1

Setting the scene

An oak tree growing in a meadow has a relatively short trunk and a familiar structure of wide branching limbs that can easily be recognised. However, when oaks grow in forests they compete with each other and develop long straight trunks; they have an appearance that is totally different from the same species growing in open country. One of us, on a family holiday in Greece, collected two tiny seedlings of the Greek fir from a mountain on the island of Cephalonia. One seedling was planted in a garden in England and, 30 years later, is 15 metres high, growing fast and with a form just like the illustrations in tree books. The second was planted in an earthenware pot and is now a hundredth the size of the other – a perfect bonsai. Such capacity to respond dramatically to the available resources, however limited, and yet survive is also seen in those mammals in which large litters are commonplace. The runt in a litter of pigs might be a tenth of the weight of its siblings at birth, but it is perfectly formed and, if given sufficient milk after birth, will survive to become an adult, albeit of reduced size, that will be capable of breeding.

Nobody will be greatly surprised by these examples, and yet the 'robustness' of development – whereby the general characteristics of each individual develop in much the same way irrespective of the environment – is often contrasted with 'plasticity' or malleability, which allows change, particularly during early development. These seemingly opposed characteristics of organisms are frequently forced into a dichotomy that is often used to explain natural phenomena: the programme for an organism's development is either closed or open; its characteristics are either immutable or subject to change; the brain is either hard-wired or changeable; behaviour is either innate or learnt. We shall argue that these opposing ideas that seem so obvious to many people are misleading and unhelpful to anybody who wishes to

understand how the body grows and the brain develops. Our aim is to draw the reader away from patterns of thought that are rooted in conventional public debates about 'nature' and 'nurture' rather than in empirical biology.

The nature/nurture dichotomy is not merely a feature of popular science and folk biology. Many eminent biologists have accepted an 'either/or' account of development. For example in his book *Sociobiology*, Edward O. Wilson (1975) tacitly accepted this position. In a large collection of reviews of the book published in the journal *Animal Behaviour* in 1976, Wilson was attacked because he had not considered the interplay between the developing organism and its environment. In response to these criticisms he wrote that, in his view, development was a black box or 'module' that could be decoupled when the relations between genes and the characteristics of the adult organism were considered (Wilson, 1976). The key message in our book is that development is much more integrated in these relationships than this decoupling image suggests.

The use of the nature/nurture distinction often involved a confusion of categories, since 'nurture' was seen as a developmental process and 'nature' was often viewed as the genetic origin of that process. For some, however, 'nature' was viewed as the adult expression of a developmental process. That point was cleverly captured by Matt Ridley (2003) in the title of his book *Nature via Nurture*. For others, though, nature was reserved for those features that developed 'robustly', unaffected by the vagaries of the environment, and nurture was used for those features that were 'plastic', greatly influenced by the conditions in which the individual developed.

The nature/nurture distinction runs through persistent arguments about the origins of human faculties. The seventeenth-century philosopher John Locke believed that all reason and knowledge was derived from experience. Charles Darwin's cousin, Francis Galton, expressed a strongly contrasting view about the development of human mental faculties, believing that education and environment produce only a small effect on the human mind and that most human qualities are inherited.

The debate continues to the present day. It extends across the full range of human faculties, styles of thinking, and behaviour. The universalists claim that these faculties are shared by and intrinsic to all human beings. The relativists argue that all the cognitive characteristics of humans emerge from the culture in which they are embedded. Reducing the problems of origin to either 'this' or 'that' is deeply

unsatisfactory. Equally unhelpful, we shall argue, is the conflation of origins with developmental processes.

These ideas and widely held views about the decoupling of development from evolutionary processes led to constipation of thought and encouraged misunderstanding of how evolutionary theory relates to, and integrates with, ideas about the development of the individual. It has been argued that Darwinian natural selection leads to evolutionary changes in the phenotypic characters of organisms. If these changes occur in stable environmental conditions, it was maintained, they must result from changes in gene frequency. Therefore, or so it was argued, adult characteristics are exclusively under genetic control. Furthermore, understanding development was not essential because Darwinian selection acted on the outcome of each individual's development. Bruce Wallace (1986) expressed a view, shared by many other eminent evolutionary biologists, that an understanding of development was irrelevant to an understanding of evolution. Ron Amundson (2005) has carefully described their position and how it contrasts with the views of those who give prominence to developmental biology.

