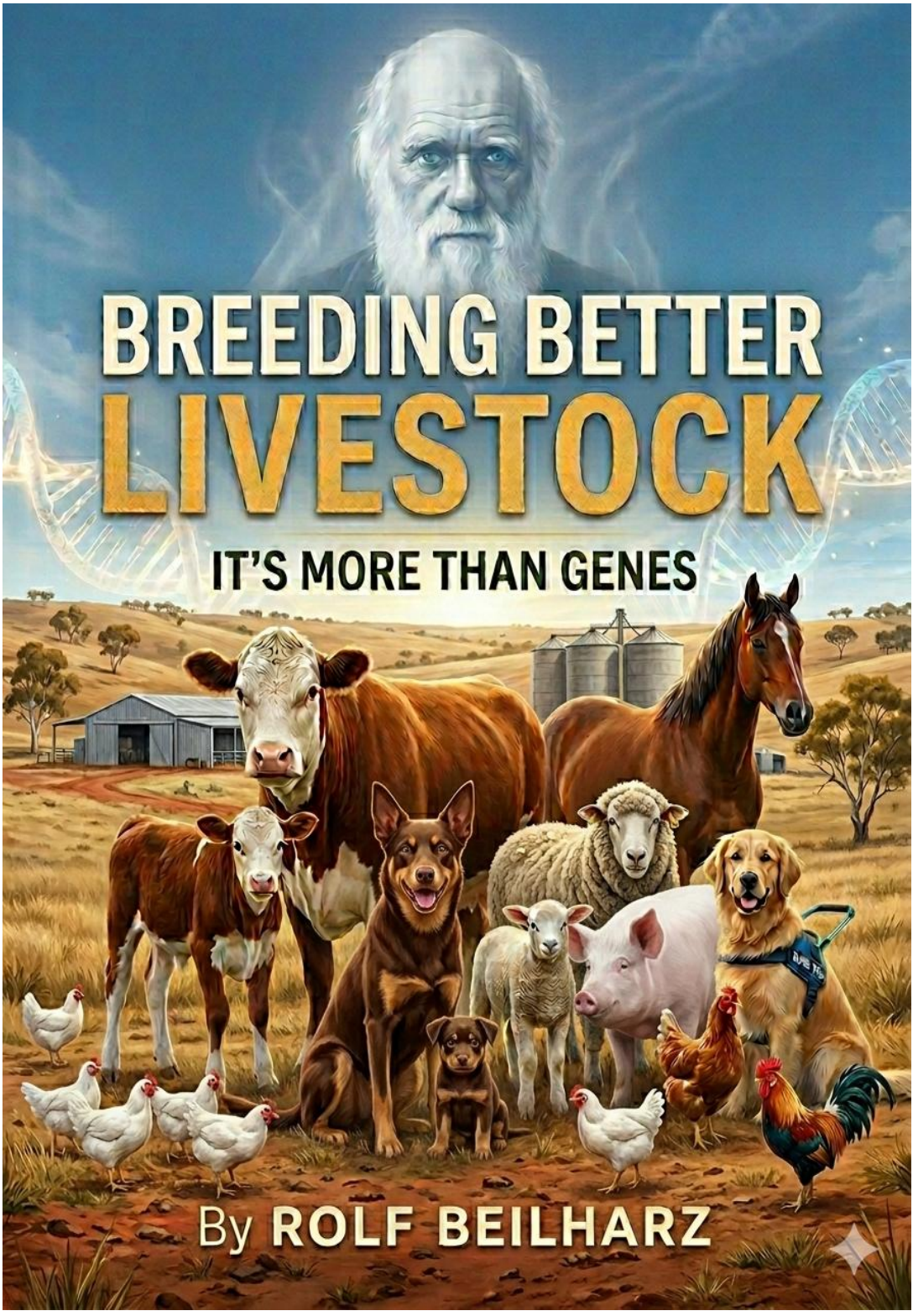
BREEDING BETTER
LIVESTOCK
IT'S MORE THAN GENES
By ROLF BEILHARZ

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Cover image: Gemini collage showing Charles Darwin gazing over examples of species that have benefited from Dr Rolf Beilharz's research.

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BREEDING BETTER LIVESTOCK

it's more than genes

Rolf G. Beilharz

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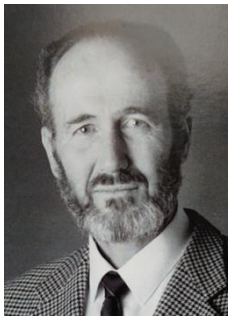

Dr Rolf Beilharz was a professor in the Faculty of Agriculture at the University of Melbourne for most of his career. A wide perspective informed his life work as a geneticist culminating in a concern that the advances of the first quantitative geneticists might have stalled as subsequent generations focused primarily on the effects of genes rather than considering environmental interactions. Hence his early draft's title, 'Welcome Back Mr Darwin'. In retirement, Rolf honed his argument into a draft that has formed the basis of this book. Two major outcomes of his work are the correction offered to modern geneticists and the critical implications of practical genetics in animal welfare.

Contents

Author's Preface

I look back with pleasure to a year of study leave during which I was studying house mice and wanted to compare the behaviour of laboratory mice with that of wild house mice. I was in Seewiesen, a Max-Planck Research Institute for the study of animal behaviour in Bavaria, Southern Germany. This is the place made famous by Konrad Lorenz, who had written charming stories about animal behaviour in the little book 'King Solomon's Ring', first published in 1952.[1] I count myself lucky that Lorenz was still active in Seewiesen when I was there.

I already had some 'selected' laboratory mice, sent over from our animal house in the University of Melbourne, Australia. How could I capture a group of wild mice without harming them, to compare with my mice?

Seewiesen had many outdoor birdcages, and in these cages, food was often in bowls on the ground. Once technical staff had left in the afternoon and no one was there, wild house mice emerged to feed on the bird food. No poison was used because it might have harmed the birds, and the mice were tolerated. Most people did not see the mice anyway, because they hid as soon as anyone approached. And herein lay the clue for catching them.

Humans rarely see wild house mice going about their business. Most people, if they see mice at all, catch just a glimpse of them escaping, often into a little hole which had not been noticed before. If you know that mice always hide in holes, then what about artificial holes, say the hole in a 20 cm length of water pipe, on the ground next to the food? Put a small pipe next to the food and wait a few days to let the mice get used to it. Then, in the afternoon quiet, you need merely to walk to the cage and a mouse will be hiding in the pipe. You pick up the pipe by putting a hand over each end. You don't open the pipe until it is in a mouse cage. If

the mouse refuses to come out, you blow into one end of it. For me this was a very reliable method of collecting my sample of wild mice.

Hiding behaviour of wild mice is an instinctive behaviour that has evolved through natural selection. Mice that do not hide or escape into small holes, safe from predators, get caught and eaten. As long as genes influence the behaviour, future generations will be made up primarily of the offspring of hiding mice.

But imagine that Seewiesen is a small island with a finite population of wild house mice, isolated from other mouse populations. Imagine further that there were lots of researchers all catching wild mice with water pipes. Then, natural selection would select strongly against wild mice hiding in water pipes, and favour those hiding in other ways. The population would then change over time. You can see that natural selection is continually adapting species to their environments. People who understand animals and their environments can predict what the environment will do to the animals living in it.

Author's Acknowledgements

For the whole of my adult life, I have been a scientist. I have thoroughly enjoyed biology and economics being applied in agriculture and animal breeding, as well as evolution and animal behaviour. I was pleased to be able to pass on my love of science to students. I have made friends in various countries, and I have learned much from them. As always happens in science, my friends have their opinions, and I have mine. Such differences of opinion lead to progress in science.

It is the same with this book. I am presenting ideas that will have the effect of overturning the way some people understand current thinking in genetics, evolution, animal welfare and other aspects of biology. I cannot avoid comparing my ideas with those of others; that is the way science works. So, please see this book as my attempt to increase understanding. And when I have used your work to compare with my ideas, I thank you for the stimulation. There are many scientists whose work has helped me without their knowing it. Jim Crow is one such. I have benefited greatly from the thoughts of others. Please accept my sincere thanks.

Some people close to me deserve special mention. Among them are my graduate students, all of whom contributed greatly to an environment in which ideas could be followed up and developed. Directly connected with the subject of this book are Mike Goddard, Brian Luxford, Julie Wilkinson, Kalaya Mitpaibon, Atakan Koc, Kathryn Champness, Ian Gillies and Andrew McLean. Among my teachers of quantitative genetics have been Stuart Barker at Sydney University and Jay L. Lush, Dave Cox, L.N. Hazel, Oscar Kempthorne and W.F. Hollander at Iowa State University. I am deeply indebted to Gerhard Nitter of Hohenheim University in Stuttgart, co-author of an important paper, for his contributions particularly relating to application of our theory to

animal breeding programs and generally in the firm disciplining of my sometimes-wayward thinking.

People interested in animal behaviour have contributed much to my understanding of animal behaviour and evolution. Important among these have been Konrad Lorenz, Wolfgang Wickler and Jürg Lamprecht in Seewiesen, my many colleagues in the International Ethology Committee, participants at many International Ethological Conferences, and my colleagues in the Australasian Association for the Study of Animal Behaviour.

I have been greatly touched by people who reacted positively to the ideas in this book. Among them are Ella Luiting, Wendy Rauw, Johann Sölkner, and Melbourne University colleagues Paul Hemsworth, Adrian Egan, Geoff Hutson, Derek Tribe, and Bill Malcolm. Franz Pirchner, then editor of the *Journal of Animal Breeding and Genetics* (formerly *Zeitschrift für Tierzucht und Züchtungsbiologie*) oversaw the publication of significant papers.

For many years the University of Melbourne, in particular the Faculty of Agriculture—now Melbourne School of Land and Environment—has provided an environment in which it was a pleasure to teach and to conduct research. I was also helped by the Australian American Education Exchange (Fulbright) scheme; a Pawlett Travelling Scholarship from Sydney University; the Alexander von Humboldt Foundation for my several periods of research in Germany; the University of California, Davis, for an exchange arranged by Ed Price; and a period of study leave at Hohenheim University, Stuttgart, Germany, where I began writing my paper with Gerhard Nitter.

Special thanks go to my wife Dr Vyrna Beilharz and our daughter Dr Margaret Beilharz for thoroughly editing this book.

Rolf Beilharz

Foreword to the 2026 Publication

Rolf was a key member of what is referred to here as the Faculty of Agriculture at the University of Melbourne in its various guises over the years. When he joined it was the Faculty of Agriculture and Forestry and subsequently became the Faculty of Agriculture, Forestry and Horticulture, the Institute of Land and Food Resources, and then the Melbourne School of Land and Environment.

Now it is the School of Agricultural, Food and Ecosystem Sciences in the Faculty of Science. Each iteration included a strong animal science component, of which Rolf was a leader. The current name of the School, containing as it does reference to ecosystems, seems appropriate given Rolf's insistence that deeper consideration of the environment is essential to understanding the expression of genes.

Rolf shared his draft manuscript with key colleagues in the Faculty of Agriculture in the early 2000s gaining some comments that assisted his redrafting. Around this time, he had requested a colleague to assist by getting it into a publishable form, but this was not to eventuate as other events overtook the project. Among others who had copies of his earlier drafts in their repositories of academic documents were his graduate students and colleagues in the Animal Science Section of the Faculty. As Rolf's ability to further refine the manuscript declined, his daughter Margie, a zoologist and scientific editor, began to edit his final draft in 2014.

This 2026 published document is based on that of 2014, which condenses some verbose passages and omits sections that were contained in earlier drafts on subjects outside the theme of the book. A couple of paragraphs in which Rolf amplified his thesis

that might seem misplaced, and occasional religious references, have been retained as being reflective of his mind and worldview. Colleagues who have reviewed the final document include Adrian Egan, Lindsay Falvey, Brian Leury, Brian Luxford, Mike Goddard, Paul Hemsworth and Bill Malcolm. Notwithstanding these learned inputs, the document is Rolf's, and it stands as his academic legacy to agricultural science.

Lindsay Falvey

Chapter 1

Genetic Puzzles in Modern Agriculture

In modern commercial agriculture, farmers rely on the advice of geneticists to develop breeding programs for their livestock—beef and dairy cattle, meat and wool sheep, chickens and so on. Agricultural geneticists know a lot about the genes affecting economically important attributes of each species, so it is relatively easy for a breeding program to produce offspring that show improvements in the particular desirable quality.

The livestock industry is enthusiastically applying genetic information in breeding programs designed to ensure that each new generation has the best genes possible. They aim to improve the genetic makeup of their herd so that it brings the maximum profit to the farm.

For example, by breeding from lineages of dairy cows that produce huge amounts of milk (usually measured when they have their first calf), a dairy farmer can increase milk production on the farm.

But it is not unusual for the animals produced in these breeding programs to also have other, less desirable, attributes. In many agricultural industries, farmers are wondering why they must invest more and more resources, including more feed and higher veterinary bills, in order to maintain their 'genetically improved' livestock.

We also sometimes see problems that directly affect farm production: cows that produce huge volumes of milk after their first calf often have difficulty getting pregnant a second time. On average, the productive life of these dairy cows is likely to be much shorter, which is not such a great outcome for the farmer who bred from the 'best' cows and bulls.

These undesirable outcomes are hints that determining a breeding program purely on genetic selection for a desirable trait is not the best way to improve a herd and maximise profitability. But they are hints that the livestock production industry by and large ignores.

In recent years, the focus on genes has become even more pronounced. Molecular biological techniques, artificial animal reproduction, genetic engineering and cloning have all expanded brilliantly, as exemplified by the sheep clone Dolly.[2] Researchers at that time expected that these techniques would revolutionise animal evolution. One such example was a CSIRO scientist, D.H.S. Hetzel, who in 1996 wrote:

> *Overall, whilst the production to date of commercially useful transgenic livestock has been disappointingly low, future prospects appear bright. … The full power of new genetic technologies will be realised when used in combination with reproductive technologies which reduce generation time and enable large scale multiplication of genetically superior lines.*[3]

We are still waiting, almost 20 years later, for the promised improvements in livestock. And some of the experiments with genetic engineering of farmed animals have provided unexpected and unsatisfactory results.[4]

Such is the investment in, and hope for, new technologies in genetics and reproduction, that few people in the industry are open to the idea that some of the problems farmers face in managing their stock arise from those breeding programs themselves.

Seeing the Problems but Not the Cause

My first, and wonderfully effective, teacher of quantitative genetics was Professor Stuart Barker, who taught me at the University of Sydney and later moved to the University of New England in Armidale, NSW. Material presented at a seminar held in his honour in September 2007, which brought together animal breeders and

evolutionary geneticists, neatly sums up the puzzlement felt by those who can see the problems but not their cause.

Let me quote just a few examples, from the book 'Adaptation and Fitness in Animal Populations' that arose from the seminar. And keep in mind that the term 'fitness' is used in the evolutionary sense to describe the number of offspring (descendants) an individual has in its lifetime that survive to breed in the next generation, relative to others in the same population.

> *Fitness of farm animal populations is clearly becoming a concern, especially in programs that have achieved substantial genetic change for "production traits" or where environmental stressors are intense …*
> *Animal breeders have clearly been very successful in achieving selection goals. In high-input production systems, dairy cows are now much more productive, sheep produce more and better wool, and cattle, broilers, and pigs now grow faster and have improved meat quality. Fitness, in the sense of general health, well-being and reproductive ability, is commonly perceived to have declined in farm animal populations particularly of developed country production systems.*[5]

But the suggestions provided for addressing the problem remain entrenched in the geneticists' world view that the answer will be found at the level of genes, and in their field of quantitative genetics.

> *One straightforward model is to consider fitness as just another quantitative trait. There appears to be a negative genetic correlation with production traits and if fitness as such is not selected for, one would expect a decline. The problem could then be resolved by simply measuring fitness and including it in the selection objective. However, fitness appears to encompass complexes of characters—do these fitness characters behave like other quantitative traits? And why is the correlation with*

> *production traits negative? Can we trust that the simple quantitative genetic model will work?*[6]

Richard Frankham recommended a higher priority on fitness characters in quantitative genetics research but still thought in purely genetic terms, such as heritability, directional dominance, gene interactions, inbreeding depression and heterosis.[7]

Mike Goddard also concluded that fitness traits should be considered in genetic breeding programs but accounted for the poor outcomes in reproduction and survival as being due to genetic interactions, specifically inbreeding depression and selection for other traits.[8]

For now, it doesn't matter what these various terms from the field of quantitative genetics mean, but these examples show that the geneticists are seeing the problem but, in looking only at genes, missing the big picture.

Taking a step back, and considering the animal as a whole, gives us a new understanding, which I outline after one more cautionary example of a selections response that did not achieve what the breeders wanted.

The Strange Case of the Mid-side Wool Samples

The background here is that 40 to 50 years ago CSIRO scientists investigated the best way to measure the 'fineness' of wool in a fleece. Fineness is important to the farmer because the diameter of the fibres in the fleece determines the price received for the wool. Wool of fine fibres, say 16 microns in diameter, commands a much higher price per kilogram than wool of 20 microns. (A micron is one millionth of a metre, or about one hundredth the thickness of a human hair). Above 21 microns, fibre diameter becomes much less important, and when it reaches 24 microns and higher it no longer affects the wool price.

CSIRO did a very thorough study, taking wool samples from many different parts of the fleece and comparing the samples with the average fineness of the whole fleece. They were looking for an area of the fleece that would provide useful information on how fine the fleece was from just a single sample. Being able to use just one sample would minimise costs for the farmer, who has to send each sample to a laboratory for measurement.

Sure enough, the CSIRO scientists found that the sample that best predicted the average fibre diameter of the whole fleece was one taken halfway down the middle of the side of the sheep. As this 'mid-side sample' was also easy to collect, it was recommended as the most economical and practical way to determine the fineness of a fleece from any given sheep.

Ever since, many Australian sheep farmers measure their flock's fleece with a sample from the mid-side of each ewe, usually collected while the sheep was young and had not been stressed by reproduction. And this fineness measure feeds into the wool breeding program, with breeding for finer fibre diameter being done based on the fineness of the wool from the mid-side sample.

My former part-time doctoral student, Dr Ian Gillies, had already had a long and successful career as a dentist before starting his PhD. He also had a sheep farm in the hilly and rather remote East Gippsland region of Victoria. For many years, Ian had bred sheep (with an average fibre diameter of about 20 microns) with advice from knowledgeable local farmers. By the late 1980s, however, he was ready to try something new.

Ian's approach was to take thorough measurements of attributes associated with wool production from his flock. He did so for 4 years, and then continued to measure the flock's progeny for years after the original ewe measurements ended. This gave him a database of measurements of the initial 222 ewes, the rams they were mated with, and the lambs that these ewes produced, all

under normal commercial farming conditions. Evaluation of this information became the content of his PhD thesis.[9]

The Australian Wool Testing Authority (AWTA) is one of the institutions that provide accurate measurements of fleece characteristics, and Ian Gillies worked with them to get his fleece measurements. The AWTA encouraged sheep breeders to select their sheep with the finest wool, and to put the wool from these sheep into a special bale so that it would attain a very high price at auction. Ian adopted this idea, selecting his finest sheep on their mid-side sample measurements before shearing, and baling the shorn fleeces from those best ewes separately.

Based on the mid-side sample and the weight of each fleece that went into the bale, Ian calculated a weighted average fibre diameter for the whole special bale. This allowed him to predict with confidence the average fibre diameter of the whole bale. Unfortunately, however, his prediction turned out to be wrong.

When wool is auctioned in Australia, each bale is 'core tested' for fibre diameter. The core sample is taken from a mixture of the fleeces from various parts of the bale. This core sample revealed the average fibre diameter of Ian's special bale to be one micron coarser than the weighted average Ian had calculated from the mid-side samples. This, of course, meant Ian obtained a lower price for the wool and spurred him to work out what had happened.

Now comes something peculiar to Ian, which I value very highly: he is an almost compulsive measurer and keeper of records. In addition to the mid-side samples, Ian had also taken a fleece sample from the front and the rear of the sheep. Seeking a solution to his puzzle, Ian calculated a weighted average using all three samples he had taken from each sheep—the mid-side, the front and the back. This new calculation matched the core sample result very precisely, the explanation being that the front and back samples had been coarser than the mid-side sample.

It is sad that Ian did not achieve as high a price as he had hoped, but it is also a wonderful demonstration that one gets what one selects for. Years of selection of wool sheep for fine fibre based on mid-side samples has given us sheep with fine-fibred mid-sides. But the fibres elsewhere in the fleece were not as fine.

We now know that if you really want to reduce the average fibre diameter of your fleeces, you need to select on several samples from different parts of the body. Because, with just one sample, selection pressure was put only on the mid-side—this was the part of the fleece that responded, and the response elsewhere was less.

This study provides a cautionary pointer for geneticists: it's vital to carefully consider what you are selecting for in a breeding program, because even a successful response, in terms of your chosen attribute, may produce an undesired or unexpected result.

Where Livestock Breeding Programs Can Go Wrong

Ian Gillies's research also produced a number of other interesting results, which demonstrate the sorts of trade-offs between traits that I mentioned above. He found, for example, that ewes producing more wool typically raised fewer surviving offspring.

My contention is that these trade-offs arise because animals typically grow and reproduce in environments in which resources (the most important being food) are limiting. Although farming offers somewhat different conditions, we must remember that farmed animals are the result of many years of both natural and artificial selection, and that both these processes are still occurring today so that populations adapt to new conditions over a few generations.

Our carefully bred dairy cow successfully produces huge amounts of milk for 10 months or more, as she has been selected to do. Producing all that milk takes lots of resources—our cow has to direct a higher than usual proportion of her energy budget into milk production. Her investment in milk has consequences for

other aspects of her life: she has less energy to put towards her own health and wellbeing, including keeping in good enough condition to become pregnant and carry another calf the following year.

Selecting for the economically desirable attribute of 'high milk output' has produced cows that produce lots of milk but it has not produced a better-quality cow overall.

In this book, I explain each of these steps:

- why resources are limiting for most animals, including farmed livestock
- how resource limitation results in trade-offs between different attributes (and why the geneticist's fall-back explanation of genetic antagonisms and other gene interactions are often not necessary)
- why selecting for a significant enhancement in one desirable attribute, such as high milk production in dairy cows, can produce offspring with reduced evolutionary fitness.

In particular, I show how each of these processes is a result of natural selection, resulting from interactions between individual animals and their environment. (For those who would like a brief refresher of the science of natural selection and genetics, I give a quick explanation and define key terms in chapters 2 and 3.)

To further our understanding of natural selection, I take another look at some common misconceptions, particularly where geneticists are concerned, including:

- that evolution is driven by mutations in our genes—it is actually driven by the environment
- that natural selection is always a force for change—it is more often a force for stability
- that natural selection always drives attributes towards their maximum expression—the optimum state is not usually the most extreme

- that selection will 'weed out' variability in attributes important in fitness (essentially reproduction and survival)—natural selection will maintain variation in the population
- that an inverse relationship between overall fitness of an animal and a particular trait important to fitness (such as litter size or lifespan) is due to genetic relationships—in many cases it can be explained by the environment.

With this clarified understanding of natural selection, I take a critical look at the shortcomings inherent in the agricultural geneticists' focus on individual genes rather than whole animals. For example, once you've understood the key role played by natural selection, you may be surprised to discover that the equations at the basis of all quantitative genetics specifically make the assumption that natural selection is not acting.

I also extend this understanding to other ideas about natural selection in wild as well as domestic animals. Darwin's original thesis remains true to this day, and some of the 'challenges' to natural selection, such as punctuated equilibrium, which I discuss in Chapter 7, are easily explained by keeping in mind the idea of resource limitation.

My primary objective in writing this book is to encourage geneticists and livestock breeders to broaden their focus from only the genetic level to include that of the whole animal.

It is by looking at the level of the whole animal that we can understand how natural selection, largely determined by the animal's environment, determines evolutionary outcomes.

