Adaptive Behaviour

Understanding the Human Animal

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2012

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To my parents, Dolores Cruz Ruiz and Manuel Soler Serrano.

Foreword

According to a Gallup poll taken in 2009 on the birthday of Charles Darwin, fewer than 40 percent of my fellow Americans accept the reality of evolution. The situation in Spain is somewhat similar, although here slightly more than 60 percent of the population “believes in” evolution. Of course, this means that more than 30 percent of all Spaniards do not think that evolution by natural selection has occurred, and even this is a discouraging figure.

Moreover, many of those in Spain and the United States who say that they believe in evolution do not really have a sufficient understanding of Darwinian theory, much less an appreciation of the way in which modern biologists use the theory to conduct their research. Manolo Soler has recognized this reality, a point that led him to write this magnificent book to help members of the general public to advance their comprehension of a scientific concept of great importance. Dr. Soler is perfectly suited to undertake this task because he has utilized Darwinian theory as a foundation for his elegant studies of animal behavior. He is part of a group of Spanish ornithologists who have experienced great success in their investigations of the adaptive value of bird behavior. As a result, Dr. Soler has the necessary background with which to explain the value of evolutionary theory for scientific research.

As Dr. Soler explains, Darwinian theory has two components. One part is the theory of natural selection, which helps provide a way for biologists to identify the adaptive value or function of the characteristics of living things that interest them. By “function”, we scientists know, thanks to Darwin, that we are talking about the role the trait plays in enabling individuals to reproduce successfully. The first part of this book provides an accessible account of this point with many examples drawn from fascinating recent studies conducted by biologists in Spain, Europe and the United States of America. All of these top researchers have made important discoveries that were dependent upon an understanding of natural selection theory.

This theory guides the investigator when he or she is trying to develop hypotheses (explanations) for some intriguing aspect of the natural world. A wonderful example of science in action that you will encounter in this book involves the behavior of the black wheatear, whose males carry many rocks to places where their mates will build their nests. Why do the males behave this way? The first step toward a solution is to develop one or several hypotheses on the possible reproductive benefit of this characteristic. Manolo Soler and his colleagues have developed several such ideas based on a Darwinian foundation. They have then evaluated each possible adaptive function of this strange behavior using each hypothesis to produce testable predictions. The research team has subsequently hunted for the evidence for or against the predictions they have in hand and in this manner, they reached the conclusion that the males were demonstrating their physical condition (a trait related to their capacity to bring food eventually to their nestlings). The females use the information they receive about male parental quality to adjust their reproductive investment in eggs. Thus the rock-carrying males benefit by getting more eggs to fertilize if they can demonstrate that they are able to fully provision their youngsters when these hatch from the eggs in a nest. Without an evolutionary foundation, the biologists involved and the rest of us would have not understood why male black wheatears behave the way they do.

The same applies to many other puzzles explored in the pages of this book. Why do so many animals reproduce sexually instead of asexually? Why are the eggs of any number of bird species bright blue? Why do females and males of many species that appear to be monogamous actually mate on the side with their neighbors? Why are altruistic acts extremely rare in the natural world? Manolo Soler presents the most recent scientific answers to these questions and many more.

The author also demonstrates the utility, indeed the necessity, of an evolutionary focus if we are going to really understand the behavior of human beings. In the last few decades, some biologists and psychologists have made tremendous progress in applying Darwinian theory to key elements of human behavior. In this book, you will encounter a clear and convincing summary of this work. After having read the evidence, I believe that you will conclude that we can learn much about the adaptive value of our actions if we accept the possibility that we, like the black wheatear and all other animal species, have evolved under the influence of natural selection.

There is another component to Darwinian theory and this element deals with "descent with modification." Darwin knew that there is a long history behind each and every aspect of living things. We need to take this history into account if we wish to construct a complete picture of the behavior of all animals, including *Homo sapiens*. We can gain a part of this picture if we realize that the adaptive characteristics of living things have changed little by little over time from a distant starting point. According to Darwin and his fellow evolutionists, each modern species has ancestors that are now extinct. Some of these ancestral species gave rise to a cluster of descendent species alive today and in these cases, we can predict that these organisms will exhibit similar attributes as a result of having inherited them from a common ancestor no long with us.

The last chapters of this book present the results of comparative studies of closely species, studies done to reconstruct the history of complex traits in various animals, including our own species. Just as Darwin and others have predicted, animals derived from a common ancestor sometimes have maintained elements exhibited by this ancient species. In certain primate species closely related to us we can see traces of the species that preceded us and that endowed us with certain key attributes. Thanks to this point, we can put to the test ideas about such things as the history of the capacity for language and the cognitive aptitude of our own species.

Readers of this book will learn that the evolutionary theories of Darwin even today have great significance not only for persons who study birds, insects and reptiles but also for those researchers that search for answers to questions about the function and history of our own species' behavior. Evolutionary biology is not a discipline of the past but a vibrant, useful and immensely productive field of research today. We thank Manolo Soler for having written a comprehensive account that demonstrates the power and modernity of the ideas of Charles Darwin.

John Alcock
Arizona State University

Preface

I took on the task of writing this book, the second in a series sponsored by the Spanish Evolutionary Biology Society (Sociedad Espanola de Biolog^a Evolutiva, SESBE), early in 2008. After delivering eighteen lectures on 'Ethology' at Granada University, I decided the time was opportune to write a book on animal behaviour based on my approach to the subject in my classes. In these, where I try to encourage students to think and participate, I pose questions on adaptation in animal behaviour which include examples from the human species. I noticed from the start that posing questions on human behaviour led to an immediate increase in students' interest and in their disposition to take part in class discussions. Nevertheless, for various and complex reasons which I consider in Chapter 1, ethology texts do not usually cover human behaviour - though some of them include one isolated chapter about this subject. For these reasons I decided to give the human species particular prominence in this book, which considers the principal themes of animal behaviour. Furthermore, this decision was supported by the enormous advances seen in recent years in relevant fields such as molecular biology, evolutionary psychology and neurobiology. The sequencing of the genome of various species and the impressive development of evolutionary psychology, together with the identification of numerous genes, neural circuits and hormones responsible for many behaviours, have very clearly shown that the fundamentals of human behaviour do not differ from those of other animals.

Eleven themes comprise this book. After justifying in Chapter 1 the inclusion of the human species in a book on animal behaviour, Chapter 2 covers fundamentals such as the scientific method and the ‘theory of evolution by natural selection’, which underpins the scientific study of behaviour. Chapter 3 summarises the history of ethology and gives an overview of current trends in this science. The three following chapters (4-6) deal with reproductive behaviour, following the logical sequence of the reproductive process: finding a mate, fertilisation and, in species with parental care, looking after the young in order to increase their chances of survival. Chapter 7 studies gregariousness in individuals that live in more or less permanent groups, which at times form very complex societies, as seen in social insects and in the human species. Groups and societies in all species, including our own, persist as a consequence of the benefits which individuals obtain through living together and helping each other. One form of helpful behaviour is known as altruism, the theme of Chapter 8. Chapter 9 studies the relationships between individuals of different species which, although sometimes resulting in benefits to both parties, most often serve the needs of one of them. Chapter 10 deals with the fascinating subject of animal communication leading to an analysis of the no less compelling subject of human language. Finally, Chapter 11 deals with the study of cognitive skills, dealing with topics such as problem-solving ability, planning for the future and tool use. In addition, this final chapter considers more rarefied matters such as culture, conscience, emotions, sense of justice, morality and religion.

The layout of all chapters is similar. Initially I present what the science of ethology has revealed on the subject in other animals followed by its application to human beings. Often, and as I like to do during my classes to assist my students’ comprehension, I start with examples that illuminate the theoretical basis of an issue. With respect to the numerous studies described in the book, those which are discussed in detail have not been taken from other works but are based on original sources, often recently published novel research.

All chapters are designed with a view to being entirely comprehensible without having to have read the preceding ones, allowing those who are especially interested in particular subjects to start the book where they please. With this in mind, scientific names are given the first time a species is mentioned in every chapter. Similarly, theories and scientific terms are cited in inverted commas on first mention in each chapter. Although I am aware that scientific names and bibliographical references interrupt the flow of the text I have decided to include them since they are indispensable to those readers seeking a deeper understanding of the subjects treated. I expect that readers who are less interested in the more scientific aspects will soon get used to ignoring these insertions, which always appear in parentheses. In any event, I believe that the scientific name of a species may be very useful for enquiring readers since it allows easy search for images or additional information on any example of particular interest of them. Thus, searching for the scientific name on Google and clicking on ‘Images’ may reveal impressive photographs of many of the described behaviours. Readers are, for example, invited to do an image search for the parasitic louse *Cymothoa exigua* that destroys the tongue of its fish host and settles in its place, or the marine racing stripe flatworms *Pseudoceros bifurcus*, which engage in fencing combat with their enormous erect penises, each attempting to penetrate the other. You may also wish to search for images of *Pan paniscus*, which will lead to video images of the frontal copulation in which bonobos indulge.

Separate text boxes are used to present the most specialised theoretical knowledge. These are independent of the text and are not necessary for understanding the chapters. They need concern only those interested in acquiring more specialised knowledge.

Acknowledgements

This book is not just the result of having a year in which to write it but is instead the fruit of my entire professional career, during which I have been privileged to learn what so many scientists have previously discovered. I am indebted to numerous persons, institutions and, indeed, learning experiences for their assistance and for their influence on me during all this time. I will try to summarise them briefly.

From a professional standpoint, and as a small tribute to Darwin in this year 2009, in which we commemorate the 200th anniversary of his birth and the 150th anniversary of the publication of his famous book ‘*On the Origin of Species*’, I first want to thank him, Charles Darwin, since his theory on evolution by natural selection converted biology into a true science and blazed a path for successive generations of biologists. It is no coincidence that both the first and the final references cited in this book are works by Darwin.

I have enjoyed and learnt much from conversations on science with many colleagues and scientist friends, both Spanish and foreign. I would not wish to omit anyone but this paragraph would be excessively long if I were to mention them all, so I will confine myself to the two persons to whom I feel especially indebted, to the extent that I consider them my mentors who enabled my education as a evolutionary biologist: Anders M0ller and Juan Moreno.

I am grateful to past and present members of my research group for their readiness to collaborate and to assist with general subjects that were not always their particular priority. This willingness has helped new recruits to the group and has made my own workload lighter. I particularly want to thank my brother Juan, the first member of my group, my ‘helper number one’ as I used to call him in the days when he preferred to accompany me into the field to inspect jackdaw nests instead of attending classes at his college. It is many years now since he started working independently and he now heads his own research group (although we continue to collaborate frequently) but I want to express my enormous gratitude to him. My professional development would have been much slower without his help and collaboration.

My thanks too to my ethology students, especially to those who enjoyed it, who were the majority (the course is optional and so most of those who choose to attend do so because they are interested in the material). The interest and enthusiasm which they showed during my lectures made my work more enjoyable. I was always fascinated by research work but until 1990, when I began to teach the subject etology, I never suspected that I would enjoy teaching so much.

With respect to this book, many people have read some of the chapters and their suggestions have helped to improve the text. They have included biologists and professional researchers such as Vittorio Baglione, Daniela Canestrari, Juan Carranza, Laureano Castro, Adolfo Cordero, Florentino de Lope, Manuel Martin- Vivaldi, Santiago Merino, Jesus Mosterin. Andres Moya, Julio Sanjuan, Juan Carlos Senar, Eduardo Tejero and Alberto Tinaut. I have also shown chapters to some friends who lack specialist biological knowledge but are interested in the various topics. Their suggestions, above all, have helped me to improve the accessibility of certain paragraphs to readers without a specialist Charles Darwin, since his theory on evolution by natural background in biology: Juan Alonso, Manuel Amezcua, Mari Carmen Arroyo, Cecilio Casado, Susana Fuentes, Jose Carmelo Hernandez, Iluminada Jimenez, Eduardo Jimenez, Luis Muriel, David Nesbitt, Jose Parodi, Eva Prados, Antonio Robles, Maria del Mar Hernandez, Francisco Sanchez and Mari Carmen Soler. I particularly wish to thank the four persons who have read the entire book: John Alcock, Juan Moreno and Juan J. Soler, whose comments improved the content, and Clara Redondo, who helped to increase its readability.

With respect to this English version I am indebted to Ernest Garda who did good work in translating into English the original Spanish text, my friend Anders M0ller who has read all the chapters providing, as usual, clever suggestions, and especially to John Alcock for encouraging me to prepare this English version and for reading once again all the book offering lot of comments and suggestions that helped improve the book considerably.

From a personal standpoint, I must begin by thanking my village, Guadix, whose landscape of steep hills and gullies so fascinated me that my preferred adolescent pastime was going on excursions there with my friends. These field trips, along with my attraction to animals from my earliest days, confirmed my calling as a naturalist. Among those friends I especially am indebted to Cecilio, since, in addition to our enjoyment of rambling over the hills and gullies, we shared a great fascination with living things. I still recall his natural history encyclopedia, of four green, hardback volumes, from which we learnt so much as children. I want to thank all my friends of those now distant days of adolescence and youth, not only my walking companions but also those who did not accompany us, because together we established an atmosphere of cultural and intellectual involvement which proved most important to our development.

Of course, I must also thank those most important to me, my family. My parents, to whom I have dedicated this book, and my six brothers. Above all, to Teresa Ortiz Vazquez, my wife and the mother of my three children who, until her death in 2001, always gave me her help and unconditional support. I thank my children too for their understanding and patience with a scientist father who gives much time to his work. I especially thank David, the youngest, for his (usually) successful efforts to behave himself. Eva Prados Arjona has become part of my family during the past five years. She is my friend and companion and I am enormously grateful to her for having brought me the happiness and peace necessary for writing this book and, more than anything else, for having restored to me the joy of living.

Chapter 1. Should human behaviour be studied from a biological perspective?

1.1. Introduction

We humans have always been fascinated by the behaviour of other animals and we have had a close relationship with many animal species throughout history. Some have been our enemies, others our prey. Some have been our competitors and others, a few, our allies. Since time immemorial this close relationship has obliged us to know them well. For our ancestors, eating, as much as not being eaten, often depended on being aware of and being able to predict the behaviour of the other animals that shared their habitat. We have hated some species; others we have loved, but nearly always we have admired other animals, recognising that in some ways they are superior to ourselves. Some cultures have even idolised some animals and venerated them as gods.

Sometimes we have even regarded other animals as role models and not only in antiquity because this still happens today. We just have to observe (even if only via television documentaries) the dedication and perseverance of birds caring for a nest full of chicks, the great tenderness and affection with which mammal mothers care for their young, or the courage that individuals of many species display in risking, and even losing, their lives to save those of their companions. On occasions such as these we can be overwhelmed by emotion and attribute the purest and most sublime sentiments to animals such as these. I recall not long ago a group of people who were watching a TV documentary on elephants. The story told how a group of females with some young were migrating during a time of drought and scarcity. They were crossing a desert area in an apparent attempt to reach a more foodrich region. The star of the documentary was a tiny baby elephant that was in quite a weak state. After each stop its mother and the other females helped it to get up and pushed it so that it would resume walking. When the little one died, the group stayed by the dead infant and its mother for a considerable time. Eventually, all elephants apart from the mother resumed their trek once again. The mother, although she had not eaten for a long time, remained for two days, preventing the vultures from devouring the corpse. At the end of the documentary, a lady rose from her armchair wiping away her tears and said ‘that was more unbearable than a weepy soap opera’.

The elephants’ behaviour revealed in the documentary was not a confection of special effects. It was real. Infancy in elephants is very lengthy and the mother and the other females, who are also related to the young, really are extremely solicitous. People who saw the documentary said such things as ‘they feel it more than many people do’ or ‘they are better than many people’. By ‘better’ they clearly imply ‘better people’ and it is curious to hear elephants described as being better people than many real people!

We humans enjoy making comparisons of this sort. One need only spend a few minutes listening to someone talking about his or her pet. Sometimes the pet owners attribute moral virtues to them, as did the watchers of the elephant programme. Often too they are regarded as possessing the highest cognitive capacities. In any event, without paying much heed to owners' opinions of their pets, which tend to be very unscientific, we can ask ourselves 'is human behaviour very different from that of other animals?' In particular, since we have mentioned parental care, 'is the behaviour of a human mother so different from that of any other type of female mammal who is caring for her young?' Surely not, fundamentally. The preoccupation with her offspring, the effort to provide it with all that it needs and the readiness to take any risk to save it from danger are common to mothers of all species in which there is parental care. Why then are there no books that treat human behaviour and the behaviour of nonhuman animals similarly?

That is the principal objective of this book, to tackle the study of human behaviour and that of other animals simultaneously and with the same approach. My intention, however, is not just to describe behaviours, but also to try to understand why they arise, by making use of the only theoretical framework that makes this possible: Charles Darwin's 'theory of evolution by natural selection' (Darwin 1859). There is an important hereditary component to behaviour and it is the outcome of evolution. Evolutionary theory allows us to apply the scientific method, that is to say to suggest hypotheses and put their predictions to the test to see whether or not they are fulfilled (see Chapter 2). This is the typical scientific focus of studies of animal behaviour. Furthermore, during recent decades it has also been applied with success to the study of human behaviour as much by evolutionary psychologists as by ethologists (biologists who concern themselves with animal behaviour).

I think it is important, indeed necessary, to justify from the start the validity of studying human behaviour as if we are an animal species with an evolutionary history, as this book does. Is it acceptable to study human behaviour together with that of other animals from the same biological perspective? Many philosophers, anthropologists, psychologists and sociologists would answer this question with a resounding 'No' for two main reasons, each in turn associated with two highly controversial matters (see Box 1.1 for a detailed explanation). Nevertheless, many biologists and also some professionals of the disciplines mentioned above would give an equally resounding 'Yes' to the same question. In this case the justification for their reply is simple and direct: for scientific reasons. On the one hand, we actually are animals, more specifically, a vertebrate, a mammal, a member of the order Primates. Behavioural researchers have demonstrated, without any doubt - as we shall be seeing throughout this book - that the fundamentals of human behaviour do not differ from those of all other animals. Furthermore, applying the evolutionary perspective of behavioural ecology to studies of human beings has produced a flood of ideas that have led to novel insights into our behaviour. This is reflected in a large number of scientific studies that have been published during the past twenty years and that have illuminated topics such as finding a partner and falling in love, conflict between partners, the sharing (or not) of parental responsibilities, social relationships, altruistic acts and many others make more sense when seen from the viewpoint of evolutionary biology. Although such a focus remains a minority view in some disciplines, such as anthropology, it is enjoying considerable success in others, especially in psychology. Here the science of evolutionary psychology has forged ahead. It is rooted in the study of the psychological mechanisms that underlie evolution as the discipline looks to find biological similarities that are common to all human beings.

Should human behaviour be studied from the same biological perspective as for all other animals?

NO

1. Because many social science professionals suppose that our culture, intelligence and consciousness have liberated us from our instincts (genetic predispositions) and hence from evolutionary forces. In contrast, biology rests on the theory of evolution by natural selection, which is based on genes (see Chapter 2).

Related controversial aspects

a. The uniqueness of human nature (which makes us different from other animals).

b. The nature-nurture debate (is human behaviour determined by genes or by the environment?).

2. Because many people believe that such a viewpoint implies justifying reprehensible behaviour. For example, they think that if violence is genetically determined, even if only partly, then murder is justifiable because it is something natural.

Related controversial aspects

a. The naturalistic fallacy: Assumes that what is natural is good and hence is morally acceptable.

b. Social Darwinism: Proposes applying to human societies the idea that those who have triumphed are the ‘most fit’ and hence that the ‘less fit’ should not be helped to overcome their situation.

