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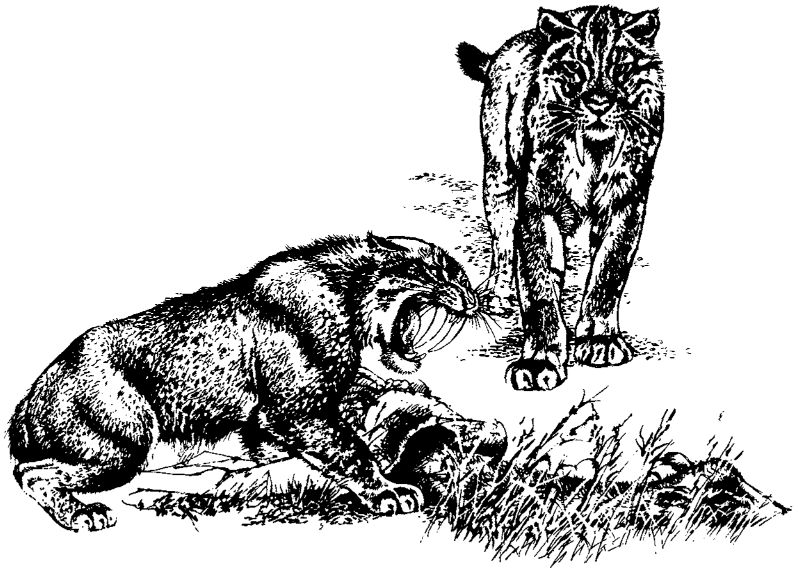
Introduction

Evolution is a subject of central importance to biologists interested in the study of behaviour. Darwin himself devoted a chapter in *The Origin of Species* to behaviour and, like so much else in biology, the growth of interest in behaviour during the past century took much of its impetus from the framework that he provided. Yet the study of behavioural evolution itself has lagged behind other aspects of behavioural work because, for various reasons, it is not an easy subject in which to achieve insights. Set against this, there are reasons to regard behaviour as an especially important field to study from the evolutionary viewpoint. What is both difficult and important about behaviour?

The most fundamental problem in the study of behavioural evolution,



as compared to that of morphology, is the lack of a fossil record. To say that 'behaviour leaves no fossils' is almost a cliche, but it is not entirely true. The physical structures that we find fossilised can sometimes give a clue to what the behaviour of their possessors must have been like. That *Archaeopteryx* had wings but no keel suggests that it glided rather than flew. Who could doubt that the sabre-toothed tiger was a carnivore? In some cases the fossil record has even allowed a closer examination of behavioural evolution. For example, marine invertebrates can sometimes leave traces of their burrows in the fossil record. The shape of these burrows indicates how they foraged so as to avoid covering the same ground twice. Furthermore, the particular way in which they refilled their tubes with material that they had processed gave a laminated structure of characteristic form to the burrows they left behind. These burrows are products of behaviour, but their form is just as characteristic of the species as are aspects of its morphology; tracing the changes in form through the fossil record shows how their foraging patterns changed as their behaviour evolved (Seilacher, 1986).

Gastropods can also leave fossil evidence of their behaviour, through the holes that they bore in the shells of their prey. Examination of prey can indicate whether or not a predatory attempt was made, whether it succeeded, where on the shell the hole was made and, by the size of the hole, the size of the predator. Changes in these features over hundreds of millions of years indicate how predators and their prey evolved (Kitchell, 1986).

Despite these examples, there is no doubt that our direct knowledge of how behaviour evolved is poor, for we can only infer it from structures that were left behind. In most cases we lack these and must rely on more indirect knowledge, comparing present-day species to determine how their common ancestor must have behaved and what changes have taken place since they split. The classic study by Konrad Lorenz (1941a, b) on the displays of ducks blazed a trail in this direction, but for many years there were few further developments. The field of comparative studies is a methodologically complex and difficult one, calling for rigorous statistical techniques: only recently have these been placed on a sound footing. As John Gittleman and Denise Decker make clear in Chapter 4, a start has been made in studies that make use of these new methods, and prospects for the future in this area look bright.

