Animal Traditions Behavioural Inheritance in Evolution

Article · January 2000

DOI: 10.1017/CBO9780511542251

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Behavioural Inheritance in Evolution

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
10 Stamford Road, Oakleigh, VIC 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2000

Printed in the United Kingdom at the University Press, Cambridge

Typeface in Swift 9.5/13pt, in QuarkXPress™[wv]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data
Avital, Eytan, 1951–
Animal traditions: behavioural inheritance in evoloution / Eytan Avital and
Eva Jablonka.
p. cm.
Includes bibliographical reference.
ISBN 0 521 66273 7
1. Animal behavior. 2. Behavior evolution. 3. Behavior genetics I. Jablonka, Eva II.
Title

QL751 .A94 2000
591.5–dc21 00-037819

ISBN 0 521 66273 7 hardback

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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 and Palestine sunbirds in Israel. These facts do not disappear into thin air just because they do not fit gene-based selection theories. In birds and mammals, the inheritance of habits, of information transmitted through social learning, is both ubiquitous and indispensable. Given the existence of patterns of behaviour that are reliably transmitted from one generation to the next and are selected at the 'cultural' not the genetic level, it is illogical to base theories about the evolution of behaviour solely on specific brain modules that were constructed via the selection of genes. The course of the evolution of behaviour cannot be adequately described and understood without incorporating 'culture' as an active and interacting evolutionary agent that affects the selection of genes. Genes are not enough.

Why culture is not enough

With respect to humans, the opposite view to that of the sociobiologists is also common, particularly among social scientists, who deny a role for genes in human cultural evolution. These social scientists argue that the range of behaviours that an individual human being with a particular set of genes can exhibit (what is known in biological jargon as 'behavioural plasticity') is very wide, practically indeterminable. What is more, they argue, people with different genes can show very similar behaviours. Gene differences are therefore deemed to be irrelevant to the behaviour seen in society, because they do not underlie differences in behaviour. Although genetic evolution may have led to the ability to produce habits and traditions, once this ability is in place, genes only limit the range of possible behaviours, and these limits are so wide that gene differences are, in effect, negligible. According to this view, the explanation of cultural differences and cultural change lies in the realm of the social sciences, not biology. Purely cultural evolution, such as that which we described in our imaginary tarbutniks, is sufficient.

We agree that genes limit rather than determine traditional or cultural differences, and in many cases variations in genes can safely be ignored. However, even when there is a lot of plasticity, variation is often constrained and organised so that among the many things that can be learnt and transmitted, some are learnt and transmitted more easily than others. For example, it is easier for a rat to associate gastric discomfort with taste than with sound, and it is easier for humans to memorise rhymes than to memorise part of the telephone directory. The need to understand the structure of plasticity compels us to think about the structuring factors, and genes are among them. Even when genetic differences do not underlie differences in traditions, we need to know how the genetic constitution influences the evolution of traditions, and how 'cultural' evolution shapes the way genes function and interact with habits. Our point will be clearer if we return to our thought experiment with the genetically identical tarbutniks.

Imagine that two populations of genetically identical tarbutniks are founded in two different habitats. The food sources in the two habitats are not the same, so the nutritional problems the tarbutniks face are different. In one habitat, (A), fruit is particularly abundant. It is tasty and easy to handle, but tends to be acidic and give the tarbutniks digestive problems. Fortunately, some tarbutniks discover by chance that eating mud after ingesting the local fruits helps their digestion. Through social learning, the mud-eating habit spreads. Tarbutniks then find that eating mud from one particular area has a dramatic effect not only on the digestion of fruits, but also on the digestion of other types of plant material. (It is because some microorganisms in this soil have enzymes that degrade cellulose.) The habit of eating the special mud also spreads. Not surprisingly, the pre-existing tendency of young tarbutniks to taste the faeces of their parents is reinforced: by eating faeces, the young acquire some of the beneficial microorganisms from their parents. The outcome of this set of feeding adaptations is that the food available in habitat A can be digested very efficiently.