Only then can we see the big picture in our quest for improved livestock.

Chapter 2

Evolution by Natural Selection: Darwin's Perspective

It is over 150 years since the English naturalist Charles Darwin published 'On the Origin of Species', the book that introduced the concept of evolution by means of natural selection to a sceptical public. Remarkably, at about the same time another Englishman, Alfred Russel Wallace, independently came up with a very similar idea, although he didn't go to the great lengths that Darwin did to explain and refine his theory. Darwin's book, which has the full title 'On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life', was published in 1859.

Both Darwin and Wallace recognised that the struggle that individual plants and animals underwent to survive and reproduce could influence future generations. Yet at that time it was not understood how characteristics are inherited from parents to offspring. But they did know about artificial selection. Darwin bred pigeons and was able to select for the particular attributes desirable for showing.

Natural selection, as described by Darwin and Wallace, is a simple mechanism for evolution, which is simply explained as changes in populations of species over time. The core of the idea of natural selection is that nature itself, which is the environment in which organisms live, favours those organisms best adapted to it. The best-adapted organisms will, in time, replace all others. This idea, evolution by natural selection, provides the perspective from which all forms of life can be seen to have arisen by the evolution of new forms from older, initially very simple, forms.

But what do we mean by 'favours' and 'adapted'? Each particular environmental niche, such as a rocky beach in southern Victoria or a sandy desert in central Australia, selects (favours) organisms whose attributes are particularly appropriate (adapted) to this niche. It follows that all other organisms are to some extent less successful.

In the words of Darwin:

> *A struggle for existence inevitably follows from the high rate at which all organic organisms tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life … otherwise, on the principle of geometric increase, its numbers would quickly become so inordinately great that no country could support the product.*[10]

Because the reproductive rate is greater than that needed to replace the present population of organisms, competitive elimination must take place. There is only a fixed amount of food and shelter (these are resources) available for each species in the environment in which it lives. As generations pass, the surviving individuals of any particular species are those that successfully master all challenges and use most efficiently the resources available in their environmental niche. It is their characteristics that get passed on to the next generation.

Five Simple Steps to Evolutionary Change

In summary, this is the classical description of how natural selection works:

- Within any species, individuals vary in many attributes, for example, body size and shape, physiology and behaviour.
- These differences are, at least to some extent, inherited by their offspring.

- All species produce more offspring than can survive to adulthood and reproduce. Plants and animals compete with others of their own species for resources such as food, shelter and mates, and many are hunted or eaten by other species.
- The attributes of some individuals give them an advantage, so they are more successful in surviving and reproducing than others. These individuals are better adapted to their environment and have higher evolutionary fitness.
- The next generation will contain more descendants of these well-adapted parents than descendants of individuals which were less well adapted.

Thus, natural selection causes populations of a species to change over time.

One or both of two things can then happen to form a new species:

- A single species can change over time until its descendants are so different that they are regarded as a new species. For example, the modern horse has descended from an ancestor the size of a fox.
- If different populations of the same species independently adapt to the varying environments in which they happen to live, a single species may over time differentiate into two separate species, which can no longer interbreed. This is what happened to the finches famously observed by Darwin on the Galapagos Islands off the coast of Ecuador in the Pacific Ocean. It is likely that one species of finch found its way to spread across the islands. Then, over time, finches on different islands, facing different environments and selective pressures, adapted in different ways. In particular, they varied in the types of food they specialised in eating, and consequently evolved beaks of various sizes and shapes.

In these two ways (change within a single population and separation of different populations into different species), natural

selection has led, and continues to lead, to the great diversity of life we now see. When we look into it further in later chapters, we will see that selective pressure can also be a force for population stability.

Since the time of Darwin and Wallace our knowledge of the mechanism of inheritance has expanded immensely and in ways that they could never have predicted.

Chapter 3

Genetics—The Mechanism of Heredity: Mendel's Discovery of Inheritance

At about the time Darwin published his book, the Austrian monk Gregor Mendel was discovering more about the mechanisms of inheritance which allow Darwin's natural selection to effect change in future generations.[11] Perhaps because his research into breeding pea plant varieties was seen as being more about plant hybridisation than a study of heredity, its significance was not recognised until it was rediscovered in 1900.

Mendel did many breeding experiments with varieties of pea plants that had clearly distinct alternative characteristics, for example:

- Seeds were either smooth or wrinkled.
- Seeds were either yellow or green.
- Unripe pods were either green or yellow.
- Stems were either long or short.
- Flowers were either purple or white.

Mendel chose parents (P generation) that exhibited different attributes, for example, yellow or green seeds. He cross-pollinated the different types, cross-breeding pure-bred yellow-seeded plants with pure-bred green-seeded plants and so on. He found that in each characteristic all of the plants in the next generation (F1) were the same; for example, they all had yellow seeds. But when he self-pollinated these F1 plants, the next generation (F2) had both colours again, that is, both yellow and green seeds. Both of the original types were represented in the F2 generation, but one type (yellow seeds) was three times more common than the other type (green seeds).

Mendel's experiments showed that inheritance is not a matter of 'blending' characteristics from both parents (which would have led to yellowish-green seeds). Nor is it inheritance of characteristics acquired during an organism's lifetime, as proposed by Lamarck, and even to an extent by Darwin.

Mendel showed that:

- Inheritance of attributes was due to a 'factor' which was passed unchanged from parent to offspring.
- For each attribute, an individual inherits one factor from each parent.
- An individual may carry a factor which does not show up but which can be passed on to the next generation.

Although he had no inkling of their nature, he deduced correctly that these factors were normally present in the cells as pairs, and that they pass from parents to offspring by means of gametes (that is, the sperm or egg) in which the genes occur singly.

Mendel was able to recognise how genes moved from parents to offspring because he chose to work with very simple attributes. Variation in a single gene controls each of the features he looked at, for example, seed colour, so the genetic make-up of the plant (called the genotype) was easily visible in the organism itself (the phenotype).

Genes and Chromosomes

Early in the 20th century, it was recognised that Mendel's factors, which we call genes, were located on the threads of genetic material that could be seen under the microscope. In each cell, genes occur in paired strings of DNA called chromosomes. Usually, every gene sits in a particular position on each chromosome, so the chromosome pair has two copies of the gene.

In cells that divide into two to produce egg or sperm cells, the chromosome pairs separate into single chromosomes. One

complete set of single chromosomes finishes up in each reproductive gamete (egg or sperm cell). At conception, a sperm from a male parent and an egg from a female parent join (following mating or pollination), and the two sets of chromosomes together make up a complete set of pairs in the fertilised egg (the zygote), which develops into a new individual of the next generation.

In Mendel's peas, the first generation (F1) plants all showed the same characteristic, even though their parents were different. This is because the yellow variant (or allele) is 'dominant' over the green one. Similarly, brown eye colour in humans is dominant over blue eye colour. When an individual has two different alleles, the dominant one is the one that 'shows through' in that individual. The other allele is called recessive.

Practical breeders readily grasped the importance of Mendel's findings after its rediscovery in 1900. Mendelian genetics was applied directly to animals to select for desirable attributes in animals through selective breeding. In some cases, it was possible to produce new, pure breeds or strains, in which all individuals had the same allele (the allele is then said to be 'fixed' in that population), after the less desirable alternative alleles had been bred out.

Population Genetics: The Study of Simple Traits

The application of Mendel's 'laws' to whole populations of organisms gave rise to the field of population genetics. Evolutionary changes can now be understood as changes in the proportion of different alleles present in a population from generation to generation.

The science of population genetics started with idea that allele frequencies in a population will remain stable from generation to generation under certain conditions: the population is infinitely large (because then even random chance will not change the relative frequencies of alleles as they move from parents into

gametes and then recombine in the progeny), and there are no forces acting to change the frequencies.

Because two scientists, the English mathematician Godfrey Hardy and the German physician Wilhelm Weinberg, independently published the idea in 1908 in their respective countries, this balanced state is known as the Hardy–Weinberg equilibrium.

In the real world, however, populations are not infinitely large and there are forces that act on the frequency of alleles—the most obvious ones being natural selection, migration, non-random mating and mutation. So, by comparing the expected frequency of an allele under the Hardy–Weinberg equilibrium with the actual frequency, we can determine the effect of the forces acting on that gene.

The Hardy–Weinberg equilibrium lets population geneticists predict allele frequencies from one generation to the next for simple traits.

Quantitative Genetics: The Study of Variable Traits

Many traits, such as height and weight, don't show just two, or a small number, of alternative states but instead vary continuously along a gradient. Tackling these attributes led to the field of quantitative genetics.

Animal breeders faced the fact that Mendelian genetics could not explain the pattern of inheritance of many traits they were interested in. In commercial livestock, it is traits such as body size, milk yield and wool production that are important, and these traits vary continuously.

Many of these attributes vary in a bell-shaped curve. The measures of most individuals are near the average measure of the trait with very few individuals showing extreme measurements in either direction.

By 1910 scientists were aware that the bell-shaped curve of variation for a character results from the action of multiple genes.[12]

We can visualise a bell-shaped curve of the attribute 'height' in a population like this: For the majority of animals, genes for 'shortness' are roughly as common as genes for 'tallness', and the optimum will be a moderate height, near the middle of the range and in about the centre of the bell curve. Such variation in the population is called 'additive genetic variation', which can be thought of as the combined effect of all the genes affecting that attribute.

It is not possible to identify the effect of any single gene on the attribute. It is also not possible to separate the effect of the genes from the effects of the environment. For example, people growing up under famine conditions will not grow as tall as they would have if food had been plentiful.

Researchers trained in statistics developed quantitative genetics to overcome this problem using mathematical equations.

Combining Natural Selection and Genetics: The Evolutionary Synthesis

Population and quantitative genetics became the main tools for explaining evolution by natural selection. They also became tools in the genetic improvement of animals and plants. A synthesis of Darwin's concept of natural selection by the environment and these various fields of genetics took place in the 1940s. Known as the 'modern evolutionary synthesis', it combines the concept of the natural selection of organisms with Mendel's mechanism showing how genes actually do pass from generation to generation. It became the central paradigm of biology and was hailed as the definitive explanation for evolution and life.

An evolutionary change is the result of changes in allele frequencies from one generation to the next. We can see that the alleles belonging to the most successful individuals—those that

produce the greatest number of offspring—will increase over generations. The term 'fitness' measures how effectively organisms pass their genes into future generations.

At the time of the evolutionary synthesis[13], it was taken for granted that the environment strongly influenced selection and the response it achieved. Yet the basic mathematical models developed by the geneticists, as I mentioned earlier, did not include the differing environmental selection challenges found in different populations.

Modern Genetics

In 1953 James Watson and Francis Crick described the structure of DNA, the material of the chromosomes in which the genetic information of every cell in an organism is coded. It has now become possible to manipulate this material directly, by biochemical means.

Biotechnology has contributed to an explosive increase in our understanding of biology as well as to rewarding commercial success. It is no wonder that, to the large numbers of scientists now working in biotechnology, the external environment is entirely irrelevant. The environment in biotechnology is tissue or cellular preparations grown in artificial media in laboratories, rather than on farms or in natural habitats.

In the past 50 years in particular, new scientific specialisations have developed: genetics, molecular biology and genetic engineering (including moving genes from one species to another). Scientists have now described the whole human genome and that of a number of other species. And for a growing number of genes, we understand the biochemical pathway through which a gene acts in step-by-step detail.

Chapter 4

The Geneticists' Blind Spot

Modern science has changed the perspective from which we view evolution, and this change has had enormous consequences. Some of our earlier assumptions regarding the natural selection of organisms have simply dropped out of focus. This loss of perspective has dangerously blinded those biologists—geneticists, molecular biologists and genomists—who focus on the level of the gene or of biological molecules. Scientists' overwhelming interest in the molecular level of life has sidelined the interest in 'old-fashioned whole organisms'.

Unfortunately, our focus on the minutiae of how genes work has put us in danger of no longer seeing the big picture. Both in popular culture, led by Richard Dawkins' 1976 book 'The Selfish Gene'[14], and in the commercial world of plant and animal breeding we now have an unhealthy focus on genes at the expense of the whole organism. We no longer see clearly one fact, which was obvious to Darwin and early geneticists: that the environment (and in particular the resources available to an individual) limits the potential of the individual organism to survive and reproduce.

The evolutionist Richard Dawkins clearly saw the importance of the phenotype (that is, the whole organism) in ensuring that genes pass from one generation to the next. Yet he chose to express this fact in terms of phenotypes being merely the vehicles by which 'selfish genes' ensure their fitness. His writings, and the catchy title of 'The Selfish Gene', have contributed strongly to the geneticists' focus on genes as the most important agents in evolution.

The following quotation from Daniel Dennett illustrates how pervasive this focus on genes has become:

> *What about those cases when … the interests of the body … conflict with the interests of the genes?*
>
> *This question was always latent in the modern synthesis. … Dawkins made the point unforgettable by framing it in terms of the concept of the selfish gene.*
>
> *The old … had dimly thought in terms of adaptations being "for the good of the species"; Williams, Maynard Smith, Dawkins, and others showed that "for the good of the organism" was just as myopic a perspective as "for the good of the species" had been. In order to see this, one had to adopt a still more undeluded perspective, the gene's perspective, and ask what was good for the genes. …*[15]

In this book I refer to many examples of agricultural livestock—dairy and beef cows, sheep, chickens and so on, and for these animals their environment is largely controlled by the farmer who provides feed, shelter and livestock management. In modern agriculture, breeding has become a highly technological, commercial business, with geneticists providing a lot of advice to farmers on how to improve the herd or flock.

Most animal breeders today focus on the genetic level in their attempts to improve their animals: powerful computing programs estimate genetic 'breeding values', which are an assessment of an individual's genetic quality. Estimated breeding values are calculated from the animals' relatives—for example, the breeding value of a dairy bull is based on the milk production of his daughters.

An individual's own performance is now seen as an unreliable guide to its breeding value. The estimation of breeding values, particularly when based on information about the animal's own offspring, often does provide more information on how good an

animal's offspring will be than would a measurement of its own phenotype.

Farmers are encouraged to buy semen for breeding their herd based on advertised breeding values, and these may be sourced from overseas or interstate. Thus, even in the breeding strategies applied to domestic animal improvement, there is a clear trend towards focusing on the genetic level while ignoring phenotypes and the environment. Thus, the emphasis on genes as the important part of all life has reached its peak among geneticists. It is not that whole organisms and the environment have been deliberately excluded, but simply that all interest in genetics has shifted to the genes themselves because there is so much to be learned there.

Assuming Natural Selection Is Absent

As in all applications of mathematics, simplifying assumptions have been freely applied in quantitative genetics. In the brilliance of the mathematical achievements, their dependence on assumptions tends to be forgotten. The environment is included as a word in genetic formulae but, as with Mendelian and population genetics (which are incorporated fully in quantitative genetics), the focus remains firmly on the genes.

Although lip service is paid to the environment, natural selection is specifically excluded from genetic equations.

A standard textbook on quantitative genetics is 'Introduction to Quantitative Genetics' by Falconer (the latest edition, published in 1996, is by Falconer and Mackay[16]). In Chapter 20 of all four editions of this excellent book, we find the following statement:

> *The absence of differential viability and fertility was specified as a condition of the theoretical development of the subject; that is to say, natural selection was assumed to be absent. Though for many purposes this assumption may lead to no serious error, a complete understanding of metric characters will not be reached*

until the effects of natural selection can be brought into the picture.[17]

This assumption that natural selection is absent is still the basis of all quantitative genetics. But can a science that assumes that natural selection is not acting make any useful statements about evolution by natural selection? And is it not likely that our use of this assumption has led us to misunderstand the evolutionary process? In fact, it is highly probable that our failure to take into account the flawed basis of population genetics has led to gross misinterpretations of the data, as will be shown in the coming chapters.

Let me just restate the situation in one sentence:

Quantitative genetics is a complete, self-consistent theoretical system which, however, does not adequately describe the real world, because in the real world natural selection is always operating.

Falconer goes on to describe those attributes that are directly related to an individual's fitness (such as life longevity and/or fertility). These tend to have low levels of heritability, that is, progeny do not so closely resemble their parents. You will see later why this is the case. Again, the answer lies in the effects of the environment through natural selection rather than the speculative, theoretical genetic explanations accepted by most.

Falconer also correctly tells us that every organism is the result of past natural selection. We cannot understand the biology of present organisms unless we are aware that past natural selection has moulded them. Falconer, the master teacher, is aware that geneticists should be reminded that they have, often unwittingly, accepted the assumption which excludes natural selection, and should consider whether this creates a problem. However, he has the same blind spot as other geneticists in not recognising the serious consequences of ignoring natural selection.

Why did geneticists develop a blind spot? Why was environmental limitation not seen as an integral part of the adaptation of all species to their respective environmental niches? All biologists recognise that adaptation occurs, but geneticists apparently believed they had covered it adequately in population and quantitative genetics. Their model calculations demonstrated that frequencies of 'better' alleles must rise, but they had no need to specify the reasons why alleles were better in any particular real environment. Model calculations could be done as long as one postulated different relative fitnesses for alleles.

We (my graduate students and I) took seriously the fact that quantitative genetics had assumed natural selection away, as was plainly stated in all editions of Falconer's textbook. But its critical significance was evidently not appreciated, possibly even by Falconer himself.

It is now clear to me that quantitative genetics has no way of formally describing how changing environmental resources cause the resulting natural selection that then changes phenotypes. When people neglect whole organisms and the environment in which these organisms exist, they are blinded as follows.

Phenotypes, the whole organisms responsible for the success of genes, are put to the test by the environment, and the success or failure of the phenotype to survive and reproduce determines whether its genes will be successfully passed on to the next generation. If this challenge of whole organisms by the environment is ignored, the resulting narrow focus on genes alone creates the geneticists' blind spot.

An incident at the 5th World Congress of Genetics Applied to Livestock Production in 1994 in Guelph, Canada, illustrated the limitations of quantitative geneticists. Johann Sölkner, in a paper with John James, discussed a theoretical genetic model in which two genes were competing for resources.[18] When resources were limited, the model produced significant curvilinearity in the

relationship between the traits caused by the genes. That is, the relationship between the two genes shows as a curved line on a graph, not a straight line.

Hearing that such work was being done was encouraging. But even more interesting was a question asked by the chairman to bridge a silence in question time. Would it be possible, over the range of work that might be of interest in practical animal breeding, to approximate and to treat the curves as straight lines? After some thought, Sölkner said 'no'.

This exchange opened my eyes to how we geneticists manage complexity inherent in the necessary mathematics. We simplify. We treat the curve as a straight line over a short range. In hindsight, I see this as a perfect illustration of how theoretical genetics has removed itself from the real world where competition for resources often leads to curvilinear relationships.

Rediscovering the Individual

Darwin's theory of evolution is not the complete story. He did not know about genes or chromosomes, or how genetic material is passed from parent to child. He did not know that the environment can affect how genes are expressed and that these environmental effects can also be passed on to the next generation (this is called epigenetics). But, despite these shortcomings, Darwin's theory, proposed over 150 years ago, still holds its own. In this book, I show the importance of keeping in mind Darwin's original idea.

Darwin held that the environment determines natural selection and that we need to look at the whole animal, not just its genes. I contend that geneticists working in commercial agriculture and focusing on genes and genetic equations have lost sight of 'the big picture'. While they can select for certain desirable attributes, environmental natural selection constrains their ability to achieve an overall improvement. Geneticists interpret the trade-offs they

see (between, say, milk yield and length of productive life) in the light of their genetic models. Yet the real relationship is much simpler, as I will show.

I also show how the narrow focus on the details of genes and their biochemical actions contribute to misunderstandings of how natural selection operates.

When you keep in mind the limits of the environment it becomes clear that natural selection as described by Darwin is sufficient to explain alternative theories of evolution, such as 'punctuated equilibrium' or 'neutral evolution', that have since been proposed.

Chapter 5

Can Farmers Improve Their Livestock's Genetic Fitness?

Practical experience on farms has sometimes provided insights into evolutionary theory that are applicable to all living organisms. Darwin's familiarity with artificial selection in the breeding of pigeons, domestic animals and plants provided the model for natural selection. The following experience with sheep breeders may provide another useful insight.

The Booroola Gene—Challenging Theory?

It is now many years since an anomaly about reproduction in wool sheep started off a train of thought that has led to this book. With other scientists and agricultural advisers, I was applying quantitative genetics enthusiastically to the improvement of farm animals. We all had confidence in the progress we were making. The particular anomaly that triggered my train of thought was as follows.

Breeders of wool sheep in Australia were advised to select ewes for twinning. Australia's world-renowned quantitative geneticists in Australia's premier agricultural research organisation, CSIRO (the Commonwealth Scientific and Industrial Research Organisation), had accurate data on lambing rates. They calculated that although twins had a higher mortality rate than single-born lambs, the production of a flock in which all ewes had twins would be much greater than that of a flock where only some ewes had twins.

Presumably the calculation assumed that all other things were equal. I now suspect that other things are never equal, but no one then was concerned about this possibility. Farmer interest was

great, and the expected economic gains were very attractive. The only drawback was the extra labour needed to identify which lambs were twins, so that they could be used in breeding the next generation. I clearly remember a field trip with undergraduate students to a large sheep property in the state of Victoria. The owner had constructed about 100 pens to isolate overnight those individual ewes judged by their udder to be on the point of lambing. In the morning the ewes with twins and their lambs were identified. The capital investment and the labour employed to record twinning in this large flock were impressive.

This was also the time in which CSIRO scientists identified the characteristics of the Booroola gene, also called the fecundity gene, in sheep. Like twinning, this gene created worldwide interest and was incorporated into commercial sheep populations both in Australia and elsewhere. Ewes with two alleles of the Booroola gene were having up to 6 young in one litter.

Yet, despite all the excitement I could not get rid of one thought, one with which all geneticists can agree when they recall Fisher's fundamental theorem of natural selection.[19] In simple terms, Fisher's fundamental theorem states that fitness usually cannot be improved. (I discuss Fisher's fundamental theorem more fully in Chapter 6.)

Yet, here we all were selecting for a large litter size, a major component of fitness, and expecting a big commercial improvement. Was Fisher wrong? Did we have a special situation in which fitness could actually be improved? Or would the gain in litter size be lost again elsewhere so that fitness would remain the same? My scepticism about achieving large commercially useful improvements in reproduction dates from that time.

Measuring Fitness in Livestock Production

Brian Luxford and Julie Wilkinson were my doctoral students during the 1980s. Brian later became the genetic controller (and

then scientific director) of a very large commercial pig-breeding program in Australia. Julie changed her career path from animal breeding to social work, but not before making major intellectual contributions to the development of our thoughts. I gratefully acknowledge their contributions to what follows.

Brian, Julie and I wanted to develop a mathematical model to describe natural selection of the character 'fitness'. Even though this model was clearly a simplification of a complex situation, its consequences provide important insights of which most geneticists are not aware.

'Fitness' describes the number of offspring (descendants) an individual has which survive to breed in the next generation. Ideally the definition should include several generations of descendants. Natural selection of fitness is nothing other than the inevitable favouring of the offspring of those individuals that provide the most breeding descendants in subsequent generations.

Furthermore, fitness is not a single, distinct biological character that can be seen, felt or measured in the same way as colour, height, weight or leg length. Fitness is the end result —the total effect— of many separate biological traits such as strength, physical stamina, survival, length of life, litter or clutch size, mortality of young, ability to gain food and so on. Each of these individual traits, in fact every bodily or behavioural characteristic which is important to an organism, contributes to fitness. And it is this combined effect of all the separate features of an organism, expressed in terms of the number of surviving young which themselves breed, that is the fitness which natural selection always favours. Those animals that have most progeny in future generations are defined as being the fittest. It is they that are represented by the largest proportion of progeny in future generations.