The early ethologists, such as Lorenz with his study of ducks, concentrated on displays; there was good reason for these to diverge between species and little reason for convergence. Species are the fundamental units

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within the animal kingdom. We can, rather arbitrarily, split them up into races or subspecies. We can equally group them into genera, families, and so on. But of all these groupings, the species is the most clearly defined (Mayr, 1963). One of the major reasons for this relates to the behaviour of the individuals that make them up, especially their displays. Behavioural changes accompany speciation, and may indeed lead to it. Differences in behaviour between species are a major reason why individuals of different species seldom even attempt to mate with one another. The topic of behaviour and speciation is considered by Roger Butlin and Michael Ritchie in Chapter 3.

A major difficulty in studying the evolution of behaviour lies in its very flexibility. While displays may be rather constant and fixed within a species, and have to be to ensure their recognition, this is far from true for many other aspects of behaviour. Taxonomists draw the distinction between homology, where two structures are the same because of common ancestry, and analogy, where they merely look the same through convergence. In tracing evolution, the distinction is clearly a very important one. Detailed studies of the bones of the forelimb allow us to conclude that the pectoral fin of a fish, the wing of a bird and the human arm are homologous: all are examples of the tetrapod forelimb. But the wing of a bird and that of an insect, while performing the same function, are simply analogous, as they are based on quite different structures. Application of the idea of homology to behaviour is fraught with difficulty (Atz, 1970). While the behaviour of closely related species is often very similar, the potential for convergence between non-relatives following a similar way of life is tremendous. Furthermore, such responses can occur within the lifetime of the individual. Thorpe (1963) defined learning as the process manifested by 'adaptive changes in individual behaviour as a result of experience'. The word 'adaptive' is there, just as it is in evolutionary arguments. When we see an animal performing an apparently well-adapted action, such as washing a potato before it eats it, we cannot tell whether the behaviour has a long evolutionary history or was learned for the first time a few moments before. That is, we cannot tell without further study. For the flexibility of behaviour, and the role that experience plays in shaping it, is not just a problem for studying its evolution; it is one of the prime reasons why the evolution of behaviour is of interest. Learning and flexibility are, of course, themselves the products of evolution, and are of particular relevance to ourselves. Dick Byrne takes up this theme in Chapter 8.

The flexibility of behaviour leads to a complex interaction between it and evolution. Animals can, by their behaviour, move to different places, choose new foods or modify the world around them in various ways. Any such actions will change the selective forces operating on them. So behaviour can modify the rules of the game. Indeed, it has been argued that such changes may be of fundamental importance in evolution, behavioural change coming first and genetic adaptation in line with it following on behind, the so-called 'Baldwin effect'. To take an example, an animal that eats only red berries will have a problem in a year when the harvest of these is poor. Only those flexible enough to switch to blue ones may survive. Learning to switch may be involved, and those that learn quickly do not starve, whereas the slow learners go to the wall. Over a series of disasters, selection may favour faster and faster learners until, ultimately, the survivors will not have to learn to eat blue berries at all but will do so on their first encounter. As Darwin would have put it, a habit has become an instinct. This may sound Lamarckian, but it is not; it is simply indicative of the complex and fascinating interplay between behaviour and evolution, which is very much a two-way process.

One problem one might expect in studying the evolution of behaviour, which is not really a problem at all, is whether or not the behaviour pattern under study has a genetic basis. Put more strictly, evolution can only take place where *variation* in a feature is at least partly genetic, so that selection can act upon it and changes are carried over from one generation to the next. Some of the arguments in this area have smacked of genetic determinism, and have rightly irritated those who thought the nature–nurture controversy long resolved in favour of an interactionist stance. Genes, as such, do not cause behaviour patterns, and it is not necessary for them to do so for selection to affect behaviour. To stress the point, all that is required is for variations in the behaviour pattern to have some genetic component on which selection can act. It is hard to imagine any aspect of behaviour of which this will not be true. Selection experiments may lead to change more or less quickly, depending on the extent to which individuals differ genetically in ways that affect the behaviour, but it is hardly likely that such an experiment would not work at all. All behaviour is genetically based, and affected by many genes; at least some of the variation in it is bound to stem from differences between individuals in their exact genotype. Ary Hoffmann explores the ways in which genes affect behaviour in more detail in Chapter 2.