Now look at what happens in the other habitat, (B). This habitat is very rich in nutritious nuts, so the tarbutniks have different problems. The shells of the nuts are hard, and rarely break when the nuts fall. However, some tarbutniks find ways of cracking the nuts open, and, through parental example, the young learn nut-opening techniques. Gradually, better techniques develop and spread through the population by social learning. Some of the materials in the nuts enhance the transcriptional activity of a gene coding for a major digestive enzyme, so the tarbutniks in habitat B digest the nuts very efficiently. Thus, in both habitats A and B, effective ways of dealing with the local food sources evolve. An unsuspecting biologist, seeing the behavioural and physiological differences between the two populations, and being unaware of the genetically identical and immutable nature of tarbutniks, might start looking for the underlying genetic differences. She would find none, of course. What has happened is that 'cultural' evolution has produced two different, but effective ways of using exactly the same set of genes to satisfy the tarbutniks' nutritional requirements. The differences in the digestive physiology of tarbutniks in populations A and B involve differences in gene expression, not differences in genes.

In this imaginary case, traditions evolved and shaped gene activity. This evolution led to an excellent fit between habits and genes, without the latter changing at all. Although in real organisms genetic variation is abundant, and genetic variation will be mobilised by natural selection, we believe that this imaginary case highlights two important points: first, behavioural adaptations are often primary, and can lead to complex sets of physiological adaptations on the basis of the set of genes already present. Second, since traditions usually evolve much faster than genes, it is much more plausible that traditions evolve to fit and utilise the existing genes, than that genetic evolution drives the evolution of traditions. Of course, in the study of *long-term* evolution, genetic variation is of great importance. Sooner or later the two inheritance systems, the genetic and the social–cultural, will interact and genes and culture will co-evolve.

The American anthropologist William Durham has given an excellent example of one type of co-evolution of genes and culture: it is concerned with the ability of adult humans to make use of the milk sugar lactose, and with the role of cows and bulls in human societies.[11] Fresh milk contains the sugar lactose, which can be broken down into its useful components (glucose and galactose) by an enzyme, lactase-I, which all mammals are able to synthesise. The level of this enzyme is normally very high in the young mammal just after birth, but decreases dramatically during weaning. Normally, therefore, fresh milk is digestible only during the suckling period. Adults outgrow their ability to digest the milk-sugar because their lactase-I level goes down. Consequently, when adults drink fresh milk, it does not yield much energy, and often gives them mild indigestion and sometimes diarrhoea. This situation is characteristic not only of non-human mammals, but also of most human populations. But there are some illuminating exceptions. There are adults who have genes that enable them to break down lactose ('lactose absorbers') and hence benefit from drinking fresh milk.[12] A high proportion of these people is found in the dairying populations of northern Europe, and among wandering pastoralists, such as the Tussi population in the Congo basin. In other populations, including many dairying populations, lactose absorbers are much less common. How can we explain this rather odd distribution?

History and ecology provide the clues. The domestication of cattle led not only to an increase in beef eating, but also, about 4000–6000 years ago, to the use of fresh milk and processed milk products such as cheese. With processed milk, there are no problems with lactose absorption, because processing removes most of the lactose. However, the life style of the wandering pastoralists of the Congo basin probably made it difficult to process milk, and so they came to depend heavily on fresh milk as a ready food source. Adults needed the ability to digest the lactose in this milk. Those with the genetic ability to do so thrived and reproduced, and the gene or genes responsible spread through the population.

What about the other, non-wandering, dairying populations with a high frequency of adults who can absorb lactose? They can and do process milk, so is there any reason why they should drink fresh milk? Is the ability to absorb lactose of any particular benefit to them? It is: lactose, the sugar found in fresh milk, is not only an excellent energy source, it also acts like a vitamin D supplement, facilitating the absorption of calcium. This is of great importance in environments where there is a deficiency of vitamin D. People living in sunny areas have a constant supply of vitamin D, because solar radiation converts precursor steroids to the vitamin. But, in regions that receive little sunlight, vitamin D may be in short supply. If so, the ability to drink milk after weaning has a great advantage, because it both supplies calcium and facilitates its absorption, thus preventing rickets, the crippling softening of the bones that results from calcium deficiency. Consequently, in populations that use cattle as a source of food and live in regions with limited sunlight, individuals who are able to absorb lactose as adults have an advantage over non-absorbers. We therefore expect such individuals to leave more descendants, and in time to become the majority in the population. The distribution of lactose absorbers fits this expectation – their frequency is particularly high in populations living in northern latitudes where there are periods of the year with little sunlight.