How does one measure something that is the outcome of the joint action of many individual characteristics, each of which could be

measured independently? The best one can do is to describe the total trait as fully as possible and, in the case of fitness, count the number of surviving descendants at some specified time in the future. It is not easy to measure fitness in practice. A complete measure should include progeny produced over the whole lifetime of the animal, as well as the fate of these progeny. There should also be a measure of the rate of turnover of generations (generation length) because, all else being equal, the faster a parent produces surviving young, the faster its genes can spread.

Because it is very difficult to record reproductive success over a lifetime of an animal, in scientific research most measures of fitness that have been studied so far have dealt with only small components of total fitness, which can lead to quite false conclusions about changes in total fitness.[20] The total number, or weight, of young weaned over a long period of time (such as the total productive life of a cow) is a far better measure of the cow's fitness than simply the number or weight of calves in her first litter, or even less directly, her ovulation rate.

An Experiment: Does Selecting for Larger Litters Increase Fitness?

In any case, my graduate students and I planned a simple pilot experiment[21] to check my concerns, using mice that we bred at my facilities at Melbourne University. The fast generation times of mice meant that we could get results much quicker than the farmers could with their sheep or cows. We tested whether selection for a higher number at birth, or a higher weight of the litter, would lead to improved overall fitness.

We used litter size at birth (the number of live young born) as the analogue of twinning in sheep. Our measure of fitness was the combined weight of offspring, which we measured at weaning (3 weeks of age) and at maturity (9 weeks). This is a reasonable approximation of fitness, as in nature it is likely that animals producing many offspring of a good size will be more successful

in passing on their genes to the next generation than animals producing few, or small and weak, offspring.

So, the question we asked in our experimental set-up was: Would selecting mice for litter size at or near birth increase total litter weight at adulthood?

We established three breeding lines:

- mice that were selected from those whose first litter was the heaviest at weaning (Line A: selection for high litter weaning weight)
- mice that were selected from those whose first litter had the highest number of live young (Line B: selection for large litter size)
- mice that were selected at random (Line C: the control group with no selection).

To avoid simply favouring the offspring of big females, we divided our data, either number born alive or total weight weaned, by the mother's mature weight. In our mouse house we routinely achieved about three and a half generations per year, so we set up our experiment and we waited to see what would happen. After seven generations of selection, we measured the fitness of the selected mice in the three breeding lines. We allowed the seventh-generation mice to breed for 9 months, which we could call a 'lifetime' of breeding, and measured the total weaned and mature weight of the resulting offspring.

Table 5.1. Breeding results for generation 7. These are cumulative values for measures of reproduction. Each population started mating with 20 breeding pairs. The highest value in each section is highlighted.

Selection line	Period of mating	Total number of litters	Total number of live young born	Total weight in grams at weaning (3 weeks)	Total weight in grams as adults (9 weeks)
A	1 month	17	166	1,244	3,275
B		19	181	1,045	2,566
C		17	166	967	2,975
A	4 months	40	329	2,887	7,554
B		56	502	3,142	8,692
C		52	456	3,743	10,269
A	9 months	70	503	4,428	10,705
B		90	734	5,206	12,999
C		99	771	6,756	16,745

Selection criteria for the lines:
A: Selected for heaviest litter weight at weaning (total weight of litter at weaning/dam's 9-week weight)
B: Selected for largest litter size at weaning (number of live young born/dam's 9-week weight)
C: Selected at random (Control)

The results of this experiment were very convincing (Table 5.1). For performance in first litters (one-month production), both selection lines, which had been selected on the basis of the first litter, had responded as selected. That is, Line A mice produced young that were heavier at weaning (and also as adults) and Line B mice produced more young.

But both selected lines fell behind the Control line (Line C) in 'fitness' (number of living mice) and total offspring weight after 9 months of breeding.

At the end of the test, the mice that had been selected for high litter weight at weaning in their first litter (Line A) showed the lowest fitness. Producing a large litter uses more resources, which stresses a young mother more than producing many young that are smaller at birth.

Our experiment showed that we could select for the traits of large first litter and heavy first litter, just as farmers could select for twins in sheep. But increasing litter size or litter weight came at a cost: overall fitness (the sheep equivalent would be lifetime production of lambs) fell rather than increased.

Many years have passed since our preliminary experiment marked the beginning of our interest. Subsequently, Brian Luxford did a great deal more mouse selection work using much larger selection lines as part of his PhD study.

Brian confirmed the responses we found and showed, furthermore, that mice selected by others for over 50 generations according to the number born in the first litter, have greatly reduced 'lifetime' fitness.

And what did happen to selection for twinning in wool sheep? I have never seen anything suggesting that there might have been a flaw in the theory, but geneticists are no longer researching in this area. The large property I visited with undergraduate students has been sold, and it was suggested that the property had lost large sums of money. The Booroola gene is also no longer of interest for wool sheep in Australia.[22]

My explanation of the Booroola gene is that natural selection results in all characters of the phenotype being selected towards an optimal intermediate size appropriate to the available resources. For our sheep the optimum litter size lies between one and two lambs, depending on the quality of pasture and the health of the

ewe. While the Booroola gene did increase litter size, this benefit to the farmer was outweighed by the lower lamb size and survival rates, higher maintenance requirements of the ewe (for nutrition and care during pregnancy and birth), and lower quality (coarser) wool in the twin and triplet lambs.[23] And after carrying more than two lambs in a single litter, ewes showed reduced fat reserves, showing that the increased investment in offspring has come at an energetic cost to the ewe.[24]

Not All Genes Are Acted Upon by Natural Selection

Only attributes that have no effect on either the survival of an individual or its reproduction are completely neutral with respect to fitness and therefore not acted upon by natural selection. Without any selective pressure for one allele or another, change in allele frequencies from generation to generation in a population can still happen—but this happens simply by chance. This is called genetic drift.

Earlier, we learned that in a large population (infinite in size) where there is no selective pressure there is no tendency for allele frequencies to change. This is the Hardy–Weinberg equilibrium. In small populations, however, genetic drift can, and often does, lead to changes in allele frequency in genes with more than one equal allele. The smaller the population, the more likely it is that over time one allele will be completely lost from the population. Given enough time, genetic drift normally results in the loss of one of the alternative alleles, leaving everyone in the population with the same allele—this gene is said to be fixed. Variation has been lost and every organism in the population is the same for that particular attribute.

Consequently, attributes that do not affect fitness generally do not contribute to the phenotypic variation in a population. They will show allelic variation whenever new mutations arise, and they may show substitution of one allele for another as a result of chance fixation of new alleles. This is the variation seen over evolutionary

time scales in genetic material that is not important and is therefore not being conserved in a particular genetic form leading to most efficient metabolism. Such allele substitutions are, by definition, unaffected by selection for fitness and should in the long term occur at rates related to the intrinsic mutation rates of the various equally effective alleles.

Natural Selection Resists Evolutionary Changes in Well-Adapted Phenotypes

Fitness has been under selection for higher values since life began. We should therefore expect that, in general, each species, having been long in its environment, is now exploiting its niche as well as is possible. Because of past natural selection, most adapted populations are now in a state of equilibrium. These equilibria are the result of many forces, such as chance, migration of individuals or groups, selection among individuals, differences between environments and so on, all acting simultaneously. The equilibrium of forces applied to any individual population of organisms may differ from the equilibrium found in every other population.

Each population is in a situation peculiar to its particular environment (geographic location, soil condition, climate, other forms of life and so on). Hence, organisms in each situation may be uniquely limited by its available resources and its attending challenges. In other words, species are limited in their fitness by the environmental resources of their niches. This must be the case for all wild animal species adapted to their respective environments. For all these species, therefore, except for completely neutral traits, all traits are being selected towards intermediate optimum values.

Jim Crow, a highly respected evolutionary geneticist, wrote a book 'Basic Concepts in Population, Quantitative and Evolutionary Genetics'.[25] Commenting on natural selection, he wrote that natural selection discriminated against extreme values in all traits. Such selection away from extremes has the further consequence

that all traits maintain additive genetic variance, which in turn allows a rapid genetic response to changing environments to take place. This permits each species to change rapidly (at least in evolutionary time scales) when the conditions of its niche alter. Here is what Crow wrote:

> *The conclusion is inescapable: A great deal of natural selection is directed against those individuals that deviate from the mean.*[26] *The overall picture that emerges from this discussion is that almost every quantitative trait in any species has an intermediate optimum. Natural selection keeps the population mean near this optimum. … The phenotype contains a great deal of additive genetic variance. This feature allows the population mean to move quickly to a new optimum whenever the environment changes. The slow change of the horse from an animal the size of a fox to its present size is not the result of directional selection, as the animal breeder thinks of it, but the continual stabilizing selection toward a slowly changing optimum.*[27]

This is strong confirmation that our theory and its consequences agree completely with what is known about genetics, natural selection and evolution. Notice how Crow, like Darwin, also wrote of a slow change, while the real point being made is that the total change of optimum size took place over a long period. As I comment in Chapter 7 about Darwin, I doubt that Crow is ruling out the possibility that the change may have taken place in bursts interspersed by long periods of tranquillity.

Crow seems almost alone among geneticists in his recognition of the features of natural selection he describes. The reason for this may be that the majority of animal geneticists work with domestic animal populations in environments of greatly increased and often ever-increasing resources. Environmental improvement during domestication seems to have lulled geneticists into thinking that the environment imposes no limit on production. Consistent with this is the lack of interest shown by most geneticists in the

environment and the corresponding shift in focus to genes, DNA and estimated breeding values.

Jim Crow said that natural selection towards higher fitness has been holding each adapted species at optimum intermediate values in every trait. Our studies (described further in Chapter 6) show why. Thus natural selection, together with environmental limitation, has actively *prevented* change in life's forms. Natural selection continues to adapt organisms to their niches until the most efficient use of available resources is achieved, and then …?

We can no longer avoid this compelling insight. The main effect of natural selection on life on earth has been to *prevent changes and maintain stable phenotypes*. Once the population is adapted to a stable environment, genetic variation continues to occur, but phenotypes that differ too much from the optimum 'average' forms are culled all the time. The evolutionary (fossil) record reveals long periods of stasis punctuated by short periods of rapid evolutionary change in many of the surviving species. This is exactly what Darwin's natural selection must do, because resources of the earth are finite and catastrophic events are rare.

Another feature expected during periods of environmental stability is the presence of size clines in warm-blooded animals—where you see increases in size from tropical to polar regions, or as altitude increases. These clines reflect the fact that, as temperatures rise, optimum values for size decrease.

Optimum size increases when conditions get colder as a simple result of the relationship between surface area and mass of the organisms. In the cold, it is easier for larger animals to maintain their body temperature because larger animals, for a given body mass, have relatively less skin area from which they lose heat. Clines are exactly what are expected as a consequence of natural selection actively holding organisms at locally optimum values.

Chapter 6

A New Look at Natural Selection: The Resource Allocation Paradigm

Here I present a new way of understanding natural selection, which began with the work I did with Brian Luxford and Julie Wilkinson in 1993.[28] We showed that the forces of natural selection in the past now constrain life. From this we have derived logical consequences for biological facts that have puzzled other people.

Natural Selection in a Resource-Limited Environment

Some farmers, for example, experience the problem of a dairy cow driven to produce so much milk that she lacks the resources needed to produce more progeny. We can show that this is because she is not able to express her full fitness with the available resources. Although it may sound simple, much modern discussion of quantitative genetics misses the fact that resources from the environment are necessary to support genetic change. This one concept—that genetic improvement to make animals give us more milk, meat, or wool, requires more resources—is the clue that leads us to the solution to many problems currently puzzling geneticists and animal breeders.

We expressed our theory in two simple equations, focusing first on the component of fitness that is directly related to reproduction (which we called Frep). The first equation states the obvious fact that reproductive fitness depends on several components:

- A—how many times a female gives birth (which, in female mammals other than humans, closely reflects length of life)
- B—how many live young, on average, are born at every birth (litter size)

- C—the proportion of the offspring born that survive to breed (survival).

When we put them together in an equation, these factors are multiplied together to produce fitness.

We can write this as:

$$Frep = A \times B \times C$$

Thus, in our equation, fitness is the number of descendants breeding one generation after the parents whose fitness we are measuring.

The second equation describes another fact most of us take for granted. When we focus on whole animals, we must also consider the food they eat. All organisms need energy to live. Metabolism, which underlies all processes going on in living organisms, requires energy (mainly food). We saw the need for metabolic resources and energy to be so obvious that no comment was needed. Yet it turns out that metabolism and the resources necessary for this had been ignored completely in all forms of genetics.

Let's call the total metabolic resources used by an animal R. We divided up the resource use into three categories. They are:

- a, b, c—resources used directly in reproduction. These resources relate directly to A, B and C, the components of reproduction in the fitness equation (above). So, for example, an animal that gives birth many times (thus having a large value for A) must be investing a lot of resources into those births (so has a correspondingly large value for a).
- x, y, z—resources used in all other physiological processes used by the animal to maintain itself, to cope, and to survive. These resources relate directly to traits X, Y and Z, which stand for all attributes that relate to survival rather than directly to reproduction (although they are obviously related, as we can't have the latter without the former). For example, X could be

size of horns; Y could be ability to run fast to escape from a predator.

- Another factor, m, is resources lost in the process of metabolism. This happens because chemical reactions may not be one hundred per cent efficient.

Typically, resources consumed by one process are not available for others. Resources used for growing horns or fighting off a predator are not available for milk production or for feeding young. So, R, representing the total resources, is the sum of the component resources being used:

$$R = a + b + c + \ldots + m + \ldots + x + y + z$$

The traits represented symbolically by X, Y and Z include all those that are not directly involved in reproduction but still affect fitness. Unless the organism copes with its environmental challenges, survives to the next breeding season and reproduces well, it cannot have a high fitness. Any trait, like X, Y or Z, that does not give the individual a good chance to reproduce is discriminated against by natural selection. Lethal or deleterious traits and skeletal and metabolic deficiencies result in low values of traits X, Y or Z.

The resource use equation describes the way in which resources are being allocated at any moment in time. For example, the cow which is using much of its resources to supply milk for sale has few resources left to prepare her calf for birth.

I have shown this equation diagrammatically in Figure 6.1, which shows that all traits that matter to an individual affect its fitness. Resources used by any one trait are not available for use by other traits.

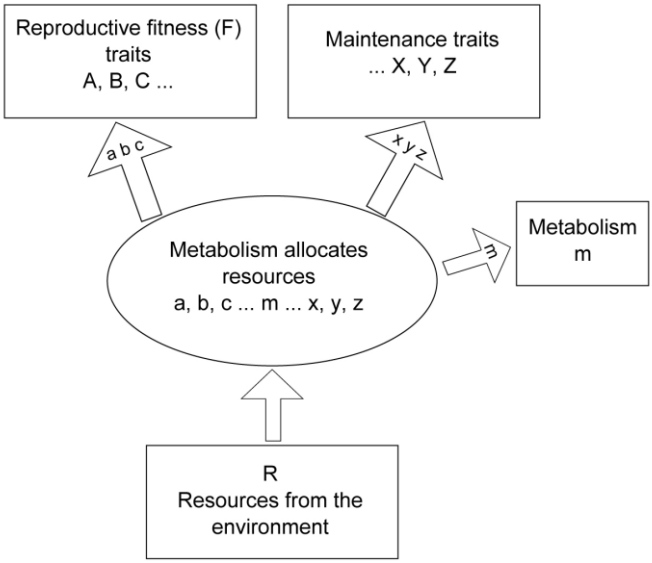

Figure 6.1. Allocation of resources from the environment by animals under natural selection. A, B and C are components of reproduction. Some resources (m) are lost because the organism's conservation of energy is not perfect. X, Y, and Z are traits that use resources to keep the individual alive. a, b, … z are resources used by traits A, B … Z. This equation can also describe resource allocation over longer periods of time, such as a lifetime. An animal that carries too much fat has fewer resources left to escape a predator and thus shortens its lifespan.

So, what do our two equations tell us?

Selection Acts towards an Optimum Level

By definition, natural selection selects the fittest organisms. Reproductive fitness (Frep) will therefore respond to selection by increasing in value if at all possible. For fitness to increase, there must be variation between individuals in those key fitness components A, B, C or in any other trait, X, Y or Z, that also affects fitness.

That part of genetic variation that can be inherited and thus allows a selection response to occur is called additive genetic variation.

As any component (say A) increases, it will consume more resources ('a' will increase) and R will increase, which will in turn allow Frep to increase. This can continue for all traits until R reaches its maximum possible value—the animal is using all the resources available from the environment.

When R reaches its maximum value, Frep can still rise a little further. This is because genetic mechanisms reshuffle genetic variation in each generation. Changes can be of alleles, or of how certain genes are arranged along the chromosomes (mutation). They also involve which individual chromosomes from mother and father form a pair in the new zygote (sexual recombination). This genetic shuffling allows the same total resources being metabolised to be reallocated to, and among, fitness components A, B and C to make resource use most efficient.

Continuing selection for high Frep will lead eventually to all animals in the population having optimum values for A, B and C. Optimum values are defined as those values which, in combination, give the highest resulting Frep. As a consequence, there will be an optimum magnitude of resources a, b and c allocated to each of the traits A, B and C.

Note that I am using the term optimum, and not maximum. This is because optimum values of traits are not the highest values the traits can have. If trait A is below its optimum, Frep will be lower than its maximum. But also, if A is above its optimum, Frep will be lower than its maximum because at least one of the other traits (B and C, or another trait X, Y, Z) must then be below optimum, because R is not able to increase.

If that sounds unlikely, let me show you in a simple example. Say our resources allow us a total of 12 fitness 'points' which can be allocated to two reproductive traits A and B. At what point is fitness maximised? Remember, Frep = A × B.

So, here are our options of A × B:

Level of A	Maximum level of B, given A	Reproductive fitness (Frep = A × B)
0	12	0
1	11	11
2	10	20
3	9	27
4	8	32
5	7	35
6	**6**	**36**
7	5	35
8	4	32
9	3	27
10	2	20
11	1	11
12	0	0

You can see that the highest value of reproductive fitness (36) occurs when both A and B are at intermediate values (both 6). Moving either number away from 6 in either direction can only lower the resulting product. That is, it reduces fitness. The same thing happens when three or more numbers are multiplied, as long as the total sum of the numbers is constrained.

Another example: if three positive numbers are limited to a total of 12, the best product is 4 × 4 × 4 with a value of 64. If you like, test other combinations to satisfy yourself that you can't achieve a higher result when you multiply them together. Our equations thus show that, when environmental resources are limiting, every major component of reproduction will be selected towards an

intermediate optimum value, because that is what will maximise fitness.

What about the other characters: X, Y and Z?

All morphological (that is structural or shape-related) features of a phenotype, their development and growth, all actions and movements, and particularly mental activity, require environmental resources. The traits using these resources do not multiply their effects with fitness components. They can't just be added into our fitness equation because their relationship with fitness is less straightforward.

But these attributes (X, Y and Z) still use up resources, leaving a smaller pool of resources available to maximise reproduction (a, b and c).

Here's an example. Hair cover is not a component of reproductive fitness, yet it affects fitness in the following way: animals lacking sufficient hair will have a greater probability of dying early in life from cold. They have a fitness of zero. So, natural selection will favour individuals with a good coat of hair. On the other hand, if an animal uses metabolic resources to grow a dense, warm coat, this again will reduce the resources available for maximising fitness through reproduction—unless resources are not limiting.

Thus, when the environment is limiting, selection will be for just the right amount of hair cover that balances the survival of the individual animal with its own maximum reproduction rate. In other words, in environmentally limited situations there will be a selection towards an intermediate optimum value for amount of hair cover.

Thus, all characters of an animal that require resources will be selected for intermediate optimum values, in the same way as components of reproduction. Metabolism itself will be selected towards maximum efficiency (highest living product per unit of resources utilised) so that the fewest possible resources (m) are lost.

The Environment Is Always Limiting for Well-Adapted Populations

Ecologists study the relationships between organisms and their environment. In ecology, it is well known that the physical environment limits the biomass of plants that can grow there; that this, in turn, limits the biomass of plant-eating herbivores; and that this, in its turn, limits the biomass of meat-eating carnivores. Similarly, in the agricultural sciences, several ideas are accepted as obvious. These are that the yield of cereal crops is limited by soil fertility, amount of fertiliser and water, and that stocking rates or carrying capacities for grazing animals are limited by pasture quantity and quality.

Thus, the notion of environments limiting what organisms can produce is common knowledge in biology with the glaring exception of modern quantitative genetics. Because quantitative genetic theory has not incorporated the environment adequately, and thus cannot model environmental limitation, the geneticists of today have inherited a blind spot, as we have demonstrated.

Theoretical geneticists typically assume resources are infinite, in that their equations don't take into account the resources available in the environment. However, we have seen that natural selection will automatically lead organisms to maximise their resource use in order to maximise fitness. Inevitably, the environment will become limiting as more and more individuals use more resources to survive longer and produce more offspring.

Because today's populations of animals are the result of natural selection, it follows that all populations in which animals are well adapted to their environment must now be limited by it. We can even take this one step further and say that complete environmental limitation can be taken as the criterion for maximum possible adaptation. 'Better' quality animals usually require more or better food in order to express their potential. In other words, animals cannot undergo genetic (or evolutionary)

improvement unless environmental resources allow genetic changes to express themselves.

Thinking back to selection for twinning in sheep described in Chapter 5, it is clear to see that it was possible to recommend twinning to wool sheep breeders only because the environmental limitation of genetic progress was absent. It is highly likely that irrigated pastures on government research stations support twinning rates at a higher level than is possible on commercial farms. Taking lambing data and mortalities at face value, without having measured how much more feed a ewe with twins needed to eat compared with a ewe with a single lamb, would suggest apparently better performances for a flock all having twins than for a flock all having singles. But the reality of limited environments turned out to be different.

We can also have another look at what happened with the Booroola gene using my above explanation. Wool sheep are typically kept on land that is not productive enough for more profitable livestock. And remember what Jim Crow already knew, that the optimal size for any trait is in the middle of the possible sizes. For sheep the middle litter size is one lamb per year. This is likely to be achieved by some genes preventing too many progeny and others preventing too few. I suggested above that a gene responsible for keeping the size down had a mutation that made this gene ineffective. Natural selection if allowed to act would quickly get rid of this gene because the mother would be unable to raise any of the too-many young. Clearly an optimum, intermediate litter size is what nature has selected and achieved. We, in our short-sighted optimism, have valued the upward disruption of nature's optimum as an important gain. We now know that it is of no use in the already difficult environments we impose on our wool sheep.

Our equations, though still a simplified model of the effect of natural selection on fitness, clearly demonstrate that organisms and their genes depend on resources available in the environment. The

immediate consequences of this understanding have already greatly changed our understanding of life and its evolution.

We have exposed fallacies arising from the way genetic theory, looking only at genes, describes life. Our equations provide a bridge between geneticists, who concentrate on genes, their frequencies and how they work, and other biologists, who are aware of how severely the environment constrains and limits life. This bridge is the recognition of the following facts:

- Fitness through reproduction is a mathematical product of important component traits of reproduction (that is, component values are multiplied together to calculate overall reproductive fitness).
- These and most other traits consume environmental resources. Resource use by different attributes must be added together to calculate the total resource use, and the total is limited by the resources an animal can obtain from the environment.
- Allele frequencies can increase from one generation to the next only if the phenotypes (whole organisms) that carry the alleles reproduce themselves successfully.
- Fitness is constantly under pressure from natural selection to increase, to the point where it can rise no further while the environment remains constant. In such environments all environmental resources available to an organism are being used most efficiently.
- In this state of adaptation, fitness is completely limited by the environment and all other traits important to the animal are constrained to a greater or lesser degree at intermediate, 'optimum' values.
- Attributes unimportant to organisms, so that they are neutral with respect to fitness, are free to drift genetically, and hence gene substitutions can occur at rates related to their mutation rates.

Our equations and their consequences comprise the 'resource allocation paradigm'.

Fisher's Fundamental Theorem: A Revision

It is good to go back to look in more detail at the fundamental theorem of natural selection, published in 1930 by Sir Ronald Fisher.