YES

For scientific motives exclusively:

a. Because we are animals (vertebrates and mammals of the order Primates).

b. Because applying evolutionary methodology has generated significant advances in our understanding of ourselves.

Box 1.1. Possible replies, with their corresponding arguments and associated controversial aspects, to the question of the validity of studying human behaviour alongside that of all other animals.

We shall now examine in detail the three arguments that are used to justify a negative response: the uniqueness of human nature, the nature-nurture debate and two historical problems, namely the naturalistic fallacy and social Darwinism.

1.2. The uniqueness of human nature

We humans have always liked the notion that we are different from other animals. Most philosophers across history have defended the idea that although other animals have instincts human beings do not. Such an opinion insists upon the uniqueness of human nature. It maintains that each and every animal species has its own characteristic nature, all except the human species that is not subject to the dictates of genes and instincts, but rather disposes of complete liberty to forge its own nature. It is unsurprising that this idea appeals since it implies that we are superior to all other animals, which gratifies our egos and offer us the hope of free will.

But can we still insist upon the uniqueness of human nature given what we now know? We are certainly different in some ways from other animals, including our closest relatives, the other primates. The chief difference, biologically-speaking, is our relatively large brain, three times larger than that of another primate of equivalent size, which implies a large increase in the number of neurons and neural interconnections.

However, although we may not like to be reminded of this very much, there are many important similarities between ourselves and other animals. We are clearly mammals and share a great many mammalian characteristics. It is also apparent that we are animals that share many features with all members of the animal kingdom. For example, as in all other cellular organisms, our cells possess a genome, the gene set that instructs the development and function of each one of us. It has always been clear that if it were possible to analyse and compare the genomes of different species, including our own, this would be the key to determining the genetic differences between human beings and other animals. Such an idea was science fiction until just a couple of decades ago, but it has now been achieved by molecular biology, undoubtedly one of the branches of biology that has advanced the most in recent years. We now know that the human genome comprises some 3,000 million base pairs, which may be likened to the ‘letters’ of an encyclopaedic instruction book that contains the information needed for our construction. These 3,000 million letters are grouped into some 25,000 genes. This result came as a big surprise because bearing in mind that since the genome of *Drosophila* fruit-flies was already known to include about 13,000 genes, it had been assumed that the human genome would have at least 100,000 genes. Humans are after all far more complex than fruit flies and endowed with vastly greater cognitive capacities. Clearly, the discovery that we have ‘only’ 25,000 genes raised some doubt about the idea that we are on a higher level than all other living beings. The surprise was still greater when it was found that the human genome is almost identical (by 98.76%) with that of the chimpanzee (*Pan troglodytes*). Moreover, the chimpanzee genome was closer to our own than to the gorilla (*Gorilla gorilla*). These findings have been taken as a personal affront by some, since they show that not only are we animals but also that we are very similar indeed to our closest living relative.

Nonetheless, although such similarities are the most striking feature of all this information, this is not to say that the differences are unimportant. As that brilliant communicator Matt Ridley (2004) has emphasised, the difference of about 1.5% from the chimpanzee genome is equivalent to no fewer than 45 million letters, which would amount to 75 Bible-length books filling a three- metre-long shelf. So, the difference may be much less than was expected, but is still very significant.

What about human behaviour? It is curious (and contradictory I would say in passing) that although nobody denies the role of heredity in matters such as eye colour or height, many people refuse to accept that our genes influence our behaviour and mental abilities. Is human behaviour inherited and so in some extent genetically determined as in other animals, or does it depend exclusively on conscious decisions based on our high mental capabilities?

In answering this question we shall analyse a behaviour that is generally considered abhorrent from a moral standpoint: infanticide in which an individual kills an infant of its species whether through violence or simply through abandonment. Infanticide is very common in many animal groups, from invertebrates to mammals, via fish and birds. We can distinguish two types: infanticide committed by individuals unrelated to the victims and that carried out by the victims' own parents.

The former type is quite frequent in many species and has been much commented upon in the case of lions (*Panthera leo*). When a group of young male lions succeeds in taking over a pride, the males accompanying the females are driven away and most cubs are killed by the newcomers. Something similar is seen in many other mammals, not just among carnivores, but also in the primates and even birds. For example, in the barn swallow (*Hirundo rustica*) unpaired males may destroy the broods of established pairs. Also in polygynous species, those where a male may pair with several females, a female may break the eggs or kill the chicks of another female paired with her male. A well-known study of this involves a small marsh bird, the great reed warbler (*Acrocephalus arundinaceus*). Staffan Bensch and Dennis Hasselquist, of Lund University, Sweden, studied a population of this species for seven years, during which they obtained data from 279 nests. Females could be classified as monogamous (the sole mate of a given male), first polygynous (the first female to pair with a polygynous male) or second polygynous (a female paired with a polygynous male who had previously paired with another female). As would be expected, first polygynous females began to lay ahead of the second polygynous females. The investigators found that during the egg stage, nests of first polygynous females were three times more likely to be destroyed by predators than those of monogamous or second polygynous females (Bensch & Hasselquist 1994). Since all nests were in the same environment, except that those of first polygynous females were in territories in which other females were still nest building, the investigators suspected that it might have been the second polygynous females and not predators that were responsible for the destroyed clutches. They tested this hypothesis by putting plasticine eggs, of the same size, shape and colour as great reed warbler eggs, in the nests. The idea was to detect marks left by individuals that attacked the false eggs indeed, when they compared the beak marks on the plasticine eggs with those made by different bird species in the area, the impression matched those of the great reed warbler, confirming that the second polygynous females were the egg destroyers.

This kind of infanticide can easily be explained in evolutionary terms. The behaviour has evolved because its perpetrators leave more descendants since natural selection favours those that practice infanticide over those that do not. Lionesses that lose their cubs because the males have killed them are ready to produce new cubs with the infanticidal males within a few months but they would not be ready to do so for a couple of years had the cubs not been killed. The infanticidal female warblers also benefit since they increase their reproductive success. When a female destroys a male's other brood, she essentially force him to concentrate on feeding her chicks. As a result the killer will leave more descendants now that all the food obtained by the male is destined for her own chicks.

The second type of infanticide, the one carried out by parents, is less easily explained. Natural selection penalises individuals that leave fewer descendants so that killing one's own offspring would seem to be an evolutionary mistake. We shall describe several examples before asking what possible benefits could arise from killing or abandoning one's own young. Infanticide by parents occurs in two types of situations. First, parents become infanticidal when they lack enough resources to raise their young. This is quite frequent among mammals where, if food suddenly runs short, a suckling female may abandon her young. Second, parents may kill their young if they are deformed, injured or seriously diseased, that is to say, when the chances that they will live to reproductive age are low. In such instances they too may be abandoned prematurely.

One of the best studies of this type of infanticide is by Dieter Mahsberg, of Wurzburg University, Germany, who worked on scorpions, invertebrates that are well known for their parental care. As is also true for some spiders, scorpions carry their young on their backs and protect them from any enemy or danger. A female scorpion does not lay eggs. The live-born young emerge from her body and climb on her back unaided. This is a difficult task and only strong, healthy young can manage it. After a couple of days the mother eats any young who have failed to climb onto her and from then on she devotes all her efforts to caring for the remaining, healthier individuals (Mahsberg 2001). The key question is whether those young who are incapable of making the climb are malformed or diseased. Mahsberg answered this question by collecting scorpion young, both those that had climbed on to their mothers and those that had not, and keeping them together in captivity under the same conditions. Most of those that had succeeded in climbing up developed into healthy adults but the majority of those that had failed to do so either died or grew into weak or deformed adults. Therefore, young that fail to climb on their mothers, and so are eventually devoured by them, would have had very little chance of reaching adulthood.

Why has natural selection favoured this type of infanticidal behaviour? The answer is that it is not sufficient simply to have many offspring, these must be of good quality so that when they grow up they can compete with rivals successfully and reproduce in turn. Young that have been underfed during development or that are born with serious defects will not grow into healthy adults and their chances of reproducing successfully will be very low. Natural selection therefore favours infanticide in circumstances where food is scarce or the young are defective since investing in such offspring is a waste of effort and resources and may prejudice the survival of siblings and even the future reproduction of the parents.

We said that the phenomenon of infanticide would allow us to draw some conclusions about the relationship between the behaviour of other animals and that of human beings. Infanticide is quite frequent in primates. Does it take place in humans? The answer is a resounding 'Yes' and a great deal of information reveals this. Without going into detail, I will list four of the many studies described by the anthropologist Marvin Harris (1997): (1) Australian aborigines used to kill up to 50% of newborn babies; (2) during the 19th century the Chinese killed between 10% and 80% of girl babies; (3) in India, also during the 19th century and among particular castes, censuses showed men to be four times more numerous than women as a result of selective infanticide of girls; and (4) European parents also disposed of many unwanted children, chiefly abandoning them in hospices, which often amounted to killing them since between 80% and 90% of children left by their parents died before they were one year old. For example, 336,297 children were legally abandoned in France in just a single decade (1824-1833).

It is certainly so that not all cases of human infanticide can be considered innate behaviour, but neither can they be regarded exclusively as the outcome of premeditated, conscious decisions. As usual (see the nature-nurture debate below) they probably involve both. Nevertheless, there is some evidence supporting that human infanticide is part of a reproductive strategy shaped by natural selection. For example, the highest percentages of infanticide in China occur in poor and unproductive regions. Here, if the first baby is a girl it was nearly always killed. This has a clear adaptive explanation. Bearing in mind that those who labour in the fields are all men, it is obvious that when resources are scarce it is important that a first child should be a boy, who can work and contribute to increasing food availability for the family. When the first child was a girl it meant another mouth to feed from the same resources obtained by her father, so that the well-being of the whole family would be reduced.

Another fact that supports the finding that infanticide is at least partly the result of a reproductive strategy is the high rate of mortality suffered by children raised by their mother and a stepfather, compared with that occurring when children are raised by their two natural parents. For example, among the Ache, a tribe of hunter-gatherers in Paraguay, 43% of children raised by their stepfather die before they reach the age of 15, whereas only 19% of those who live with their fathers die (Hill & Hurtado 1996). Proportionally similar data exist for our own societies. Thus Daly & Wilson (1988) showed that child mortality was very low when children are raised by their biological parents (fewer than ten children under two years old per million). But, when one parent was replaced by a stepfather or a stepmother that mortality rose to nearly 650 children per million. However, Daly & Wilson (1988) suggested the possibility that step-father infanticide is a maladaptive side-effect of a generally psychological mechanism, namely the neural circuitry that causes people to favour their own genetic offspring and to feel far less interest in the offspring of others. Anyhow, the psychological mechanisms involved in this process that obviously require genes for their development, and thus our behavior, have been shaped by natural selection.

Evidently, in the remote past, men who did not concern themselves with previous children of their mates, and allowed (or caused) these to die, left more descendants than those that did not behave in this way. The former ensured that all the pairs' resources were dedicated to their joint offspring and so natural selection would favour this behaviour. There is no reason why step-parents should always by chance be 'worse people' than true parents, thus there is no reason to think that their neglect of their step-children should always be due exclusively to conscious decisions.

Although some of the instances described above can be considered to be culturally-acquired learnt behaviour (given that cultures may reinforce conduct that benefits individuals in terms of their reproductive success; see Chapter 8), the fact that infanticide appears in a great diversity of cultures, and always in situations where resources are scarce, suggests that it may be an adaptation.

Therefore, most behavioural biologists and evolutionary psychologists have concluded that it is impossible nowadays to maintain that human nature is in a category of its own and distinct from the nature of other animals. Discoveries emerging from different scientific perspectives, especially biological ones, indicate precisely the opposite. Human beings do have many species-specific characteristics, which are present in all societies and cultures, and such characteristics are the outcome of the evolutionary processes that gave rise to our species and that define and set the boundaries of human nature. As Jesus Mosteriii. one of the most prestigious Spanish philosophers has said, contrary to some of his colleagues: 'in our times, the only intellectually honest way of regarding the topic (of human nature) is with an evolutionary focus' (Mosterm 2006).

1.3. The nature-nurture debate

The famous nature-nurture debate, also known as the nature-environment or the inheritance-environment debate, is intimately related to the subject of human nature. This debate started off as a discussion between scientists and, as tends to happen in such matters, each side pushed the other to take up ever more extreme positions. The most radical geneticists maintained that all behavioural traits are genetically determined and that living things are puppets directed by their genes. Conversely, the most extreme environmentalists maintained that human beings are 'blank slates', born with nothing predetermined, and that the brain is like an empty book that is gradually filled by our day-to-day experiences and it is these which forge our characters (see Pinker (2003) for a convincing argument against the blank slate idea). Such extreme ideas now receive scant support but, nevertheless, the debate continues, especially fanned by the media since journalists take advantage of any news that may generate sensationalist headlines, and, unfortunately, as a result, many people reject the idea that genes could play an important role in human behaviour, for the simple reason that if this were so instincts that could provoke morally unacceptable behaviour, such as selfishness, violence, sexism and so on, would have to be accepted since they would be inbuilt and unavoidable.

This debate is pointless and scientists rarely bother with it today. Most ethologists accept that behaviour is the developmental result of a complex interaction between both genes and environment. I have no interest in taking this debate forward since not only has it proved to be one of the most sterile in the history of human knowledge, but it has also given rise to disastrous consequences when attempts have been made to apply its most extreme proposals. We have for example Pol Pot, leader of the Khmer Rouge regime that governed Cambodia between 1975 and 1979. He studied in France and there accepted the notion that the human brain is a blank slate on which experience is written. On his return to his country he succeeded in taking power and set in motion a plan to create 'a new society'. He shut off Cambodia from all external influences and took a series of drastic measures. Among others, he forced the population to abandon the cities and he forbade the use of money, schools, religions and all manifestations of culture. His aim was to produce more obedient, cooperative and austere citizens. Between 1.5 and 3 million people died, according to different sources (nearly a third of the Cambodian population!).

At the opposite extreme, the viewpoint that genes are all that matter, is linked to the eugenics movement, whose advocates wanted to improve the human race by controlling who is able to reproduce. Hence, for example, in the 1920s, government officials in USA and many European countries, starting from the basis that intelligence is heritable, began a program of sterilisation of the mentally retarded to prevent them from reproducing.

Setting aside these historical aspects of the naturenurture debate, in which it is clear that there were neither winners nor losers, let us consider the current situation. Both viewpoints have received important support in recent years. On the one hand it has been demonstrated that not only does the environment have a great and direct influence on certain aspects such as intelligence, but also it may affect others that to many seemed to be principally determined by genetic inheritance. For example, a suitable environment may encourage an athletic child to take up sport or a studious child to read and practice other intellectual activities, in both cases because these will be most rewarding for them. On the other hand, studies comparing the behaviour of identical twins, who share the same genes, raised together or separately, have shown that nearly all personality traits have a significant inherited component, even such culturally-influenced ones as the degree of religiosity or political affiliation.

However, it has also been revealed that personality does not derive from genetic determinism, in which there are specific genes for every aspect. For example, there is an important inheritable component to criminality, but this is not to say that murderers carry one or more genes that are responsible for their criminal behaviour. What happens is that there are personalities with a greater disposition to get into trouble with the law and such personalities are inheritable since they result from variation in how many genes interact. In other words, geneticists were correct when they asserted that genes are determinant and the environmentalists were also right in saying that the environment is decisive, but both were mistaken when they maintained that the other component was unimportant.

More recently, and especially thanks to developments in molecular biology, there have been important advances which reveal that, the better we know the genome, the more susceptible genes are found to be to environmental influences. By way of an example we shall consider an interesting study of depression, a common and widespread psychological condition that is provoked by seriously stressful circumstances and may even drive some people to suicide. However, not all people respond to stressful circumstances in the same way. Some are highly sensitive, and may even be depressed by relatively minor matters, whereas others seem unaffected by even the most serious situations. Why do people respond to adversity in such different ways? In order to try and answer this question Avshalom Caspi, of King's College London, UK, and his co-workers conducted a study that involved monitoring 1,037 children, who were evaluated every two years from birth until the age of 26 years. They analysed the relationship between the number of stressful episodes they experienced and any depression suffered during that period, taking particular account of the form of the 5-HTT gene that each individual possessed. This gene has two alternative forms, or alleles, one short (s) and the other long (l). These alleles code for the synthesis of a single protein, one that regulates levels of the neurotransmitter serotonin reaching the neurons.

Without getting bogged down in details that are not essential for comprehending this study, the research demonstrated that individuals fall into three groups according to the types of 5-HTT alleles that they possess: two short alleles (ss), one of each (sl) or two long alleles (ll). Why was this gene investigated and not some other one? This was because the 5-HTT gene had already been discovered to have an important role in stress resistance in rhesus macaques (*Macaca mulatta*).

The results of the human study proved very interesting. Individuals who possessed the short allele (ss or sl) suffered more depressive episodes and suicidal thoughts the more stress they had during the course of their lives. Only 10% of those who did not suffer any stressful experiences developed depression, whereas 33% of those who experienced four or more stressful episodes became clinically depressed. In contrast, those who lacked the short allele (genotype ll) were not affected by the number of stressful episodes that they encountered and only 10%-17% of them suffered any depression, irrespective of whether or not they had had any stressful experience.

What do these results mean? Clearly the short allele does not by itself cause depression -only 33% of carriers were affected at worst. But likewise not having the short allele did not exempt people from depression since at least 10% of such individuals became depressed. What the data do show is that a person whose genome includes the short allele is much more likely to suffer depression, but only in an environment in which stressful episodes are frequent. This gene affects such responses by interacting with very many other genes, but the difference between alleles is enough to influence the outcome of such interactions.

The overall conclusion from this and many other similar recent studies is that ‘innate’ does not mean ‘inevitable’, what means that the genetic programme is flexible. There is ever more evidence that genes behave as if designed to be guided by the environment. Some genes act by activating other genes, and whether or not they do so may depend on environmental circumstances. In conclusion therefore we can say that both genes and the environment have an important part to play. We have no need to fear genes. We are not their puppets but equally neither are we inevitably subject to the whims of our environmental circumstances.

1.4. Historical problems: the ‘naturalistic fallacy’ and ‘social Darwinism’

As we said earlier, a second reason that explains the traditional opposition to studying human behaviour from a biological viewpoint is the belief that this angle justifies morally unacceptable conduct. It is regrettable that such an idea is still quite widespread in some intellectual circles, notably among humanists and students of social sciences, because it is rooted in errors of interpretation of evolutionary theory that have given rise to social problems across history. These errors are known as the ‘naturalistic fallacy’ and ‘social Darwinism’. The former maintains that what is natural is good and thus morally acceptable. Such a perspective leads to the conclusion that natural tendencies, such as personal effort, will power and the drive to overcome adversity, bring about the social advancement of the individual and human progress in general. If true, those who triumph are the fittest and, conversely, that those who are less fit should not be assisted. This is what is known as social Darwinism, an argument advanced by Herbert Spencer, a 19th century philosopher who must have possessed great powers of conviction since he succeeded in getting many of his contemporaries to accept his ideas. In reality, however, the belief that the socially triumphant are the fittest has nothing to do with Darwinism, since what is achieved by effort is not encoded in the genes and thus cannot be transmitted to descendants and be subject to evolution. It should perhaps be known as ‘social Spencerism’, never Darwinism, since it runs contrary to Darwin’s theory (Moreno 2007). Evolutionary fitness means something quite different from social Darwinists meant by ‘fit’.