As mentioned earlier, developments in the comparative method, allowing us to reconstruct the course of evolution from studies of extant species, have done a great deal to enhance our understanding of behavioural evolution in the past few years. Comparisons are the essence of science, and here we are talking of comparisons between species or 'taxa'. A quite different approach to comparison has had even more impact, and this is the comparison between the way animals behave and evolutionary models of how they would be predicted to behave. Since Maynard Smith and Price (1973) applied game theory to the fighting behaviour of animals, and coined the phrase 'evolutionary stable strategy' (ESS), models relying on this approach have burgeoned. Some of them are highly mathematical and not all of them have their feet as firmly in the real world as the more innumerate of us might like. But they have had a strong impact, both on our thinking about behaviour and on our understanding of it, as the frequent references to ESS theories in this book will testify. Chapter 5 is specifically devoted to models of behaviour such as these: in it Ian Harvey skilfully covers this ground without assuming that we all have a degree in mathematics.

Darwin (1871) was aware that sex was something rather special, so he devoted much of *The Descent of Man* to it. A century and more later, it is still a central topic for evolutionary discussion. Indeed, where 20 years ago behavioural conferences were dominated by talks on foraging strategies and the application of optimality theory in that area, today breeding systems and mate choice seem the focal subjects. The diversity of animal mating systems and understanding them in terms of natural selection are in themselves intriguing. So is the role of sexual selection in leading to the lavish displays, ornaments and weapons shown by many species. But the importance of sex in evolution runs deeper than these. There is no doubt that sexual reproduction, with its capacity to generate variety through recombination, is a potent force for change in evolution. What remains in some doubt is why sex evolved. Just what advantage is it to a female to throw half her eggs away by producing males rather than producing entirely asexual daughters? This and other perplexing aspects of sexual reproduction are dealt with by Tim Halliday in Chapter 6.

Darwin's theory was delightfully simple; T. H. Huxley remarked on how stupid he was not to have thought of it himself. But it has been, and remains, subject to a great many misunderstandings. There have also been changes in thinking. The neo-Darwinian will agree with much in *The Origin of Species*, but he also has ideas of his own. Perhaps the most significant difference comes from the development of kin selection theory, largely dating from the two classic papers by Hamilton (1964a, 1964b). The level at which natural selection is best viewed as acting, whether on individuals or on genes, remains a subject of debate, but few would doubt that the theory of kin selection gives the right perspective on the issues. If mate choice is the most popular seminar topic in behaviour today, kin recognition must run it a close second. Realisation of the importance of kinship in behaviour has led to many studies in this field; these are amongst the topics explored by Peter Slater in Chapter 7.

If, as kin selection theory predicts, animals should behave in such a way as to benefit their genes rather than, for example, the group or species to which they belong, we can account simply and elegantly for much of the great diversity of behaviour that we observe in the natural world. But a few interesting problems remain. Altruism is one, although there are remarkably few well-documented examples of animals behaving apparently in the interests of others rather than themselves, as the account of the subject in Chapter 7 shows. Another problem area is social structure and organisation, which Phyllis Lee discusses in Chapter 9. How do such phenomena as complex social structures emerge from groups of individuals, if each is acting purely to enhance its own inclusive fitness? Are kinship and reciprocal altruism the sole keys we need to find a solution to this question, or do animal societies have emergent properties that we must address at a different level? Herbert Spencer viewed an orchestra as an immoral organisation because it forced the individual to become subordinate to the group. Few would take such an extreme stance when it comes to human organisations, but do animal groups consist of more than just collections of individuals playing their own tunes?