Fisher's fundamental theorem states that the rate of increase in fitness at any time is proportional to the (additive) genetic variance in fitness at that time.

Additive genetic variation is that variation which allows a selection response to occur. That is, there is variation between individuals and some of that variation is heritable. Geneticists tend to view additive genetic variation as an indication that some individuals in the population have alleles that make a poor contribution to fitness, and they aim to replace the poor alleles with better alleles to increase fitness.

Fisher's fundamental theorem recognised the fact that, in populations at equilibrium, organisms cannot improve their fitness. But he attributed the lack of further improvement to the population having no more additive genetic variation left in the trait 'fitness'. When there is no more additive genetic variation in any trait, that trait can no longer respond to selection and hence stays where it is. But exactly what does 'no additive variation in fitness' mean?

We have seen that fitness is not a single tangible biological trait that can be measured by itself. Rather, it is the overall result of the joint action and interaction of many other individually measurable traits, each important in its own right. The fitness we measure, the contribution of genes to future generations, is the total result of variation in many other traits. 'No additive genetic variation in fitness' must imply that there is no variation in any other trait important to life. This is an extremely unlikely possibility.

From the point of view of genetics, evolutionary progress requires the assumption that genetic variation lost through response to natural selection is compensated for by an increase of variation through mutation so that longer-term evolutionary change can be maintained. This is because natural selection in the traits that matter is seen as directional towards higher values. Each trait is therefore seen as approaching the point in which additive genetic variation in that trait disappears, because only the best alleles remain at each gene contributing to the particular trait being considered.[29] Yet, this mechanism for maintaining variance is not convincing.[30]

Few geneticists will dispute that if an adapted population is selected towards *lower* fitness, fitness will decline, as the selection picks up animals showing deleterious recessive genes in any important biological trait. This demonstrates that additive genetic variance in fitness (that which allows a selection response in fitness to occur), has not disappeared, even when fitness cannot rise.

There are many ways in which these other important traits can interact and vary, even when the overall result, fitness, does not increase. Remember Crow's statement that much variation remains present in the component traits when fitness is prevented from rising further. This is shown most simply when one component trait of fitness, say A, rises in the usual situation of limited environmental resources.

As A rises, at least one other trait, say B, has to fall. Geneticists then say that A and B have a 'negative genetic correlation'. At equilibrium, when fitness is maximum, each of the separate traits A and B has a zero correlation with fitness, but A and B are strongly negatively correlated with each other, so that A can rise only if B falls, and vice versa. In this situation fitness cannot rise. But it can fall if either A or B moves away from its optimum level. Note that if fitness were a trait in its own right, then zero additive genetic variation in fitness would mean that fitness cannot respond to selection, either by rising or by falling.

Fisher's theorem reflects, and has in turn contributed to, the geneticists' focus on genes as the cause of evolutionary changes.

I propose an alternative theorem, which takes a more holistic view and recalls Darwin's earlier insight: natural selection of organisms by the environment is responsible for evolutionary changes through the resources and challenges that each environment presents.

Many people will find the thought of natural selection preventing genetic changes (conserving genes) counterintuitive. Yet it must be so for all organisms adapted to their environment, until that environment changes. Adapted animals conserve important genes and gene sequences, hence only the genetic material that is unimportant to organisms can drift and show evolutionary changes in adapted populations.

To argue this, I present the alternative explanation of why, in a stable environment, fitness can't generally be improved: the theorem of optimum fitness through natural selection. This theorem points out in six very simple statements that the environment usually limits further selective development of organisms. Whatever is done, attempting to improve genotypes beyond this natural limit is counterproductive.

Note that my theorem is an alternative to Fisher's fundamental theorem, not an alternative to Darwin's theory of evolution by natural selection.

The Theorem of Optimum Fitness through Natural Selection

- Organisms require resources (mainly energy) from the environment to grow, survive, reproduce and raise young; that is, to live and reproduce (to be fit).
- Genes provide the instructions controlling the development, maintenance and reproduction of organisms. However, an organism's full genetic potential can only be realised in an

environment in which essential resources are adequately supplied.

- Natural selection favours those organisms whose genes enable them to utilise available environmental resources most efficiently. Those using all available resources effectively will succeed better than those using only some. Those maximising fitness on the available resources are selected above those using resources in any other way.
- In every evolutionary niche, and on every farm, organisms respond to natural selection by increasing in fitness until fitness can improve no more. That is the point at which successful organisms are using all the resources available in the environment most efficiently for highest fitness. (On farms, artificial selection is added on top of the results of natural selection and is likely to reduce fitness—I discuss this later).
- Optimum fitness is achieved when contributing attributes are at intermediate values. That is, the optimum values of individual traits are not the highest values the traits can have. Additive genetic variance in the traits contributing to fitness remains present.
- The resources available in the environment determine the optimum phenotype and therefore the optimum genotype. All other genotypes, whether resulting from random mutations, from selection for higher estimated breeding values or from biotechnological intervention, will have lower fitness than that imposed by the genotypes chosen by natural selection—unless the environment is currently improving.

Evolutionary Change Is Driven by the Environment

The theorem may of course be applied to the derivation of the findings of my research work, presented in Chapter 5. As long as environments remain stable, they continually select those alleles that produce the optimum phenotypes appropriate to each environmental niche. Periods of environmental change lead to

both some extinctions and some rapid changes in surviving populations as they radiate and adapt to the new environmental circumstances.

The existing fossil record of major rapid evolutionary changes interspersed between long periods of stability is an expected consequence of the environment limiting fitness after fitness has responded genetically to natural selection. Further, during long periods of environmental stability, all traits important to fitness, and the alleles responsible for them, are conserved by natural selection in their optimum forms and allele groupings, respectively. Only neutral genes, those which do not influence important traits, are free to drift by chance.

As selection occurs in response to the environment, it is the environment that either prevents evolutionary change (by selecting for optimum phenotypes in a stable environment) or encourages evolutionary change (by selecting a more favourable phenotype in a changing environment).

Mutation and sexual genetic recombination continually produce genetic changes. However, genetic changes rarely cause evolutionary changes in important traits unless the environment is not limiting, such as when an environmental change frees up resources and the population is not yet adapted to the improved environment. Genetic changes in animals cannot result in sustained increases in weight, milk production or reproduction beyond the levels that can be supported by the available environmental resources.

The six very simple statements of my theorem are based on the obvious concept that animals need resources to achieve their genetic potential for living and reproducing—yet researchers in animal biotechnology, geneticists, animal breeders and investors in commercial agriculture continue to act as though environmental limits do not exist.

Chapter 7

Darwin's Theory Withstands Challenges

Two theories are commonly raised as alternative theories of evolution that contradict Darwin's theory of evolution by natural selection: the theory of punctuated equilibria proposed by Eldredge and Gould[31] in 1972 and the neutral theory proposed by Kimura[32] in 1983. A brief comment on these two theories in the light of my work shows how apparent 'problems' can be explained both by my theorem and by Darwin's theory.

Punctuated Equilibria and the Rate of Evolution

Darwin described evolution as gradual, resulting from small changes from generation to generation—a process that has come to be known as phyletic gradualism. And since Darwin's time biologists have generally accepted that evolution is slow, even imperceptibly slow. Yet, the fossil record shows that evolution makes jumps—it appears that fossils remained the same for long periods of time and then changed significantly over a shorter period.

Eldredge and Gould's theory of 'punctuated equilibria' was proposed to explain this episodic pattern, where major bursts of evolution were separated by long periods of tranquillity in a particular location. Is such a pattern in conflict with the concept of slow, gradual evolution of a population over time as described by Darwin?

Eldredge and Gould suggested that the 'jumps', or sudden changes in a particular species seen in the fossil record at a particular location, come about as follows:

- Gene pools of large populations are relatively stable, because there are many different selective pressures acting and gene flow occurs between locations of different selective pressures. Therefore, changes in gene frequency (and particularly, selection of a gene to fixation) do not occur easily and the population doesn't change much over time.
- Natural selection is more likely to result in population gene pool changes in small populations on the edge of a large population, especially if they become isolated for some reason.
- Over time, the large population doesn't change much (stability in the fossil record) but the isolated, small population adapts to some environmental feature, becoming different to its ancestors.
- When circumstances bring the populations back together, the better-adapted individuals from the small population spread over the area, so the fossil record shows an abrupt change (the 'jump').

So, is this in fact in conflict with Darwinian selection? Not even Eldredge and Gould said so.

Mayr explained that Darwin used the term 'gradual' to mean 'lack of jumps'.[33] A gradual change is what one sees in a population being selected in a specific direction. In each generation, the population changes slightly on average as the proportion of favoured individuals increases. Such gradual change per generation can appear to be very fast in the geological time scale.

Eldredge and Gould's theory of punctuated equilibria is precisely what Darwin's theory of natural selection requires. Environmental change is often not slow, gradual and continuous but occurs in shorter periods of major environmental or climatic change interrupting longer periods of general tranquillity. For most of

evolutionary time on earth, these static conditions have been such that natural selection actually prevented evolutionary changes.

The resource allocation paradigm adds more to the explanation, as follows:

- First, natural selection has not disappeared during periods of environmental tranquillity but is in fact the cause of the lack of change.
- Second, no mechanism other than genetic recombination and natural selection is required during the periods of rapid evolutionary change.

As Crow said, selection towards intermediate optimum values maintains additive genetic variation in all traits.[34] This allows rapid selection responses to occur when environmental conditions change. The first response to major environmental changes is likely to be the extinction of many species. The fossil record confirms this. There are clear signs that this is also happening now as a result of the presence and activities of us humans. Extinction makes available environmental resources to new users, which explains the radiations of new types after extinctions. Mammals are an example: in the time of the dinosaurs, mammals were restricted to a few, narrow niches, but they radiated when the dinosaurs became extinct.

What has already happened during domestication of animals by humans will also become evident in the future as a very rapid succession of fossil types. Relatively uniform wolves will be found to have been replaced in many regions by a great variety of dogs. The same will apply to fossils from sheep, goats, cattle, horses and so on. No one has claimed that any mechanism other than selection, by man or by nature, has been acting in the production of the great variety of sizes and shapes of our domestic animals, and domestication started only about 20,000 years ago.

We now see that the theory of punctuated equilibria poses no challenge to Darwin's theory of evolution by natural selection.

Neutral Evolution

A different challenge is raised by the theory of neutral evolution championed by Motoo Kimura.[35] As geneticists became more adept at studying the genetic material itself, they found more and more genetic material that apparently drifts at random, neutrally, rather than being selected by the environment. When you study the constituent material of genes, DNA, you see that the most rapid evolutionary changes occur in genetic material that imposes only minor effects on the phenotype (the whole organism). Genes controlling important attributes change relatively slowly or not at all.

Why do important genes change so slowly? Why does only the unimportant genetic material evolve rapidly? If genes really are the important units of evolution, as Richard Dawkins said in his book 'The Selfish Gene'[36], then randomly drifting genes pose a serious challenge to the Darwinian idea. If genes drift at random, what has become of the natural selection required by Darwin's theory?

Crow wrote about evolution at the molecular level:

> *One of the biggest surprises … the rates of molecular evolution are much less variable than the rates of change of bodily form and function.*[37]
> *The principle that emerges is that those proteins that have the fewest constraints evolve the fastest. … Intervening sequences (regions of the gene that are not translated) evolve faster than translated parts. Pseudogenes (non-functional copies of genes that have arisen by duplication and have lost their function) evolve faster than functional genes. … The conclusion is clear: The smaller the effect that is caused by a nucleotide change, the more rapid that change is in evolutionary time.*[38] *[Crow's emphasis]*

And about evolution by random drift (the neutral theory):

> *The findings just discussed show, somewhat paradoxically, that the less strongly a nucleotide or amino acid is selected, the more*

> *rapidly evolutionary substitutions occur. This relationship would seem to argue that selection is not the driving force.*[39]
> *Although acceptance is increasing, it [the neutral theory] remains controversial. One point is abundantly clear, however: molecular and mathematical studies have shown that any selective forces bringing about molecular changes are at the most very, very weak.*[40]

It is amazing how well Crow has described the consequences of our equations describing the resource allocation paradigm before we wrote them and without recognising the great importance of what he wrote. Let's see how the resource allocation paradigm explains neutral evolution.

Earlier I said that only attributes that are neutral with respect to fitness were not held to optimum values by natural selection. The genes underlying these neutral traits are free to drift at random.

Our equations tell us that phenotypes are held at optimum values. We therefore expect genes that contribute to these phenotypes to be held (and conserved) in forms that ensure development of the optimum phenotype. Only the unimportant genetic materials (genes that have lost their function) are free to change by random drift, because natural selection does not prevent this. Their genetic substitution is not being prevented and hence will occur over evolutionary time at 'constant' rates related to the mutation rates of the genes involved.

For this unimportant genetic material, selection is not the driving force. The neutral theory of evolution is true. But it applies only to genetic material that has no effect on fitness. It may be a disappointment for adherents of the neutral theory of evolution to find that this theory is relevant only for unimportant genes. Fortunately, the facts are not in dispute. Opinions differ only about whether or not people take the neutral theory to be important for evolution. As Crow wrote while describing the 'paradoxical' aspects of the neutral theory, it is only non-functional genetic

material that evolves rapidly, by random drift. We need not concern ourselves with genetic material that has no function.

The neutral theory is irrelevant to all traits that are of significance to organisms. For all the traits that interest us in the evolution of whole animals, Darwin's natural selection is acting strongly, preventing changes from existing optimum values for most of evolutionary time. Our equations do indeed have very important consequences. Whereas the findings about the neutral theory were paradoxical to Crow, to us they are a necessary consequence of the model described by our two equations. Only when we realise that the environment normally (for the majority of evolutionary time) limits organisms and acts to prevent change in important genetic material, will we see that the neutral theory has nothing to say about important traits in organisms. Darwin wrote about traits that mattered to organisms; he was not interested in characters or genetic material with no effect on fitness.

The Evolutionary Synthesis Still Rules

I can sum up this chapter as follows: at least in principle, a synthesis of natural selection and genetics still validly explains the evolutionary process of traits that matter to organisms. The theories that have apparently challenged the evolutionary synthesis either are, in fact, consistent with it, or refer only to unimportant characters and genes. We will need to restate the evolutionary synthesis in words that reflect current knowledge, including the recognition that evolutionary change is not bound to a uniform slow rate. And we also have to state clearly what exactly natural selection acts upon: it discriminates between whole organisms not between their genes.

This in no way diminishes the importance of genes in evolution—without genes there would be no evolution and no life as we know it. But the genes are selected within the whole organism they have created, not by themselves. Because geneticists have not accepted this truth, a huge blind spot has developed in modern genetics.

Under conditions of purely natural selection, all important traits interact in such a way that fitness reaches the highest possible value when all other traits are at their 'optimised' values. The phenotype balances all traits optimally. At the optimum value for each individual trait, that trait's correlation with the measurement of fitness is zero. As the trait falls below its optimum value, fitness falls and the correlation is positive. Above the optimum value the opposite occurs, with fitness falling as the trait rises, resulting in a negative correlation between trait and fitness. All traits other than those not contributing to fitness will have mutually negative correlations. The more severe the resource limitation, the more negative will be the correlations.

Reeve and colleagues in 1990 published calculations confirming these statements about populations in equilibrium.[41] They pointed out that even traits important to fitness had zero correlation with fitness when a population is in equilibrium and wondered whether that was support for the neutral theory of evolution. My students and I have clearly differentiated unimportant genes or traits, which have no effect on fitness at any time, from those traits important to fitness, which have zero correlation with fitness only at that point when all traits are optimised to obtain highest possible fitness within the available resources. The neutral theory does not apply to traits that affect fitness and hence does not contribute to understanding evolution in nature or how animals diverge into different breeds.

Chapter 8

Incorporating Natural Selection into Quantitative Genetics

We know that fitness is the end result (in terms of surviving descendants) of all of the attributes that allow an organism to contribute genes into future generations. I have shown that the resources available to an organism must be divided up between the various attributes affecting survival, growth and reproduction. We have seen that in all stable environmental niches, natural selection will lead to the limitation of phenotypic change according to the level of available resources. This happens regardless of the original conditions in which the organisms found themselves.

We often debate whether an attribute is the result of nature or nurture. What an organism is like, its phenotype, is a result of both its genes and the environment. Geneticists put this in a simple equation—

$$\text{Phenotype (P)} = \text{Genotype (G)} + \text{Environment (E)}$$

—where phenotype is the animal or that attribute of the animal being measured, genotype is the genetic make-up of the animal and E the part of the phenotype influenced by the environment.

This simple equation is the start of more equations describing more and more items which can affect the measured phenotype. I'll leave out the intervening equations that increase the complexity of the quantitative genetics equations being used and get straight to the point. Within all the complexity of items affecting the measure of phenotype there has to be added one item, which 'measures' the environment in which the animals are being farmed.

I call this Er, the regional environment in which the animals are being raised and held.

All organisms, including farmed livestock, have already been subject to evolutionary pressure. Therefore, the animals we now deal with have responded to natural selection in the past, usually by becoming 'optimum' for the environment to which they have adapted.[42] Different genotypes of livestock have been favoured in different agricultural regions, just as in wild animals. For example, eastern grey kangaroos (*Macropus giganteus*) are favoured in the forests of eastern Australia while red kangaroos (*M. rufus* [now *Osphranter rufus*]) are favoured in the deserts of central Australia.

Er will differ between, say, a dairy farm in the moderate climate of South Gippsland, Victoria, with relatively high rainfall and plentiful pasture, and a dairy farm in dry, outback NSW where the resources available to the cows are much less. And as Er differs, so will other aspects of the genetic equation that results in the overall phenotype of animals. Different phenotypes (and therefore different genotypes) will be favoured in different environments.

For example, cows that produce huge amounts of milk in Gippsland may do very poorly in outback NSW. The cows may still produce relatively large amounts of milk but then have difficulty in becoming pregnant again, and because they are not thriving the farmer may need to spend a lot of money on veterinary care. It follows that farmers choosing semen from bulls to breed with their herd should be critically aware of the environments in which the semen has been produced and those in which the genes are going to be expressed.

Adaptation will occur to the level of the environmental component Er in every environmental niche. So, we should not collect data for calculation of genetic values across populations that have been selected in different environments. For example, semen contributing to the high production of milking cows in feedlots in

the United States is not appropriate for the pasture environment of New Zealand dairy cattle.

The environmental variable (Er), describing the different amounts of resources made available in each region or locality to the organisms living in it, must be added to the current equations underlying quantitative genetic theory.

Quantitative Genetics' Minimal Recognition of Environmental Factors

Genotype–environment interactions (GE) were the closest that quantitative genetics came to recognising Er before the publication of our papers. That many GE interactions exist is well recognised in quantitative genetics, but apart from different environments being mentioned in the description, little effort has been made so far to explain how different environments cause genotypes to vary unequally in this way. Why do these interactions occur?

GE interactions result from two facts:

- Different environments require from organisms a different optimum allocation of resources to meet the different challenges imposed by each environment.
- Different genotypes place unequal demands on environmental resources.

Genetic Antagonisms

We should also understand what geneticists mean by genetic antagonisms. Technically, genetic antagonisms are negative 'genetic' correlations between different characters. An example: if the genetic value in trait 1 rises, the genetic value of trait 2 falls. Geneticists and animal breeders have generally assumed that the antagonisms among traits found in the wild or in production systems, must be caused by genes. That is, they are the result of differential action of the same genes on different characters. This is called pleiotropy. For example, pleiotropy occurs when a gene

affects two attributes, M and N. If selection for the gene causes the value of M to rise, and also causes the value of N to fall, then M and N are genetically antagonistic.

How Genes and the Environment Really Interact under Natural Selection

Now let's look at GE interactions and genetic antagonisms in the light of what we know about Er.

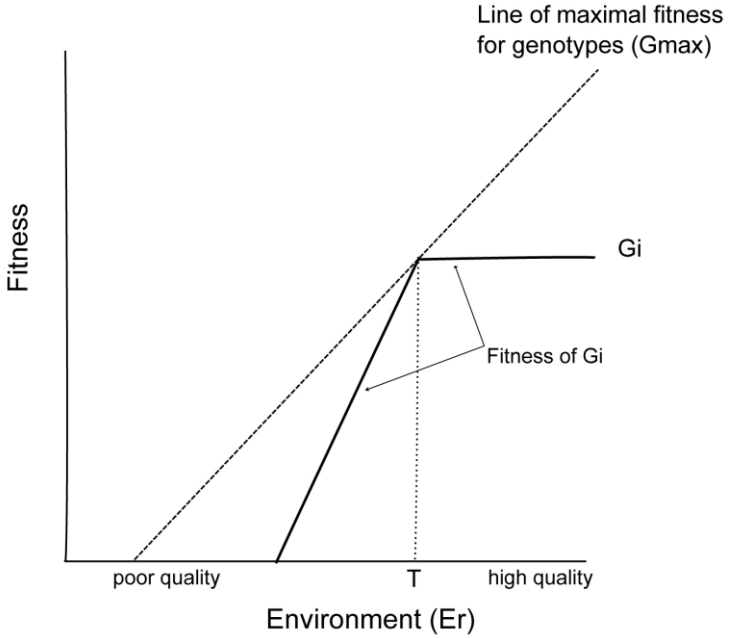

Figure 8.1. Relationship of the fitness of an individual genotype (Gi) to the environment (Er). Fitness of Gi has been selected to be maximum at the environmental level T.

Figure 8.1 shows a graph of the fitness of an individual of genotype Gi across a range of environmental values. The dotted diagonal line shows the maximum fitness possible for an individual that is optimised for that environment. Each point on the sloping line

indicates the highest value for fitness (Gmax) that a genotype can have for that particular environment Er. In the poor environment (on the left of the graph) the environment provides inadequate resources (low Er) and maximum fitness is low. In the good environment (on the right of the graph), resources are plentiful (high Er), and an animal selected for that environment will have a high fitness.

Take an individual with a genotype that we can call Gi. We can describe Gi in terms of the resources that its genes require for full expression of its maximal fitness. The bent line indicates that individual's fitness depending on the available resources. The genotype of that individual reaches its maximum fitness at point T (where it meets the line of maximum possible fitness). If the environment improves (to the right of T), the fitness of that individual will not have any increase, because its genotype, which is already expressing its maximum genetic potential, cannot make use of the extra resources.

In poorer environments (to the left of T), the individual's fitness will decline. Because it will be in environments for which it is not optimally adapted, the individual's fitness will be less than optimum. At a certain, low level of Er, the resources will be inadequate for that individual and it will not succeed in passing on its genes to the next generation—its fitness will be zero.

Different genotypes will have their maxima for fitness at different levels of Er depending on the demands their genes make on environmental resources. All traits other than fitness itself will take those phenotypic values they are allowed to achieve given that each trait competes for resources with other traits within the limit set by the total available resources.

In environments where resource levels are lower than those required for maximum fitness, all important traits must show trade-offs, among themselves and with fitness, resulting from the environmental limitation. Geneticists interpret these trade-offs as

genetic antagonisms, yet it is clear that the ultimate cause of these trade-offs must be environmental limitation.

If Er is higher than T, each trait can be more fully expressed without necessarily causing decreased expression of other traits. If negative genetic correlations persist in such unlimited situations, then pleiotropy is most likely to be the responsible mechanism. But the situation in which organisms are not adapted to their environment, when the environment is not limiting, is very rare in nature. On farms or in nature, when new resources are supplied, it is highly likely that most 'genetic antagonisms' are actually caused by environmental limitation as attributes compete for limited resources. When the environment is limiting, then whatever the genetic situation is, there is only one phenotypic result possible: an antagonism.

In a typical resource-limited environment, as one trait increases, one or more others, and fitness, will drop. This will certainly be the case when breeders genetically increase one particular production trait in adapted animals. The apparent 'genetic' depression of the other traits, demonstrated by their fall as the selected trait rises, must be a result of environmental limitation and will occur even in the complete absence of pleiotropy. In my opinion, pleiotropy only rarely interferes with what breeders wish to do, whereas environmental limitation is to be found everywhere in nature and on farms.

