such as identical twins, can display different behaviours as a consequence of differences in diet, education and family relationships and for other complex reasons. However, the sociobiologists argue that, since the *range* of cultural practices depends on genes, the genetic level is the preferred level of explanation. Thus they argue that what needs to be explained is not the evolution of a particular 'cultural' practice, such as Christmas dinner or the Jewish Seder, but rather the evolution of the genetically determined psychological mechanism, the genetic strategy, that leads to food-sharing. It should be noted, however, that not only is it assumed that a defined strategy is inscribed in the genetic material, but it is also often assumed that the regulation of this strategy by the environment is genetically determined. Robert Wright, one of the spokesmen for modern human sociobiology, asserts that not only are the 'knobs of human nature' (for example food-sharing) genetically determined, but so also are the ways in which the 'knobs' can be calibrated (where, when and how to share food). The calibration is accomplished 'by a generic, species-wide developmental program that absorbs information from the social environment and adjusts the maturing mind accordingly'.[6] According to such sociobiologists, it is possible to explain not only general cognitive, emotional and social patterns of behaviour in terms of genes, but also more specific ones – self-deception and a sense of duty, humour and a hatred of strangers.[7]

This way of thinking has led most human sociobiologists to argue that the genetic strategies that have evolved are embodied in the mind of man as highly specialised semi-autonomous cognitive units, which they refer to as 'modules'. A neural module is a dedicated neural circuit in the brain that processes only a certain type of incoming information (e.g. information about potential mates) rapidly and in an unconscious way.[8] These genetically determined modules, which underlie our allegedly very definite human nature, are the consequence of past selection in 'the environment of evolutionary adaptation' or 'the ancestral environment'. This environment is that imagined for our hominid ancestors, starting about two million years ago, when *Homo erectus* first roamed the plains of Africa. By making fitting assumptions about what the 'ancestral environment' was like, the past function of each and every behaviour is inferred. A specific psychological mechanism is then assumed to underlie each observed type of behaviour. It is assumed that genes for each mechanism have been selected, so that it is embodied in the brain as an independent cognitive module. The same explanatory strategy is used to provide explanations for all social behaviour patterns, however esoteric. Since this type of argument can readily explain every conceivable behaviour, why do we maintain that evolutionary biologists need to incorporate an additional inheritance system into their explanations? Why are genetic strategies not enough? What is wrong with the assumption that the mind is an assembly of separately selected semi-autonomous cognitive modules?

There are several reasons why something is wrong. As we shall discuss in more detail in the next chapters, for some traits in animals and man there is little evidence for substantial genetic determination. In fact, even seemingly 'fundamental' and 'innate' patterns of behaviour, such as whether or not a relationship is monogamous, or how the young are cared for and by whom, differ between populations of the same species.[9] It is often impossible to predict the mating system or the type of parental care that will be found without knowing the ecology and history of the population. Moreover, not only are there many ecological and historical variations in patterns of behaviour, but we also know that some of them are passed on from one generation to the next. They are cultural and heritable. Many people argue that using the term 'culture' for animal traditions is inappropriate, and we shall discuss these difficulties in a later section. For the time being we will use the term 'culture' in a diffuse and intuitive manner to mean social traditions and sets of social traditions. One example of what we regard as animal culture is the well-studied food-handling behaviour of the group of Japanese macaques living on the small, wooded island of Koshima. These monkeys used to live and forage in the forests, but Japanese primatologists started to feed them by scattering sweet potatoes on the sandy beach. Soon, the monkey troop began to leave the forest and feed on the beach. About a year after the feeding started, a young female monkey was observed to wash the potatoes in a nearby brook, actively removing the adhering sand. Within the next few years, potato-washing spread through the troop, and the practice was transferred from the brook to the sea. As well as potato-washing in the sea, several other habits associated with feeding on the sandy beach are now well established in the group of macaques on Koshima. The habits are transmitted from mothers and other group members to the infants.[10]

Japanese macaques are not the only animals to have changed their behaviour in recent times. In many cities and towns, European red foxes have successfully adapted to their new and complex urban habitat over a period that has been far too short to allow adaptation through the selection of genes. The same is true of common racoons in America