The increase in the frequency of the genes enabling adults to make good use of fresh milk is therefore the result of a cultural change, the domestication of cattle. Domestication was beneficial for individuals in all communities in which it was practised, because beef and milk products are energy-rich foods, but in some populations, such as those of the wandering pastoralists and the populations of northern Europe, fresh milk became particularly important. What is fascinating is that in these populations we see not only a high frequency of lactose absorbers, but also a high cultural regard for fresh milk. According to Durham, in the creation myths of the Indo-European people, the importance of the cow, the source of fresh milk, becomes greater the higher the latitude. In the myths of the most northern populations, the first animals or the first bovines to be created were female cows, who produced a lot of milk. Their milk was drunk fresh by giants and gods, and is considered to be the source of their great size and strength. The first bovine of creation was not used for food or sacrifice, but continues to nurture the world. These myths thus reflect the importance of fresh milk and at the same time reinforce and encourage its consumption, leading to even stronger selection for lactose absorbers; the increase in the frequency of adult lactose absorbers further enhanced the 'educational' value of the myth. A positive, multigeneration, feedback-loop between genetic and cultural evolution was thus formed. Culture and genes co-evolved, affecting one another. Culture alone was not enough, although it became the guiding selective force, opening up new possibilities of genetic evolution.

The evolution of lactose absorption is an example of harmonious and simple co-evolution between genes and culture. Other, less straightforward types of co-evolution are possible, but we will leave these for later chapters. Social learning is usually the driving and directing force of this co-evolution, leading organisms to construct, regulate and stabilise their biotic and social environments, and consequently to influence the selection pressures the environment imposes on them. Acquired and socially transmitted behaviours occupy the driver's seat because adaptations to local changes occur more quickly through behaviour than through genes.

Genes and culture: new studies and new problems

Human cultural evolution, and the interplay of genetic and cultural factors in the evolution of cultural practices, have been the subjects of some important theoretical work during the last twenty-five years. Geneticists Cavalli-Sforza and Feldman pioneered this new approach, which was soon taken up and developed by others, notably the anthropologist Robert Boyd and the ecologist Peter Richerson. All borrowed the mathematical tools of theoretical population genetics, quantitative genetics and epidemiology, and applied them to culture. To follow the changes in frequency and the spread of new cultural practices in populations, they treated cultural practices as if they were discrete transmissible entities, much the same as infectious viruses.[13] New fashions in music or clothes, for example, were assumed to be transmitted, and to spread like measles or chicken-pox.

This genetic–epidemiological viewpoint has highlighted several major differences between genetic and cultural transmission. First, cultural offspring need not be genetic offspring: genes are passed on only to one's children, but behaviour can be learnt by both kin and non-kin 'students'. Second, cultural variations are not 'random': they are acquired by a process of learning, and learning is not a 'blind' process, even when there is an element of trial and error in it. It is guided by goals, and organised by rules that allow effective categorisations and generalisations. Third, while, with very few exceptions, genes are all transmitted according to the stable laws of genetic segregation, which results in each gene having the same transmissibility (present in 100% of the offspring of an asexual organism and 50% of those of a sexual organism), patterns of behaviour have variable transmissibilities. If one particular pattern of behaviour is more easily perceived, learnt or memorised than others, it becomes more common in the next generation even if it does not have a particularly beneficial effect on the animal. Imagine, for example, a monkey population in which the young learn from their mothers what is good to eat. Two new types of food are introduced into the environment of such monkeys. The animals eat both foods, which are equally abundant and energy-rich, but one food type has features that make it more tasty, or slightly addictive. Naturally, this is the one that mothers are soon eating most frequently, and from their mothers the young learn to eat it too. The less tasty but equally nutritious food is ignored by the youngsters, at least for the time being. Such 'biased transmission' is rare in the genetic system, but it is probably the rule rather than the exception in behavioural evolution. One behaviour may be more easily learnt and remembered than another because of its inherent qualities, as with the monkeys' food, or because of the way it is acquired. For example, if the behaviour can be learnt from multiple 'teachers' (through the influence of parents, neighbours and other individuals), it is more likely to be both acquired and passed on.