Natural phenomena and behaviour need not be ethically acceptable. In fact, in most cases (lethal competition, predation, parasitism and many others) the conclusion may be the opposite -what is natural is often ethically repugnant. If infanticide is adaptive and natural, this does not mean that infanticide is morally desirable! Natural selection itself is neither morally good nor bad nor does it pursue any particular objective.

Despite being mistaken, the naturalistic fallacy and social Darwinism have profoundly influenced human thinking and historically they have been used to justify the unjustifiable. The horrors caused by Hitler and Stalin are extreme and opposite examples. What is worse is that these ideas continue to be used to justify the ends of some pseudo-intellectual and social circles, including ultra-feminists, assorted progressives, some religious representatives and extreme right groups, among others. Nevertheless, as we have said, both the naturalistic fallacy and the misnamed social Darwinism are erroneous and they cannot be the basis of any valid reasoning. A further problem is that both leads people to reject evolutionary thought unnecessarily.

1.5. Another controversial matter: the differences between men and women

Let us conclude this chapter with another issue related to human nature, the possibility that the sexes are behaviourally different in our species. Since throughout this book we shall often refer to men and women, I think it is as well to clarify some aspects of sexual differences from the start.

Nobody denies that differences exist, often very considerable ones, between the males and the females in most other animal species. The difficulty is that when men and women are considered, a controversy arises that may have social repercussions, since speaking of such differences is not considered politically correct in some circles. There is a widespread and mistaken impression that to speak of such differences is to highlight male superiority, although there is no reason why that should be so. The existence of differences is not to say that men are superior to women, or women superior to men, it only means that they are not the same.

The existence of important differences between men and women is so obvious that you would have to be blind not to accept it or, more to the point, resolved not to do so. Apart from the sexual organs and other external sexual characteristics that distinguish the sexes, there are many other important differences, notably the physical, psychological and hormonal ones. For example, with respect to external morphology, men are larger and more muscular as well as having distinctive patterns of hair distribution and body fat. There are also clear and significant differences in characters associated with fecundity and lifespan. Men have higher juvenile mortality and they die younger than women. Women reach puberty ahead of men. There are also genetic differences, males have two different sex chromosomes, X and Y; women have two X chromosomes. The key hormonal difference is that men have higher concentrations of testosterone in the blood whereas women have more oestrogen. These hormonal inequalities are responsible for important aspects of behaviour. Testosterone makes men more competitive, ambitious and aggressive on average than women, as well as being responsible for the generally larger size and greater muscle power of men.

Also, and this is what is most controversial, important differences exist in brain anatomy and in cognitive abilities. There are many differences in brain anatomy but among the most important are that the amygdala (the region responsible for impulsive responses such as fear, anger and aggression) is more developed in men, whereas the prefrontal cortex (which controls emotions) is more developed in women. As far as cognitive abilities are concerned we shall mention only three of the most important that distinguish each sex. Males tend to do better at mathematics (although not at arithmetic), have a better sense of direction and are better at solving spatial problems than women. On the other hand, women have greater linguistic fluency, are better at tasks involving precise manipulation and do a better job than men at detecting and evaluating negative emotions (see Brizendine (2006) for a detailed account of the subject).

Clearly what we have given are general tendencies, not absolute differences. For example, we have said that men are taller than women but, as we all know, there are many women who are taller than many men. The same may be said of all the characteristics that we have mentioned, but the statistical trends are clear and significant. A statistical difference cannot be denied by anecdotes and exceptions, as some seem to believe.

Clearly, the idea that men and women are equal is mistaken. This is not however a case of one sex being better than the other, but simply a biological reality. Biology, like evolution, is not guided by any moral imperative. However, the biological differences in no way justify any social discrimination. Proving that the sexes differ does not imply that one has more rights than the other. The historical discrimination to which women have been subjected is properly rejected in modern society and evolutionary biologists applaud the laws and regulations necessary to do away with sex discrimination. Social equality does not require that the sexes be the same biologically.

1.6. Conclusions

We need to forget the sterile nature-nurture debate once while also accepting our evolved human nature. We are mammals of the order Primates and we have much in common with these our closest relatives. Naturally, we also have some peculiarities of our own that make us different. Many such have been proposed, among them language, intelligence, culture, our complex societies and so on, although most of these characteristics are present in other species, even if only in an incipient form (see Chapters 10 and 11).

As we have emphasised, accepting our animal condition does not mean that we are enslaved by our genes. Indeed, one of the things that sets us apart from other animals - and I think that it is the most important difference - is that we are the only species that has proved capable of rebelling against the evolutionary imperative that drives individuals to produce the greatest possible number of high quality descendants. Birth rates in many developed countries are now well below replacement levels. For example in Spain the rate is 1.3 children per couple. This shows that we can confront our instincts and overcome them. Genetic predispositions favour the expression of particular behaviours, but they can never obstruct the mind to the extent that nothing can be done to counter an innate tendency.

I am sure that we stand to learn a great deal about ourselves the day that we come to accept our animal nature. It will allow us to see some problems for what they are, problems of evolutionary biology. Many aspects of our societies, including violence, pair formation, caring for children, parent-child relationships, altruism and social relationships, would be easier to understand were they analyzed from an evolutionary viewpoint (see Chapter 2). This is what we shall do throughout this book and it is my hope that it will serve to open the eyes of some of my readers.

Chapter 2. The scientific method, natural selection and other fundamental matters

2.1. Introduction

As the title indicates, this book covers the study of animal, including human, behaviour. This is the concern of several sciences and ethology is one of them (see Chapter 3). As with any other science, it employs the scientific method and requires an appropriate theoretical framework, permitting investigators to make predictions that may be tested to check their hypotheses. The theory that supplies such a framework and makes scientific advances in ethology possible is the ‘theory of evolution by natural selection’, the very same theory that underlies all the biological sciences. Given their importance, this chapter examines these two fundamentals: the scientific method and the theoretical framework in which it is applied.

2.2. The scientific method

Although less evident than fire, writing and the wheel, the scientific method may be said to be one of the greatest human discoveries. It has certainly been responsible for the enormous scientific and technological advancements of recent centuries, which have enabled an incredible improvement in the standards of living of human beings, at least in the industrialized countries. Nevertheless, this is not to say that all its outcomes have been positive. I cannot avoid pointing out that it has also provided our species with machines and technologies that are highly effective in resource exploitation and in large-scale destruction, to the extent that it has given humankind enormous power, sufficient to exterminate all life on earth in the short term. Humanity is becoming aware, little by little, of the danger that our development poses for the planet. There is more and more talk of 'sustainable development' and yet for those in government this concept may be no more than a slogan to employ when seeking to justify continuous economic growth, which each country wishes to achieve as rapidly as possible. The notion of sustainable development is utopian, given a global economy based on irrational consumerism and ongoing economic growth. Controlling population growth is the sole measure that would allow us to continue to inhabit this planet for a long time in a truly sustainable way.

The scientific method may be broadly defined as the collection of techniques, methodologies and analyses that allows puzzling phenomena to be explained, from a starting point of previous scientific knowledge. Applying the method makes scientific advances possible. This definition may seem obvious but achieving the acceptance of the scientific method has not been easy. The tendency throughout most of human history has been (and continues to be except among the educated and scientifically literate) to explain natural phenomena and to answer all sorts of questions in terms of supernatural causes, religious doctrines, traditions and malevolent powers, and the like, which are fundamentally anti-scientific.

Box 2.1 outlines the usual steps of the scientific method. Starting from existing knowledge, scientists propose hypotheses to explain new phenomena, draw predictions arising from these hypotheses and put them to the test, to establish whether or not they are valid. A given hypothesis may generate a variety of predictions and the more of these that are not refuted the more the hypothesis is sustained. In any case, new questions arise continually and generate new hypotheses that may complement or improve upon their predecessors. Thus, when a hypothesis is sustained in many different situations it may come to be known as a theory. It should be added, however, that some theories arose as general models that had great predictive value from the start, the ‘theory of universal gravity’ and the theory of evolution by natural selection are examples.

THE SCIENTIFIC METHOD: The collection of techniques,
methodologies and analyses that enables the science to advance.

Phenomenon requiring explanation

3

HYPOTHESIS: Proposed possible explanations for a phenomenon of interest.

3

PREDICTIONS: Outcomes or results that must be obtained if the hypothesis is correct

3

TESTING: Carrying out the necessary tests to see whether or not the predictions are met

METHODS FOR TESTING A HYPOTHESIS

- Comparison between individuals
- Comparative method (at the level of species, populations, etc.)
- Experimental method

THE EXPERIMENTAL METHOD: Consists of manipulating the characteristic responsible for producing the behaviour (according to the initial hypothesis) without affecting anything else. This would involve the ‘experimental group’. In addition, a ‘control group’ for which nothing is manipulated is also considered. The hypothesis is considered demonstrated if significant differences are found between the results obtained for the experimental and control groups.

RECOMMENDATIONS

- Hypotheses must be based exclusively on existing scientific knowledge.
- Hypotheses should be based on an adequate theoretical framework and thus cannot employ supernatural causes, religious doctrines, traditions, philosophical standpoints, political ideologies etc.

Box 2.1. Definition and usual stages of the scientific method, testing methods and some important recommendations.

We will consider in detail a very interesting example of animal behaviour which will help us to understand the scientific method better. It involves a study of a remarkable behaviour of a passerine bird, the black wheatear (*Oenanthe leucura*). In this species, the pair, but mainly the male, has the curious habit of carrying stones in its beak which are then dropped usually at the base of the nest but sometimes elsewhere, even far from the nest. This activity is clearly very costly. On average a bird weighing only 40g carries 300 stones, a burden of nearly two kilogrammes! The reproductive behaviour of this species was little known until recently but, nevertheless, the stone-carrying habit drew the attention of ornithologists and was described early in the 20th century. The obvious question posed by this observation is ‘why do black wheatears carry pebbles?’ They must derive some benefit from it to make the high energy cost of flying when carrying pebbles in the beak worthwhile.

Five of us formed a research team to study stonecarrying by the black wheatear in Guadix district (Granada province, Spain), an area where this species is relatively abundant. We devoted the first year to gathering detailed information on the reproductive biology and stone-carrying behaviour of the wheatear, since the existing data was merely anecdotal. This initial study allowed us to establish certain relevant parameters which were important in answering our original question. The principal ones were: (1) birds carry pebbles at the start of the nest building stage, (2) pebble carrying chiefly involves the males (sex that carries approximately 87% of pebbles), (3) only some of the pebbles (about a third) are deposited at the nest base, (4) pebbles sometimes form a wall at the entrance to the nest cavity, (5) pebble size is fairly uniform by a given nest (some nests have large pebbles and some have smaller ones), (6) the number of pebbles transported is highly variable, ranging from 0 to 1,300, and finally (7) pebble carrying takes place during short periods of intensive work.

Based on this information, we proposed five hypotheses to explain pebble carrying (Moreno et al. 1994), all of them based on the theory of natural selection, which we will now consider briefly. The first hypothesis (nest support) proposed that the stones are used to provide a solid nest-base. This explanation generates various predictions, principally that the number of pebbles brought would depend on how irregular the surface was on which the nest was to be built. However, neither this nor other predictions relating to this hypothesis were met, there being no relationship between pebble numbers and nest-base condition. Furthermore, nests were sometimes built in sites to which no pebbles at all were transported and sometimes the stones were carried to places where nest construction was not possible. This hypothesis is therefore probably invalid.

The second hypothesis (thermoregulatory function) suggests that the pebbles could play an important part in moderating broad temperature fluctuations that could prove prejudicial during incubation. Four predictions were derived from this hypothesis but, again, none of them was met. The most important of these was that the pebbles would help to reduce the cooling rate of the nest. We tested this by an experiment using old nests. We inserted a plastic bag of warm water and a temperature sensor and recorded how long it took for the water to cool from 40°C to 30°C. We then removed the pebbles and repeated the measurement. The stones had no effect on cooling rates, and thus, this hypothesis too was invalid.

The third hypothesis (climatic protection) proposed that the pebbles serve to protect the nest from wind and rain. The most important of the predictions generated by this hypothesis was that the stones would reduce the negative effects of adverse weather conditions both on the eggs during incubation and on the brood during its stay in the nest. This prediction was not fulfilled, nor were others based on this hypothesis, since analyses of the outcome of 167 nests for which we had complete data showed that none failed for weather- related reasons.

The fourth hypothesis (defence from predators), which suggested that the stones would difficult predator access to the nest, also generated various predictions. The principal of these was that successful nests would have more stones than predated ones. Neither this nor the other predictions were met so this hypothesis too was rejected.

The fifth and final hypothesis (sexual display) proposed that stone carrying enables a male to display to a female his good physical condition and readiness to work during the breeding period, which would lead the female to adjust her reproductive output (the number of eggs laid). Given females of similar reproductive capacity, those whose mates brought many pebbles (showing that they were strong enough to bring much food to the chicks) would lay more eggs than those paired with males that carried few stones. This hypothesis is based on the 'theory of sexual selection' (see Chapter 4), but it should be noted that stonecarrying is unrelated to courtship, given that it is preceded by pair-formation. This hypothesis predicts that various parameters related to reproductive success would increase as the number of stones carried by the male increased. By applying the 'comparison between individuals' method of testing a hypothesis (see Box 2.1) we established that several predictions were met. For example, pairs that transported more pebbles laid more eggs and raised more chicks, that is to say they proved more effective at leaving descendants, in accordance with the hypothesis. The comparison between individuals method is insufficiently rigorous to establish hypotheses. These results did not allow us to consider it demonstrated but they encouraged us to start an experimental study (see Box 2.1), a much more reliable approach.

Wheatear territories hold a variable number of old nests that contain pebbles transported in earlier years. We were able to show in a previous analysis that more pebbles were carried during each breeding event in those territories that contained more 'old' stones. It was thus necessary to clarify the effect of those 'old' stones since it was possible that the best males preferred the territories with most 'old' pebbles, because these were better territories. We began with three distinct hypotheses: females could be evaluating male quality according to the pebbles transported, according to the quantity of 'old' pebbles present in the territory or by taking both these variables into account. Two experiments were designed to test these hypotheses, the first of these to determine the role of 'old' stones and the second to determine the effect of pebbles transported prior to a given breeding attempt (Soler et al. 1996). In the first experiment we started by manipulating the number of 'old' stones present in the territories before the breeding season began. All the territories were randomly divided into two groups. In the first one we took away all the 'old' stones from the experimental group and in the other group we left all the nests as we found them for the control group (see Box 2.1). Our prediction was that if 'old' stones played an important role in affecting female egg laying decisions, removing them would have a negative effect on the reproductive success of the pairs that used the experimental territories. Instead removing 'old' pebbles had no effect on the number of stones transported or on the number of eggs laid or young raised by the various pairs. The prediction was not fulfilled and thus it may be concluded that stones from former years have no effect on breeding behaviour in the wheatears.

We carried out another experiment to test the hypothesis that what is important is the transport of pebbles before each nesting attempt. All nests were randomly divided into three groups. We added as many stones as had been transported by the breeding pair to the nests of the first group. We removed half of the transported stones from the second group. We neither added nor removed stones from nests of the third group although we visited them with the same frequency as we did the others (every two days). More stones were transported in the territories from which we removed pebbles than in the other two groups, indicating that the birds tend to replace the lost stones. On the other hand, those nests to which most stones were transported also had greater breeding success, pairs at these nests raised nearly twice as many chicks as did the pairs in the other two nest groups. These results support the idea that the female black wheatear adjusts her reproductive effort according to the number of stones that the male transports in her presence, and not according to the number of stones previously accumulated in the nest cavities. This finding is further supported by the fact that on all the occasions in which we saw males carrying pebbles, not only were the females always present and attentive, but also we sometimes saw them picking up some of the pebbles that the male had brought, as if to judge the weight of the stones that he had delivered.

This example clearly demonstrates the process of generating alternative hypotheses and deriving predictions, as well as some of the testing mechanisms, the steps which comprise the distinct phases of the scientific method (see Box 2.1). However, this is not the end of the matter. The scientific method continues even after a hypothesis has been sustained as new hypotheses and related predictions are proposed and put to the test. A new hypothesis arose in this manner from the wheatear study: if most pebbles are carried by males then it may be predicted that, since a larger wing area would make carrying them easier, natural selection (see below) would favour a greater wing area in males than in females. We found in an earlier investigation that males do have a wing area (taking body size into account) which is significantly greater than that of females. Moreover, we obtained another interesting result that also supported the hypothesis. We found that the greater the males' wing loading (the mass supported per unit area of the wing) the fewer stones it carried to the nest. Having obtained these supportive findings by the method of comparison between individuals (Box 2.1), we began another experimental study to test the hypothesis that males have evolved a larger wing area as an adaptation for stone carrying (M0ller *et al.* 1995). We proceeded as follows. Males were randomly assigned to either of two groups. Two feathers were cut from the wings of males in the experimental group. Males in the control group were captured and measured, as were the experimental birds, but no feathers were removed. The most evident predictions were that, since cutting feathers would increase wing loading, the experimental males would carry fewer and lighter pebbles than the control males. Both predictions were fulfilled so we accepted the hypothesis that males have evolved a larger wing area as an adaptation to pebble carrying.

The experimental method - in conjunction with the comparative method - is the most powerful and reliable when it comes to testing hypotheses, but it has the problem that the individuals in the experimental group have to be manipulated, which may affect their behaviour. The problem is solved by considering another group, the control group, in which the manipulation is faked. For example, if paint is being used to change the colour of some part of the bodies of the experimental group, a control for this handling would be to paint the same part of the bodies of another group using just the solvent of the paint used, i.e. without changing their colour. If this faked manipulation affects the behaviour of the control individuals, the experiment cannot be regarded as valid.

Another problem with experimental handling is that it may harm the subjects of the study, raising an ethical matter that must always be taken into account. The ethical problem particularly applies to humans, a species in which no experiments involving either bodily or mental manipulations can be performed, so that most experiments are carried out by employing photographs or images after which the subjects are asked questions that will provide the desired information.

We will now examine a type of experiment with human subjects that, thanks to its ingenious construction, succeed in testing a hypothesis which could not be explored previously in any other species for ethical and experimental design reasons. Staying with the sexual selection theme on which the wheatear study was based, it is frequently the case in many species (humans included) that males and females perform more or less complex dances during courtship. A hypothesis derived from this observation is that if the dance is used in mate selection, it should convey some important information about individual quality. Since it is known that the degree of symmetry is an indicator of biological quality (known as 'fluctuating asymmetry', see Chapter 4), it is possible that dancing allows the evaluation of a partner's symmetry. This hypothesis had never been tested because it seemed impossible to separate the effects of the dance from the physical appearance and other morphological features of the participants, which would provide direct information on symmetry. William Brown, of Rutgers University, USA, and his collaborators found a way to test this hypothesis in a human population. It consisted of evaluating the dancing ability of different persons to see afterwards whether it was related to their fluctuating asymmetry indices. To do this they filmed numerous people while they danced under special conditions. They attached markers to 41 key body points (hands, feet, shoulders, elbows, wrists etc.) of each subject and filmed them with eight special 'motion capture' cameras, which only record signals from the markers. The cameras were set up to cover entirely the eight cubic metres (2x2x2m) within which the subjects had to dance. The images thus obtained resemble indistinct dancing robots, which therefore avoids transmitting any information on physical appearance, as was intended. As predicted, Brown's team found a significant relationship between symmetry and dancing ability and this was greater in men than in women (Brown et al. 2005).