Let's now compare individuals of three different genotypes adapted to use varying levels of resources. Figure 8.2 follows the same format as Figure 6.1, but shows three individuals G1, G2 and G3.

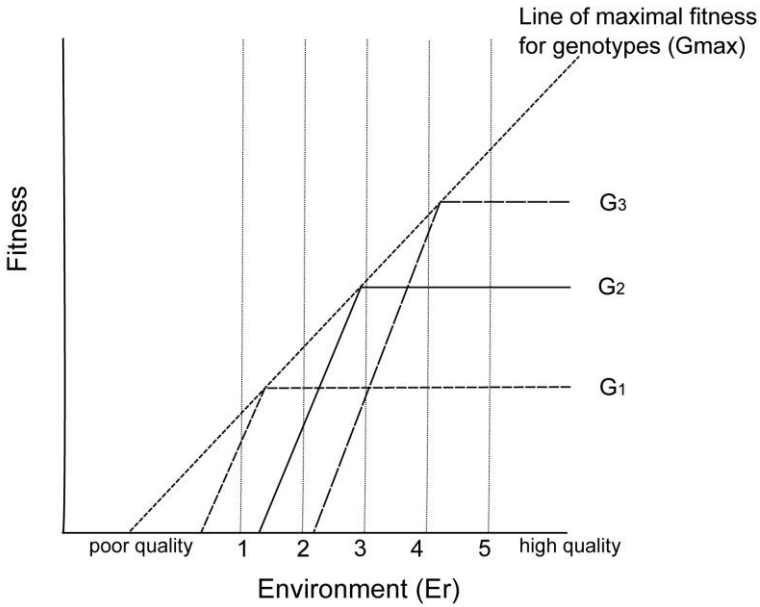

Figure 8.2. Relationship of fitness of three genotypes (G1, G2 and G3) to different levels of resources provided by the environment (Er). The measure 'fitness' shows a typical genotype–environment interaction.

The figure illustrates how our model, based on environmental resources, leads to typical GE interactions observed in quantitative genetics, and shown here for the measure fitness. Compare what happens at the different environmental levels:

- At environmental level 1, G1 is the only phenotype that can survive in this rather poor environment.
- At environmental level 2, G1 is fitter than G2, and G3 can't survive.
- At environmental level 3, G2 is fitter than G1 and G3.
- At environmental level 4, G3 is fitter than G2 while G1 continues to show its genetically poor phenotype.

- At environmental level 5, to which none of the genotypes is fully adapted, the genotypes line up according to their genetic values.

Note that the scenario at environmental level 5 is how geneticists automatically think of genotypes: G3 is better than G2, which is better than G1. This is a typical genotype–environment interaction observed in quantitative genetics, but genes are not driving it, the environment is driving it. This understanding contrasts with almost all current explanations of the mechanisms of evolution, which imply that it is genetic changes that drive or inhibit evolutionary changes.

Figure 8.2 shows that explanations requiring genetic changes to be the mechanism that drives evolution are relevant only for environments that are not limiting, that is, environments as good as, or better than, Er level 5. At that level, G3 would be favoured by selection over G2 and G1. But genotypes will only be not limited by the environment if the environment has recently been greatly improved, or in the purely theoretical situation in which natural selection is assumed to be absent.

As long as 'highly productive' semen is used for inseminating dairy cows across all levels of environments, it is inevitable that cows outside the highest production environments must show problems. And the problems have clearly become obvious enough for geneticists to try to find out why. Geneticists typically search for genetic solutions. Usually there is no hint that looking at the environment would find the answer.

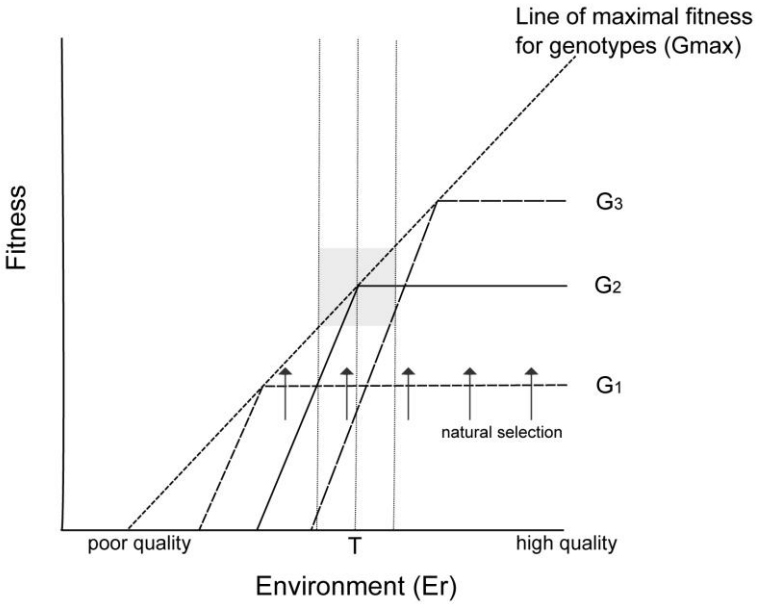

Figure 8.3. Natural selection in the environment at level T. G2 is selected. Both the 'genetically better' genotype G3 and the genetically worse genotype G1 are worse than G2 at Er level T.

So, let's look at a model of the real world, where different individuals in a population are being selected within a particular environment. Figure 8.3 shows what happens to three individuals in a population being selected in three environments (Er). Every environment continuously selects fitness upwards. Fitness responds to natural selection by moving upwards until it meets the line of maximal fitness, at the point of intersection of the line Gmax with T. The 'real world' in this model doesn't include anything to the right of the level of T because T is the maximum resource level of the environment.

What can we learn from the fitness of the three individuals where Er is T:

- The genotype G1, because of its genetically poor phenotype is not able to reach Gmax so its fitness remains low and it is eliminated by natural selection in favour of G2.
- The genotype G3, which cannot express its full genetic potential for fitness in T because its resource demand is too high, is also eliminated by natural selection in favour of G2.
- Genotype G2, with perfectly matching resource demand, prevails.

In practice there will be fluctuations in the environment T from time to time. The right boundary of the 'real world' we are considering would then move between the fine lines shown on both sides of T. These fluctuations will lead to variations in optimum fitness within the shaded box shown around the average optimum point T. But genotypes as different from G2 as are G1 and G3 will never be selected.

This discussion makes clear why, except in populations where fitness is lowered through inbreeding, natural selection never allows a situation to persist in which phenotypes are well below the fitness possible in the environment to which the population is adapted. Such poor phenotypes, whether they derive from genotypes that are 'poor' (such as G1), or that are 'too good' (such as G3) for this environment, will very rarely contribute genes to future generations. Larger environmental changes reducing the availability of appropriate resources will cause either extinction, or selection for animals capable of living on fewer resources, for example, selecting G1 in Figure 8.3.

Again, we can see that environmental limitation is the real cause of 'genetic antagonisms' and selection plateaus.

The Environment Drives Both Evolutionary Change and Stability

Living organisms require resources from the environment in order to live and reproduce, that is, to be successful in evolution. This statement is now obvious to readers of this book and has been so in papers of geneticists such as Sölkner and James[43] and Luiting and others.[44] Yet, in genetic models for explaining evolution, very little attention has so far been paid to its core, the requirement of resources. In this chapter, the addition of new theory allows the need for resources in the development of phenotypes to be expressed in quantitative genetics. Consequences important for understanding evolution (and the genetic improvement of domestic animals) include the following:

- Relations between environments, genes, phenotypes and how organisms come to change as a result of selection are complex and cannot be fully understood if the availability of resources is ignored. Quantitative genetic theory requires the inclusion of a new environmental component (Er), which represents the environmental resources and challenges found in different regions to which local populations adapt by natural selection.
- The environment determines which organisms will thrive in any given situation, while genes provide the variation in phenotypic development necessary for organisms to adapt to their environment.
- Most modern theoretical models of evolution have been presented in terms of genes driving or preventing evolution. This view is now clearly demonstrated to be wrong. Genes do not, by themselves, drive evolution, nor are they responsible, in most circumstances, for lack of changes in evolution or animal breeding. Darwin's original idea that the environment selects the most suitable organisms remains true and is completely sufficient for describing evolutionary change. Environmental changes favour the selection of those genes

that produce appropriate phenotypes precisely on the basis of those phenotypes.

- Explanations of evolution must include the concept of genes being actively conserved in those forms that guarantee the production of unchanging 'optimum' phenotypes when the environment, or the need for a specific gene product or phenotype, remain constant. This also includes the genetic canalisation of important phenotypic features, such as constant body temperature. Canalisation refers to the ability of the genotype to produce the same phenotype regardless of the particular environment the organism finds itself in.

Chapter 9

Genes, Phenotypes and the Environment

My work and that of my students has been accompanied by a series of new insights as time has passed and our findings have accumulated. Each little new realisation is important and satisfying when it occurs. However, have we perhaps achieved more than merely a sum of individual small steps? Let's briefly review our findings and the new worldview these open up. In the following chapters I discuss and, where appropriate, speculate further on other consequences of our findings.

Despite recent doubts and apparent controversies, the thrust of Darwin's insight into natural selection in 1859 remains true: the environment selects the organisms best fitted to each niche. But the metaphoric way this insight is presented by neo-Darwinists, as resulting from the selection of genes, is incorrect. The environment selects in every environmental niche those whole organisms that thrive best in that niche. It is not possible to select genes on their own, and genes do not determine evolutionary change. Neo-Darwinists' misunderstanding, or at least misrepresentation, of Darwin's theory constitutes a remarkable irony in that it has contributed seriously to a misunderstanding of the basic mechanism of evolution.

Talking about selfish genes as if they were particularly important in evolution is like talking about selfish eggs being particularly important in the commercial success of laying hens. Like genes for phenotypes, eggs are important in the commercial success of laying hens. Neither genes nor eggs can exist without organisms or hens, respectively. But we still talk about poultry and the selection of hens for their egg production, not about selfish eggs. Eggs are in no way more important than the hens. In evolution there is also

no way in which the genes themselves are more important than the organisms they develop. It is the success of phenotypes (whole organisms) that determines whether genes will get to the next generation. Ernst Mayr[45] has made similar comments.

Our work shows why environmental limitation holds fitness at its highest possible level in a given environment and holds all other traits at intermediate values so that this fitness remains at its highest level. This is the mechanism by which natural selection prevents evolutionary change. Natural selection, far from being inactive, has actively imprisoned optimal phenotypes in every niche. This is also the reason why important genes become conserved and why antagonisms between traits are so widely present.

We have identified the criterion by which we can recognise the organism that is best adapted to its environmental niche—it is the organism that makes best use of the available environmental resources. Genetic variation remains present[46], yet phenotypes will not change and there may even be an accumulation of feedback mechanisms of different kinds to ensure constancy of phenotypes. Phenotypic clines, such as the size of warm-blooded animals increasing with rising altitude or latitude, result from optimum values of body size changing as temperature varies.

The most important effect of natural selection has been to prevent change. This is because environments are stable for longer periods of time than they are in upheaval. In stable environments, organisms can do no more than adapt perfectly to their niches and remain there. This concept may take some getting used to, given the prevailing view that 'natural selection is the agent of continuous change'. I suspect that even Darwin did not see natural selection as usually preventing change, but this significant new insight provides the explanation for many previously misunderstood consequences.

Environmental change usually follows either cosmic or geological events or climate changes. These cause losses, or reduction in quality, of environmental niches. Extinction of species adapted to these niches usually follows. Resources freed after extinctions of earlier users (and environmental changes for the better) allow evolutionary changes to occur in surviving species. These evolutionary changes continue until all new and changed niches are again filled with species adapted to them. Natural selection as understood by Darwin is thus continually the cause of adaptation of animals to their niches, whether the niches are changing or remaining constant. The function of genes and of genetic change is to produce new genetic combinations from which phenotypes most appropriate to changing environments will be selected.

The evolutionary record shows that mechanisms allowing genes to vary and to be continually reshuffled into new combinations have been overwhelmingly successful in animals (including humans). Drastic environmental changes favour rapid genetic changes that allow phenotypes to adapt as fast as possible. This is the likely cause of the selection of the sexual recombination mechanism, which has been ubiquitously successful, despite theoretical doubts among neo-Darwinist evolutionists, who questioned the efficiency of needing two parents, rather than having cloning with single parents.

One can argue back from this evident evolutionary importance of the genetic recombination mechanism. Perhaps periods of environmental change have been frequent and periods of tranquillity have been short. More likely, and consistent with the fossil record, environmental changes occurring after long intervals have been so large that other mechanisms were too slow for species to survive. The rapidity of change with the genetic recombination mechanism was just too fast compared with cloning and other mechanisms, so that these other species were left behind in evolution. Recent, complex forms of animal life all have the sexual recombination mechanism.

We might also note that as evolution produced new life forms, this immediately created new environmental niches for other life forms to exploit. In summary, what have evolved are life forms that can rapidly change their genetic constitutions, and that so far have survived all environmental changes to which they have been exposed.

In evolution there has been no hint of selection for genetic uniformity in any higher form of life. Natural selection by a stable environment is sufficient to hold phenotypes constant even when the genetic recombination mechanism continually produces hopeful new variants. This opens our eyes to another irony. Reproduction scientists were putting huge efforts into cloning, when evolution has so clearly rejected the production of clones in all complex forms of animal life. Surely, we must expect massive problems if we revive a reproductive process abandoned long ago by animal evolution. Reproduction specialists should think deeply about the wisdom of trying to resurrect cloning.

With this overview of genes, phenotypes and environment, and with the realisation that natural selection has led to adaptation of organisms to the extent that they become limited by their environment, we are now equipped to consider, and reinterpret, other areas of biology as well.

Evolutionarily Stable Strategies (ESS)

Competitive allocation of resources when the environment is limiting reminds me of the concept of evolutionarily stable strategies (ESS) developed by John Maynard Smith.[47]

For ESS calculations one postulates different arbitrary strategies that animals can use to gain resources. These are limited because other animals are also competing for them. Then one specifies point values that are gained or lost depending on whether or not a strategy is successful at winning the resources in an encounter with another individual using the same or a different strategy. With

appropriate point values, there are many situations in which there is no single winning strategy. A balance is reached in which, on average, several strategies have equal success. In such a situation, when one of these strategies is used by fewer than the equilibrium proportion of individuals, this strategy will have higher success, and its carriers will increase to the equilibrium point where all successful strategies have equal success. This entirely arbitrary game or set of rules mirrors exactly what our theory about allocating resources tells us must happen when resources become limiting. That resources must become limiting follows inevitably from natural selection in every environment in which resources are not continually increasing.

The concept of ESS is a very useful analogy which describes what must follow when (a) different traits within an organism, (b) different individual organisms, or (c) different species, are in competition for limited resources. What has been called parent–offspring conflict describes what happens when parents and their own offspring are competing for limited resources. Here natural selection must find the optimum allocation of resources for the parents, who must stay alive if they are to continue feeding the current young and to breed again, and the young, which must reach a certain size before the parents stop feeding. Natural selection achieves this automatically as it maximises the number of young surviving to enter the breeding population in the next generation.

Different species can compete in two different ways: either both compete for the same resources or one preys on the other. In the first case, a typical result of natural selection is that the two species divide the total niche into two sub-niches, which in time become fully separated niches. In birds this often means that one species uses the lower part and the other the upper part of the tree canopy. If sub-niches cannot be achieved, one species will become extinct in the areas in which both previously coexisted. This happened when humans introduced dogs (dingoes) into mainland Australia, where up to then the niche had been utilised by a marsupial (semi)

equivalent, the thylacine. In this case dingoes (together with humans) caused the thylacine to become extinct in mainland Australia, while it survived on the island of Tasmania where there had been no dingoes or other dogs until the advent of European settlement.

'Arms races' describe the situation in which one species preys on another. If the predator runs faster, the prey must also run faster to survive. But running faster requires more resources. In every situation in which we record an existing balance between predators and prey, natural selection must have arrived at an appropriate utilisation of resources in each species separately, to allow both species to survive. For each individual species, what happens in the other species constitutes an environmental change.

When natural selection does not achieve a response in the prey to an improved predator, and the predator wipes out the prey, the predator may well die out itself. If that has happened in the past, we now find only fossils. Among living animals, predators and prey must have been in an ESS balance achieved by natural selection (at least before humans affected their environments).

Natural selection is always operative. No population of organisms on earth is ever free of it. The artificial selection practised by breeders and the direct manipulation of genes can only add their metabolic demands to the already existing process of natural selection. People may think that natural selection is no longer acting when their domestic farm animals are protected from predators, because such protected animals are no longer selected for vigilance or for the energy reserves needed for escape. But natural selection acts on the total organism, and this comprises much more than escape behaviour in potential prey. We can probably visualise this best by considering what has happened to dogs during domestication.

Wolves living nearby would have benefited from the food dropped by humans. Natural selection would then have raised their fitness

as their resources increased. Those wolves that evolved into dogs benefited in fitness as environmental resources increased greatly. The original environment of wolves is challenging. In the wild, it normally requires a pack of wolves to raise one litter of perhaps 4 pups per year. Often, only the dominant female has a litter, as she prevents other females in the pack from mating. Four pups in a year is on average a rate of between one half and one pup being raised per adult per year, or between 1 and 2 pups per adult female. Wolves are able to produce more young per year when their environment offers more resources. Thus, wild wolves have a mechanism for reducing their fitness to the one litter the pack can raise when conditions are difficult. By contrast, in today's domestic environment, a single bitch, without help from other dogs, can raise two litters of 6 to 8 pups every year.

Breeders did not select this enormous increase in fitness. It is entirely a result of natural selection in the domestic environment which now provides dogs with a much higher level of metabolic resources, plus veterinary support to overcome otherwise fatal deficiencies.

Chapter 10

Evolution in a Resource-Rich Environment

Remember the resource use equation:

$$R = a + b + c + \ldots + m + \ldots + x + y + z$$

R is the total amount of resources available to an individual for growth, survival and reproduction, and R is usually limited, which in turn limits fitness.

However, fitness is not limited when the available resources exceed requirements. For example, when:

- animals have entered a new environment in which some non-reproductive traits (for example, X, Y, Z) that normally consume resources (x, y, z) are no longer required
- the animal's management system has recently been changed such that a reproductive component, for example, long reproductive life (A and its associated resource a) is no longer required
- specific resources, such as the amount or nutrient quality of the feed, are being continually increased (increasing R).[48]

Under any of these three conditions, rapid genetic progress in many traits is possible and fitness can increase.

In the first two examples, investment in traits that are no longer necessary can decline, even if the resources available are stable. In the third situation the environment is continually gaining more resources, and consequently R can keep rising.

We emphasise continual improvement for this last case because a once-only increase of resources will produce a once-only response.

While this may last 10 or 20 generations, it must end rapidly, at least in evolutionary time scales.

Domestication

The domestication of animals has been an evolutionary process in which all three conditions have played a part. The initial domestication in fenced-in pastures, or under the protection of shepherds and dogs, has greatly reduced the danger from predators and increased the security of good nutrition. Domestic animals enjoyed increased fitness both through the greater availability of food, which resulted in higher birth rates, and through the absence of predators, which led to greater survival of both young and parents.

More recent intensification of animal production, as with broiler chickens or egg layers in sheds and beef and dairy production in feedlots, has resulted in a second wave of greatly increased, and very costly, resources. Intensive animal production was not practised before the middle of the 20th century, and it is possible that animals have not yet adapted fully to these conditions of husbandry. Intensification of animal production was accompanied by the development of computer software and very effective artificial selection based on estimated breeding values, in the dairy industry calculated largely from the performance of the daughters of individual bulls.

Yet, even though the evolutionary time scale has been short, many intensively reared animals already show unwanted side effects of their selection for maximised output: broiler poultry, bred to maximise growth rate and size, suffer from heart problems; dairy cows, bred for maximum milk production, have difficulty becoming pregnant to produce a second calf and therefore can't supply milk for as long as they used to. These unwanted trade-offs are a sign that resources are again limiting fitness, even in these new environments that farmers are supplying with costly resources such as protein-rich food in greater quantities.

Even major environmental improvement in animal production, when accompanied by effective artificial selection on breeding values of production traits, has rapidly exhausted the extra environmental resources. Clearly, we can only expect long-term genetic improvement without severe trade-offs if environmental resources can be improved continually in cumulative steps.

All selection of domestic animals before the second half of the 20th century was based on phenotype selection. 'Genetic' antagonisms could therefore not become severe because the most productive animals would have performed poorly and not been bred from. A selection plateau, an equilibrium between production and fitness, would have been established without serious side effects.

Major Evolutionary Steps That Freed Up Resources

At various stages in evolutionary history, major developments resulted in the availability of significant quantities of new resources. These include:

- the ability to exploit oxygen in metabolism (once oxygen became available in the atmosphere)
- the evolution of eukaryotic cells (cells characterised by having their genetic material contained in a nucleus)
- the appearance of multicellularity
- the ability to leave water and live on land
- the achievement of precise temperature control in mammals and birds
- the evolution of the human brain.

Once these developmental steps took place, the resulting organisms had available to them new environments that were previously unused. New forms of life could then exploit these new resources, which at times would have been in limitless abundance, as they radiated from the initiators of the major developmental step.

Let's have a look at the last example. Glen McBride explored the evolution of humans from the common ancestor that we shared with other primates, and it alerted me to another set of possibilities for increasing resources.[49]

Evolving humans developed increased mental abilities, presumably at least as a result of genetic changes. Improved mental ability allowed them to utilise their existing environment more effectively even when the physical or biological resources of the external environment remained static. Here, then, is an example of a species evolving even in the absence of change in the resources of its environmental niche. Existing available resources were used more efficiently after genetic changes had allowed the phenotypes to better utilise the available resources. It is only very recently that humans have realised that even these resources, like coal and oil, are also limited.

Clearly, increases in available resources in niches occupied by humans then strongly selected further increases in mental abilities. This set in train a series of events with positive feedback. In 'Figments of Reality—The Evolution of the Curious Mind', Stewart and Cohen describe the situation like this:

> *Evolving humans, because of their increasing mental abilities, started to influence their environment in such a way that it would make available more resources. This led to further selection of even higher mental abilities.*[50]

These authors write about the complicity of humans with their environment as they evolve.

Given this example, geneticists could argue that new genes always have the potential to bring about such a result. New genes could potentially create other situations in which existing resources could be utilised more effectively than was previously possible. I cannot deny this, but point out that such an increase in mental ability, which allowed the environment to be changed to release previously unavailable resources, appears to have happened only once to date

during the evolution of life on earth. Therefore, the probability that evolution has been driven by genetic, rather than environmental, change, is vanishingly small. Animal breeders are unlikely to reap practical benefits from such genetic changes.

A particularly important step in human evolution has been the invention of symbolic thinking and language. This development opened up a new world of possibilities by means of communicating, recording and using experiences and techniques formulated by others. The culture and the artefacts created in this way comprise a further modification of the environment. The end result of this evolutionary process has been an ever-increasing pace of modification of the whole earth. This has now reached a dangerous point. The ecological feedback systems that have, until the last few thousand years, maintained reasonable climatic boundaries on earth, seem now to be under strain. We cannot yet foresee where this evolutionary trend will end.

Richerson and Boyd[51] discussed in detail how culture, the product of human thought with its resulting artefacts, has become a force that now affects human evolution as much as genes and the original natural environment do. The authors make the point that three forces now affect human evolution: genes, the natural environment and the culture created by humans. Human evolution is a unique process. The evolving human species, by virtue of its increased mental abilities, largely freed itself from the limitations imposed on all other forms of life by their respective environmental niches. Nevertheless, there have also been other situations that have facilitated major bursts of evolution.

Apart from the evolution of humans by virtue of their increased mental abilities, and the identifiable major evolutionary steps opening up completely new resources for new types of organisms, all other evolutionary changes remain subject to environmental limitation as described so far in this book.