The evolution of behaviour, how natural selection acts on it, and the adaptations that have been produced as a result are a particularly exciting research area today. Not only is there the superb diversity of nature to be accounted for, but there are also some clear and ingenious theories against which to test it. Finally, a battery of tools has been developed which puts us in a powerful position to carry out such tests. If Charles Darwin were alive today, surely this would be his field – and he would certainly be in his element!

2

Behaviour genetics and evolution

A. A. HOFFMANN

2.1 Introduction

Behaviour genetics is concerned with the genetic analysis of individual differences in behavioural traits. These differences may occur naturally or they may be induced by a researcher in the form of mutations.

Naturally occurring variation forms the basis of traditional behaviour genetic approaches. Much of the early literature in this area is concerned with demonstrating a genetic basis for individual differences. Studies tended to focus on simple behaviour patterns that could be easily and rapidly measured under laboratory conditions with a high degree of repeatability. Organisms were used that could be easily maintained in laboratory cultures, in particular fruit flies and mice. This enabled researchers to accumulate observations on a large number of individuals, which is a prerequisite for any genetic analysis.

Examples of these early studies include geotaxis in *Drosophila melanogaster*, in which flies were forced to make a series of up or down movements in a vertical maze (e.g. Hirsch, 1963), and 'emotionality' and 'open field behaviour' in rats and mice, which was measured as the rate of defaecation and urination when rodents were placed in a new environment (e.g. Broadhurst, 1960). By selecting over successive generations for individuals with high and low emotionality scores or negative and positive geotactic responses, lines were created which differed markedly for these activities. Such studies illustrated that genetic differences existed among individuals and that behavioural traits, just like morphological and physiological traits, could be subjected to a genetical analysis.

Naturally occurring variation also forms the basis of human behaviour genetics, which has traditionally been concerned with testing whether individual variation in human behaviour has a genetic component. In particular, much effort has been devoted to the study of intelligence as measured by IQ tests, and personality as measured by responses to questionnaires. More recently, human behaviour genetics has moved beyond simply determining whether or not behavioural variation has a genetic component. The impetus for this development has come from psychology in which behaviour genetics is seen as a tool for further understanding behavioural variation rather than as a means of studying the functioning of genes underlying variation. For example, recent genetic research on intelligence has focused on the extent to which the same genes influence different intellectual skills, and on the roles of genes and the environment in different stages of intellectual development (Hay, 1986; Plomin, DeFries & McClearn, 1990).

Induced behavioural mutations, particularly those altering the nervous system, have been used extensively to understand how nervous systems are assembled and how their components function. This work comprises the relatively new field of neurogenetics, and has been largely carried out using protozoans, nematodes and *Drosophila* (Hall, Greenspan & Harris, 1982). Neurogenetics is expanding rapidly with the availability of techniques from molecular biology to study specific genes and their products.

This chapter is concerned with aspects of behaviour genetics relevant to evolutionary processes. Because neurogenetics and human behaviour genetics have generally not addressed evolutionary questions, these areas will only be discussed briefly. Early behaviour genetic studies will not be considered in detail because the ecological significance of many traits used in these studies is not clear. For example, it is difficult to imagine how the response of fruit flies in a tube to light or gravity is relevant to their ability to locate resources in nature (Rockwell & Seiger, 1973). Similarly, it is not known how defaecation and urination rates of mice in an open field experiment relate to their exploratory behaviour in nature (Hay, 1986). The discussion will therefore focus on recent research using traits relevant to the ecology of animals.

The chapter starts with a brief look at the way genes can influence behaviour. This is followed by examples illustrating the genetic analysis of variation for ecologically relevant behaviour. Some complications and limitations evident from these examples are discussed. The genetic analysis of differences between populations is then considered to illustrate behavioural adaptation to different environmental conditions. A final section considers the genetic analysis of behavioural differences between closely related species.