2.3. Biological evolution

With the exception of those religious fundamentalists who interpret the Bible literally, nowadays nobody seriously denies that all life on earth has changed over time and that all living things are derived from a common ancestor. Biological evolution is a fact. Some 80 million years ago our planet was overrun by reptiles, large mammals did not exist (although there were many small species) nor did human beings. Now, in contrast, reptiles are relatively scarce and mammals, especially humans, abound. Nowadays series of fossil remains, very complete for some groups, are available to us. These clearly record changes over time and they always reveal a perfect relationship between the sequence of appearance and a logical process of structural development in organisms. For example, jawless vertebrates appear earlier than jawed fish, which in turn appear in the fossil record before terrestrial vertebrates.

Many biological sciences, and not only the study of fossils, have provided incontrovertible evidence for evolution. This book's objectives do not include presenting all the evidence in favour of evolutionary theory. However, I wish to point out that not all the evidence favouring evolution is of a historical nature. There are also robust indications that evolution is active today, even in our own daily activity. For example, as all readers are surely aware, many bacteria have become resistant to a diversity of antibiotics, posing a grave threat to public health. How has this resistance been acquired? When a genetic mutation arises in a bacterium, which allows it to resist the effect of a particular antibiotic, it will survive exposure to it and will produce many copies of itself that are also resistant. Its non-resistant companions die when we use the antibiotics so that quite soon most of the bacterial population is resistant, the non-resistant ones having died off. This is clear evidence of natural selection in action. For all intents and purposes, the data in favour of evolution are so numerous and compelling that biological evolution may now be regarded as a scientific fact, as demonstrable as the existence of the atom or the orbit of the Earth around the Sun.

What is evolution? In Darwin's own words it is 'descent with modification' and this is a good definition. To be a little more specific, it may be said to be a change in the characteristics of populations of organisms over the course of successive generations. But what changes? The reply might be that what changes are the diverse morphological characteristics or behaviours of individuals. Nevertheless, this reply would not be entirely correct because it describes only what is apparent (the phenotype) and natural selection cause evolutionary change when acting upon genetically determined characteristics, which are what are transmitted to the next generation and can bring about evolutionary change. Evolution only occurs when there is a change in the gene frequencies (the genotypes) of a population.

All organisms and their characteristics are the outcome of evolutionary changes. The processes of natural selection (see below) are not the only ones that can produce evolutionary changes but they are regarded as the most important. Evolutionary theory may be applied to any biological discipline, certainly including the science of animal behaviour (Soler 2002). The methods and analyses of evolutionary science have directly helped us to increase our understanding of the world around us and indeed of ourselves. Furthermore, these methods, together with the resulting knowledge, are contributing decisively to advances in applied science in fields as diverse as the conservation of endangered species, the management of natural zones and hunting reserves, medicine, agriculture, animal husbandry and biotechnology, among others.

2.4. Natural selection

How is the change that we have described above and which is the key to the evolutionary process produced? In reply to this question, Charles Darwin (1859) proposed the most celebrated of his ideas, a mechanism that he called 'natural selection'. This is relatively simple and easy to understand if we follow the steps proposed by Darwin himself (Box 2.2).

NATURAL SELECTION: Differential reproduction by hereditary variants. It penalises the less fit and so increases the proportion in the population of variants that result in improved chances of survival or in enhanced reproductive output.

1) The individuals that comprise a population differ among themselves (**variation**).

2) Some of the characteristics responsible for individual variation may be transmitted from parents to offspring, i.e. they are heritable (**heritability**).

3) Individuals have enormous reproductive potential and each generation gives rise to many descendants that never succeed in breeding as a result of competition for limited available resources (**competition**).

4) Survival and reproduction are not chance events. Those individuals that possess the most favoured characteristics will survive better and leave more descendants than those which lack these features. Hence a higher proportion of the favoured characteristics will pass to the following generation.

Box 2.2. Definition and summary of the mechanism of natural selection

What is natural selection and how does it operate? The superb studies carried out by Peter Grant and Rosemary Grant, of Princeton University, USA, will help us to understand the process. These biologists have studied the Galapagos finches for over 30 years on the islet of Daphne Major (0.34 km^2) and have obtained conclusive proof of the evolutionary effects of natural selection in those populations. There were only two finch species on the island when they began their study: the common cactus-finch (*Geospiza scandens*) and the medium ground-finch (*G. fortis*). A third species, the large ground-finch (*G. magnirostris*) colonised the island in 1982 and these three species remain there today. The common cactus-finch feeds on the pollen and fruits of cacti but the other two species are seed-eaters, which crush seeds in their beaks, and they are potential competitors since their diets overlap. The medium ground-finch feeds on smaller seeds but the larger individuals also take the seeds of *Tribulus cistoides*, which are larger and comprise the favourite food of the large ground-finch. Upon the arrival of the large groundfinch, which logically was expected to eat the largest seeds — those of *Tribulus*—, the investigators predicted that an evolutionary change in the medium ground-finch would result. They supposed that there would be selection for a smaller beak in the medium ground-finch, which would reduce competition with the other species and at the same time would increase their efficiency in exploiting medium-sized seeds. That is to say, the consequence of the larger-beaked invaders exploiting large seeds better than the indigenous species would be that those natives that specialised on medium-sized seeds (those with smaller beaks) would leave more descendants than those specialising on larger seeds.

The investigators were able to detect the evolutionary change that they had predicted in 2004, by which time the two species had coexisted for 22 years. By then the population of the large ground-finch was sufficiently large to reduce the availability of *T. cistoides* seeds considerably. Both species suffered great mortality after a severe drought in 2003 and 2004, which brought about a reduction in seed availability. No significant difference was observed between the beak sizes of those large ground-finches that died and those that survived. However, there was selective mortality of those medium ground-finch individuals that had larger beaks. As the observers had predicted, this resulted in an evolutionary change in that mean beak size declined in the medium ground-finch population. It was on average 11.2mm before 2003 and 10.6mm in 2005 (Grant & Grant 2006): a 5% reduction in just two years!

This is a very specific study but it can help us to understand the mechanism of natural selection that gives rise to evolutionary change, as set out in Box 2.2. The first point, the existence of variation, is fundamental to the finch study and takes the form that in each species there are individuals with small, medium-sized or large beaks. The second point, the heritability of beak size, had previously been demonstrated by Grant & Grant. They found that small-beaked individuals had small- beaked offspring and large-beaked ones produced large- beaked offspring. These two points together indicate that there is genetic variation in beak size. This is a key finding since, as we have pointed out, evolution only occurs if genetic variation exists. The third point, the deduction that many more individuals are born than succeed in reproducing, was not investigated in these finches but it is a general finding across the animal kingdom. Numerous studies of different species have shown that up to 70% of the individuals that are born die without leaving any descendants (the percentage is much higher still in species where there is no parental care, as occurs in most fish and marine invertebrates). With respect to the fourth point, which affirms that those individuals that survive to reproduce are those possessing the most favoured characteristics, the finch study demonstrated that this was the case since the medium ground-finches which survived to reproduce were principally those with smaller beaks.

Although the finch study did not collect data on subsequent breeding, to have a complete view of the more or less stable evolutionary effects of natural selection we would need to take note of the long-term consequences of the process. It is evident that largebilled medium ground-finches would leave few descendants in future years since the majority of them had died. This would mean that smaller-billed medium ground-finches would predominate in the next generation, the type which would continue to exploit medium-sized seeds, those of optimum size for their beaks.

Natural selection is enormously powerful and it may give rise to important evolutionary change in a population in a short period, as we have seen with the finch study. Nevertheless, caution is needed since the evolution of characteristics by natural selection is not always adaptive in the sense of improving the effectiveness of the characters under selection. Sometimes it simply acts to conserve what is useful. Since the development of many characteristics requires time and energy, i.e. is costly, if a feature is conserved it is because it is necessary or is not costly. Otherwise it would be eliminated by natural selection. Individuals that did not waste time and energy developing unnecessary characteristics would be able to devote that time and energy to producing more descendants, which in turn would displace individuals which continued to maintain costly characteristics from which they derived no advantages.

There are the numerous well known instances of cave-dwelling animals which have lost their sense of vision. Another fascinating example is provided by the giant tube worms (genus *Riftia*) of the undersea thermal vents. These vents comprise a very peculiar deep-sea habitat where hot sulphurous emissions provide an additional source of energy. The worms and other animals of these vents have developed special adaptations permitting them to live off these sulphurous emissions. *Riftia* worms that obviously evolved from ancestral species with mouths and anuses may reach two metres in length but possess neither mouths nor anuses. Instead they harbour great numbers of symbiotic bacteria that metabolise the sulphur and provide the worms with all their requirements.

2.4.1. Natural selection in modern human societies

Does natural selection act upon human beings in modern industrialised societies? This is a very important and highly topical question for two reasons. Firstly, because many people maintain that the important advances in medicine have reduced mortality and have prevented natural selection from operating. Secondly, because some professionals in the field, after having carried out studies intended to check adaptive hypotheses and having reached negative or conflicting results, have suggested that in human societies, people do not behave in accordance with Darwinist predictions.

With respect to the first of these, although medical advances and the decline in mortality are certainly real, they need not impede the operation of natural selection, given that this acts principally on differential reproduction, i.e. if a feature makes reproduction more effective in those individuals who possess it, and that trait is heritable, it will become more frequent in the population generation after generation.

The second question is much more worrying since the criticism is based on situations in which features that should result in larger numbers of descendants, according to Darwinist theory, not only do not do so but may even have the opposite effects. We shall examine this problem further because critics of the application of natural selection to human behaviour have made much of it.

A clear prediction of Darwinist theory (for reasons that we treat further in Chapter 4) is that people who possess more resources (wealth) should leave more descendants than poorer people. This prediction has been found to be met in numerous studies of existing hunter-gatherer societies, especially those which allow polygamy, and in pre-industrial societies. Nevertheless, conflicting results have been found in some modern societies, i.e. in these cultures richer people have fewer offspring than poorer ones. Nevertheless, various recently published studies have identified some procedural problems in certain earlier studies and they have also found that adopting more rigorous methodology does yield the results predicted by Darwinism.

Among the principal problems that have stood out are, firstly, that the analysed samples have tended to include young men in the middle of their reproductive lives. Secondly, these studies use socioeconomic status as a measure of wealth, making no distinction between richness and cultural attainment, parameters that may have contradictory effects. Thirdly, it is also necessary to consider the economic attainment of men and women separately, since these two may have opposing effects. A good example of a recent study that confirms Darwinian predictions is that by Rosemary Hopcroft, of UNC- Charlotte, USA. After analysing data from a United States sample between 1989 and 2000, she found some compelling and very interesting results. On the one hand it is true that both men and women of higher educational attainment produce fewer children but, on the other, men with higher salaries not only indulge in sexual relationships more often but also leave more offspring that do those whose salaries are lower (Hopcroft 2006).

Another study whose results confirm and complement the previous one was carried out by Martin Fieder and Susanne Huberc, of the University of Vienna, Austria. They worked with a Swedish population sample and found that with less marked distinctions both in levels of salaries achieved and educational attainment, when both parameters rose there was an increase in the number of offspring left by men (though the number declined in the case of women; Fieder & Huberc 2007). (See also the more comprehensive study by Nettle & Pollet 2008, described in Chapter 4).

2.5. Adaptation

The word 'adaptation' has a starring role in the vocabulary of evolution. Probably everyone has an idea of what it means but, unfortunately, that idea is not always correct. Hence it is worth clarifying that, although an adaptation may arise during development, this is not true evolutionary adaptation. An example will explain this. An individual who has practised swimming from a young age for several hours a day may be capable of swimming fast and far and might be said to be adapted to swimming. Another individual who has similarly from a young age dedicated many hours to playing computer games may come to be an expert player, although he well not be a great swimmer. Improvements that are acquired through lifelong practice have no effect on the evolutionary process since they cannot be transmitted to offspring. Hence, although the word adaptation may be correctly used linguistically in the sense of becoming accustomed to new circumstances, this meaning does not correspond with the idea of evolutionary adaptation. In evolutionary terms an adaptation is not the same as 'adaptability'.

What then is an adaptation from an evolutionary standpoint? It may be defined as any characteristic that increases the biological efficiency (fitness) of individuals that possess it and which is developed through natural selection, and thus is the result of genetic changes. Biological or Darwinian efficiency is the ability of organisms to survive and to produce descendants that are efficient in their environment. The beak sizes and seed-crushing behaviour of Darwin's finches which we studied above are clearly adaptations that increase individuals' chances of survival, which in turn enables them to reproduce and pass on the genes for a particular beak size. The pebble-carrying behaviour of black wheatears is also an adaptation that, although it does not increase survival chances, does serve to augment the fitness of individuals that carry many stones, when it comes to leaving descendants.

It is easy to imagine the process which has given rise to the adaptation in these and in many other cases. Consider the eye. A cell -or a group of cells- that is sensitive to ambient light may be considered a rudimentary eye. Nevertheless, in comparison with individuals which lacked such an eye, an individual that had one would derive many advantages, not only in finding food but also in avoiding being eaten. Any improvement that might be produced in such an organ would bring the same advantages, so that it would be expected that individuals that inherited these improvements would leave more descendants in turn. In this way, natural selection will have benefited those individuals with more highly developed vision and, after millions of generations, will give rise to the highly efficient eyes that have evolved independently in a variety of animal groups. Then, why there exist some organisms with simple eyes? The answer to this question is that only when the benefits of improved vision exceed the costs will a fancier eye to spread through a population.

Imagining the evolutionary process which has given rise to an adaptation is not always so simple. There are many existing bizarre adaptations whose evolution is a genuine enigma. A remarkable example is a parasitic crustacean (*Cymothoa exigua*), a fish louse that replaces the tongue of its host. It enters its victim through the gills when it is very small, attaches itself to the tongue with its three pairs of anterior legs and then destroys the principal tongue artery. The tongue gradually atrophies through lack of blood and the parasite replaces it with its own body, attaching itself to the muscles that remain of the appendage. From then on, the fish uses the parasite as if it was its own tongue and it suffers no further damage. The parasite feeds whenever the fish does so and it grows as its host grows (Alvarez & Flores 1997). It is hard to imagine the adaptive process by which the parasite became converted into a tongue. Perhaps it originally only lived in the fishes' mouth and the tongue-replacement strategy emerged little by little.

2.6. The adaptationist method

Most of the complex features of living organisms to which a task or function may be assigned are considered to be potential adaptations and one of the principal activities of evolutionary biology has been, and is, showing what these are. This type of investigation is termed the ‘adaptationist method’. It consists of proposing a hypothesis regarding the benefits supposedly conferred by a characteristic and then demonstrating that individuals that possess it leave more descendants than those which do not.

The adaptationist method is sometimes criticised for being, on occasions, overspeculative. Caution is called for and at least three considerations must be borne in mind. Firstly, an ingenious idea, however evident it may seem, proves nothing by itself but has to be tested (there are three methods of testing hypotheses: comparison between individuals, the comparative method and by experiment. See Box 2.1). Secondly, alternative hypotheses must always be considered and different possibilities need to be analysed critically. Finally, not all the characteristics of an organism need be adaptations -some may be by-products of other adaptations-, and neither need all adaptations be perfect, they may be in the process of refinement.

Another matter regarding the adaptationist method needs to be considered and is important, although relates more to the terminology than to its substance. Our language is intrinsically anthropomorphic, i.e. we tend to attribute purpose and intention to animal and even to plants. Students of animal behaviour often use phrases such as ‘by allowing himself to be devoured by the female’, the male mantis succeeds in fertilising more eggs and thus in leaving more descendants. But this does not mean that the male has consciously evaluated its behaviour to achieve its end and that it finally has decided to allow itself to be eaten. This is simply a linguistic shortcut. Such language has the advantage that it is very useful. The correct way to describe the behaviour of the male mantis to avoid anthropomorphism might be something along the lines of: ‘the male mantis is devoured by the female during copulation because during the course of evolution, natural selection has favoured those males that are eaten over those that succeed in escaping, given that the former leave more descendants because they are able to copulate for longer and therefore to fertilise more eggs’. In other ways, without using some anthropomorphic language, a sentence becomes a paragraph.

Although a little anthropomorphism is both inevitable and useful, it is necessary to be very cautious and always to make clear to one’s audience and to oneself that it is only a manner of speaking and that you are not implying that animals are making conscious decisions. Rather, there are instinctive behaviours or adaptive strategies that have been selected for because they confer advantages, because they increase survival chances or because they increase reproductive efficiency.

2.7. Evolutionary theory: its importance and some errors of interpretation

The theory of evolution brought about a great revolution in biology, thanks to its enormous range of application and predictive capacity. Prior to Darwin, the biological sciences were largely descriptive. It was the theory of evolution by natural selection (Darwin 1859) which provided an adequate theoretical framework that permitted hypotheses to be produced and predictions made that could then be tested (Box 2.1). All this converted biology into a true science.

Although, as we have seen, evolution by natural selection is not an excessively complex idea, it is not easily understood and as a result misinterpretations are widespread not only within the general population or among enthusiasts of natural history but also - and this is more serious - among teachers and professionals in biology. The most frequent errors are summarised in Box 2.3 but we shall only comment briefly on the most important ones.

ERRORS	**SOLUTIONS**
Natural selection acts for the good of the species.	The species does not come into it. Natural selection acts mainly at the level of the individual.
It is possible to produce adaptations to prevent future conditions.	Natural selection is 'blind'. It never acts towards a particular end, let alone that of solving future problems.
Natural selection acts to produce improvements and to increase complexity.	It only improves adaptation to the environment. Although it may well produce an increase in complexity this is not always its outcome.
Natural selection may provide an organism with the adaptations that it needs.	Adaptations are the outcome of selective processes but selection can only act on existing variation, with no ultimate aim.
Vertebrates are more 'evolved' than invertebrates	Organisms cannot be said to be more or less evolved. All existing species are well adapted to life on our planet. Degree of evolution should not be confused with degree of complexity.
Evolutionary trees indicate levels of perfection.	Evolutionary trees only show the phylogenetic relationships between different groups.
The human being is the most evolved species.	Evolution is not a ladder with human beings at the top but rather a pattern of branches in which we occupy a particular position.

Box 2.3. The most frequent misinterpretations of the theory of natural selection and their corrections.

One of the most frequent errors (which is still unfortunately widespread in many countries even among biologists) is the belief that individuals act for the good of the population or the species (what is known as 'group selection', see Chapter 8). For example, there is the idea that the members of a pack of wolves or a pride of lions do not fight among themselves for the good of the species, since they would injure themselves seriously or kill each other and the species could become extinct. This has been shown to be incorrect. Natural selection favours individuals which behave in ways that maximise their reproductive success, no the group's chances of survival. Those contests involving threats and displays between males are the result of natural selection since both contenders benefit if conflicts can be resolved without serious cost to the participants (see chapter 10).

Another frequent error, which occurs frequently in televised nature documentaries, is to assume that natural selection generates progress and increases complexity. It is certainly true that evolution produces improvements in efficiency which, over time, tend to increase complexity. This is logical since the earliest living things were very simple and thus any changes that evolved would tend to make species more complex. However, evolution only favours improved adaptation to the environment. Hence there are many examples of selection that acts favouring the maintenance of a characteristic (stabilising selection) and also of selection that results in a loss of complexity. For example, many parasitic species have lost the digestive systems that their ancestors possessed; snakes and cetaceans have lost their limbs and birds have lost their teeth, among very many other examples.

Another very similar error is to believe that the human being is the most highly evolved species. Evidently this idea is highly comforting to our egos but it is nonetheless false since evolution has not progressed as a linear ascent to reach our species but rather in the form of a tree. It is a series of branches, not a ladder.

Following this introduction to the scientific method and to evolutionary theory, which underpin biology and hence also the science of animal behaviour, we are now ready to begin our study of ethology.