Evolutionary changes usually follow environmental changes, and the role of genes is to rapidly produce those phenotypes that most quickly and best exploit changed environments.

Self-Domestication in Environments Associated with Humans

It is worth looking briefly at species that have adapted to more favourable environments that resulted from human activity without, however, becoming fully domesticated. Some such species are sparrows, pigeons, mice and rats. Starlings, seagulls, crows, ravens and other scavenging and more omnivorous species have also been affected positively by human activities. Sparrows and pigeons clearly benefit greatly from the food dropped by people in cities and towns, resulting in large populations of these birds wherever many people live.

When humans first settled in an area where sparrows or pigeons occurred naturally, the few birds present presumably had the level of fitness that such birds can achieve in nature in the absence of humans. Humans built structures providing more nesting places and, knowingly or unknowingly, provided extra food. Fitness of individual birds then rose. This higher fitness included greater survival of more young, thus causing an increase in population. Eventually, the competition arising from the increasing numbers will have again reduced individual fitness.

A balance between rising individual fitness and reduced fitness resulting from the larger population will be achieved, as predicted from 'evolutionarily stable strategy' calculations (see Chapter 9). Such a balance will lead to the maintenance of a large population in which individual fitness could actually be higher if fewer individual birds were there to compete for food and nesting resources. Such situations now exist in all urban areas. In such populations, 'harvesting a surplus' of individuals could well result in the maintenance of a vigorous population at high individual fitness levels on resources that are essentially the waste of human

activity. It is not unreasonable to consider maintaining and harvesting a free-flying population of pigeons. More likely, however, the 'love' humans show for these birds, expressed by many people putting feed out for them, will not permit harvesting, for 'ethical' reasons. Biologically, harvesting surplus pigeons from a healthy population would not reduce average fitness.

There are many similar situations in which humans have, for whatever reason, given animals access to resources which were not available to them in their original wild state. Examples are the feeding of game animal populations in the European winter to 'save them from dying in the cold', and the provision of watering points for sheep and cattle in Australia, which in turn has allowed kangaroo numbers to rise. Whether and how such situations should be used for harvesting meat deserves rational consideration

One thing is very noticeable about partly domesticated species living among humans. In most sparrow populations, for example, individuals always remain just outside the reach of human hands. So, there must still be strong natural selection for escaping when humans come close, but only then. Escape behaviour requires greater energy expenditure than not escaping. This is clearly illustrated by the difference in escape behaviour of 'wild' house mice and rats, and 'laboratory' mice and rats. Humans have not deliberately selected laboratory animals for absence of escape behaviour. Much reduced escaping has resulted simply from natural selection in the cage environment, because we cannot breed with those individuals that jump from the cage and escape. Often a large increase in litter size and body size in laboratory mice has also resulted from natural selection, as mothers now utilise the continually present, high-quality food and the metabolic resources no longer needed for fleeing.

Changes in behaviour, accompanied by changes in musculature, reduction in brain size and so on, are the consequence of natural selection in our various domestic animals in all environments we

provide. This effect is likely to be less strong in birds that continue to fly free.

Many people say they prefer meat of truly wild 'game' animals, claiming that it differs in taste and nutritional quality from that of domestic animals. This may be related to the need for escape behaviour as much as to the more variable diet available in the wild. We should at least consider this possibility in our 'new animal industries', such as farming deer or trout. High fences will create natural selection in deer to reduce the escape response. Will a commercial deer industry on farms still supply the venison taste that currently makes deer meat valuable, or will the meat end up indistinguishable from beef?

As I have emphasised in this book, natural selection is active in every population. We would be wise to think more about its pervasive action in everything that we do with animals and ourselves.

Chapter 11

Natural Selection Acts on Life History Genes from Zygote to the Next Generation

So far, we have discussed natural, theoretical attributes that influence fitness, such as A (length of life) and B (average litter size). How should we visualise those traits important to fitness expressing themselves in real animals in the real world?

Genes usually contribute to a system moving along a track in time, a developmental path. What does it mean to recognise the action of a gene for 'anything'? Take a gene for horns as an example. Many genes together influence the formation of horns on deer, cattle and sheep. Are genes for horns the only determinant of horn growth?

No! Sex hormones, which are the result of other genes, contribute to horns taking a shape in males different from the shape developed in females. Thus, physiological factors in the body, but outside the immediate developmental system for building horns, influence their development. Similarly, if particular nutrients are in short supply in the food, stunted horns may result. Here the genes are doing their best, but if the substrate for their chemical make-up is missing, they cannot supply the product necessary for a fully formed horn.

So, the development of horns occurs within an external environment which needs to be adequate, in a physiological environment in which hormones influence sexual differences and, of course, within a system in which many genes are cooperatively contributing structures and control of the developmental sequence.

Cattle evolved horns a long time ago to protect themselves from predators. Today, however, farmers find them much easier to handle if they are hornless. Consequently, effort has gone into breeding hornless (or polled) cattle, whose progeny never grow horns.

Cattle breeders talk about 'genes (strictly alleles) for horns' or their alternative 'alleles for polledness'. What are these 'genes (or alleles) for horns'? Although it happens only rarely, every gene can mutate from one allelic form to another. In a population in which horns are reliably formed in every individual, the alleles present at each of the structural and controlling genes contributing to full and complete horn formation are called the 'wild type', or normal, alleles. If random mutations occur at any one of the structural or controlling genes, the development of complete horns can be interfered with by the new mutant alleles. A reaction can be slowed down or diverted from the normal path, resulting in abnormal horns, or the process may be interrupted completely, so that no horns form at all.

Alleles for polledness, the complete absence of horn production, could be alleles of any one of many genes that must work together to achieve the final product. Cattle breeders do not care which gene is responsible, as long as they get the phenotypic result, no horns. But is such an allele for 'polledness' a 'gene for no horns'? Surely, a better name would be 'gene (allele) for complete interruption of horn formation'.

You cannot use the wild-type form of that allele by itself to create horn production in a test tube unless you also have wild-type alleles at all the other genes involved in the process. The news media often proclaim that yet another 'gene for a particular medical problem' has been discovered; recognising such a gene may allow one to repair a particular interruption to the pathway to health, but it does not guarantee that an interruption at a different locus affecting the same path to healthy development will not appear.

Genes with Mendelian expression, say for coat colour or breed characteristics such as erect or floppy ears in dogs, are genes that show the effects of particular allelic combinations directly in the phenotype. Such genes also have naturally selected wild-type alleles associated with a complete developmental path, and 'mutant' alleles representing noticeable interruptions or distortions of the complete biochemical sequence at particular stages. Floppy ears in dogs result from the interruption of the process that made the ears of a wolf stand erect and be highly mobile so that even faint sound from any direction in which ears are pointed can be picked up. Animal coat colour also illustrates well how a complete path to dark pigmentation can be modified. The 'albino' allele, in double dose, blocks the formation of all pigment, leaving the skin without protection. Hair is white and blood vessels under the skin leave a light pink colour showing through.

At another genetic locus (the locus is the position of the gene in the total chromosome set), a mutant allele, in double dose, blocks full production of black pigment, leaving the coat red or brown. At yet another locus, a mutant allele causes pigment granules in the hair to clump rather than be evenly distributed, making the colour weaker ('dilute').[52]

Mendelian genes constitute only a small proportion of the total set of genes important to fitness. They and most other genes are cooperating in sequences in time, either by providing material substrates to the sequence or contributing to the timing of the sequence. A gene taken in isolation is an unhelpful concept in the complex forms of life we encounter today. We should think of a living organism as a sequence in time, starting from the fertilised zygote and ending with chemical decay of the formerly living phenotype when the biochemical reactions that maintain life stop at death. We must now convert the theoretical notions of reproductive and other fitness traits into concepts that help us visualise the life of an organism as a developmental sequence of biochemical reactions from fertilisation (conception) to death.

Organisms as Developmental Sequences in Time

What does our resource allocation model of Chapter 6 mean in terms of organisms, which are developmental sequences in time, controlled by varying genetic instructions, in an environment which rapidly becomes limiting? We can begin by saying that length of life (or, more directly, the number of litters produced) is an important character. Natural selection must have brought it into optimum relationships with all other reproductive and survival traits. In real life, metabolic decisions about where resources must go will be taken moment by moment. During the development of a bird or mammal embryo, important metabolic decisions are made in the mother, either when provisioning the eggs she lays, or nurturing the foetus inside the uterus. These embryos are usually well protected from the external environment.

Once young are hatched or born there is usually still much help from parents for some time, but the young must fend for themselves more and more as time passes. In other words, the external environment starts to challenge individual young growing animals and soon they must obtain by themselves all necessary resources for further development and survival. As they approach maturity, there is a period during which animals are still growing but reproduction is possible and will take place if resources are plentiful. Otherwise, the animal delays reproduction for another season until it is more mature. Thereafter, the animal essentially spends its time reproducing (or attempting to do so) and then recovering from the metabolic drain of putting resources into offspring.

Natural selection removes, by death, all individuals in which at any moment metabolic processes have left the animal unable to cope with the next challenge. It also discriminates against parents less able to compete and thus having fewer young. Similarly, the simple loss to a rival of an opportunity to mate is another way for natural selection to penalise an individual organism.

There is thus continual balancing of a vast range of biological factors. Examples of unsuccessful evolutionary strategies are:

- Litter size is too large when there is no mechanism to reduce litter size, and the mother dies.
- Reproduction starts too early in life, the stress of reproduction now being too great for the survival of the still-growing animal through the next difficult season.
- Growth is inefficient, taking too long, or demanding too many resources from the environment.
- Metabolism does not use all available resources, causing the animal to have fewer young.
- The animal's body is too small or too large to be efficient in the local climate.
- Coat colour is too light against a dark background or too dark against a light background.
- A mother produces too much or too little milk to match the needs of its young.
- Young animals walk up to 'strangers' when they emerge from their protected nests.
- Ground-nesting birds make nests on cliff ledges before young have acquired an 'instinctive' avoidance of cliff edges (in humans we call it 'fear of heights').
- Animals need to learn escape responses by experience, rather than using instinctive 'fleeing' or 'freezing' reactions.

You can think of many other possible deviations from the most efficient developmental path. All these will be penalised by natural selection. Every metabolic 'decision' is made independently at each moment. However, natural selection rewards genetically controlled phenotypic changes that anticipate coming challenges along the lifetime developmental path in the given environmental niche. This means that adapted organisms in predictable environments already inherit pre-programmed developmental paths in which resource needs for an efficient path are anticipated and prepared for.

Examples are laying down reserves such as fat or starch for anticipated future needs, giving young animals emerging from safe nests an instinctive fear of strangers, and giving nestling birds on cliff ledges a 'fear of heights'.

A Thought-Provoking Adaptation

One thought-provoking adaptation for handling reproduction in unpredictable environments is the strategy of brood reduction found in some bird species. At an international ethological conference in 1987[53], Doug Mock and his colleagues described this in great blue herons (*Ardea herodias*) breeding in swamps in the USA. Great blue herons raise two young in an average season. When the season is really good, three will survive. In bad seasons only one or none survives.

The mechanism for adjusting each clutch to available resources is strikingly simple. Usually, three eggs are laid and brooded. There are gaps of several days between egg layings and, as a result, consecutive young hatch several days apart. The parents always feed the chick begging most strongly. This is usually the hungriest and often the oldest and strongest. Simple reactions by the parents to this begging stimulus achieve the required result.

If the season is good there is enough food to raise all three chicks. If the season is average, the second young, which is hungry, starts to kill the third young. This is a slow process as the second chick is not strong and its young bill is not a refined killing weapon. After perhaps a week of life the third chick dies. Unless the season gets worse the second chick gets just enough food to survive. If the season turns really bad the first chick starts to kill the second chick, again taking days to achieve the result. Then only this first chick survives. The parents do not interfere in the fate of their individual young. There is some evidence that size of food particles affects whether defending food is successful and whether the killing of siblings will take place.

What thoughts does this example provoke in you? To me, the killing of siblings with no interference from parents seems to run counter to all the feelings about 'rights' of individuals, and parental 'love and care' that civilised humans have developed. Why do the parents not care and not prevent the murder? And why does the cruel killing take so long?

Because nature selects the best outcome precisely on the basis of this outcome: the number of surviving young. Apparently, this mechanism achieves the best possible fitness for these herons in their particular environment when food particles are of a particular size.

The slowness of killing the weakest young is itself a selected mechanism because it ensures that the next two will survive if the big first chick dies accidentally or is taken by a predator. If the first chick is no longer there, food flows to the two smaller chicks, which then both survive in a normal year. There are many animal species in which parents seem to be as 'moral' as humans in the way in which they defend and care for their young. They have adapted to environmental niches in which such 'apparently moral' behaviour on the part of parents achieves highest fitness.

The insight that nature uses whatever mechanism is available to achieve maximum fitness in an environmental niche should cause us to pause and reflect on our feelings about 'animal suffering'. Our intuitive judgments about animals may be completely inappropriate in individual situations. What animals need depends on what environmental conditions they are adapted to.

Whether or not genes prosper depends on how well the developmental path launched and guided by the genes of each zygote or clone is able to handle the challenges of the environment. I have an overriding conviction that developmental paths of organisms are continually under pressure, metabolically, to keep the organism alive. Among the products of evolution that nature

has provided, there is very little scope for an individual animal to 'take it easy' on its development path.

Variation in Life History

Let your mind's eye wander over the variety of animal species that has evolved. We will find species with short lives which breed only once (for example, males of the small Australian marsupial *Antechinus flavipes*). Even some species with longer lives, such as Atlantic salmon, breed only once. Individuals of such species release a huge, single output of reproductive material and then die shortly after. Male antechinus and both sexes of Atlantic salmon indulge in frantic mating or spawning activity over a period in which they neglect everything else and show clearly visible signs of impending death. This is an odd biological strategy that must have arisen by natural selection as the most efficient adaptation to the particular environments of these species.

At the other extreme, there are larger animals in variable environments where droughts and bounty alternate unpredictably within the lifespan of an individual. Such species have often evolved with females having small litter sizes and mechanisms for scaling down reproduction or abandoning the young altogether when times get bad. However, individual females survive to breed again over many future years, and such females clearly are reproducing as well as they can every year. Domestic livestock on pasture still provide evidence of flexible increases in reproduction when pasture is good.

If a ewe loses a lamb by accident early in the lambing season, she lays down metabolic reserves and often produces an extra lamb the following year. In a reasonable season she is likely to rear both twins, but if she then encounters poor environmental conditions in the following season and neither lamb dies, the strain on her metabolism may so run down her condition that she fails to breed at all in the following season. The environment sets a variable ceiling to reproduction every year. Female phenotypes are selected

to respond as well as possible to environmental fluctuations and to have a long life. Long lifetimes with small and reducible reproductive output each season must be a good way to achieve high fitness in variable and unpredictable environments.

In some breeds of sheep, we still find phenomena such as the 'flushing' effect. Extra feeding early in the breeding season raises the lambing percentage. In this case, ewes are responding to signs of a good season ahead by increasing their reproductive rate (by releasing more ova). A related phenomenon is seen in the less-husbanded breeds of sheep such as the Australian merino. Introducing rams early in the mating season brings many ewes into oestrus, so that mating takes place over a short time interval about 2 weeks later. Such synchronisation of the time of birth must have been selected because it lowers the risk of loss of young to predators when compared with a staggered lambing season.

Similarly, the simultaneous migration of many vulnerable animals in large groups is selected because it gives each individual more chance of avoiding predation than if it migrated alone. Predator populations cannot increase merely by anticipating a large food harvest. If the vulnerable young and other prey animals are present over only a short period of time, predator populations cannot increase. Thus, many more prey, although still individually hard to defend, remain alive because the relatively few predators are no longer hungry once they have filled their bellies.

All of these phenomena show how well natural selection in the past has achieved lifetime patterns (individual developmental paths) of animals well adapted to prevailing environmental conditions. Such lifetime strategies are following 'optimum' rates of development, growth and reproduction at maturity in the environment of each species.

Optimum Lifetime Patterns

If we accept that natural selection has achieved for each species a lifetime pattern of development, growth and reproduction that has resulted in the highest fitness possible in its environmental niche, then we should be able to derive general expectations of what we should find. What do we expect, and do our expectations match our observations?

If we think of the life cycle as starting at birth, one complete generation will have passed by the time the offspring of the individual under consideration are born. Only after all offspring have been born will we know when the 'average offspring' was born, which will then tell us the length of time in the life cycle from the birth of the individual under study to the average time of birth of its offspring. A more practical way to estimate the average length between generations is to calculate the average age of the parents when progeny are born, giving equal weight to father and mother. Parental age at birth of young defines the period from birth of the parent to birth of its young. Taking a random sample of young gives an appropriate sampling of parents with first-borns through to last-borns, and this average age provides an accurate measure of generation length.

We already know that it is difficult to distinguish the fitness of one individual from that of its progeny, and also from that of its parents. So, let us proceed cautiously. When an individual is born or hatched, its parents invest many resources in its survival. Thus, the environment of the young depends greatly on parental input, or parental effort as Trivers[54] called it. Our focus individual must now get to reproductive maturity as efficiently as possible. This means that the growth and development to the point at which full reproduction is functioning should take a relatively short time compared with its subsequent reproductive effort, and that this non-reproductive preparatory period should consume as few resources as possible.

Parent–offspring conflict is a well-studied topic in animal evolution. In mammals and birds, it leads to an evolutionarily stable set of strategies in which the goal of minimising the provisioning of offspring by parents is balanced by the goal of the young striving to achieve maximum growth from the food brought by the parents. In birds, parents often continue to provision young well beyond fledging as the family flies from one feeding ground to another. The end result is always an ESS balance.

Studies of growth curves of fully fed young animals have revealed remarkable uniformity in growth rates, even between different breeds of domestic animals selected for different growth rates. Taylor shows that when growth of the whole animal, or its parts, is described relative to the mature size of the animal, the growth curves obtained are remarkably similar in the two sexes, in different breeds of the same species and even across different species.[55]

We should expect the environment to impose selective pressures in favour of the most efficient developmental path to bring the organism from the zygote stage to the start of breeding. After all, this is reproductive downtime; the organism experiences danger while not yet being in the position to produce offspring. We should expect this growth phase to use the fewest possible environmental resources to most efficiently bring the animal to mature size, able to reproduce, and then having the most efficient total lifetime of reproduction possible in its environment. It follows that all animals, in the absence of special requirements for local adaptations, should follow mathematically the same optimum growth curve relative to the animal's mature size, just as Taylor has found.

I find it difficult to illustrate lifetime pattern of fitness itself by means of sketches or graphs. This is because fitness is influenced by so many factors. Reproduction is only one part of it and is restricted as to the time it can occur. Fitness also includes the biological processes of survival and the necessary development

required to ready the body for reproduction. Can individual survival to the point in time when reproduction becomes possible be expressed in the same currency as the number of viable young produced when the surviving animal starts reproducing?

I define metabolic resource use as the use of resources for all purposes that increase fitness. In Figure 11.1 I have tried to illustrate the point I made at the 5th World Congress of Genetics applied to Livestock Production in Guelph, Canada.[56] It shows the developmental path of an organism (b) selected early in life for greater size or for any comparable metabolic effort compared with a wild-type organism (a) adapted to the local environment and showing more moderate early growth and a longer life overall. As fitness in this environment cannot be higher than that achieved by natural selection, selection for higher earlier metabolic effort must result in a shorter life.

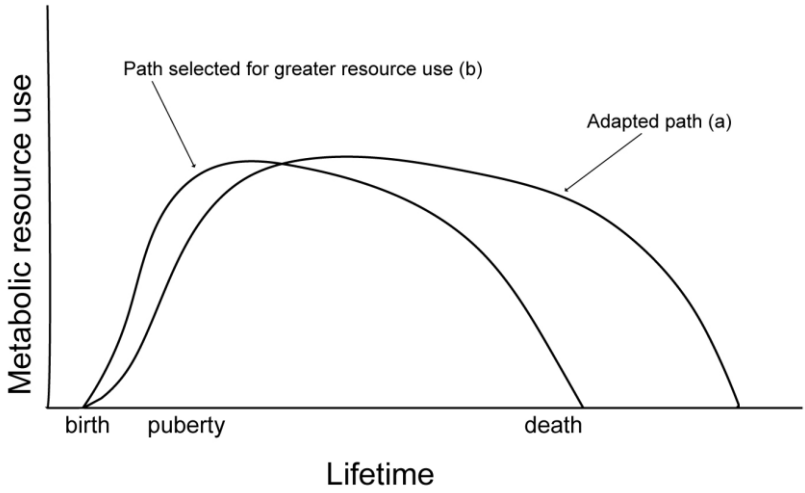

Figure 11.1. Two lifetime developmental paths of 'metabolic resource use' showing an initial phase of growth, then puberty, reproduction and death shortly after reproduction. Path (a) is an organism adapted to the local environment. Path (b) is an organism that has been selected for high early metabolic resource use.

In Figure 11.1, the growth Taylor describes is that part on the left of each lifetime path, before maximum size and maximum metabolic effort have been reached at puberty.

Clines of size in wild birds and mammals, such as increasing body sizes from the equator to the poles, also demonstrate that there is an optimum, most efficient mature body size for each species in each environment. Animals that deviate from either the optimum mature size or the optimum lifetime developmental path are likely to achieve lower total fitness. Are these ideas pure speculation or is there real supporting evidence?

There is much supporting evidence, but it mostly comes from studies in which people were looking for genetic mechanisms for ageing, for selection plateaus, or for other topics of genetic interest, but not for limitation by a paucity of environmental resources. Typically, researchers have not been aware of the overriding need for metabolic efficiency as required by organisms adapting to limiting environments. We can take as examples two papers by the highly respected geneticist Eric Bradford and his graduate students J. Eklund and N. Barria.

The paper by Eklund and Bradford was published in the prestigious journal *Nature*.[57] A line of mice (line G) had been selected earlier for increased growth between 3 and 6 weeks of age. This selection had greatly increased liveweight and also altered food intake, body composition and reproduction. The paper reported what had happened to body weight and length of life. Male and female mice from line G and from an unselected control line (line C) were allowed to grow up in appropriate conditions and weighed regularly until they died. They had good food and were not challenged metabolically by breeding or any other potentially stressful stimulus.

Table 11.1. Average lifespan in weeks of mice selected for early growth (line G) and controls (line C). Data from Eklund and Bradford (there were 16 male and 16 female mice in each line).[58]

Selection line	Males	Females
C (control)	112.1	119.5
G (growth)	51.1	82.3

The mice selected for increased growth did indeed grow larger (heavier) than the control line mice, but the data in Table 11.1 show that they died much younger. The males of the control line had a slightly lower average lifespan than did the control females, but the difference was not statistically significant—it could have resulted simply from chance variation among individuals. However, the control group lived significantly longer than did the selected group, for both males and females. And the selected males lived significantly shorter lives than the selected females.

Hence, both sex and selection line had real effects on longevity, with the effect of selection line being very much greater. There was also a significant interaction between lines and sexes—the effect of the selection was different for male and female mice. This is shown by the shorter longevity of males in the G line than the C.

This effect of sex was significant but not large and will be discussed again in the next chapter. Much greater was the difference in weight between the two lines. The G line had peak weights between 60 and 80 grams while the C line had peak weights between 30 and 40 grams. This provides very clear evidence for my statement that movement from the optimum size and developmental path reduces fitness. In this case, fitness was measured by length of life. A mouse can be expected to have more litters, and therefore the more progeny, the longer it lives.

Barria and Bradford looked at reproductive characters (fertility, ovulation rates, embryo survival) in relation to weight.[59] This study

(after that of Eklund and Bradford) used the same lines G and C discussed above as well as other lines derived from G by (a) stopping the selection for faster growth and (b) reversing this selection, that is, selecting back towards slower growth.