2.2 How genes affect behaviour patterns

Mutations which block or alter behaviour patterns provide a useful tool in understanding how genes influence behaviour (Hall *et al*., 1982). Two types of information can be obtained from comparisons of mutant and normal individuals. First, mutations provide a way of disrupting behaviour, similar to disruptions obtained with direct surgical intervention or drug treatment. For example, the importance of the antennae in the behavioural response of an insect can be investigated by surgically removing the antennae of a normal individual or by isolating mutant insects which lack antennae. Mutations are particularly useful when disruptions cannot be readily obtained by experimental manipulation. For example, in the analysis of the visual behaviour of flies, extensive use has been made of mutants which lack or change particular cell types in the eye (Hall *et al*., 1982), alterations that would have been difficult to obtain by surgical intervention. However, a limitation of mutations is that they are often less specific than direct intervention techniques because a single mutation may cause disruptions in several different traits.

Second, mutations provide a way of isolating genes and gene products affecting behavioural patterns. Enzymes and other proteins involved in the development and control of the nervous system can be identified. This approach has been particularly useful in isolating genes and gene products involved in complex processes such as learning and memory (Dudai, 1988).

Most neurogenetic studies have been carried out with micro-organisms and invertebrates. This is partly because the effects of mutations at the biochemical and physiological levels are easier to determine in simpler organisms. It is hoped that an understanding of gene products influencing behavioural processes such as learning and memory in invertebrates will provide insights into these processes in higher organisms. In addition, mutations with drastic effects can readily be isolated in micro-organisms and invertebrates by 'screening' for individuals with radically altered behaviour patterns. Screening is normally carried out after individuals are exposed to a treatment inducing mutations, such as exposure to a mutagenic chemical. Mutations can also arise without mutagenic treatments, but such 'spontaneous' mutations occur at a much lower frequency than induced mutations and they are therefore not easy to detect.

The following studies illustrate some of the ways mutations have been used to understand behaviour patterns. The example of defaecation in nematodes shows how mutants are isolated and the type of information they readily provide. Research on learning in *Drosophila* indicates how mutations can lead to the isolation of gene products involved in a complex process. Finally, the shiverer mutations in mice illustrate how the effects of specific genes can be studied in mammals with the help of molecular biological techniques.

2.2.1 Defaecation in **Caenorhabditis elegans**

The nematode *Caenorhabditis elegans* has been used extensively for the genetic analysis of behaviour. The nervous system of this nematode is relatively simple and well known, and can be altered substantially without causing death. These features make *C. elegans* particularly suitable for understanding the neurobiological basis of behaviour patterns. Many mutations have been isolated which influence behaviour such as egg laying, osmotic avoidance, locomotion and touch sensitivity. More than 200 genes are now known that have specific effects on the nervous system of *C. elegans*.

An example of a screening for behavioural mutations is a study by Thomas (1990) on defaecation. As outlined in Figure 2.1, defaecation is achieved when nematodes undergo a cycle of muscle contractions, starting with the contraction of the posterior body muscles which causes the gut contents to be pushed forwards. The muscles relax and the gut contents accumulate near the anal region. The intestinal contents are then pressurized and the anus is opened to enable expulsion. Each cycle therefore consists of three phases, the posterior body contraction, the anterior body contraction, and finally the expulsion of faeces.

Thomas (1990) obtained mutations by feeding nematodes a mutagenic chemical (ethylmethanesulphonate). To isolate the mutations, adults were kept individually and produced F1 progeny (the *C. elegans* strain used was a self-fertilizing hermaphrodite). Most newly arisen mutations are recessive rather than dominant and will therefore not be expressed in a diploid organism unless they are in the homozygous form. Any recessive mutation arising from the mutagenic treatment should be in a heterozygous condition in the F1 generation and not recognizable. To identify mutations, F2 worms were produced from the F1 generation. Following the basic rules of Mendelian genetics, some recessive mutations will be expressed in the F2 generation because $\frac{1}{4}$ of the progeny should be homozygous for a newly arisen mutation. Mutants could therefore be identified by observing the defaecation behaviour of F2 individuals under a microscope.