Recognising that cultural inheritance is not only possible, but also can be profitably modelled, challenged the sociobiological view of human social evolution. Yet the cultural inheritance approach did not become mainstream, either in anthropology or in behavioural ecology. On the one hand, the anthropologists argue that the 'units' of cultural inheritance on which the models are based are too artificial: cultural practices cannot be treated like 'atoms' because they are part of a practically indivisible whole, a cultural 'package'. Even if one traces the evolution of a relatively simple human cultural product, for example, the pre-fabricated house, one has to take into account changes in family size and standards, immigration, supply and demand, political consequences, the strength of trade unions and so on. All of these affect the production and marketing of the product, and may also introduce modifications into the design of new models. Hence, social organisation not only affects the selection of the product, but often introduces alterations into the actual technological innovation itself, as well as influencing its rate and mode of transmission. The anthropologists stress that culture is a system of practices and institutions that is very difficult to tease apart, and information is transferred and reconstructed at several levels of social organisation. Moreover, every change in behaviour, practices or ideas can have direct modifying effects on a whole repertoire of behaviours, and reverberate through the whole system.

Most behavioural ecologists, on the other hand, tend to ignore cultural evolution theory. Often it has been presented in a rather inaccessible mathematical form, and it was not clear that it could offer them any interesting new insights into animal behaviour. Since culture is generally assumed to be of major significance only in humans, and to have only very minor influences on animal behaviour, the cultural–evolution approach seemed to be of little importance for understanding the evolution of the social behaviour of mice, rats and bee-eaters. Only rarely have the analytical tools offered by the cultural evolutionists been applied to the social behaviour of birds and mammals.

The general framework used in the theoretical studies of the cultural-evolution school is the one that we are using in this book. Our approach, however, is different in two principal ways. First, we are focusing on transmitted behaviour in birds and mammals, rather than in humans. We shall use the rich field data on social organisation and interactions to re-examine the evolution of behaviour from a perspective that incorporates social learning and traditions as agents of evolution. This approach provides some simple (and testable) evolutionary interpretations of patterns of behaviour that have not been explained satisfactorily within the conventional framework. It also provides additional or alternative explanations for some behaviours that do have orthodox explanations. Second, we are going to stress the networks of ecological and developmental interactions in which particular patterns of behaviour are embedded. We shall be looking at the ways in which these networks are constructed and reproduced anew every generation, at the conditions that make them stable, and at the kind of heritable variations that they can support. In other words, we shall not treat patterns of behaviour in isolation, but rather as dynamic packages, parts of a developmental system that, in most cases, is transmitted and evolves as a whole.

The way non-human animals pass on learnt patterns of behaviour has been studied both by experimental psychologists, in the controlled and unnatural conditions of their laboratory, and by ethologists, under natural field conditions. Unfortunately, until about twelve years ago, many of the field observations were anecdotal, and were rarely integrated with laboratory studies and brought under a common theoretical roof. Although in 1980 John Bonner and Paul Mundinger published pioneering reviews on the evolution of culture in animals, and these reviews increased interest in the subject, the study of animal cultures has remained marginal. Mundinger's comprehensive review had little direct impact, while Bonner and the few evolutionary biologists who followed him were concerned mainly with the genetic basis of the ability to produce culture, not with the evolution of animal culture itself or its effects on genetic evolution. They regarded cultural evolution in animals as limited in scope, as a product rather than an agent of the social evolution of behaviour. However, this view of animal cultural evolution has been changing.[14] Several excellent symposium volumes that document and analyse social learning and 'cultural' practices in animals have been published during the last twelve years; collaboration between experimental psychologists and behavioural ecologists is growing. Increasingly it is recognised that, if we are to understand how animal psychology develops and how it has been evolving, social learning has to be considered. Today there is hardly an issue of an evolution-oriented behavioural journal that does not publish at least one article on social learning or the local traditions of animal populations. This interest in animal traditions should lead to a better understanding of the relationship between genes and culture during evolutionary time. At a more general level, it will alter the way in which we think about the processes that drive evolution.