Chapter 3. The science of ethology

3.1. Introduction

Behaviour is characteristic of animals and it provides them with a host of adaptive responses to their environment. In its simplest form it merely involves movement, although a lack of movement -including resting or even sleeping- may also be regarded as behaviour. In essence, really the only time an animal is not behaving is when it is dead.

There are many definitions of animal behaviour. One of the most widely accepted, although it is too simple and mechanistic, is 'the response of an organism to a stimulus'. It may also be said to be the assemblage of mechanisms and strategies that living beings use to resolve the problems that confront them during their life cycles. Behaviours range from very simple and predictable to highly complex and unpredictable. Animal behaviour, and thus also human behaviour, is highly varied and may be studied from a diversity of viewpoints that are the province of various sciences (see Box 3.1).

Ethology (behavioural biology): Mainly concerns the behaviour of animals in their natural habitats. This field, the science that is most directly associated with animal behaviour, may also include humans as an object of study.

Anthropology: Deals with the behaviour of present day human beings. The most important of its various branches are cultural anthropology, which studies human cultures that may have promoted the same lifestyle for hundreds of years, and physical anthropology, which is concerned with how humans evolved.

Psychology: Aims to understand the mental processes of humans and other animals, and why they behave as they do. Chiefly, deals with the mechanisms responsible for behaviour. Studies that employ animals other than humans are usually laboratory-based instead of observed under natural conditions.

Sociology: Sociologists study human societies, how humans manage to conduct social life and the cultural basis for human social behaviour.

Sociobiology: Deals with animal social behaviour, analysing the causes underlying the evolution of animal societies. Has since broadened its scope to encompass an adaptationist focus on animal behaviour, which means that it now also comprises what it known as behavioural ecology.

Box 3.1. Sciences whose objective is the study of animal behaviour, including that of human beings.

3.2. Ethology: a brief historical overview

Human interest in animal behaviour is long standing. During the Greek classical period, Aristotle devoted two volumes of his famous work *Historia animalium* to the subject. Among others, he gave detailed accounts of the contests between courting wild boars, the incubatory behaviour of pigeons and the reproductive strategy of the common cuckoo (*Cuculus canorus*), a bird that builds no nest but instead lays eggs in the nests of small bird species, which then take on the task of raising the, for them, gigantic cuckoo chicks.

However, as happened with many other sciences, the quest for knowledge then faded for many centuries. This was especially the case with the study of animal behaviour since in the 17th century, when other sciences experienced a resurgence, the influential French philosopher Rene Descartes, came up with a disastrous notion that succeeded in destroying any interest in the subject. Descartes maintained that animals functioned as machines and therefore that knowing the machine (its morphology) and its workings (its physiology) left nothing further worth studying. This view retarded ethology for two hundred years. It is a pity that nobody gave Descartes a dog when he was a child; had they done so perhaps he would not have come up with his unhelpful conclusion.

Virtually nobody took an interest in studying animal behaviour until the 19th century, when Charles Darwin, in his famous work *On the origin of species*, used numerous examples of animal behaviour to advance his theory on evolution by natural selection. In particular, he proposed hypotheses to explain behavioural evolution, which led to enormous advances not only in ethology, but also in biology in general (Darwin 1859).

The study of animal behaviour developed greatly in Europe during the first half of the 20th century thanks to the impetus given by Darwin's work. Following studies by Whitman and Heinroth, there emerged the personalities of Konrad Lorenz, Karl von Frisch and Niko Tinbergen, who received the Nobel prize in 1973 for having essentially created a new science: ethology. That ethological school was based on studying animals under natural conditions while giving maximum importance to the analysis of instinctive behaviour, which ethologists regarded as distinct from learning. At the same time, in the United States, a school of thought emerged known as comparative psychology (also known as 'conductism' or 'behaviourism'), which was opposed to ethology and maintained that what mattered was to study the mechanisms of learning under laboratory conditions. Its leading advocates, chiefly Thorndike, Watson and, in particular, Skinner, maintained that only reflexes are innate (the ‘classical conditioning theory’ developed by Pavlov) and that all else is learned by animals based on the rewards and setbacks they receive from the environment. The dispute between both camps was very fierce at times, but gradually their differences lessened, both regarding their methodology (field or laboratory) and their theoretical frameworks. Nobody nowadays maintains that animal behaviour is composed entirely of instincts or learned behaviours; all ethologists agree that every behaviour is the outcome of a very complex interaction between genetic and environmental factors.

Without a doubt, the most important revolution in ethological belief came when ethologists accepted that behaviour depends upon the expression of an organism’s genes, and hence heritable and subject to natural selection. This means that behaviours of individuals will have been optimised by natural selective processes to maximise their reproductive success. It is this adaptationist approach that dominates ethology today and it has given rise to the discipline known as behavioural ecology, which may be defined as the branch of ethology that studies behaviour from an evolutionary viewpoint and that maintains a close relationship with both ecology and genetics. In fact, behavioural ecology has achieved such prominence that it may be considered to be modern ethology, so giving it a distinguishing name no longer makes much sense.

3.3. Behavior is heritable

Before going any further it is important to have one point clear: behaviour has a genetic basis. Take, for example, the case of web-spinning spiders. Their parents will have disappeared by the time they are born yet, despite being alone, they know how to build their webs perfectly well, from scratch and without being taught. However, this is not to say that there exists a gene, or a group of genes, responsible for web building, genes only direct protein synthesis and do not cause behaviour directly. The fact that an individual may carry the gene or genes responsible for a particular behaviour means, only, that the individual possesses the hereditary information needed for the development of the behaviour, but it is not certain that it will carry the behaviour out (see Chapter 1). Two circumstances may intervene: either the environmental conditions necessary for the development of that behaviour may not arise, or one or more of the genes may not be expressed adequately. Behaviour, as we have said, is the outcome of the interaction between genes and the environment and neither of these components can be said to be the most important. Invariably, the maturity, development and experience of individuals are decisive when it comes to performing a behaviour.

The development of a particular behaviour has been compared to baking a cake and this is quite a useful analogy. The outcome depends on two things: the recipe (equivalent to genetic information) and the temperature and baking time (the environmental conditions). If an ingredient (gene) is missing you get a different cake. If several are missing or one of the most important ones is absent the outcome may be disastrous. The cake may also be fit only for the bin if it stays too long or too briefly in the oven, or is baked at too high or too low a temperature.

3.4. The objectives of ethology. Tinbergen's four questions

Ethology considers all possible approaches to study how and why animals interact with each other and with the environment in which they live. Niko Tinbergen, in his classic and influential work published in 1963, considered that there are four principal factors involved in the study of behaviour: causal, developmental, evolutionary and functional or adaptive. These can be expressed in what have come to be known as Tinbergen's four questions (see Box 3.2).

We shall consider each of these questions about behaviour by making use of a particular example, a striking and spectacular behaviour that has often been commented upon: the egg-eviction behaviour by the chick of the common cuckoo and other parasitic cuckoos. The common cuckoo does not build a nest and instead, as we have noted, the females lay an egg in a nest of another bird species, which not only incubates it but also cares for the parasitic chick. Shortly after the chick hatches it sets about lifting all the other nest contents onto its back, be they eggs or other chicks (95% of the time they are eggs since the cuckoo chick tends to hatch ahead of the eggs of the host species), and tips them one by one out of the nest. Marcel Honza, of the Czech Institute of Vertebrate Biology, and his coworkers have made a detailed study of this behaviour (Honza *et al.* 2007), using continuous filming at nests, and the following account is based on their work except where indicated. This egg-eviction behaviour, which may even take place in the presence of the adoptive parents without their doing anything to intervene, is responsible for the typical image of a cuckoo-parasitised nest: it contains only one chick, the cuckoo. It is important to note that such behaviour may be very costly to the cuckoo chick, not only in terms of the time and energy expended but also because it may be dangerous. The cuckoo chick's determination to do a thorough job sometimes results in it too falling from the nest (Wyllie 1981).

1)) Causal

What causes an animal to behave in a particular way?

2)) Ontogenetical or developmental

How does behaviour change as an individual grows and develops?

3)) Historical or phylogenetic

What is the evolutionary history of this behaviour?

4)) Functional or adaptive

How does this behaviour influence the chances of survival and effective reproduction by individuals?

Box 3.2. Tinbergen's four questions

3.4.1. The causal approach

Animal behaviour is highly complex and hence demands high levels of control and coordination as well making use of a great deal of information both about external environmental conditions and about the internal state of the individual. So, when we ask, what is the physical cause of behaviour, one answer focuses on the nervous system and hormonal system, which take charge of coordinating information received and bringing about the appropriate behavioural response. The resulting behaviour is actually performed by the locomotor system, both muscular and skeletal, and a great diversity of structures that make specific behavioural patterns possible. This, in summary, is the basic machinery responsible for behaviour. The nervous system integrates and coordinates both external stimuli and internal drives and thus oversees different behavioural possibilities, giving priority to some over others. Hormones affect motivation, among other things, and may increase or reduce the chances that a particular behaviour will occur.

Questions associated with the cause of a particular behaviour may be considered from a diversity of viewpoints, depending on what is of greatest interest to a researcher. Thus, for example, in the cuckoo case a neurobiologist would study the nervous system when exploring the relationship between the cause of the behaviour and its effect (how the chick receives stimuli and what changes occur in the nervous system to make the chick empty the nest of its competitors). An endocrinologist would study the hormonal changes that happen in the young cuckoo before it performs its behaviour. A cognitive psychologist would try to explain the mental processes responsible for egg-eviction. An experimental psychologist, after identifying which stimuli provoke the behaviour (detecting via the sense of touch that there is something else in the nest) would be interested in obtaining more information on the stimuli and mechanisms that result in the egg-eviction. He or she would design experiments that would establish exactly which stimuli are effective and which are not. In contrast, an ethologist might attempt to investigate such aspects as the influence of time and temperature, of the presence or otherwise of the adoptive parents, of the size of the eggs requiring expulsion (which varies according to host species) and of the depth of the nest wall that needs to be climbed.

3.4.2. The ontogenetical or developmental approach

The cuckoo chick does not set about expelling its nest companions the moment it hatches. Most authors say that it only does so some hours later, but Honza *et al.* (2007) have found that starts even later, after 40 hours on average. All observers agree however that the difficult task of climbing the nest wall with an egg on its back is performed with considerable effectiveness from the first attempt. Moreover, once the chick begins it works obsessively, hardly pausing even to eat. If eggs or host chicks are repeatedly replaced in the nest, they are ejected time and again, the cuckoo chick continuing to work until it may even die of exhaustion. However, the drive to perform this behaviour does not persist throughout the cuckoo chick's development in the nest, but tends to disappear after seven or eight days.

Several important points can be derived from the above information. The nervous and locomotor systems must be sufficiently developed to make the behaviour possible. Also the fact that the cuckoo chick can carry out the task highly effectively from its first attempt, without prior learning, implies that the behaviour is innate, that is to say it is instinctive. This is not to say that the behaviour is genetically determined in the sense of depending solely on the genes within the cuckoo. Rather, it means that the gene - environment interactions that occur during the development of the chick enable it to carry out a complex task the first time the chick responds to particular stimuli in the nest. In general, this is not always the case since behaviours often require prior learning before they can be carried out correctly.

The developmental approach to behaviour gave rise to three key concepts that mark the scientific beginnings of ethology: instinct, learning and imprinting. We shall now consider these briefly.

Instinct

Behaviour is heritable, as noted above. An instinctive behaviour is one that is genetically determined in a large extent and that does not require learning in order to be performed to perfection. The spiders' web example above is a classic case. The egg-eviction behaviour of the cuckoo chick also clearly illustrates the nature of an innate behaviour: a very complex process is carried out impeccably from the first attempt and, furthermore, with enormous dedication. Nevertheless, although the term 'instinct' was highly important during the period of classical ethology, it is practically never used in modern ethology since even behaviours that have a marked genetic basis need suitable environmental conditions for them to be carried out and their performance may vary according to such conditions.

Learning

Learning may be described as the modification of behaviour through experience. Very many behaviours, among them foraging for food and nest building, have been shown to increase in effectiveness through practice.

All animals are capable of learning. An example that illustrates this unequivocal statement come from studies of the nematode worm *Caenorhabditis elegans*, a very simple organism that lacks a brain. It has been studied very thoroughly and its nervous system is known to be comprised of exactly 302 neurons, interconnected in a pattern that seldom varies. Marie Gomez, of the Central Nervous System department of the Swiss company F. Hoffmann-La Roche, and her eight coworkers, showed that these worms were nonetheless capable of learning to find food. *C. elegans* is able to move around guided by the temperature of its medium. It was shown that when the worms found food somewhere which was at a specific temperature, they remembered it and thereafter showed a preference for environments that were at the same temperature. If the situation was altered and food ceased to appear at that temperature and was presented at another temperature, the worms progressively forgot the first temperature and starting preferring the new one. This whole process, involving both memory and learning, is regulated by the NCS-1 gene (Gomez *et al.* 2001). This illustrates what we have previously pointed out, that neither genes alone nor the environment produce a behaviour. The learning process associated with specific environmental conditions is also regulated by a gene (or genes).

Animals are capable of learning the most extraordinary behaviours (just see the videos of animals on *You Tube*), but learning requires some prior capabilities. There is a widespread myth that the learning capacity of humans is greatly superior to that of other animals but, this is not entirely true. For example, rats are better than we are at avoiding poison, carrier pigeons navigate in wide open spaces much better than we do, and few people can match the ability of bees to remember a wide range of food sources that they have only just discovered. In any event, it is important to realise that each species has evolved to learn only such behaviours as will tend to advance its reproductive chances in its environment. Natural selection does not favour individuals with excess learning capacity because the running costs of a nervous system are very high, both in terms of energy and nutrition. Rats do not learn to search for nectar nor bees to avoid poisons because such abilities do not benefit them in their environments (see Chapter 12 for a more detailed treatment of this topic).

Imprinting

In those vertebrate species in which the young are cared for by their parents the general rule is that the young do not immediately know to which species they belong and they must learn this during their earliest hours or days. They possess a special sensitivity during this brief period during which they tend to regard whoever or whatever they see as their parents. The mechanism by which animals ‘learn’ to what species they belong is known as ‘imprinting’. This type of learning was studied in detail by Konrad Lorenz, who collected eggs of greylag geese (*Anser anser*) and kept them in an incubator. When the goslings hatched they followed him as if he were their mother. In addition, Lorenz was able to show that such imprinting could be achieved with whatever sort of object (a box, a ball and even a flashing light) the goslings first saw during a relatively brief period after hatching. He also discovered that once imprinting has occurred, and the ‘sensitive period’ has passed, it becomes irreversible. Lorenz used these findings to present imprinting as proof that what is innate predominates over what is learned.

However, such reasoning proved to be neither so straightforward nor so clear. When Lorenz repeated his work with another species of waterfowl, the mallard (*Anas platyrhynchos*), he was surprised to find that mallard ducklings would not follow him. After much further experimentation he found that for imprinting to occur in mallard ducklings they not only have to see something that moves but also they have to hear the callnote specific to their kind.

We now know that the phenomenon of imprinting is much more complex and flexible than was first thought. Studies of brood parasites, to which we referred previously in this chapter, whose young are raised by individuals of a different species, have yielded very interesting information on imprinting. For example, it has been found that not all stimuli are equally effective (those offered by the true parents are far more effective than those provided by the adoptive parents), that the sensitive period may be delayed considerably and even that re-imprinting on the correct species may occur later, even during the juvenile period. Another member of the cuckoo family, the great spotted cuckoo (*Clamator glandarius*), is also a brood parasite like the common cuckoo. It lays its eggs in the nests of members of the crow family, which then raise the parasitic chicks. In studies of this species by my own research group we saw that adult great spotted cuckoos sometimes visited parasitised nests and they were also seen with the juveniles once the latter had flown. We interpreted such behaviour as being a necessary mechanism enabling imprinting by young great spotted cuckoos. It appears that, contrary to the belief that brood parasites are an exception and have innate knowledge of which species they belong to, juvenile great spotted cuckoos need contact with their own kind to help them to imprint on their own species. We tested this hypothesis experimentally by placing great spotted cuckoo chicks in the nests of magpies (*Pica pica*) in areas where the cuckoos did not occur (chiefly in Freneusse, France), so as to avoid any contact between the young birds and adults of their own species. As we predicted, once the cuckoo nestlings fledged from the French magpie nests they behaved as did the magpies' own young (remaining in the territory of the pair that raised them), instead of behaving as do cuckoo nestlings in places where they normally occur (here they form groups independent of the territories of the adoptive parents). This experiment showed that despite being brood parasites, great spotted cuckoos need to undergo imprinting in order to 'learn' to which species they belong (Soler & Soler 1999).

3.4.3. The evolutionary approach (phylogenetical or historical)

Behaviour evolves, as does every other characteristic of living beings. Hence a key question that ethologists may ask of any behaviour is how it began and how has it changed; in other words, 'what is its evolutionary history?' A generalized starting point is that complex behaviours, for example the songs of modern birds, have evolved from the simpler behaviours of their ancestral species.

There are two distinct ways of studying the evolutionary history of behaviour: by examining suitable fossils or by means of a comparative study of living species. The former has fairly limited application since, strictly speaking, behaviours do not fossilise; instead, on rare occasions, structures associated with behaviour may do so. For example, the origin and evolution of flight in birds has been studied by examining fossil wings and feathers of avian ancestors. The other way of deducing history, the comparative method, involves analysing a specific behaviour in living species that display it and comparing it with the behaviour of related species that do not exhibit the trait in question. Some general assumptions tend to be made; for example, that if the behaviour is very widespread then it was probably present in an ancestral species of all the current ones. On the other hand, if the behaviour is found in only one or a few species in a genus this probably means that it only evolved relatively recently. In this way it is possible to reconstruct the evolutionary history of a behaviour in a group of related species. Even ancestral states can be reconstructed from the behaviour of current species and the phylogenetic relationships.

A comparative study in relation to our example of egg-eviction behaviour by cuckoo chicks would be most interesting but the problem is that we lack enough information. Most genera of the subfamily Cuculinae (parasitic cuckoos) are known to show this behaviour but it is not displayed by at least two of them (*Clamator* and *Scythrops*). Unfortunately, no reliable information is available on the situation in many of the other genera of cuckoos.

3.4.4. The functional or adaptive approach

As we have seen, the evolution of different behaviours is the result of the process of natural selection. Many behaviours thus comprise adaptations that have been selected since they provide reproductive advantages for the individuals that perform them. Thus, the adaptationist approach (see Chapter 2) is based on asking what these reproductive advantages actually are. As noted previously, there are two principal approaches to answering these questions: the experimental method and the comparative method. Both involve proposing hypotheses that are then put to the test, in the former case through suitable experiments and in the latter by means of an appropriate comparative study.

Returning to the egg-eviction behaviour of the common cuckoo, the key question would be: ‘What advantage does the cuckoo chick get from behaving in this way?’ The benefit must be significant since, as we have noted, the behaviour is very costly. The benefit seems obvious, by ejecting its nest companions, the cuckoo gets all the food brought by its adoptive parents and does not have to share it. This benefit may well be decisive. The host species are small in size and their capacity to bring food to the nest is limited. The parasitic chick may grow to be ten times heavier than its hosts. It also needs much more food than the hosts’ chicks would require. It is thus easy to imagine the scenario in which egg-eviction behaviour may have evolved. The survival of the chicks of an ancestral cuckoo species that used small-sized host species, offering limited food-provision ability, may not have been very high. As soon as there emerged a rudimentary form of a behaviour, such as egg-eviction, which resulted in the parasitic chick receiving most of the food brought by its hosts, the survival chances of chicks that displayed it would increase. Such chicks would leave more descendants than those that lacked the behaviour, so egg-eviction would rapidly spread throughout the population. Natural selection would gradually favour individuals that improved the effectiveness of this mechanism and in this way the current situation evolved so that now all common cuckoo chicks hatch capable of ejecting all their nest companions. In other words, the behaviour is now universal within the common cuckoo for a simple reason: all cuckoo chicks are descendants of cuckoos who were capable of eliminating all possible competitors when they themselves were chicks.