Fertility, ovulation rates and embryo survival rates had fallen greatly in the mice selected for heavy weight (line G). These reproductive characters rapidly increased again as weight fell rapidly in the mice now selected for low weight (Gb). They rose, but more slowly, in the mice in which selection for heavy weight was stopped (Ga). Weight also fell in this line, but more slowly than in the reverse selection line. In other lines where inbreeding was superimposed on selection, the well-known deleterious negative effect of inbreeding on reproduction was added to the negative effects of selection for rapid growth on reproduction just described in the lines without inbreeding.

This paper, also, demonstrates a beautifully consistent set of results. As growth rate and size increase above the naturally selected optima, fitness characters, in this case aspects of reproduction, decrease. Whenever adapted growth paths are distorted by extra metabolic demands, fitness must decline, and the evidence here is that it does so in many of the traits contributing to reproduction and overall fitness.

My explanation based on limited available resources is well supported by all of these results. In the absence of awareness of environmental limitation, Bradford and his students postulated possible genetic explanations. Barria and Bradford suggested a model with genotypes A1A1, A1A2 and A2A2 having values 2, 1 and 0 for growth and 0, 2 and 2 for reproduction. The values postulated for reproduction in the model show dominance of allele A2 over allele A1. This is necessary to explain the negative effects of inbreeding found in reproductive traits because deleterious genes are usually recessive.

It is true that such a genetic system would work to produce the results found. As selection for growth shifted allele frequencies from A2 towards A1, growth would increase and reproduction would decrease. But there is no evidence that any genes involved were actually working in these mice in this way. In fact, dozens if not hundreds of genes affect reproduction and growth, and it would be highly unlikely that a simple seesaw system such as proposed by Barria and Bradford is operating alone. Speculation on genetic possibilities is easy. To my mind, limitation of resources and selection away from optimum use of these resources provide a much more satisfying explanation.

Why Do We Age and Senesce?

Life history is another name for developmental path. It is the name under which a specific branch of biology (life history studies) has developed. After looking briefly at this, we can make some useful speculations on the topics of ageing and senescence.

A good introduction to life histories is found in the book 'The Evolution of Life Histories' by Stephen C. Stearns.[60] Stearns introduces the scientific field and discusses the theory. He also tells us what is known about life history traits. The book concerns a very important aspect of biology. It also presents much evidence related to fitness characters that supports the statements I make in this book. The quantitative genetics available to Stearns did not yet include my explanations about Er and limitation by environmental resources. The recognition that natural selection, by adapting organisms to their environments, then limits them to the most efficient uses of available resources was not yet available in 1992, although it was taken for granted that the environment limits organisms.

As in the papers of Bradford and his students, Stearns, and the many scientists whose work he reviews, was looking for genetic explanations for trade-offs and other fundamental relationships. Stearns is also suspicious of quantitative genetics. I agree with

Stearns that organisms have lifetime developmental paths. People, very understandably, are interested in their own later lives. Can they slow the process of ageing and ward off death?

As in other efforts to increase lifespan, Stearns was looking for genetic mechanisms and assumed that genes drive evolution and the consequences flowing from this. We now know that the environment limits fitness and hence the optimum developmental path available to animals. Therefore, we should expect that length of life depends on the shape of the optimum path selected to provide highest fitness, and on whether any particular path has to vary from the optimum by putting in extra effort.

Natural selection must arrive at the optimum length of life in an amazingly complex situation. On the one hand, breeding longer and getting older raises the fitness of the individual parents. On the other hand, the continuing presence of dominating parents may depress fitness of their young when parents are not allowing space for the young to breed. So, natural selection, as it deals with the parent–offspring problem when offspring are young, must also find the optimum time for ageing parents to leave available resources to their offspring to start breeding.

Natural selection solves this complex problem automatically merely because the individuals breeding best at any time, whatever their age, are likely to get more young into the next generation than will individuals breeding poorly. I can't deduce from this situation what the optimum length of life will be, but I trust natural selection to have found the answer, even if the answer is flexible depending on the environment. I conclude that the particular age at which an individual reaches each life stage will be found to be optimum for any species in the niche to which it has adapted. Computer modelling to determine optimum ages under specified conditions may shed light on how natural selection optimises length of life.

Bradford and his students showed very clearly that mice that put in extra effort to grow faster and to become bigger than the

naturally selected optimum size had greatly reduced lifespans. To have a long lifespan, you must ensure that you follow an optimum developmental path in terms of metabolic effort close to that which natural selection would select in your environment. This is another major leap in understanding that follows from recognising that environmental resources limit evolutionary changes. Are we wasting research funds presently going into the study of ageing? Presumably we will find out much about mechanisms that lead to death, but I doubt that we will achieve more than minor extensions of lifespan by looking at old age. We must focus on the early part of life and consider quite generally the effects different lifestyles are having on the metabolic efforts we require to satisfy our lifestyles. Presumably, the effort required to grow and carry around a large body will decrease lifespan, as happened in Bradford's mice.

Ageing is a consequence of what happened earlier in life. The specific mechanisms of how we deteriorate with age are less important than what happened to us earlier in life.

There is, in fact, one medical researcher who has evaluated human data from this point of view. In the book 'Mothers, Babies and Disease in Later Life' David Barker related epidemiological information about diseases causing death in people to data on the same people as babies and on the pregnancies that had produced them.[61] He has found that what happens in these early stages of life has great influence on diseases contracted in later life and the causes of death. Here is a summary from Barker's book:

> *Studies of programming in foetal life and infancy are now established in the agenda for medical research. They have two goals: preventing disease in the next generation and understanding disease in the present one. The search for the causes of coronary heart disease has hitherto been guided by a "destructive" model. The causes to be identified act in adult life and accelerate destructive processes—the formation of atheroma, rise in blood pressure, loss of glucose tolerance. This book has proposed a new "developmental" model. The causes to be*

identified act on the baby. In adapting to them, the baby ensures its continued survival and growth at the expense of its longevity. Premature death from coronary heart disease may be viewed as the price of successful adaptations in utero. We need to know more about these adaptations: what are they; what induces them; how they leave a lasting mark on the body; and how this gives rise to the diseases of later life?

Here we have another sign that the thesis of my book is echoed in other fields, in this case in human medicine.

Barker also noted that the growth trajectory of boys is more rapid than that of girls from early in embryonic life. Boys are therefore more vulnerable to under-nutrition, and this could have consequences later in life, such as higher rates of coronary heart disease. From the arguments of my book, the extra metabolic effort that boys put in, even very early in life, has a metabolic cost which contributes to a shorter life, however this is mediated.

To this point we have deliberately not followed up sex differences, because I have reserved the next chapter specifically for this topic—the differences between the sexes.

Life Histories are Optimised by Natural Selection

The model of fitness and its inheritance offered in chapters 5 and 6 is a simplification. How do genes really cause the development of phenotypic traits? A living organism should be seen as being on a developmental path starting with the fertilised zygote and concluding with death. Genes influence each step along this path. Natural selection eliminates all organisms that at any moment have insufficient metabolic resources to cope with the next challenge from the environment and discriminates against all those not using available resources efficiently. This in turn selects for the laying down of reserves as a buffer against predictable changes in resource needs, such as seasonal or pregnancy-related extra efforts.

Organisms inherit programmed lifetime developmental paths. These programs include mechanisms for adjusting reproductive effort to the environment. In each environmental niche there are optimum sizes and optimum developmental paths. Natural selection uses the genetic processes to achieve optimum lifetime paths. Deviations towards higher resource use than required in optimum sizes and optimum developmental paths incur metabolic costs. These typically lead to reductions in reproduction and longevity. 'Premature ageing' is a consequence of above-optimum resource use, often early in the lifetime path. There is evidence in humans that costly adaptations to environmental stress, even in babies in the uterus, reduce longevity.

Chapter 12

Life History Differences between the Sexes

Here I investigate the ways in which sex affects natural selection and life histories.

The recombination mechanism for shuffling genes has been very important in the evolution of life because it produces more-varied offspring than a clone can do. It requires two sexes, or at least two different sex organs, on separate individuals in typical animals and on the same individual in typical plants. These organs have complementary differences which permit fertilisation—the mixing of genes from father and mother. We normally have little difficulty separating the two sexes in animals. In many species there are substantial morphological differences between sexes, called sexual dimorphism.

Let's investigate the magnitude of the phenotypic differences between males and females. Why do males and females differ in form, size or lifetime developmental path?

This leads to the distinction Darwin made between sexual selection and natural selection. Sexual selection is the selection by females of certain males for mating, and vice versa. He discussed this in the book 'The Descent of Man, and Selection in Relation to Sex', published in 1871.[62]

Sexual selection differs from natural selection, which is selection by the environment for enhanced survival and reproduction of individuals. Most evolutionists since Darwin have faithfully followed him in looking at sexual selection as a mechanism completely separate from natural selection. We are left with the impression that sexual selection must be investigated separately.

In natural selection, the environment provides challenges that organisms must meet and overcome if they are to mature and reproduce successfully. Let us repeat this truism from the point of view of a male animal. A male animal must meet and overcome the challenges of the environment if it is to mature and then reproduce successfully. Finding females, mating with them and keeping rival males away are environmental challenges for this male individual just as are finding food and escaping from predators. If the individual is successful, his genes will move into the next generation and his fitness will be appropriately high. We can say exactly the same thing about the fitness of female animals.

Thus, within any given species, members of both sexes comprise part of the environment imposing natural selection pressures on mating and reproduction of the individual. Members of each sex must evolve appropriate responses to rival individuals of the same sex and to mating partners of the opposite sex, in the same way as individuals of each sex must evolve appropriate means of obtaining food and escaping from predators.

It follows that sexual selection, mate choice and same-sex rivalry are part of natural selection in evolution. There is no need to separate sexual selection into a special topic as Darwin did. Here we have a rare chance to make biology a little less complicated. We can treat all of evolution as being by natural selection among individual organisms, whatever their sex. We should seize this opportunity.

The principle is: individual organisms are selected by, and adapt to, their environment. The environment, however, includes individuals of the same species, both of the same and of the other sex. These two sentences neatly resolve those awkward situations where we are not sure whether our investigation belongs to natural or to sexual selection.

Sexual Dimorphism

Sexual dimorphism is the name for any recognisable difference between the sexes of the same species. Some species show no sexual dimorphism—males and females look the same. In other species, males and females differ considerably, in size and weight, features (such as horns) or exaggerated decorations (such as the famous male peacock's tail). In some walruses, males are more than twice as heavy as females, and in some birds of prey females are larger than males, so sexual dimorphism need not always mean bigger males.

All of us accept that colour patterns and physical features in males often differ from those in females. In humans, bald men can't express hair colour, and women don't have beards like their husbands, fathers or grandfathers. We all know that beards and baldness express themselves differently in men and women. Such characters not expressed equally in both sexes are called sex-limited characters.

Up until now we have thought of animals without considering their sex. We have spoken of the environment as selecting animals without paying any attention to the possibility that the same environment may not treat a male and a female animal identically.

Does the environment differentiate between the sexes in natural selection? We normally assume equal treatment of the sexes when considering Darwin's natural selection. By contrast, in sexual selection, males select among the females of their species the one or more females they will mate with. Females select among the males of their species in exactly the same way. Clearly such 'mate choice' is different from culling or other discrimination between individuals in natural selection. But it would be wrong to assume that the selective pressures of the environment will be the same for males and females of a species.

It soon becomes obvious that there are many ways in which a male individual may face different selective pressures to those faced by

a female individual in the same environment. For example, a predator could more easily see a larger male. On the other hand, the large male may not be attacked, but the smaller female taken instead. And what about reproduction? In many species mothers spend much time raising a small number of young, while individual males may have many offspring from mating with many females.

Wolfgang Wickler and Uta Seibt[63] have looked closely at the evolution of sexuality and the differences between the sexes. They point out that the first recombination of genes from different individuals, using recombination of genetic material, was among bacteria and other similar ancient life forms for repair of the genetic instructions.

As organisms became more organised and efficient, the diploid, double-stranded genetic material permitted repair of one strand by direct transfer of the information present in the other strand. As we have already noted, creating genetic variation by sexual recombination became important.

Particularly in 'lower' animals, asexual reproduction without much genetic recombination does occur. Some animals, like some fish and snails, are hermaphroditic while others, like starfish and some worms, can reproduce by cloning—breaking into parts and regrowing whole individuals from the parts. But, as life forms became more complex, sexual recombination and the complete separation of roles between the female and male sexes increased. The typical female role is producing large yolk-filled eggs and nurturing the young. The typical male role is to produce many small sperm and to ensure that the sperm find their way to as many eggs as feasible in order to fertilise them.

The efficient use of resources is always favoured by natural selection. Wickler and Seibt state that no other combination of gamete cells can surpass the division into large, yolk-filled eggs, of which few are produced, and small sperm, individually cheap and produced by the millions. Given limited resources, complementary

specialisation must win. There will be individuals producing few large eggs full of resources for a successful start to an individual of the next generation and individuals producing very many small sperm whose few resources are targeted on finding eggs and fertilising them.

This is so even in fish that release eggs and sperm into the open water. Sperm swim rapidly to find and fertilise a large egg. Land animals reproduce by means of eggs with protective shells or within a uterus in the body. Here, the initial size difference between female and male gametes has, in many species, been selected further to make the roles or lifetime developmental paths of male and female animals also dimorphic. This results in greater competition among males for the reproductive resources offered by females, with more males than females missing out completely on reproducing.

Optimum Lifetime Strategy for Each Sex

The separation of the roles of the two sexes is the result of natural selection for the highest possible efficiency in utilising resources to get offspring into future generations. This selection has led each of the two sexes of animals to specialise so as to be at its most efficient, given that the other sex exists. Appropriately dimorphic sexes are the ESS solution for each environmental niche.

Females must cope directly with the challenges of the environment. Typically, they also play the larger part in the nurture of the young. They will be selected for a lifetime developmental path that directly reflects the immediate challenges of the environment. The timing of readiness to mate is selected into the most favourable season for the newborn young to find food and shelter. As well, females efficiently use other predictable changes in the environment, for example by synchronising mating in the herd. They will also exhibit appropriate mechanisms to deal with unpredictable environmental fluctuations. These can be phenotypic responses to a good season, such as the flushing effect

in sheep. There can also be brood reduction as in the American herons discussed earlier. Under harsh conditions, female kangaroos and wallabies can discard the young in the pouch while simultaneously keeping an embryo in suspended growth until the environment improves. It is probably reasonable to say that the lifetime pattern of female animals is close to the optimum developmental path for which a theoretical population of animals reproducing directly, say by cloned spores, would have been selected in each environmental niche.

For males to reproduce, their need to mate with females leads to competition between individual males. Males obtain matings either by competing physically with other males, or by becoming so attractive that the females prefer to mate with them. The latter has been called mate choice. It is typically choice of males by females but does exist with sexes reversed in some species.

Competition between males requires them to either become big and strong (for fighting or as an intimidating display) or to grow decorations (to attract females). The horns of deer and other ungulates can be both attractive and also the tools with which strong males win matings. Feather crests and exaggerated tails, as in the male peacock, and equivalent decorations in reptiles and mammals, such as the manes of male lions, are likely to have been selected because they made the individual males attractive to the females of their species.

Every variation from the typical efficient female life path is important. Most males require more environmental resources early in life than are used in the course of the optimum life path of females. If the males did not invest heavily in growth early in life, they would not achieve matings at breeding age. We already know that such alterations of the life path at a young age are deviations from 'optimum' developmental paths and therefore come at a cost. We should not be surprised that male *Homo sapiens*, being generally larger, have shorter life expectancies than women. Although data are sparse, I expect that similar situations exist in other species.

The mice bred by Bradford and his students provided one such example.[64] The growth-selected, big G male mice had a much shorter average lifetime than G female mice. Both sexes of the smaller, unselected C mice enjoyed much longer average lifetimes than did the G mice. It would be interesting to systematically record length of lifetime of those birds of prey where males are smaller than females.

Males and females exhibit different lifetime patterns because each sex is selected to be most efficient in achieving high fitness, given that the other sex exists. The environment, therefore, always selects sexual dimorphisms, unless the two sexes have exactly identical environmental requirements.

Homo sapiens: A Special Case

Humans exhibit an early growth phase that is very long relative to the rapid efficient growth curve found in other primates and many other animals. Presumably this was selected to allow human children to develop the brain capacity needed to cope with the complex world of culture in which humans now exist. Malcolm Potts and Roger Short express this opinion strongly, among many other fascinating details about sexuality, in their book 'Ever Since Adam and Eve'.[65]

These changes in optimum lifetime pattern of humans have been accompanied by another evolutionary oddity. Sexual activity is not confined to hormonally determined periods of 'heat' in the female when fertilisation is likely and mating takes place. Ovulations in humans are hidden. Copulation is frequent and typically continues over many years in each heterosexual pair of humans.

Procreation results from it, of course, but most other animals achieve procreation far more efficiently, with sexual activity restricted to when females come on heat. Has continuous sexual activity, and the pleasure it provides, been selected in humans for an important reason? Yes! Sexual activity with a well-known

partner maintains the parental bond. Again, Potts and Short emphasise this point.[66] Human children benefit from a long period of relaxed, undisturbed protection by two parents as the children approach maturity and become confident adults. For the species *Homo sapiens,* the high frequency of sexual intercourse clearly achieves much more than procreation.

I suggest that continuing sexual activity in humans between breeding partners is the strongest mechanism bonding the parents. A strong bond facilitates the full intellectual and social development in children. The enormous complexities of human culture that children need to master in order to become successful adults has led to an increase in longevity, away from the earlier optimum, most efficient, growth curve of most other animals. This recognition exposes a sad irony in some Christian religions.

Most religions have recognised mankind as being 'like God', different from other forms of life. The difference lies in the human capacities of thinking and spirituality, and includes the higher mental abilities necessary for coping with fully developed human culture. Yet the sexual mechanism which achieved our evolutionary change to become humans 'in the image of God', namely our strong instinctive urge for sex, was seen by certain Christian leaders as an evil lust. Complete service of God was seen to necessitate complete rejection of this 'lust' in favour of a life of celibacy. This behaviour modification is diametrically opposed to the powerful, naturally selected instinctive urge to have sex. This theological mantra is likely to have contributed significantly to the growing number of revelations of sexual molestation of young people by priests. In plain scientific words, this human-made theological problem results from the great difficulty any organism has to act against a strongly selected instinct. This fact also leads us to the obvious solution of the problem: let each male priest have a wife so that he can enjoy normal sexual behaviour and as a result be better fitted to express full humanity to the children in his charge. To be properly inclusive, I am happy to say that any priest,

male or female, should be allowed to have a partner, whether heterosexual or homosexual.

The strong human instinct to have sex, like all other attributes under the control of natural selection, will have mutations in genes or environmental disturbances of the action of genes, as is happening all the times in the whole genome. Unless sperm meets an egg, there will be no descendants. Hence natural selection will have tended to reduce the presence of same sex attraction.

Once we became humans with the ability to modify our environment, natural selection lost much of its power. This applied particularly to the last and current centuries because our medical knowledge and tools allowed certain individuals, who would have in earlier times died young, to live on.

One thing is clear: instinctive attraction to others has a genetic base. As in all other parts of the genome, this genetic base will have mutations, and different people will grow up to be different. We should fully accept all people within the community, including those attracted to others of the same sex.

The well-known palaeontologist Niles Eldredge in his book 'Why We Do It'[67] argues correctly that natural selection in evolution does not literally choose between genes as is implied by a simplistic interpretation of 'selfish genes'. He also comes very close to my contention that sexual activity binds human partners. He writes:

> *Moreover, sex has become decoupled from reproduction in human life, forming the "human triangle" of sex, reproduction and economics. … sex exists for its own sake in human life and has, as well, intricate connection with the economic world quite apart from reproduction.*[68]

So, I am not alone in claiming that ongoing sexual activity has been important in human evolution, even though Eldredge's explanation of the cause differs from mine.

If my explanation of human sexuality is correct, then we must look at the sexual urge in a positive light, in contrast with the theological views held in religions that demand celibacy. We should positively applaud sexual relations between bonded partners as a wonderful mechanism that contributes to the healthy development of their offspring.

Natural Selection Has Resulted in Different Optimal Life Histories for Males and Females

Continuing recombination of genes has clearly been very successful in evolution. In most animal species, two distinct sexes have been selected to complement each other. Each sex has been selected for its own optimum developmental path, or life history, given that the other sex exists. In many species this has resulted in quite different optimum sizes and developmental paths for the two sexes. Treating sexual selection as different from natural selection is unnecessary. The environment selects individuals of each sex towards highest fitness. For each individual, the environment includes conspecific members of the same sex and the opposite sex. Securing matings is just one of the many environmental challenges for every individual to master.

Chapter 13

Animal Behaviour and Welfare

Animal welfare and behaviour are also best understood in the context of animals adapting to their environments. Can we do better than to assume that well-adapted animals feel well in their environment? I doubt it.

An example to help us think this through is an Australian marsupial adapted to deserts, the crest-tailed mulgara (*Dasycercus cristicauda*). This small, stocky, rat-like marsupial does not need to drink. It gets its moisture from the food it eats, and its kidneys conserve water extremely efficiently. Animals specialised in this way have little competition in their difficult environment. However, the physiological adaptations that allow them to survive in deserts must be metabolically very costly. The fact that the mulgara does not drink is not a problem for this animal. Other mammals, not adapted and hence not competing for the insects and small reptiles and mammals available in the desert, will die rapidly when they have no water to drink. Thus, the 'basic welfare requirement of fresh water every day', as is typically thought necessary for animal welfare, is completely unnecessary for the welfare of mulgaras and similarly adapted species.

Wellbeing, if it is to have any useful meaning, must accompany the state of normality in which an adapted animal lives in harmony with its environment. As we saw in Chapter 6, adapted animals have the highest fitness (lifetime reproduction and survival of young) that such an animal can possibly have in its environment. This is the result of earlier natural selection in this environment. A disturbance of this harmony is likely to reduce wellbeing. We humans can never actually experience the feelings of other animals. What we can say, however, is that disturbed harmony often leads

to visible symptoms indicating physiological and behavioural efforts by the organism to re-establish harmony. It is reasonable to believe that one accompanying consequence will be that the animal feels unwell.

The Two Components of Adaptation

In 1982 I discussed how animals adapt to their environments.[69] In brief, there are two distinct components in the process. The first concerns how individual animals adjust during their own lifetimes (a learning process); the second concerns which among the developing phenotypes of the various individual animals remain in the populations and survive and reproduce. This second component reflects the genetic adaptation resulting from natural selection.

Constant environments, or predictably recurring stimuli that always require a uniform response, select for rapid, often invariable instinctive responses. These include 'fear of heights' in chicks of cliff-nesting birds. Other examples are the reaction to gravity and all the reflexes that come into play when animals fall, the suckling response of all mammalian babies, and the freezing and fleeing responses of prey animals.

Rapid responses, not involving much brain activity, require relatively few metabolic resources. Hence, much behaviour in many species is controlled in this way. Early ethologists, such as Konrad Lorenz (who studied the behaviour of wild animals), recognised correctly that these instinctive behaviours were part of the genetic adaptation of animals to their environment.

In contrast, variable, unpredictable environments favour the selection of a flexible path of development and much more variable behaviour as adults. In this case, learning by experience (say by conditioning, learning to react to recurring stimuli) by each individual becomes important.

Of course, if individual learning by copying from others is efficient, mechanisms facilitating copying of behaviour from others will be favoured. Andrew McLean suggested that, when it is efficient for animals to have higher mental abilities, the environment will select whatever mental abilities are necessary and an appropriate genetic response will occur.[70] This has happened in relation to cooperative hunting, in complex animal societies, and in the development of mental maps to handle challenging environments. We must remember, though, that brains are expensive tissues requiring many metabolic resources. For brains to grow, the demand for higher mental abilities must be strong and continuing. Helmut Hemmer found that domestication in many animals has typically led to decreased brain sizes compared with those of their wild progenitors.[71] This emphasises the continuing need for selection of mental abilities if those abilities are not to be lost and brains are not to decrease in size. Thus, environments of different degrees of variability select for different degrees of learning ability. Complex, unpredictable environmental niches select for greater complexity of behavioural responses than do simpler and more predictable environments.