As the genetic or 'hard heredity' model formed around 1900, other scientists who were focused on the biology of development started to integrate emerging genetic, and later molecular biological, concepts with the developmental framework. Wilhelm Johannsen (1909) separated the organism's 'genotype', or the set of hereditary factors, from its 'phenotype', the organism's developed characteristics. Indeed, he introduced these terms. Richard Wolterek (1909) developed the concept of the 'reaction norm' to denote the range of phenotypes derived from a single genotype under developmental influences. Scientists whose orientation was developmental did not consider development to be immune from the environment. Pioneers in experimental embryology, such as Hans Spemann (1938), identified the role of diffusible factors in the transition from an undifferentiated zygote into a multicellular organism. In the mid-twentieth century Ivan Schmalhausen (1949) and Conrad Waddington (1957), whose work we shall discuss later in this book, provided conceptual and empirical observations that started to show how developmental and evolutionary processes could be reconciled. Richard Lewontin (1983) showed how an organism's activities in changing its environment could affect the evolution of its descendants. In the twenty-first century, influential insights were also provided by Mary Jane West-Eberhard (2003), who suggested – provocatively to some – that phenotypic change was not just a passive follower of genotypic evolution but that phenotypic

plasticity could in fact influence evolution, thereby focusing on the importance of developmental phenomena. Similar points were made by the advocates of developmental systems theory (Oyama et al., 2001). Susan Oyama (2000) had already written eloquently on the subject.

Advances in scientific thought in relation to the transactions between the individual organism and its environment are seen especially clearly in the psychological literature (Sameroff, 2010). Encouragingly, some of the advances have passed into the popular domain. David Shenk (2010) has described how each individual interacts with his or her environment in such a way that potentialities may be revealed or suppressed by circumstances. The message is optimistic and has major implications for public policy. Shenk's perspective was presented as an interaction between genes and environment; an image which he drew from the scientific literature (Meaney, 2010). The interaction is often abbreviated as 'G × E'. As we shall outline in later chapters, some problems arise from this formulation because it conflates ideas about sources of variation in populations with those about an individual's development – a point that is powerfully emphasised by Evelyn Fox Keller (2010). It is the person who interacts with the environment, not his or her genes. While genes are definitely activated or repressed by some environmental conditions, the organism can change its environment or choose which environment in which to live without necessarily producing changes in the expression of its genes.

A plethora of ideas and observations have emerged, and we hope to clarify this confusing literature and identify the key concepts. Our overall purpose is to provide an overview of how developmental processes are integrated. We focus on how two superficially opposed sets of processes – those generating robustness and those generating plasticity – operate together in development. However, as we shall explain in Chapters 3 and 4, these are not unitary processes; these apparently simple terms encompass a wide variety of mechanisms operating from the level of the gene to that of the organism.

Undeniably, species are generally recognisable for what they are, and readily seen as distinct from each other. Animals and plants are usually identified correctly by skilled naturalists as members of their own species. Whatever his or her experience, nobody would confuse a human with a rhesus monkey. The general characteristics of each individual develop in much the same way irrespective of the environment in which he or she lives. Many of these features do, indeed, develop robustly in the face of variation in the environment. We shall examine how such robustness comes about at a variety of levels of

biological organisation. At the same time, malleability or plasticity during development is a widespread phenomenon in both the plant and animal kingdoms. In many species, a variety of distinct phenotypes may develop from a single genotype, depending on local conditions. Phenotypes may form a continuous range, as in the birth sizes of mammals, or they may be discontinuous, involving quite distinct bodies and behaviour, as in the female honeybee. Plasticity is a term encompassing multiple processes regulated in a variety of different ways. We shall argue that robustness and plasticity are complementary, often integrated in development and therefore difficult to separate. They should not be seen as being in opposition to each other.

Our discussion in this book will encompass both consideration of the whole organism and its mechanistic underpinnings. This means that frequently we will move between different levels of organisation. Many of the same issues about the development and control of the whole organism are also reflected in considerations of its component parts and in the molecular structure and role of the gene. A commonly held view among modern biologists is that primacy and centrality should be given to the gene alone. However, we shall argue that gene expression is profoundly influenced by factors external to the cell nucleus in which reside the molecules making up the genes: the deoxyribonucleic acid (DNA). A willingness to move between the different levels of analysis has become essential for an understanding of development and evolution.