3.5. Applied ethology

To end this chapter on the science of ethology it should be emphasised that the study of animal behaviour is not only important for its contributions to knowledge but also that it has made valuable inputs to such subjects as animal welfare, neuroscience, psychology, psychiatry, resource management, environmental management and the study of human behaviour. We shall consider the application of ethology to three of the most important of these.

3.5.1. Animal wellbeing

The concept of animal welfare has changed a great deal over recent decades. Formerly it was thought that animals were fine as long as they were neither ill nor injured. However, the drastic changes wrought by the emergence of modern systems of farming industry (such as overcrowding, confinement and social isolation) in rich countries have revealed the serious problems that may affect animals when they are kept in extremely unnatural circumstances. There have also been recent increases in biomedical investigations in which literally millions of animals, most of them mammals, are used as experimental subjects. These two developments, together with greater social concern for animal suffering, have encouraged a modification of our concept of animal welfare. It is no longer considered to refer solely to physical health but also involves an animal being able to experience a suitable environment.

These new concerns led to the emergence of the science of animal welfare, whose chief aim is diagnosing the physical and mental health of animals. In order to do this, indicators of physical health and other aspects of animal welfare, based on physiological parameters that quantify stress, have been developed and behaviours associated with pain, fear or frustration have been identified. We now also know that the basic needs of animals are more than simple physical requirements, such as water, food and a suitable temperature. It is also essential to bear their ethological needs in mind or at least to provide them with an adequate environment in which they can perform all their basic behaviours. Recent studies have made it clear that animals do not have to be able to carry out all types of behaviour, but they need to be able to perform those for which they are motivated at a particular time.

3.5.2. Conservation

Until quite recently, ethology was hardly involved at all in programmes for conserving endangered species. This was because ethologists have traditionally shown little interest in taking part in such programmes and conservationists have been little concerned with ethology. The situation has changed sharply and knowledge of animal behaviour is now considered so important that conservation programmes cannot ignore it. Awareness of territoriality, foraging behaviour, mateseeking strategies and suchlike is indispensable both when designing conservation action plans and when predicting the possible effects of any measures taken.

The following example illustrates the importance of keeping behaviour in mind in what is currently such an important field of knowledge as conservation biology. A group of investigators led by Isabelle Cote of the University of East Anglia, UK, were studying the conservation problems of a small European river fish of the blenny family, the river blenny (*Salaria fluviatilis*), with a view to proposing measures to halt the continuing decline of its populations (Cote *et al.* 1999). The most important problem confronting this species is habitat loss due to removal of stones and sand from rivers for use as building materials. Male blennies set up nests beneath stones and attract females to spawn there. The females lay their eggs under the stones and the males protect the eggs from predators and oxygenate them until they hatch. The investigators devised a model that simulated stone extraction, using data on stone distribution from affected (extracted) and unaffected areas. Without considering data on stone selection by males, no minimum size limit of stones was included and the conclusion of applying the model was that stone extraction had no effect. However, when the reproductive behaviour of these fish was borne in mind (males prefer to select the largest stones as nest sites) the conclusion reached by the investigators was very different. Reducing mean stone basal area from 200cm^2 to 50cm^2 would lead to a 47% reduction in nest density and a 75% fall in egg production. By comparing fish reproduction in extracted and non-extracted zones they found that extraction had an even more negative effect than the second, more realistic model predicted.

3.5.3. Human societies

Many of the problems of human society are related to the interaction between conduct and environment or, and this amounts to the same thing, between genetics and behaviour, which are the fundamentals of behavioural ecology. It is thus to be expected that ethological methods can be employed when studying social problems and human behaviour in general (see Chapter 1). Thus, for example, the adaptationist approach has given interesting results in studies of murder in human societies, and hypotheses developed in studies of infanticide in other species have been applied with considerable success to understanding the maltreatment and abuse of children (see

Chapter 1). The available statistical data have been found to correspond with what has been observed in other animals. For example, male child abusers are most often the current partners of the mothers and not the genetic fathers of the children involved.

In other cases the results obtained from studying the behaviour of different animal species have been applied successfully to understanding some of the problems of human societies. For example, studies of how chimpanzees and other primates engage in reconciliation after a dispute have helped in the development of new treatments and strategies aimed at reducing aggression between children in establishments, such as orphanages and schools for disruptive children, where this is a particular problem. Another example is seen in the classic works on social development in rhesus macaques in which it was shown that, given the choice, baby macaques preferred to cling to a terry cloth-covered metal doll than to an uncovered one nearby even though this mannequin offered the infant a milk bottle. Studies such as this proved to be of vital importance in advancing ideas on child development and for psychiatry in general.

Chapter 4. Reproduction, finding a mate and sexual selection

4.1. Introduction

Human beings, and all the living organisms on Earth, are the descendants of individuals which succeeded in reproducing themselves, thus passing their genes on to succeeding generations. This means that the most effective reproductive strategies have been under the influence of natural selection since the beginning of the evolutionary process.

When we speak of reproduction we immediately think of sex, of sexual reproduction, but not all organisms reproduce in the same way, other forms of leaving descendants exist. Reproduction is quite a complex process which, in one way or another, succeeds in transmitting an organism's genes to the next generation. Different species pass on their genes via a range of mechanisms (see below), sexual reproduction is the best known of these simply because it is the one we employ. From an ethological viewpoint and in a logical sequence, sexual reproduction comprises various stages: finding a mate, fertilisation and care for the young. Each of these receives a chapter in this book. Here, in addition to the different reproductive methods, we shall study mate-seeking and the evolutionary mechanism that directs the process, which is sexual selection.

4.2. Reproductive methods

Living beings have developed many reproductive methods in order to produce descendants, whose differences from their parents will be more or less considerable according to the method used. Box 4.1 summarises the principal methods and the genetic changes in descendants to which they give rise. The box only outlines the topic since it is incomplete. Furthermore, a species may use more than one method. For example, many plants and animals can reproduce both sexually and asexually.

Different reproductive methods have evolved in different species according to their habitats and ways of life, which is to say, they may be considered as adaptations that enable effective reproduction in particular conditions. This explains why such a diversity of methods exists, something that may seem strange to us. Thus, for example, there are species in which all individuals are both male and female at the same time; others in which sex changes (individuals start as females and later change into males), and vice-versa; others in which males are virtually non-existent and even others in which there are more than two sexes.

In general, all types of reproduction may be considered to come under either of two major types: asexual and sexual. The main difference is that there is no genetic exchange during production of descendants by asexual reproduction unlike sexual reproduction. Hence individuals resulting from asexual reproduction are genetically identical to their parents, whereas those produced sexually bear new and unique genotypes, such that almost every individual is genetically unique. There are some species in which both types of reproduction alternate, for example, the aphids (Simon *et al.* 2002).

Mitotic parthenogenesis: Females produce diploid eggs by mitosis, which give rise to offspring genetically identical to their parent.

Meiotic parthenogenesis: Females produce haploid eggs by meiosis that develop directly without needing to be fertilised by a male gamete. The offspring are nearly genetically identical to their parent.

Hermaphroditism: Individuals produce male gametes with which they fertilise their own female gametes. The offspring are nearly genetically identical to their parent.

Sexual hermaphroditism: Each individual produces both male and female gametes but there is no self-fertilisation: the male gametes fertilise the ova of another individual. The offspring are substantially different genetically from their parents.

Sexual isogamy: Males and females produce gametes of equal size that combine to give rise to fertilised eggs in which both parents have invested equally. The offspring are substantially different genetically from their parents.

Consanguineous sexual anisogamy: Males and females are related to a greater or lesser extent and produce gametes of unequal size that combine to produce fertilised eggs. Females invest much more than males, since ova are much larger than spermatozoa. The offspring are substantially different genetically from their parents, but less so than in the following method.

Non-consanguineous sexual anisogamy: Males and females are unrelated, produce gametes of different sizes and have descendants that are significantly different genetically from their parents.

Box 4.1. Some of the most important reproductive methods, indicating their consequences for the genetic differences between parents and offspring. Haploid: cells containing half the genetic complement of a particular species. Diploid: cells containing the full genetic complement of a particular species. Mitosis: asexual cellular replication. Meiosis: cell division giving rise to haploid gametes (two successive divisions result in four haploid gametes).

Female aphids, which feed by sucking plant sap, reproduce asexually in spring and summer, laying unfertilised eggs that give rise solely to daughters, which also reproduce the same way. This reproductive arrangement yields a rapid increase in numbers when conditions are favourable. The ability to produce only daughters, which in turn are capable of reproducing quickly themselves, allows a female to give rise to a much greater number of grandchildren and greatgrandchildren than would have been possible by producing both males and females through sexual reproduction. Furthermore, since such daughters are genetically identical to their mother, they share 100% of their genes with her, and not 50% as would be the case with sexual reproduction. Hence, asexual reproduction generates greater efficiency in producing descendants and in transmitting one's own genes to the next generation. Sexual reproduction lacks these two advantages and has a third important disadvantage: time and energy must be expended in finding a mate and achieving fertilisation, which is also risky since it increases the probability of attracting predators or of contracting infectious diseases (see Box 4.2. for more detail).

Why then does sexual reproduction exist? It clearly must confer some advantage in order to prevail despite the described costs. However, before answering this question (in the next section) we shall continue describing the aphid life-cycle, which will also give us some insight into these foreseeable advantages. The aphid reproductive system changes with the arrival of autumn, when the females lay eggs that now give rise to both sexes. These males and females pair-up and produce a new generation of eggs by sexual means. It is these eggs which overwinter and hatch early in the following spring.

COSTS	BENEFITS	
1	The chance of transmitting gene copies to the next generation is reduced by 50%.	
2	Finding a mate requires time and energy.	It gives rise to genetic variation upon which natural selection can act.
3	Courtship and pairing increases risks of injury and predation.	New gene combinations are created, which may enable solutions to environmental problems.
4	Sexually-transmitted infections may be contracted during copulation.	It permits harmful DNA mutations to be countered.
5	It provokes fierce intermale competition.	
6	It provokes major and costly conflict between males and females.	

Box 4.2. The most important costs and benefits of sexual reproduction when compared with asexual reproduction.

4.3. Why does sexual reproduction exist?

Contrary to what many may believe, sexual reproduction is not a relatively recent evolutionary development. Although the earliest organisms undoubtedly reproduced asexually, the appearance of descendants bearing a genome resulting from an interchange of genetic material between two or more reproducing individuals arose very early in the history of life on Earth, much earlier than the emergence of the first eukaryotic cells (those enclosing their genetic material in a nucleus). Currently, and again contrary to what many may think, sexual reproduction is not restricted to multicellular organisms but also occurs in some bacteria.

Given its widespread occurrence, it is evident that sexual reproduction has been an important evolutionary success. Nevertheless, the existence of sex is one of the great paradoxes of evolutionary biology, given that it has numerous and conspicuous disadvantages whereas its advantages are fewer and less obvious (see Box 4.2). Some twenty hypotheses have been proposed to explain the benefits of sexual reproduction and these fall into two categories: genetic and environmental. The most important are defined in Box 4.3 but we shall not explore the matter too deeply since, highly important though it is from the viewpoint of evolutionary biology, it is not so relevant to the behavioural aspects which are the theme of this book. It is enough to highlight a couple of conclusions. Firstly, sexual reproduction may be more or less adaptive depending on environmental conditions and on the demographic characteristics of each organisms' population. Secondly, maintaining sexual reproduction is not the consequence of a single factor but rather of a number of factors, so that some hypotheses may be valid for some organisms and different hypotheses for others. Nearly all hypotheses refer to an advantage of sexual reproduction which, in theory, amounts to an important disadvantage for asexual reproducers. Nevertheless, these latter have not only not died out but also, in many cases, they enjoy considerable evolutionary success, although less than that of sexually reproducing species. Asexuality tends not to spread since asexual species rarely give rise to new species. Furthermore, it is very difficult for asexual reproduction to reappear once sexual reproduction has evolved. The definitive answer to the enigma posed by the existence of sex still seems remote and much work remains to be done on the problem.

GENETIC HYPOTHESES

- Muller's ratchet: Harmful mutations will accumulate inexorably where reproduction is asexual but will be eliminated, thanks to recombination, by sexual reproduction.

The latter will give rise to individuals with various mutations, which may be less successful and leave fewer descendants, but it will also result in descendants free of such harmful mutations, and these will produce a greater number of descendants.

- Kondrashov's hatchet: The accumulation of mutations does not have a progressive effect but instead once their number reaches a certain level they become intolerable and individuals which pass this threshold die. In sexual reproduction, the elimination of harmful mutations is more effective since recombination spreads such mutations among all descendants and those that exceed the threshold die without leaving offspring.

- Accumulation of advantageous mutations hypothesis: Helpful mutations are much less frequent than harmful ones. In asexual organisms, for a helpful mutation to benefit descendants, it must arise in individuals with few harmful mutations, which is improbable. Also, for two advantageous mutations to coincide in the same asexual individual, they must have been produced in the same lineage. In contrast, in sexual organisms, thanks to genetic recombination such helpful mutations are as likely to coincide as to be separated from harmful ones.

ENVIRONMENTAL HYPOTHESES

- The lottery hypothesis: It is in the interest of reproducing individuals to produce variable offspring (especially when the environment is itself variable). Such variation, which is the consequence of sexual reproduction, increases the chances that some descendants may bear suitable genes to survive in the environment into which they are born.

- The Red Queen hypothesis: In antagonistic systems (those in which two species are mutually inimicable, e.g. parasite-host relationships), the variation resulting from sexual reproduction favours the emergence of new defences in the attacked party and new weapons in the attacking party (see Chapter 9).

Box 4.3. The principal hypotheses explaining the evolution of sexual reproduction, one of the great enigmas of evolutionary biology.

Both in this chapter, and in the two that follow, which deal with reproductive behaviour, we shall focus on sexual reproduction, which is the richer and more varied alternative regarding the behavioural strategies employed. We shall begin with its two protagonists, the two sexes: male and female.

4.4. What is the main difference between males and females?

In most species, males are quite different from females in various respects (in morphology, in reproductive organs and in hormonal make-up, among other things). Every year, when we reach the topic of sexual reproduction I ask my students 'what is the main difference between males and females'? After discussion between themselves they tend to come up with twenty or so differences but they usually fail to agree which is the most important (although from time to time some clever individual who knows the answer pipes up and stifles the debate). The following example will help us to answer the question in the manner of evolutionary biologists.

The anglerfish (*Lophius piscatorius*) is highly esteemed for its flesh, sold as monkfish, which may be found at fishmongers all year round. It has an enormous head with large jaws and pointed teeth, lacks scales and may be a metre long. This description matches those on the fishmonger's slab but it is not a complete description of the species since all those on sale are females. The males are very different, they are much smaller (by up to forty times) and they live attached to the females. When a male encounters a female it bites through on her belly, penetrates beneath the skin and takes up residence there. Little by little he degenerates until he is little more than a pair of testes. His circulatory system connects with that of the female, so that he can obtain all necessary nutrients from her bloodstream. In short, the male turns into a small lump in the female, ready to fertilise her eggs when she decides to lay them. He is a true parasite and was regarded as exactly that for a long time before it was discovered that he was the male of the species. A similar reproductive arrangement is found in the 200- plus species of this family (Lophidae). The differences between males and females are seldom so exaggerated. Normally there are many similarities between them although, however similar they may be, they always differ in ways that vary from one species to another. Nevertheless, there is one difference that never varies (except in very rare examples) and this distinction applies also to most plants: the type of gamete that each sex produces. Typically females produce a limited quantity of large gametes, the eggs or ova, which contain significant amounts of nutrients for the embryo. In contrast, males produce motile spermatozoa, consisting of little more than DNA and a store of sufficient energy to move. However, since sperm are not costly to produce they are generated in astronomical quantities. This last is no exaggeration. For example, according to the most conservative estimates, human males release some 180 million sperms per ejaculation (they are produced at a rate of some twelve million per hour), whereas human females produce a fixed number of ova during their lives, some 400 of them. All this means that just 20 ejaculations release 3,600 million sperm, more than enough to impregnate all the women of reproductive age currently existing on Earth. Some simple calculations have suggested that during the course of his life a single man may produce enough sperm to impregnate all the women who have ever existed throughout history.

On the other hand, it should be borne in mind that the males of our species are not especially prolific when it comes to sperm production. Far from it! Many species far outstrip us. For example, our closest relative the chimpanzee (*Pan troglodytes*) produces some 600 million sperm per ejaculation (and it copulates much more frequently that human males do), but it too is far from the most sperm-productive species. Male fairywrens, small Australian birds (genus *Malurus*) produce no fewer than 8,000 million sperm per ejaculation. But even this total is very low compared with the output of male domestic pigs, which transfer nearly half a litre of semen per copulation, containing some 750,000 million sperm! Considering these figures, it is an understatement to say that males can produce astronomical quantities of sperm.

Another important distinction between the gametes is in their size, which also presents overwhelming differences. In our species, whereas an ovum is almost visible to the naked eye since it measures one tenth of a millimetre across, a spermatozoan only measures some twenty-five thousandths of a millimetre in length, despite having a very long tail. In volume terms, the ovum is a million times larger than the sperm.

The difference in the sizes and numbers of gametes produced by males and females is the most important one between the two sexes, not only because it applies very generally and is seen in nearly all species but also because it determines the reproductive behaviour of both males and females and has very important implications. It means that, from the very start, females invest more than males in reproduction, to which we may add that females also invest significantly more than males in the subsequent stages of the reproductive process. This is evident in mammals but also in most other animal. Very often, the males' involvement in reproduction does not extend beyond fertilising the eggs. They could be said to be parasites, not in such a literal sense as in anglerfish males but because, as a general rule, they deliver little more than their diminutive and insignificant-looking gametes. Very frequently it is the females who have to provide all the necessary resources for the development of the offspring.

4.5. Seeking a mate

Sexual reproduction generally does not allow a living being to reproduce all by itself, it requires the fusion of two gametes, each donated by an individual of a different sex. Hence, males and females are obliged to engage with each other if they wish to leave descendants. Finding a suitable mate is not at all easy and the matter raises numerous questions. Among the most important of these are: is mate-finding as difficult for males as for females?, do males and females employ the same strategies?, and are the priorities the same for both sexes? As a way to introduce these questions, we will consider the case of the pied flycatcher (*Ficedula hypoleuca*), one of the best studied bird species.

The males arrive first at the start of the breeding season. They choose and occupy territories and sing frequently to advertise their possession, actively defending their space against other males if necessary. When the females arrive they immediately begin to seek a mate by visiting a number of different territories, and hence males. When a female hears a song that attracts her she approaches the male, who escorts her while he courts her, indicating the cavity that he has chosen as a nest site and showing her around his territory. The female may choose to remain with a male or to leave and find another. Should she decide to stay the male will have succeeded in finding a mate, but he may not settle for just her. Many males try to acquire a second mate, although only 10-15% succeed. A few even obtain three females (Lundberg & Alatalo 1992).

Having described mate-seeking in a species whose behaviour is typical we may now address the three questions that we raised previously. Clearly, the answer to all three is ‘no’. Males find it harder to obtain a mate than do females. They must arrive earlier, compete with other males for territories and then perform costly displays (in this case song which precludes feeding and may attract predators) until a female accepts them. Moreover, the two sexes do not use the same strategies, males must attract females and the females then choose their males. Finally, the sexes differ in their priorities: for females the priority is to find an adequate male (or territory), but males are concerned with attracting as many females as possible.