Adjustment to New Environments

When animals are placed in new environments, individuals of some species can adapt their behaviour rapidly by learning and conditioning. If each individual can adjust its own behaviour flexibly, wellbeing need not be compromised and there will be no strong selection for genetic change in the population. Where individuals cannot change their phenotype flexibly, successful adaptation must involve genetic changes. Those individuals whose genetic settings allow them to cope best with the new environment will be favoured even if their welfare is likely to be less than optimum until selection responses have again harmonised developmental paths with the stimuli of the new environment.

Domestication is an evolutionary process in which animals have adjusted genetically quite rapidly to the different environments provided by humans for their animals. This process is still continuing whenever animals are put into changed environments as happens, for example, when animal production is intensified.

Problems with Poorly Adapted Animals

Reduced wellbeing is likely to occur among poorly adapted animals in recently changed environments. Animal keepers should learn to identify situations in which animals are not adapted to their environments. The goal is to remove mismatches between the biological settings of animals and the stimulation and resources they receive from their environment. Personally, I look for various symptoms indicating reduced welfare.

Such symptoms include low fitness, indicated by low reproduction and high mortalities. Wounds and scars on animals are other signs, as are odd behaviours, including stereotypical or repetitive behaviour, such as an elephant swaying to and fro in a patently inadequately stimulating enclosure. However, stereotypical behaviour is not simple to interpret; individual animals may be using stereotypical behaviour as a means of coping with their environment. What is certain, however, is that stereotypical behaviour would not develop if the match between environmental stimulation and genetic settings for responses in the animal were harmonious.

Picture in your mind a wolf pacing around the perimeter of its zoo enclosure. Wolves have been selected to cover much ground in search and capture of prey. Their motivation for movement is high and cannot be reduced quickly. Hence a wolf in a zoo is driven by its internally set motivation to do a lot of 'stereotypic' movement around the perimeter of its enclosure. This seems pointless to us, yet pacing might be precisely that which keeps the individual wolf healthy. If he also has the opportunity to mate, he may reproduce well. So, this wolf itself may not be suffering in any way.

Nevertheless, he is not adapted to enclosures, even though his 'stereotypy' allows him to cope.

Removing Problems of Mismatch

Genetic adaptation, where possible, is one sure but slow way to eliminate mismatch. In most situations it is important not to prevent it, but rather to allow genetic adaptation to take place. However, it is unrealistic to wait for genetic adaptation to solve an existing problem of reduced wellbeing, one that is of concern right now. On the other hand, animals such as laboratory mice have already adapted completely, genetically, to laboratory cages in controlled laboratory environments. This is a result of natural selection as well as any artificial selection of the past 100 years of life in laboratory cages. Scientists did not deliberately select for adaptation. It happened quite by itself because we always bred from the progeny of those animals that reproduced well in cages. As a result, laboratory mice have vastly different instinctive behavioural settings from those of wild mice. Their motivational levels and threshold stimuli for escaping behaviours such as jumping and fleeing have changed. When we compare laboratory and wild mice we see different frequencies of the same fixed action patterns. It would be just as wrong to 'liberate' laboratory mice from their cages as it would be to 'imprison' wild jungle fowl in commercial egg-layer cages.

Over recent years, zoos have greatly changed the way in which animals are kept. The aim has been to make the environment as natural as possible for the species involved. The efforts have often been rewarded by successful breeding where this had not occurred before. This is evidence that harmony between genetic settings of animals and stimulation by the changed environment has been improved; at least to the point at which mating and birth of offspring can take place.

Environmental Enrichment

People concerned with animal welfare have been keen to enrich the environments of domestic, zoo and laboratory animals. This pursuit can include providing toys, possibilities for climbing and exercising generally, as well as stimulating challenges for the animals to obtain their food. There has been research in environmental enrichment, and people feel good that welfare of the animals is being improved. However, some important questions must be clearly stated and answered before we go on. Why are we keeping the animals? Is it for entertainment for the public, for study, for medical research related to human health, or for conservation to prevent extinction? Will we allow genetic change to occur or not? Each of the above situations may have a different answer as to whether the animals should be allowed to change genetically or whether they are to be conserved exactly as they were in their earlier (presumably wild) state.

Animals kept in zoos for the purpose of species conservation should be managed in such a way that they remain truly representative of their wild species. Genetic changes should be prevented and, as far as is possible, natural environments should be provided, even if, for their temporary survival, we have to hold them in small spaces. Each animal with complex, flexible behaviour can successfully adapt to most environments, and selection pressure to change their genotypes need not be strong. However, simple environments do not apply any selection pressure which would lead to the maintenance of complex mental abilities. The heavy demand brain tissues place on metabolic resources inevitably leads to loss of complex behavioural abilities unless the animals are stimulated to develop these abilities. Therefore, their environmental enrichment should be designed to force the animals to use their higher mental abilities and their many behavioural responses in a variety of different ways. Clearly, environmental enrichment that is varied, unpredictable and presents real mental challenges to animals is important for

primates being kept in zoos. This is particularly so if they are a reservoir of animals destined for release into the wild. Similarly, primates being studied for their complex behavioural abilities, or the physiology underlying these, should also be provided with appropriately complex and varied environmental enrichment.

The brains of domestic animals have, relative to body size, become smaller than those of animals in related wild species. Dogs selected for 'showing' have had a similar reduction of working abilities, simply because they were selected for appearance rather than for their working abilities. The long-time successful breeder of Australian working Kelpie sheepdogs, Tony Parsons, wrote in his book:

> *By the 1940s … the show-bred Kelpies had deteriorated rather badly in working ability. … That the best looking dog might be the poorest worker has seldom concerned the show breeder of Kelpies, who is seeking a dog that will win in the show ring. … It is not considered to be very important if an award-winning dog at Sydney or Melbourne Royal Show … is a poor worker or not a worker at all.*[72]

For rats, mice and rabbits kept for physiological or biochemical studies of metabolism or diseases, I see no need for the extremely complex environmental enrichment that will prevent adaptation towards simpler behaviours. Environmental enrichment may well be useful here also, but its purpose in this case is to maintain the general health of the animals, just as human office workers in sedentary jobs use gyms to keep themselves physically fit. This will be achieved even with simple regimes of environmental enrichment. It is likely to be beneficial in this case if the behavioural responses of the animals involved become adapted to simpler laboratory environments in which the animals are happier and less costly to maintain.

Wellbeing is Achieved in Animals Adapted to Their Environment

Animal wellbeing should be seen in the context of animals adapting to their environments. Well-adapted animals must be assumed to have as high a degree of welfare as is possible in their environment.

Two distinct components are involved in the process of adaptation. These are changes (behavioural, physiological) that occur during the animal's life, and longer-term, evolutionary (genetic) changes.

Poorly adapted animals suffer problems of various kinds and may well suffer reduced wellbeing. The goal of animal keepers should be to create environments that harmonise with the biological settings of animals so that appropriate behaviour continues to keep the animal healthy.

Chapter 14

Back to Darwin

Evolution is driven by environmental change, and genes allow affected species to make the phenotypic changes needed to cope with the new environment. This chapter presents more examples to reinforce this paradigm.

The New Understanding of Biology: A Recycled Paradigm

Earlier I noted that Darwin's original thesis remains true to this day: the environment (nature) selects those organisms most suited to its challenges. This selection process induces changes favouring 'better' traits because there is a genetic mechanism, first recognised by Mendel, that means that progeny of selected parents are more likely to express the 'better' traits than are progeny of animals that were not selected.

By the end of the 20th century, the mechanism of biological heredity (DNA, genes and chromosomes) was elucidated with spectacular success. Scientists can now manipulate the genetic material itself and transfer genetic material from species to species. The downside of this major achievement is that biologists in many specialised fields have become so fascinated by genes and DNA that the wider world in which biological changes take place has faded from their view.

Yet out there, in the real world, the natural selection recognised by Darwin continues to control evolution in the wild, and influences everything we do with our domestic animals and plants. These effects are powerful, and if we shut our eyes to this wider world, we can only blame ourselves for misunderstanding biology.

I emphasise the continuing effects of natural selection on animals, both wild and domestic. Variant theories of evolution, apparently in conflict with Darwin, arose because neo-Darwinists thought genes, not organisms, were being selected in the course of evolution. We now know that the neutral theory applies only to genetic material with no effect on phenotypes. Those of us interested in whole organisms in the real world need not concern ourselves with it.

Palaeontologists quite rightly saw that evolution is not slow, gradual and continuous. In contrast, we see long periods of tranquillity with no changes interspersed by short periods of change with extinctions and rapid bursts of evolution of surviving species.

I show that when you understand how natural selection works, punctuated evolution (in bursts) is exactly what Darwin's natural selection must produce. Natural selection cannot achieve more than to adapt organisms perfectly to their environment. Adapted animals cannot improve unless the environment improves. Thus, during tranquil periods, all adapted species are actively held by natural selection to their optimum forms in their respective environmental niches.

What my book gives us is a new way (though recycled from Darwin) of seeing evolution in the big picture of life. This picture is consistent across the many specialised fields of biology. The clue linking all these fields is the (formerly obvious) need for organisms to obtain metabolic resources and, conversely, not to waste metabolic resources on unnecessary adaptations.

Natural Selection is Naturally Efficient

I'll illustrate this consistency with two simple examples from very distinct fields: super-effective stimuli for ground-nesting birds and vitamins for humans.

The appeal of bigger eggs: Introductory books on animal behaviour often describe the following example of instinctive behaviour: birds that nest on the ground, such as seashore birds and geese, have an egg-retrieval response. An egg may end up outside the nest accidentally or because it is put there by an experimenter. The brooding bird then stretches out its neck and rolls the egg back into the nest. If there are two eggs outside the nest, the brooding bird shows a strong preference for rolling in the bigger egg. This preference extends to eggs that are very much bigger than any normal eggs ('super-effective stimuli'). Why does the bird not recognise that the outsize egg cannot be its own?

The answer is that birds do not reason like we do. Natural selection on fitness has given these birds a preference for big eggs because little eggs often do not produce viable young. This simple mechanism achieves all that is necessary. As an egg larger than those the bird can produce never lies outside the nest in nature (unless an experimenter puts it there), there has never been a need for the bird to evolve a mechanism that discriminates against large eggs. In nature, eggs will not get larger than an optimum size because natural selection never produces unnecessary strategies.

Vitamins in our diet: Many vitamins (A, B, C and so on) are nutrients that human bodies cannot make by themselves, and which therefore need to be obtained from our diet. Many other species can make these compounds themselves. Given that our own body readily makes many other compounds, why does it not make all the chemicals that we need, thus freeing us from our dependence on the environment? It is because we adapted to environments in which these vitamins were freely available in the foods we ate.

Again, natural selection has not created metabolic mechanisms when they were not needed. If our ancestors had used resources to make all possible vitamins in their own bodies, their fitness would have been lower, and we quite possibly would not be here. You will be able to think of many other biological peculiarities that

make sense in terms of resources required or not required in environments to which organisms have adapted.

Successful Phenotypes are Efficient

Curiously, Darwin and the original geneticists already accepted this paradigm as obvious. All living individuals (phenotypes) are subject to limitations imposed by the resources available in their particular environments. Successful phenotypes are those that balance available resources most efficiently so that each trait contributes to the most efficient total phenotype. It is only when geneticists or animal breeders focus on individual genes, or individual traits, that the resulting theory leaves out environmental limitation of whole organisms. The metaphor of gene selection, introduced to help explain evolution, fails to include the important detail that nature selects those organisms that make the best-balanced use of existing resources.

Richard Dawkins' 'The Ancestor's Tale'

Under the heading 'The Polypifer's Tale', Dawkins discusses ecological communities such as coral reefs or rainforests. He wrote:

> *There is balance in a rainforest, structure in a reef, an elegant meshing of parts that recalls co-adaptation within an animal body. In neither case is the balanced unit favoured as a unit by Darwinian selection. In both cases the balance comes about through selection at a lower level. Selection doesn't favour a harmonious whole. Instead, harmonious parts flourish in the presence of each other, and the illusion of a whole emerges.*[73]

Two paragraphs supporting harmonious species flourishing in successful communities follow. Then this following paragraph closes the chapter:

> *What I want to add to that familiar point is that the process is mirrored at the level of every species' 'own' genes. The entire*

> *genome of a polar bear or a penguin, of a caiman or a guanaco, is an ecological community of genes that flourish in each other's presence. The immediate arena of this flourishing is the interior of an individual's cells. But the long-term arena is the gene pool of the species. Given sexual reproduction, the gene pool is the habitat of every gene as it is recopied down the generations.*[74]

I interpret this last paragraph as follows: Dawkins is still using his metaphor that natural selection is at the level of genes in the total pool. He still sees genes as the most important factors in evolution. To Dawkins, the total genome of each species is an 'ecological community of genes that flourish in each other's presence'. This is a lovely poetic metaphor which would also be true if that important level of the metaphor, the individual organism, were recognised as the item being selected. In my opinion, Dawkins slips unnecessarily to the level of genes in gene pools rather than staying with whole organisms, for which balanced use of resources is vital.

Can you visualise how selection pressure can be exerted on two different individual genes in the gene pool without needing to select whole organisms? I can't. In contrast, it is crystal clear that phenotypically unbalanced individual organisms cannot match the success of those balanced individuals that succeed in raising many young in their particular environmental niche.

A Comment on Genomes

In the year 2000 and in early 2001, the (partial) completion of the draft and the publication of the whole human genome, respectively, were heralded as the most important events that had ever occurred in biology. Great promise was held out for medicine. We were told that humans have between 27,000 and 40,000 genes. This relatively low number was unexpected. Because humans are so complex, researchers had expected to find up to 100,000 genes. The discrepancy caused a flurry of comment along the following lines[75]:

> *It's not how many genes you've got, it's what you do with them that counts. …*
>
> *For example, genes usually come in segments. By "splicing out" some segments of the RNA templates for proteins, or using one segment rather than another, a single gene can yield many different proteins. The same gene can be used to make one protein in, say, muscle, and another in the brain. Up to 60 per cent of our genes produce these "splice variants".*

All explanations of the complexity of humans were at the level of the genes and the immediate effects that individual genes may have. The fuss made about the human genome was a celebration of the complete focus on genes to the exclusion of everything else. However, the relatively low number of genes shocked people into thinking about where the complexity of whole organisms, particularly humans, comes from.

When we lift our eyes from the level of genes to the level of organisms in their environment, we can see that organisms have adapted to limiting environments. They use available resources as efficiently as possible. They achieve this by accumulating genetic instructions and physiological and behavioural feedback mechanisms that control optimum lifetime patterns of development, growth, size, reproduction and nurturing of young. Any single gene is likely to have just small effects, probably in several physiological traits, but always in a way that harmonises with the effects of all other genes. The same gene in different species may well be harmonising in different ways and with different genes in different species.

If organisms are to change to meet a new environmental challenge, then selection for the now-required phenotype will put pressure on all the physiological mechanisms that must change. To survive, all those genes that have to change their effects to achieve the phenotypic result will change as required. We need to accept that

such changes are occurring, even if we don't know the details of precisely which individual alleles are being selected.

So where is the knowledge of the human genome going to get us? Probably well short of what geneticists and the public thought in 2001. Useful effects may be achieved only after much more research has elucidated the 'complexity' now drawn to our attention because we have relatively so few genes. I sincerely wish that medical researchers can use their knowledge of genes to find cures for specific diseases; I am merely pointing to likely difficulties.

The main, completely overriding difficulty is that any genetic material that is to be altered or added to existing DNA, must work in harmony with all the other processes that produce the already existing optimum lifetime patterns. When you think only about individual genes and their effects, you are unlikely to appreciate the importance of this harmony. An animal in which genetic material has been artificially altered is like an individual in which a large mutation has occurred. We know that individuals with large mutations are unlikely to allocate resources as efficiently as those following previously optimised pathways. The same is true for drugs given to patients to overcome deficiencies caused by particular genetic alleles. In many cases, unexpected side effects arise after drugs have been taken, requiring further medication to contain the deleterious side effects.

Michael Rutter, in his book 'Genes and Behaviour' concerning molecular biology in the service of medicine, is very much aware that the study of individual genes affecting specific medical problems is still in its infancy.[76] The amount of information needed to understand how many genes act together to create, for example, a symptom of mental illness in humans, is likely to be huge. It is likely to require many more years of medical biotechnology. Current molecular biology research works from the bottom up. Details of the action of many individual genes are being put together to in an attempt to understand a complex whole. I believe

that the top-down view provided by the resource allocation theory, of lifetime paths of whole animals being constrained by limiting resources, gives a better framework for understanding how different genes must work together to produce normal development and behaviour.

'Group Selection' Picks up Traits Unavailable at the Individual Level

The book 'Unto Others' by Sober and Wilson drew my attention to an example in which selection of animals in groups achieved further commercial gains after traditional selection on the basis of individuals had reached a plateau.[77] Sober and Wilson use the example to demonstrate that group selection can be successful, as they argue their case for group selection. However, the example also illustrates my point that one gets only what one selects for.

Group selection is selection operating at the level of groups of organisms, not the individual (or gene). Generally, selective pressure at this level (between groups) is weaker than selective pressure between individuals, but successful group selection has been demonstrated in a few cases.

Bill Muir, in a paper published in 1995, described applying group selection to egg-laying poultry being kept in groups in wire cages.[78] In modern egg production, keeping groups of hens in cages has economic advantages due to increased efficiency in the handling of large numbers of birds and eggs in the available space. However, when hens are selected only on their individual egg-laying records, there is no way in which selection can capture any benefits that may be available to egg layers if, as a group, their behaviour is congenial to social harmony. When selection was applied on the basis of the total production of groups in cages, a substantial increase in production was achieved. This is a beautiful example of successful selection on phenotypic results in an environment, which allowed behavioural traits contributing to group harmony to express themselves.

Notice that this result was achieved without any knowledge of which behaviours or genes were involved. It was selection based on an outcome and incorporated all the changes in phenotypes that were necessary to achieve the outcome. Behaviours are just as dependent on genes as is egg laying. When the selection environment was allowed to include congenial behaviours, whatever was responsible for congenial social behaviours among hens was picked up without compromising egg production. This is how natural selection works. It always selects on outcomes, within the available environment.

Nature Selects on Outcomes

Sober and Wilson's book has left me wondering whether I have been clear enough in what I have said about evolution, the evolutionary synthesis, and what Darwin had written. Let me therefore say clearly how I understand evolution to work.

Sober and Wilson wrote about 'altruism'. They presented a convincing argument that 'group selection', as in the case of hens laying eggs in group cages, and in humans, is much more important in evolution than was thought by geneticists and evolutionists. In the literature on evolution, the concept of nature selecting genes rather than whole organisms has prevailed in the last quarter of the 20th century and beyond. Selection of groups was even less popular than selection of whole individuals.

The second part of their book discusses 'psychological altruism', where psychologists look at why humans are often more altruistic in social groups than they are as individuals. Like many others, psychologists take for granted that in evolution there are *ultimate goals*, for example the beneficial behaviour acting as an evolutionary adaptation, and *proximate mechanisms*, for example the motivation of altruism, which ensures that the ultimate adaptation comes about in the phenotype.

The following sentence from the book's last chapter illustrates what I wish to tell you:

> *All adaptations require proximate mechanisms that actually cause those adaptations to be expressed in the lifetimes of individuals.*[79]

Evolutionary considerations therefore focus on finding possible proximate mechanisms which could explain how natural selection came to achieve the results seen in evolution. If one finds the mechanism, then an evolutionary explanation for phenotypes becomes acceptable.

Let me say it quite clearly: The emphasis must be the other way around! Nature selects whole organisms. It selects on what happens to organisms, on outcomes. And the outcomes are offspring breeding in future generations. If the outcome is improving, it does not matter whether we have found a possible proximate mechanism or not.

If phenotypes have available to them the resources that will enable them to become even better (that is, evolutionarily fitter), they will become better. Evolution, the achievement of the best outcome, will utilise any available mechanism. The evolutionary improvement will be made even if we do not yet know how the improvement has occurred.

Evolution Explained: The Resource Allocation Paradigm

Eldredge and Gould are correct when they recognise that evolution has occurred in bursts, often among many kinds of life at the same time, separated by long periods of tranquillity when fossils remain unchanged. The major cause of these bursts of evolution is the extinctions produced at the end of periods of tranquillity, usually caused by a cosmic, geological or climatic catastrophe. The resources freed by extinctions allow surviving

organisms to evolve further. Now come the new, original insights of this book.

The resource allocation paradigm shows that abundant environmental resources facilitate evolutionary change, and that limited environmental resources lead to evolutionary stability.

Fossils remain unchanged for long periods because, after natural selection has achieved the most efficient phenotype for each niche, neither 'better' nor 'worse' phenotypes can exist in any niche until the environment changes, or until a rare event such as development of human cognition occurs which allows even more efficient use of the same present resources. The organisms being selected follow tightly controlled developmental paths that harmonise lifetime phenotypes with the predictable challenges of the environment. This understanding follows directly from Darwin's central idea that nature selects the organisms that are most adapted to any given environmental niche. It also requires the recognition of the need of the living organisms for appropriate environmental resources.

Depending on the amounts and variety of resources made available when an extinction occurs, a surviving population can radiate into a limited range of niches, producing, say, new species or families, or a larger range of niches, producing whole new orders.

When dinosaurs became extinct, mammals and birds replaced them, the latter evolving from small dinosaurs. The original surviving mammal progenitors were able to replace dinosaurs in so many niches that a whole new mammalian fauna appeared, ranging on land across herbivores, carnivores, omnivores and scavengers. Some variants found niches in oceans (for example, whales), while others (such as bats) developed wings and took to the air. Clearly the original mammals, presumably due to their control of body temperature, had an advantage over reptiles and amphibians in being able to take advantage of many available niches. The initial radiation of mammals is 'unusually rapid' only when compared

with the later tranquillity that occurs when all individual niches prevent further evolutionary changes.

Another consequence of the resource allocation paradigm is that we will have to rethink the method of measuring elapsed evolutionary time when estimating relatedness among species. The rate of change in evolution results from calamities causing extinctions. This rate of change is far from constant, except in neutral genes with no effect on fitness. Dating the ages of fossils from the rocks in which they are found seems to me more reliable than estimating time according to differences in the fossils' morphology or their genes.

Without genes and their duplication mechanism there would be no complex life. Further, genes also prevent selected phenotypes from dissipating again. Nevertheless, the explanations of evolution we have considered did not require any detailed understanding of genes. Will biological and medical scientists again look seriously at animals and people, rather than mainly at their genes? Will animal breeders understand that they cannot seek continued improvement in their livestock without simultaneously increasing the resources available to their animals, or otherwise face problems with animal health, productivity and longevity? Will geneticists pay more than lip service to the environment in their equations and look to the whole animal to tell them how successful their selection strategies have been?

If so, we should at least offer a smile in the direction of the picture of Charles Darwin and acknowledge that he gave us the big picture of life, the large frame within which we were able to learn so much about life's details. This picture, although now refined, remains as true as it always was.

The environment selects the fittest individuals in every species and in every environmental niche exploited by the species. These selected individuals allocate metabolic resources optimally into all traits that matter in the current environmental niche.

Environmental changes drive evolution. Genetic alleles and gene combinations are continually changing. These continuous changes result mainly from sexual recombination, a feature of all complex organisms. It, together with genetic mutations, supplies in each local area the phenotypes that will quickly become adapted. This interaction between the environment and the organisms produced by genes describes all that we need to understand why and how evolution has worked.

To end this book let us look once more at the big picture. It gives us a better understanding of life than we can get from a study of DNA and particular genes. The big picture of biology shows how various forms of life disappear when they can no longer adapt to a fast-changing environment, even with the continual mixing of genes that is produced by sexual reproduction, while other forms thrive.

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