Selective and instructive processes in evolution – Darwinian Lamarckism

Cultural evolution involves natural selection between alternative patterns of behaviour. It is therefore Darwinian. However, the origin and transmission of some of the behavioural variations on which natural selection acts depend on learning. Since animals can adapt by learning, and through social interactions can pass on some of their new adaptations to their progeny, changes in heritable behaviour can occur in direct response to changes in conditions. Such evolutionary change is said to be 'Lamarckian', by which most people mean that it involves the inheritance of acquired characters. In modern biology Lamarckism has usually either been ignored or ridiculed. In recent books on evolution, it has been almost a rite to point to the weakness of Lamarckism in order to illustrate the strength of Darwinism. The problem has been that, for as long as there seemed to be no evidence of a mechanism through which newly acquired adaptive characters could be transmitted while non-adaptive ones were not, Lamarckism seemed to introduce some kind of mystical goal into evolution. However, now that it has been recognised that there are inheritance systems (of which social learning is but one) that make it possible for adaptive characters to be acquired and transmitted, the ghost of teleology can be exorcised. Some acquired characters can be transmitted because there are inheritance systems that have evolved to do exactly that.

There is nothing surprising or unusual about the evolution of the ability to transmit some acquired characters. It is the outcome of natural selection: those individuals who could transmit to their progeny the beneficial adjustments that they had made during their lifetime were reproductively more successful than others, so the genes that made this possible spread. Lamarckian mechanisms thus evolved under the auspices of Darwinian ones, through the natural selection of random genetic variations.[15] The Darwinian origin of the mechanisms that transmit acquired characters does not diminish the evolutionary importance of these mechanisms once they are in place. Darwinian evolution, based on the selection of largely random genetic variations, has constructed new (Lamarckian) rules for the evolutionary game. To interpret evolutionary phenomena without incorporating these new rules is unreasonable. Lamarckism is not an alternative to Darwinism; it complements it to form a broader theory of Darwinian evolution.

So why is it so commonly assumed that Darwinism and Lamarckism are irreconcilable alternatives? The answer seems to lie in the fascinating sociological and historical developments that led to simplifying assumptions about each of the two theories.[16] A fundamental (and artificial) dichotomy was created between them. Darwinian theory focuses on selective processes – on choice between alternatives, while Lamarckian theories focus on instructive processes, on the acquisition of transmissible information. When selection is considered to be the major (or exclusive) cause of adaptation, the origin of variation is deemed unimportant; the most extreme and simplest selectionist model would, in fact, assume that the origin of variation is totally random with respect to selection. On the other hand, when variation is supposed to be acquired (by learning or any other process), the simplest instructionist model assumes that instruction results in a single typical result, and therefore in a population of similar individuals in which selection could play no role. If all mother hens acquire a preference for red grains, and this preference is passed on to the chicks as they observe their mothers eating red grains, selection seems irrelevant to the ultimate fate of the acquired variant, since all chicks are assumed to prefer red grains.

Such an extreme instructionist example is, of course, only a convenient straw man. Some of the chicks in our example may not learn at all and, among those who do, there may be differences in the strength of the preference (some of the mothers from whom the chicks learn may be very choosy, others less so), or in the time it takes to learn the preference, and so on. Some of these variations, if heritable, can be transmitted and provide the raw material of natural selection. A brief look at our own experiences reveals more clearly the fallacy of the assumption that behaviourally acquired characters lead to uniformity. When we learn a new skill, for example how to paint a room, we often modify somewhat the method that we have learnt from our teacher. We may use the various brushes in somewhat different ways, or paint doors, windows, walls and ceilings in a different sequence. A maladaptive variant, such as omitting to take down the lamp-shades before starting, is usually selected out. Only rarely will we observe a single technique in the population; as the techniques are passed on, we see clusters of variant methods. Thus, learning defines the direction