4.6. Sexual selection: competition between males and mate-selection by females

Why are there such clear differences in the mate-seeking behaviour of male and female pied flycatchers? It is because the reproductive potential of males and females differs. As we have already highlighted, the general rule is that females produce only a limited number of nutrient-rich ova and, furthermore, it is they who normally care for and feed the young. In short, the number of descendants that females leave depends above all on their capacity to raise them. As a general rule, males invest little or nothing into raising their descendants (although this is not so in the pied flycatcher, where male parental investment is considerable), and, as we have also pointed out, they make enormous quantities of relatively cheaply produced sperm. The males' situation is thus very different, their reproductive success depends above all on the number of females that they are able to fertilise.

In addition to the males' greater reproductive potential, another extremely important factor explains why males compete for mates and females choose them. The sex ratio, that is the proportion of females to males, is generally 1:1, one female per male. Clearly, if there were several females to every male then competition for mates between males would not be so intense.

Darwin proposed his 'theory of sexual selection' to account for the showy and extravagant ornaments shown by males of many species (the 'secondary sexual characteristics', which we will deal with later) since these could not be explained by his 'theory of natural selection', given that many of these adornments posed survival problems. He started from the premise that males compete among themselves for females while the latter choose among the former. However, Darwin never fully understood why this was so. It is explained by the arguments that we have previously expounded, which are the basis of the theory of sexual selection. Sexual selection may be defined as the selection pressure that acts upon characteristics that are solely related to increasing success in pair and the numbers of descendants that result. The intensity of sexual selection is determined by the relative investment of either sex in the reproductive process. It is strongest in the sex that invests least in raising the offspring.

The flycatcher example clearly shows how the process of sexual selection has two distinct components, competition between males (intrasexual selection) and mate choice by females (intersexual selection) (See Box 4.4). However, it must be emphasised that these two processes are not independent of each other. Indeed, very often the second is the direct consequence of the first. In many species in which the males play no part in raising the young, the female pairs with the male who succeeds in expelling any rivals. When a female African elephant (*Loxodonta africana*) is in heat she emits a loud trumpeting that attracts all the adult males in the vicinity. The largest and strongest male will succeed in driving away the competition and it is he who mates with the female.

SEXUAL SELECTION: that which acts on characters that affect the pairing-success and the numbers of descendants produced.

Intrasexual selection: competition between males for females.

- It acts by favouring the ability of one sex (normally the male) to compete for matings.
- Such competition may be direct (by fighting), or may be more subtle (for example defending a territory, defending resources needed by females or creating a social hierarchy).
- It is responsible for the emergence and evolution of weapons used by males in fights with other males (antlers, horns, tusks, spurs etc.)
- Where it is intense it often results in males evolving a larger size than females.

Intersexual selection: choosing of males by females.

- Acts to favour the characteristics of one sex (usually the males) that are effective in attracting individuals of the other sex (usually the females).
- Promotes (chiefly among males) the emergence and evolution of adornments that tend to be exaggerated and extravagant.
- Is much less evident than intrasexual selection and is much harder to explain (see Box 4.5).
- Females may base their choices on several secondary sexual characteristics at once.

Points to note:

- Both types of selection often act simultaneously.
- It is not always the males who compete and the females who choose.
- Post-pairing sexual selection may also occur when some characteristic of a pair member may influence future investment by the other.

Box 4.4. Definition and chief characteristics of intrasexual and intersexual selection, the two components of sexual selection.

Post-pairing sexual selection may also exist (Box 4.4). Juan Moreno, of the Museo de Ciencias Naturales in Madrid, Spain, and Jose Luis Osorno, of the Universidad Autonoma de Mexico, have suggested that the blue colour of her eggs may provide a signal indicating whether a female is in good physical condition, information that the male uses to adjust his parental investment in his mate's offspring. This idea rests on the fact that biliverdin, the pigment responsible for blue egg colour, is a powerful antioxidant. That a female could take on the handicap (see the 'handicap principle', Box 4.6) of using this costly substance to colour her eggs, instead of retaining it within her body to combat the free radicals responsible for oxidation, may indicate that she is in such good condition that she can afford to squander this valuable pigment for such a purpose. Hence, bluish eggs will indicate to the male that the eggs laid are of high quality and merit parental investment, from which it may be predicted that males paired with such females will work harder at feeding and caring for the chicks than would those paired with females who had not laid such blue eggs (Moreno & Osorno 2003).

4.6.1. Competition for females among males

In general males have to compete among themselves to obtain females, although there are exceptions, including species in which the opposite applies. Such competition may take a considerable diversity of forms: from direct fighting over females to trickery and the most subtle deceptions (such as joining forces with other males in order to steal the females of the most dominant individuals or even disguising themselves as females, see Chapter 5).

Two of the most frequent forms of competition include the defence of resources or territories, which the females need in order to raise their offspring, and the establishment of dominance hierarchies, which typically occurs in social animals that live in groups, including many mammal species, especially the primates. Males in gregarious species habitually weigh each other up and, as an outcome of these aggressive interactions, each learns from whom they must withdraw, since direct conflict would lead to defeat, and whom they could subjugate. This gives rise to a society with a clear hierarchy in which the most dominant individuals have preferential access not only to food but also to the females.

Susan Alberts of Duke University in Nairobi, Kenya, and her co-workers have shown, in a fairly recent study of a wild yellow baboon (*Papio cynocephalus*) population in east Africa, which not only do the higher ranking males copulate with more females but they also father most of the babies whose mothers were in heat when those males were present. When a female is in heat her genital area begins to swell and so becomes very visible to all males in the troop. The first males to notice are displaced by more powerful ones until the only one left is the most dominant individual who does not happen to be occupied with another female at that particular moment. He remains close to the female (mate guarding, see Chapter 5) copulating frequently with the result that he fathers her offspring in a high proportion of cases. DNA samples were taken from 213 babies born during the study period and from most of the males and females in the troop, in order to test this direct effect of the hierarchical rank on paternity. Molecular analysis, which is highly reliable, established who was the father of each baby baboon. The results were very clear (Alberts *et al.* 2006): topranking dominant males had 60% more offspring than the second ranked male, and three times more than the third ranked individual (thirteen levels could be distinguished in the hierarchy, without including the juveniles). Males of the sixth rank or lower produced practically no offspring at all.

4.6.1.1. Competition between human males

Our own species also provides examples of all manner of male-male competitions. Thus, direct competition involving violent conflict, which may even end in the death of one of the rivals, has been very frequent throughout human history. At other times competition among men is indirect. History books are full of cases where the powerful disposed of their rivals in order to usurp their women. Surely the most notorious case is that of King David who, the Bible tells us, was captivated by the beauty of Bathsheba, wife of the soldier Uriah, whom he sent to the most dangerous part of the battlefield. Uriah died and thus the king succeeded in acquiring Bathsheba. Such violent mating competition among men remains common today in hunter-gather communities as well as in modern societies. For example, some 40% of Yanomami males have participated in at least one murder and these have twice as many wives and three times as many children as those men who have never killed (Chagnon 1988). Our Western society is no exception here, it is well known that a high proportion of murders are inspired by sexual jealousy.

Competition to acquire resources or to acquire a high position in the social hierarchy is also important in our own species. Strong competition exists among men - more so than among women - for resources and for social status. A positive relationship has been demonstrated between wealth, or social status, and the number of children produced, both in traditional huntergatherer societies and in pre-industrial ones. Nevertheless, some studies have found that this latter relationship does not apply in various modern societies. However, methodological problems inherent in such studies have been identified recently and firm results have been obtained in favour of a positive link between wealth and number of offspring (see Nettle & Pollet 2008 and Chapter 2 for a detailed account).

A study that has yielded particularly clear and convincing results was conducted by Daniel Nettle and Thomas Pollet of Newcastle University, UK. They analysed a sample of almost 20,000 people born in England during the week of 3-9 March 1958. They examined educational attainment, salary and number of children at age 46. They found that men with higher salaries had more children that those with lower salaries, and a higher percentage of the latter had no children at all. Also, as in other recent studies (see Chapter 2), they found opposite results for women: those with higher salaries had fewer children than the lower-earners.

They also carried out a comparative study in which they calculated an index termed the ‘standardised linear selection gradient’, which allowed the intensity of natural selection on a character to be estimated for the English population and seven other human societies. They found that the selection gradient for wealth in men was lower in modern industrialised societies and higher in subsistence societies (hunter-gatherers, farmers, herders and fishermen), especially in those where a man could marry with several women. Nevertheless, they emphasise that even the lowest selection gradients obtained for this character were similar to those obtained in field studies of other animal species (Nettle & Pollet 2008). That is to say, natural selection has always acted, and will continue to act, penalising those men who are ineffective accumulators of resources or wealth.

With respect to competition, the strategy of alliance formation is frequent among male primates (see Chapter 7). In these cases, several males cooperate to overcome another male and acquire his resources or females. Without doubt, such alliances are most frequent and large-scale in the human species. Throughout human history, wars between settlements, tribes or nations have been provoked, more or less deliberately, to deprive neighbours of their resources. The anthropologist Marvin Harris provides much relevant information in his recent book (Harris 2006). Such conflict not only was, and remains, the norm: whole societies specialising in this system of pillage have existed as demonstrated by the Vikings and the Iroquois. In many cases too, another important motivation for conflict has been to steal the adversaries' young women, still habitual among the Yanomami today.

4.6.2. Male selection by females

The female of most species invests much more in her offspring than the male does, as we have indicated. Because the female is going to devote much time and many resources to caring for her offspring, we can expect that she should choose her mate with care. Making the right choice will determine her reproductive success to a large extent. For this reason, females often spend much time in finding a suitable male, irrespective of the energy cost and the risk incurred in moving around to visit several males. Evidence of such active mate-seeking by females occurs in groups as diverse as insects, fish, amphibians, birds and mammals.

A study by Patricia Backwell and Neville Passmore, respectively of Natal and Witwatersrand Universities, South Africa, provides a good example. They studied the mate-seeking behaviour of females of the fiddler crab (*Uca annulipes*). The males live in burrows and the investigators found that females visit several males before making their choice. On average each female visited 7.5 males, although one visited 24 different males (Backwell &Passmore 1996).

But on what do females base their choice of mates? We shall deal with this question in the next section. However, it must be stated that although females often do the choosing, it is not always the case. There are instances where males also are selective about their mates and even examples in which the males choose and the females compete for them. When might such a situation arise? Following on from the earlier argument, it is to be expected that the male will be choosy when he too invests in his offspring and that in those species where males care for their young (there are some, though not many) the females will compete for males and the latter will choose their mates (see section 4.6.2.3).

4.6.2.1. What is it about males that females select?

Blackwell & Passmore (1996) found that, in the case of females of *Uca annulipes* that we have just described, mate choice has two stages. Females first decide which male to approach according to his size (they prefer the larger ones). They then decide whether or not to stay according to the quality of the male's burrow. This example demonstrates the two types of features that females tend to consider when choosing males (see Box 4.5): resources (the burrow in this case) and good genes (male size here). Therefore, we can answer our previous question in few words. Females base their choice on the benefits that they may obtain (which does not imply a conscious decision; see Chapter 2) and these benefits may be direct (material) or indirect (genetic).

Direct benefits: resources

Females looking for a mate could benefit from acquiring any of the direct benefits specified in Box 4.5, since all of them may increase the number of descendants that they contribute to the next generation. A territory that is food-rich and that offers abundant hiding places and suitable breeding sites will be a good choice. For a female bird, such as the pied flycatcher, evaluating territory quality can be quickly achieved, but obviously this will not always be the case. There are many species whose capacity for movement is limited and these will have to rely on less direct and more subtle pointers when assessing territory quality. A very interesting example is provided in a study by Susan Walls and her collaborators of the University of Southwest Louisiana, USA, of the red-backed salamander (*Plethodon cinereus*). Walls and her team showed by experiment that females of this species are capable of determining the quality of a male's territory by inspecting his excrement. If the remains of poor quality prey, such as ants (which have too much exoskeleton and produce formic acid), abound in these deposits the females will move on. However, if they find a male's excrement with remains of more appetising prey, offering more nutrients and fewer toxins, they remain and look for the territory owner (Walls *et al.* 1989).

Direct benefits: Those that bring immediate advantage to the female, such as obtaining resources that she may use to improve her physical condition or her own survival chances or those of her offspring.

- A good territory offering abundant resources.
- A secure breeding site.
- Nuptial gifts.
- Parental care by the male.
- Fertile sperm.

Indirect benefits: Those obtained on a genetic level when the genes of the chosen male are passed to the female's offspring which benefit from their father's 'good genes'. Known as good gene selection.

- An attractive father who will be chosen by a female and who will pass his attractive qualities on to his offspring.

- A father of quality, who will be good at competing, avoiding predators and obtaining food, who will pass these qualities to his offspring.

- A disease-resistant father, who will pass such resistance to his offspring.

- A male whose genes complement those of the female, which will increase the viability of the offspring.

Box 4.5. Females choose males according to the benefits that they may obtain from them (which does not imply a conscious decision) and these benefits may be direct (resources needed to raise the young) or indirect (good genes).

If females choose males according to the resources that they value, it follows that males will compete among themselves to secure those resources, since these are what will allow them to obtain mates and leave descendants. The females of *Lamprologus ocellatus*, a small cichlid fish that inhabits Lake Tanganyika, breeds by laying her eggs inside snail shells on the lake bed. Such shells are the most important resource for females whereas the food they eat consists of current-borne particles that are equally abundant everywhere. Thus males strive to obtain shells. Bernhard Walter and Fritz Trillmich, of the University of Bielefeld, Germany, found that each male defends a small territory of about a square metre. He chooses shells and buries them partially in the sand with the openings pointing upwards. Each male endeavours to acquire more shells to bury in his territory. When an egg-laden female arrives, looking for a shell to move into and a male to fertilise the eggs when she lays them, the male unearths one of his shells and invites the female to stay. If she accepts, she moves into the shell and lays her eggs several days later and these are fertilised by the male. A male that owns several shells can continue courting more females. Hence, a fortunate male who owns several shells may fertilize the eggs of several females (Walter & Trillmich 1994).

Another type of direct benefit arises when males offer food or another type of nutritive resource to females during pairing (Box 4.5). Bengt Karlsson, of Stockholm University, Sweden, studied copulation in the green-veined white butterfly (*Pieris napi*) and discovered that a virgin male of this species can deliver a highly protein-rich ejaculate to a female, which is energetically equivalent to the seventy or so eggs that she lays. He was also able to show that the nutrients delivered by the male were used by the female to produce a larger number of eggs (Karlsson 1998). Such nutrient delivery, a kind of 'nuptial gift', is common in many insect species. Because the nutrients delivered to a female in the ejaculate tend to be used by her to produce additional eggs, the male investment not only benefits the female but also to the generous donor. He gets to fertilise more eggs than he would if he did not make his nutrient donation.

Nuptial gifts may sometimes be more substantial than nutrients transferred during or just before copulation. For example, in some spiders and scorpionflies, courting males present themselves to females bearing the largest and most appetising prey possible. After capturing a good prey item, males of the black-tipped hanging-fly (*Bittacus apicalis*), a scorpionfly, hang from a twig by their first pair of legs, holding the prey in their third pair. They emit a pheromone, a chemical signal, to communicate their readiness to mate to nearby females that approach and inspect the prey. As shown by Randy Thornhill, of the University of New Mexico, USA, a male may copulate for as long as a female keeps eating, which depends on the size and quality of the prey item. The more prolonged the copulation, the larger the quantity of sperm transmitted -and therefore the greater the number of eggs fertilized. However, when the prey is large enough, once the mating has lasted for the optimum period to fertilise the eggs, the male tries to make off with what remains of the prey. The female does not cooperate and tries to keep it, leading to a struggle (Thornhill 1976).

In some vertebrate species, especially birds, males share in caring for newly-born young (see Chapter 6). In such cases it is clear that it will benefit a female to choose a male who is disposed to invest much time and effort in caring for their offspring. That is to say, selection involves choosing a good father and therein lies the problem: how can a female know whether or not a male will be a good father? This is very difficult to evaluate, but females have shown themselves capable of doing so on many occasions. The selective pressure here is very strong since females who are capable of picking out and pairing with a good father will leave more descendants than those who choose a father who subsequently contributes little to caring for the young. Thus, in monogamous species in which both parents invest in feeding and caring for the young, behavioural norms have developed which inform the female during courtship of the predisposition of a male to be paternal. The nuptial gifts that we have mentioned above are an example. In birds the male frequently brings food to the female during courtship and it has been shown that this does not solely benefit her nutritionally but also allows her to evaluate the male's disposition to feed to the chicks afterwards. For example, David Green and Elizabeth Krebs, of Simon Fraser University, Canada, showed that the frequency with which fishes are brought by male ospreys (*Pandion haliaetus*) to females when courting correlate with their qualities as fathers. The greater the rate of prey delivery to the females, the greater the subsequent delivery rate to the chicks and the faster the nestlings grow before fledging (Green & Krebs 1995).

Courtship feeding does not occur in all bird species but recently another way in which a female may evaluate a male's paternal qualities has been identified, namely the nest-building behaviour of the male. A high level of involvement in nest building by a male is a good indicator to the female of his predisposition to invest in caring for the chicks (Soler *et al.* 1998). A bulkier nest will result if the male works a great deal at nest construction, and its size may act as a signal that allows the female to adjust her investment in reproduction. Our research group showed in an experimental study that after manipulating the size of the nests of magpies (*Pica pica*), the females laid fewer eggs in nests which we had reduced in size and more eggs in those which we had enlarged or in the control (unmodified) nests. Studies such as this show that females judge the males' disposition to work at caring for the young, and they lay more or fewer eggs according to this evaluation.

Indirect benefits: good genes

Conceptually the differences between both direct and indirect benefits are clear but it is worth noting that, when it comes to selecting a mate, a female will nearly always base her choice on a mixture of the two types. For example, given that males compete among themselves for territories and, in general, for the resources needed by the females, high quality males genetically speaking, may be expected to acquire the best territories and the best resources. It is therefore very difficult to conclude that a female has based her choice only on direct benefits. The salamander *Plethodon cinereus* offers a good example. We have used it as a case of how females obtain direct benefits, which it certainly is, but it was no simple matter to demonstrate this. The straightforward observation of males being chosen through their excrement was not convincing proof since these waste material also contain hormones that could serve as indicators of male quality and the female could in fact have been choosing a male for his good genes. The investigators carried out an ingenious experiment on captive salamanders that allowed them to conclude that mate choice was based on direct benefits. The same males were offered ants for a while and later termites over another period. The resulting faeces were collected and presented to females in pairs: one with ant remains and one with termite remains, both from the same male. In this way male quality assessment from the faeces was controlled. The females still preferred excrement with termites, showing that their choice was based on direct benefits (Walls *et al.* 1989).

As defined in Box 4.5, indirect benefits are those that females obtain through mating with their chosen males, whose genes are passed on to the females' descendants. Such indirect benefits are less apparent than direct ones. Can a female really derive genetic benefits depending on which male she chooses? The fundamentals of genetics tell us that the offspring of sexually reproducing species receive on average 50% of their genes from their father and 50% from their mother. Hence, if the female succeeds in being fertilised by a strong, fast, agile male who is a strong competitor, a successful forager and good at evading predators, as well as being attractive, then such characteristics may be passed on to the female's offspring, which in turn will have increased chances of survival and reproduction, thus resulting in numerous grandchildren for the female. In contrast, were she to be fertilised by a dud male, the chances of her offspring surviving and reproducing successfully would be much reduced and she quite probably would have no grandchildren.