The understanding of the molecular basis of many of the phenomena that we shall discuss is changing rapidly. Increasingly, developmental phenomena can be explained in terms of the differential regulation of gene expression and, in particular, by epigenetic mechanisms that lead to changes in gene expression without a change in nucleotide sequence (see Chapter 5). In some cases these epigenetic effects may be transmitted to the next generation through meiosis, reflecting one of several potential mechanisms of non-genomic inheritance (Gluckman et al., 2007b; Jablonka and Raz, 2009) which must be part of any modern understanding of the essential conjunction of evolutionary and developmental processes.

We shall examine from a biological perspective the interplay between the processes of robustness and plasticity, considering how they evolved and, in turn, how they affect evolution. As active agents in the evolution of their descendants, individuals' mechanisms for responding to change can have profound effects on the rate of evolution and, indeed, on macro-evolutionary processes. We shall go on to consider the particular ways in which these evolutionary processes may work.

Our overall approach arises from the need for a wide variety of disciplines to have a better understanding of developmental processes at this time of immense explosion of empirical data and conceptual understanding. Like many others, we feel that it is crucial to re-integrate development into evolutionary thinking, and to counter the damage done by the emphasis given in so much biological thought to the nature versus nurture dichotomy.

2

Clarifications

MEANINGS OF WORDS

Anyone involved in interdisciplinary research quickly discovers that words do not mean the same to all people. For some, a term is used in the colloquial sense, while for others it has one or more technical meanings. The word 'fitness' is a good example. For the person in the street it refers to physical health and well-being and for the sports physiologist it means something similar, but for the biologist it has a much more technical meaning to do with how likely it is that an individual's characteristics will appear in future generations. Further confusion can be generated by the extensive use of metaphors such as strategy, selection, conflict, design, imprinting, programming and reinforcement, which are borrowed from everyday language but are given technical meanings that sometimes differ from each other across different communities of scientists. In this chapter we attempt to clarify what we mean by the terms that we use throughout this book, and explain why we have chosen not to use some others. In our view this is essential, as much of the literature on development and its relationship to evolutionary process has been confused by misunderstandings that have arisen from alternative usages of the same words. As George Bernard Shaw put it, when talking about the English and the Americans: they are 'two peoples separated by a common language'. Not all our scientific colleagues will agree with our terminology, but at least our meanings will be explicit.

As we have already indicated in Chapter 1, and along with many others, we do not accept the nature/nurture dichotomy, where nature refers to that which is genetically determined and nurture that which is environmentally determined. Inasmuch as we use these terms at all, nature stands for the characteristics of an organism and carries no

implication about how they developed. Nurture stands for the processes by which the characteristics develop. In other words, for us the conventional opposition of these two terms is necessarily false.

Later in the book we refer to a number of developmental and evolutionary processes where definitions have been unclear, or where different authors have used different meanings. Such terms include canalisation, stabilising selection, genetic accommodation and genetic assimilation. We shall defer consideration of these terms until subsequent chapters, where clarification of them is appropriate.

ROBUSTNESS

During development, many characteristics of organisms are relatively unaffected by substantial perturbation of the environment and cryptic genetic variation. Their development is, in that sense, 'robust'. Robustness is generally defined as the consistency of the phenotype despite environmental or genetic perturbation (Nijhout, 2002). This implies either insensitivity or resistance to such potential disruption.

We use the term robustness without implying any single or particular mechanism. Indeed we shall argue that many different mechanisms are involved. Robustness is emphatically not an all-or-none phenomenon; it need not affect all systems or organs of the organism in the same way, and it has multiple dimensions reflected in multiple mechanisms. In the next chapter we describe in greater detail the many ways in which robust phenotypes are produced.

PLASTICITY

During their development, individuals with the same genotype may respond to their environments in innumerable and sometimes qualitatively quite distinct ways. We consider plasticity in detail later (Chapter 4) where we describe the overall phenomenon and explain it in terms of multiple unrelated mechanisms. Plasticity includes accommodation to the disruptions of normal development caused by mutation, poisons or accident. Much plasticity is in response to environmental cues, and advantages in terms of survival and reproductive success are likely to arise from the use of such mechanisms. An organism that has been deprived of certain resources necessary for development may be equipped with mechanisms that lead it to sacrifice some of its future reproductive success in order to survive. Plasticity includes preparing individuals for the environments they are likely to encounter in the

future on the basis of cues obtained from previous generations; the course of an individual's development may be radically different depending on the nature of these cues. Plasticity may also involve one of the many different forms of learning, ranging from habituation through associative learning to the most complex forms of cognition.

ONTOGENY

The term 'ontogeny' or 'development of the individual' often refers to the processes by which an individual acquires its characteristics, generating what is known as the 'phenotype'. What happens after it has reached adulthood is not included. For us, however, development of a kind continues until death, involving many processes that were also involved early in life. We do not, therefore, distinguish between early learning and adult learning except that the context may make a difference to the outcome, as in behavioural imprinting.[1] Whether or not the underlying processes differ from each other is a matter for empirical study. The stage in the life cycle can be important when defining how resistant or sensitive an organism is in relation to changes in its environment. Furthermore many organisms, humans included, use specialised mechanisms at particular periods in their lives, an example being suckling in mammals. Some mechanisms, such as play by young animals, may be the biological equivalent of the scaffolding used for erecting a building, and are no longer required when the job has been accomplished.

GENES

Some people suppose incorrectly that the characteristics of an organism are encoded in the genes, in the sense that all the information required for its development is contained in DNA. The notion of genes coding for phenotypic characteristics was always problematic, but its limitations have become increasingly apparent as molecular and biological knowledge has expanded.

[1] Imprinting is a word used in quite distinct ways in different scientific fields. In this book we deal with two distinct phenomena: behavioural imprinting, whereby an animal forms a preference for a class of stimuli to which it was exposed in early life; and genomic imprinting, whereby certain genes are expressed only from one of the two parental alleles. Behavioural imprinting is divided up into filial imprinting affecting the social preferences of young animals, and sexual imprinting affecting the sexual preferences of adults. It may also refer to the development of other preferences.

For example, a person carrying two copies of the mutated gene that gives rise to cystic fibrosis is destined for illness and a high likelihood of death in early to mid-adulthood. However, the survival of such a person will be influenced by the specific mutation that they carry (at least 1,000 different mutations have been identified in the gene), the lifestyle they lead, the number of respiratory infections they have had, how they are medically treated and so forth.

Much epidemiological research in recent years has been based on sequencing the entire human genome and looking at mutant alleles that correlate with disease. A surprise of these genome-wide association studies has been that even when large populations are studied and the disease of interest is common, such as diabetes, few significant genetic effects are found and the effects of any one specific polymorphism are generally small. Single-gene effects are unusual and largely restricted to relatively rare diseases such as phenylketonuria or haemophilia (Maher, 2008).

Genes have been defined in many different ways: as units of physiological function, units of recombination, units of mutation, or as units of evolutionary process – when they have sometimes been imbued with 'selfish' intentions in order to help with understanding (Dawkins, 1976). The problem of definition has been made worse as it has become clear that the same strand of DNA may serve in processes that differ in function. Indeed, the same strand of DNA might be transcribed in one direction to serve one function and in the other direction to serve a different function. Griffiths and Stotz (2006) emphasise how, in the post-genomic era, the emerging concepts of the gene pose a significant challenge to conventional assumptions about the relationship between genome structure and function, and between genotype and phenotype.

The word 'gene' never had a clear unambiguous meaning: for some it meant simply a sequence of DNA, for others it referred specifically to those segments of DNA that are transcribed into ribonucleic acid (RNA) and then translated into a protein. To be set against that, some segments of RNA – the so-called non-coding RNAs – have regulatory functions, and the term 'gene' is extended by many molecular geneticists to include the DNA sequences coding for these RNAs. These different meanings of gene get conflated, with subsequent confusion of thought (Keller, 2000). As the philosopher of science Lenny Moss has put it with respect to genetic determinism: 'The idiom of the language-of-the-gene became written not by those whose hypotheses were successful but rather by those whose metaphors were successful' (Moss,