In many species the males supply no direct benefits to a female or her offspring but, nevertheless, it is well known that the females do not pair with the first male they meet but rather that they devote time and effort visiting several various males, in order to choose the best one. Since such males only donate sperm to fertilise the female, her choice must be based on what the males' genes may contribute to supporting her descendants. But do females really choose males whose genes result in higher-quality offspring? The peacock (*Pavo cristatus*) has a starring role in debates about sexual selection. Peacock males provide nothing that might appear to benefit a female: they only donate their sperm. Their sole preoccupation is showing off by spreading their spectacular trains when courting females and then to fertilize as many as possible. In the early 1990s Marion Petrie of Oxford University, UK, carried out various studies of sexual selection in peafowl that were living under semi-natural conditions in a park. Her studies revealed that the males with the most impressive trains mated with a greater number of females. In a follow-up study, she showed that males whose fathers had the most striking trains - with a greater number of eye-spots - grew and survived better than the sons of males with less showy trains. She reached this conclusion by isolating single males and females together at random, thus compelling some females to pair with showy males and others to do so with less attractive ones. To ensure that female quality during brooding had no effect, the eggs were placed in an incubator and once they had hatched all the chicks were raised in captivity under the same conditions. The first interesting result was that the sons of males with most elaborate trains grew more rapidly than those of males with less spectacular trains. Once the chicks had grown she released some of them into the free-living population in the park. She monitored each of them and found that the sons of the showy males survived better than those of the less attractive ones (Petrie 1994). This study thus demonstrated female mate choice for good genes.

4.6.2.2. How do females choose good genes?

The peacock example that we have studied in detail is only one of many recent studies which have shown that females choose males on the basis of their genes. Nevertheless, although the idea of obtaining genetic benefits seems quite reasonable, clearly females cannot inspect the males' genome directly in order to base their decision on actual genetic information. We can therefore ask two questions: 'what do females go on when selecting good genes?' and 'what mechanisms direct such choices?' The answer to the first question is that females base their choice on adornments, the often striking and extravagant structures displayed by males of many species - which go under the name of secondary sexual characteristics (see below). The second question is very difficult to answer given that it deals with a highly complex and controversial topic. A long list of mechanisms has been suggested and the results of numerous studies, both observational and experimental, have been published supporting one or other of the various proposals. Still, none is generally applicable, it is difficult to distinguish between them and the mechanisms are not incompatible i.e. several could be acting at the same time in a given species. The following two sections are devoted to these two problems. We shall first consider the secondary sexual characteristics themselves and then the mechanisms proposed to explain the selection of good genes and hence the evolution of those secondary sexual characteristics.

Secondary sexual characteristics

For many species it is easy to tell males from females since they do not look alike. These differences may be the outcome of natural selection, sexual selection or both. Few distinguishing features are solely due to natural selection. An example might be the brood patch, the bare belly region that female birds develop (in species in which incubation is done solely by females) when incubating to allow their eggs to be in direct contact with their skin. Differences due to both types of selection acting together are more numerous. For example, the body size difference between sexes that exists in many species, symmetry and motor coordination are as much due to natural selection as to sexual selection. Undoubtedly, however, most differences and especially the obvious ones are due almost exclusively to sexual selection. These are the typical secondary sexual characteristics which include weaponry (horns, enlarged mandibles, tusks etc.) developed by males in many species for inter-male contests; structural ornaments (tail ornaments in birds, fin ornaments in fish, crests in amphibians) and striking coloration that may or may not accompany these structural features. Secondary sexual characteristics based on auditory and olfactory signals have developed in numerous animal groups. Auditory signals are especially developed in insects, birds, some fish and many amphibians and mammals, whereas olfactory signals are more often exhibited by male reptiles and mammals (see Chapter 11).

A final group of secondary sexual characteristics, those based on behavioural displays, is also worth highlighting. These often accompany structural ornamentation and striking coloration since males often perform dances, leaps and other movements, which serve to display their adornments in all their splendour. Sometimes, however, such secondary sexual characteristics may solely comprise an exaggerated and extravagant behaviour without accompanying structures. A good example is provided by the black wheatear (*Oenanthe leucura*), a bird species in which females base their investment in reproduction on the quantity of pebbles that males are capable of transporting in their presence (see Chapter 2).

The most exaggerated and extravagant secondary sexual characteristics occur in species in which the males invest nothing in parental duties whereas in monogamous species, where males collaborate in feeding and caring for the young, secondary sexual characteristics are much more discreet. Furthermore, in those species where the males invest in parental care and are themselves selective in mate choice, the females too may develop more or less exaggerated ornamentation. Why do females select males according to the latter's secondary sexual characteristics? In the case of the black wheatear above, it is evident that the male demonstrates his physical fitness and disposition to work through his pebble-carrying display. More generally, secondary sexual characteristics are indicators of fitness or quality. Most studies show that females choose them because they are honest indicators, which implies that they must be costly to produce and maintain. Clearly pebblecarrying is costly for the male black wheatear since it requires considerable energy consumption. But what about brightly coloured and extravagant ornaments? They too are costly and in more ways than one. First, they may make an individual more conspicuous to predators. Also, developing such adornments may consume essential nutrients that have other specific functions, for example in defence against disease and parasites (see 'the immunocompetence handicap hypothesis' in Box 4.6).

A relationship between exaggerated ornamentation and reduced survival chances is to be expected since the former poses problems of camouflage and escape from predators. Nevertheless, where this has been studied it has been found that within a given species those males with the most highly developed ornaments are those which survive best (Jennions *et al.* 2001). This is because secondary sexual characteristics are honest indicators of quality and hence individuals with the most extreme ornaments are also the best survivors despite producing a trait that is costly to make and maintain. Thus, the only way to demonstrate that ornaments are indeed costly and have a negative effect on viability is by an experiment in which individual quality can be controlled.

Anders M0ller of Pierre et Marie Curie University of Paris, France, and Florentino de Lope of the University of Extremadura, Spain, carried out an ingenious experimental study on the barn swallow (*Hirundo rustica*), in which they demonstrated the costs associated with the exaggerated tail shown by males of this species whose tail is some 20% longer than in females. Earlier studies by Anders M0ller and his coworkers had already shown the importance of the tail in the context of sexual selection. Thus, for example, longer-tailed males succeeding in pairing earlier and with higher quality females and, in addition, they were the ones who most often indulged in extra-pair copulations (i.e. mating with females other than their mates. See Chapter 5). To determine whether the long tail incurred a significant cost independently of male quality, they manipulated tail length. Males were divided into three groups: the tails of one group were shortened, those of another group were lengthened and those of the third group were untouched. Thus males had tail lengths that were unrelated to their own quality, since the type of treatment received by each individual was decided at random. Once the experiment had run its course they found that males with lengthened tails had less chance of being alive the following year than those whose tail had been shortened. They concluded that a longer tail is costly for male swallows (M0ller & de Lope 1994).

Why have multiple adornments?

Males of different species very frequently exhibit more than one type of ornament. An exaggerated structure is usually accompanied by striking colours and some kind of acoustic signal. One of the ornaments normally overshadows the rest but sometimes there may be several highly developed types. The most extreme example is surely the lyrebird (*Menura novaehollandiae*), a large Australian passerine bird. The male has a majestic lyre-shaped tail formed by the two external tail feathers and twelve central ones comprising a fine tracery. He also has a very showy appearance with grey, brown and white markings. Male lyrebirds do not contribute at all to caring for the young and instead dedicate all their efforts to attracting and pairing with as many females as possible. They establish a small area on the forest floor which they keep clear of leaves and twigs and where they perform their displays. When a female appears they raise their tails so that the feathers form a lacy veil over their heads. They then begin to perform an elegant dance, all the while emitting the most varied vocal repertoire, which includes imitations of many of the sounds of the forest, from the song of other species to the sound of a chainsaw.

Since an ornament may be an honest indicator of male quality, why have multiple ornaments? We are still far from answering that question but three possibilities have been proposed to date. Firstly, perhaps each type of ornament provides information on a different attribute of the male. Secondly, different secondary sexual characteristics may provide redundant information but may enable the honest signal to be evaluated more easily by the female. Finally, some of the characteristics may provide no relevant information at all about the male and instead may be evolutionary relicts of ornaments that were functional in the past.

Mechanisms proposed to explain mate choice for good genes

The topic of mate choice for good genes has attracted much investigation and various alternative hypotheses. Nevertheless, although all these explanations have attracted some support, none so far has been so broadly applicable as to be regarded as definitive. Attempting to analyse the various ideas by commenting on examples of the experimental studies supporting each of the hypotheses would lengthen this chapter excessively. Thus I have opted for Box 4.6, where the theoretical background is treated in more detail than usual, and less attention is given to the topic in the text.

Fisher's runaway selection model suggests that a female will select a very attractive male simply because her offspring will then also be attractive and will be selected by many females and leave her many grandchildren. The alluring character need not be an indicator of anything, it need only be attractive to females. In contrast, models based on mechanisms indicating good genes assume that the offspring of a female who has been fertilised by an attractive male will not only be themselves more attractive but they will also have inherited other advantageous characteristics that will allow them to enjoy greater chances of survival.

4.6.2.3. It is not always the males who compete and the females who choose

Since we began considering sexual selection we have been applying the general arguments that are the basis of the theory. For example, females invest more than males in reproduction and males may increase the numbers of their descendants by mating with more females, whereas females can only increase their reproductive success by choosing higher quality males and securing the best resources.

The runaway selection model: This model, proposed long ago by Ronald Fisher, suggests that females select attractive males, that is those with highly developed secondary sexual characteristics, not because these are indicators of good genes but simply because they are attractive. He proposed the existence of a genetic relationship between the genes that determine the preference of a character by females and those genes that determine the development of that character by males. This genetic relationship would be mutually self-reinforcing, favouring very rapid evolution (which is why it is described as 'runaway').

Mechanisms indicating good genes: This group includes various models whose starting point is that features which make males attractive are indicators of genetic quality (see the peacocks' train example in section 4.6.2.1.2). In order to be honest indicators such features must be costly to develop and/or maintain. An important theoretical problem here is that such mechanisms imply very strong directional selection, which is to say, if males with the most exaggerated characters are always selected, genetic variability will soon disappear, which would mean that females gain nothing by being choosey. This has been termed the 'lek paradox' since it is especially striking in species that pair at leks (see Chapter 6).

- The handicap principle: Amoth Zahavi proposed that the most exaggerated ornaments are burdens that reduce the survival of the males which bear them. Hence, a male whose ornamentation is more exaggerated than that of other males is indicating that he is very fit since he is capable of surviving despite the handicap of his ornaments.

- The parasite-resistance model: William Hamilton and Marlene Zuk suggested that attractive adornments and showy colours indicate the absence of parasites to the female and hence that the male has parasite resistance that he may transmit to his descendants. This model offers a possible solution to the lek paradox given that parasites differ each year and in each area and so resistance to them would not be uniform.

- The immunocompetence handicap hypothesis: This proposes that since the development of ornamentation is under the influence of the endocrine system, investing heavily in such adornments may prejudice the immune system. There are two important versions of this hypothesis. One is related specifically to testosterone, a hormone that has the effect of exaggerating sexual display behaviour while also having a negative influence on the immune system. The other is related to carotenes, the pigments responsible for structures coloured yellow or red. Carotenes are not manufactured in the body but have to be ingested in the diet, thus an important trade-off exists between dedicating these chemicals to sexual signals or to their important role as antioxidants.

- The fluctuating asymmetry model: Many studies, both descriptive and experimental, have shown that in a great diversity of organisms (insects, fish, birds and mammals) the females select symmetrical males (those with a low level of variable asymmetry) and hence the greater the symmetry of a male, the greater his attractiveness, and consequently the higher his reproductive success. The biological justification for the preference for symmetry is that, in theory, an individual who has grown up in perfect conditions should be entirely symmetrical. Hence any deviation from perfect symmetry would be the outcome of problems encountered during development and indicate that a potential partner could be defective in some way.

Genetic compatibility mechanisms: It has been demonstrated in diverse organisms, humans included, that females may select males on the basis of their genetic complementarity (the match between the male and female genomes) because this brings advantages in the form of greater fertility and increased viability of progeny. The clearest results have been obtained in studies of the Major Histocompatibility Complex (MHC), a group of linked genes strongly associated with the immune system and resistance against disease.

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Direct phenotypic effects: As Fisher suggested, females may begin choosing a male adornment because, at first, this structure could offer a direct benefit. For example, in a bird a slightly longer tail might experience some advantage in flight. Also an ornament could indicate certain abilities of a male when the time came for it to carry some material benefit.

Exploitation of female sensory biases: A male ornament may confer an advantage simply because it offers something that females already tended to seek. That is to say, if for whatever reason females prefer some existing characteristic, be it for its form or colour or whatever, that males with that character will be preferred as soon as they happen to acquire it.

Box 4.6. Some of the most important mechanisms proposed to explain the selection of males by females based on genetic benefits. Two hypotheses that may explain the origin of secondary sexual characters are also included.

These are general rules but it is important to emphasise that they do not always apply, for two reasons. Firstly, there are exceptions that do not contradict sexual selection theory but instead support it, since they fulfil predictions derived from it. Secondly, because recently published studies have shown that, contrary to the standard view, both competition between females for access to males and mate-selection on the part of males are more frequent than was supposed (Clutton-Brock 2007).

An impressive study relating to the second point is the work by Leah Domb and Mark Pagel, of Harvard University, USA, and Reading University, UK, respectively, on sexual selection in the yellow baboon. In this species, as noted earlier in this chapter, females in heat develop a striking pink genital swelling. The authors thought that this could comprise an ornament indicating female quality, similar to the very different ornaments exhibited by males. They found that the females with the largest swellings began breeding earlier and their offspring had better survival prospects than those of females with less developed swellings. They therefore concluded that the swelling is a sexual ornament that indicates a female's reproductive potential. Accordingly they also found that males fought longer over the females with the most prominent swellings. An important question is 'why do females develop a costly ornament - it may amount to 14% of their body mass - that indicates their quality honestly, as do those of males, if it is the females who do the selecting? The answer suggested by the authors is that given that contests between males are costly, such a signal serves to motivate a dominant male who may already be with a female in heat. A female who displays her greater reproductive value may ensure that the best males compete for her and that her offspring's parent will be the fittest male of all (Domb & Pagel 2001).

In accordance with the first reason given above, there are important exceptions to the general rule that males compete and females select, which nevertheless do not contradict sexual selection theory. It is certainly the case that when males make a significant parental investment, it may be predicted that such males will not accept just any female. We can also predict that in such circumstances it will be the females who will fight among themselves to acquire a preferred partner. This most extreme case of this sort is known as 'sex-role reversal'. A particularly striking example is provided by the jacanas, members of the bird family Jacanidae. Sexrole reversal has been documented in seven of the eight jacana species. In these the males perform all parental care, including incubation and care of the chicks. The females, who are substantially larger than the males, fight among themselves and defend large, food-rich territories. Within a female's territory, the males defend their own territories against other males. If a female's territory is sufficiently large and rich in resources it may include up to four male territories, that is to say the female possesses a 'harem' of four males. She will copulate with one of them and lay a clutch for him to care for. She will then lay another clutch into the care of another male, and so on successively (an instance of polyandry; see Chapter 6).

The above examples allow us to draw a very important general conclusion: although normally males compete and females select this is not always so but rather depends on the parental investment of either sex. If males invest more than females, it is the males who will be selective and if it is the males alone who care for the young, they will be as selective as the females of those species where care for the offspring is a female responsibility. In such cases it will be the males who are selective and the females who compete for mates, the opposite of the more general situation. Nevertheless, where both males and females invest in parental care, both sexes may evolve mate choice behaviour and both may evolve appropriate secondary sexual characteristics.

4.6.3. Mate selection in humans

This topic is highly controversial. The approach presented here may even damage romantic sensitivities. Therefore I want to begin by clarifying two points. First, mate-seeking in our own species, both in the short and long terms, is not wholly a conscious decision. Secondly nobody should take what we conclude in this section personally; although we make generalisations here, remember that they are always from the point of view of statistical tendencies and there may be many exceptions to the general rule.

The first point, that not all human decisions need be conscious ones, needs to be clearly understood and is worth dwelling on briefly. To make this point, we shall examine a now famous study that was carried out by Claus Wedekind and his co-workers at the University of Berne, Switzerland, who examined the influence of the Major Histocompatibility Complex (MHC; see Box 4.6) on pair formation in humans. Couples with varied MHC genes are capable of producing children who have a greater diversity of defences against parasites than do those whose genes are more similar. Hence, if a female were able to choose a male with an MHC distinct from her own, she would tend to have children who were more resistant to diseases and parasites. This idea had received strong support from a study of mice (Potts *et al.* 1991), and Wedekind and his team designed an experiment to see whether there was a similar effect in humans.

The study was carried out on students of their own university. Males were given a T-shirt which they were asked to wear for two consecutive nights and during this period they were not to wear either deodorant or perfume nor were they allowed to drink alcohol or smoke, or do anything else that could mask their personal body odour. After this the members of a group of females were each given six of the T-shirts and they were asked to rank them according to how attractive they found their odour. The investigators found that the most attractive T-shirts to those females who were not taking contraceptive pills were those worn by males whose MHCs were most different from their own. Moreover, the odour of males whose MHC was most different resembled that of the female's current partner more closely than that of males whose MHC was more similar. This finding provides quite strong support of the fact that the MHC can also influence unconscious mate choice by women today.

What I wish to emphasise after describing this example is that the women who took part in the T-shirtodour study were unaware of both the identity and the appearance of the T-shirt wearers, still less were they able to compare the MHCs of the latter with that of their current partner. This example thus allows us to conclude that even in our own species, which we like to regard as intelligent and conscious of everything we do and decide, in these matters -as in many others- we very often take decisions that are not entirely based on reasoned evaluations and conscious reflection. Often even the most preconsidered decisions are based, at least partly, on evolved psychological mechanisms that supply adaptive solutions for the problems implicit in reproduction.

After all, today's humans are the descendants of ancestors who were successful when it came to producing surviving offspring. Leaving progeny is no easy matter since, among other things, it requires finding a suitable mate, competing with same-sex rivals and ensuring that conditions are right for raising offspring successfully. Therefore, the selective pressures that have acted over the long period of human evolution should have given rise to numerous psychological and behavioural adaptations that shape how we behave when pairing off and reproducing.

In order to understand human pair-selection strategies we need to bear in mind the theoretical considerations emphasized throughout this chapter since these explain a large part of the strategic differences between men and women. For example, in accordance with the general rule, since human males, along with those of most other species, produce large amounts of sperm, they could increase the number of their descendants by impregnating more women. In contrast, women produce a limited number of ova and cannot increase the numbers of their offspring by increasing the number of men with whom they have sexual relations. Instead, ours is a species in which the females, in accordance with the general rule, invest considerably more than the males in producing descendants, although human males, unlike those of most other mammals do participate in parental care.

The theoretical considerations highlighted above indicate that although natural selection will favour those men and women who leave most descendants, the two sexes should have different strategies for achieving this since they are subject to different selective pressures. Women may attain this outcome if they choose men who make an effective contribution to parental care or whose genetic contribution is of high quality. Men, on the other hand, will maximise their reproductive success by impregnating as many fertile women as possible.

Applying this evolutionary theoretical framework has reshaped the intellectual and scientific environment of the academic discipline of psychology. It has resulted in hundreds of hypotheses and predictions that have been translated into thousands of papers in specialised scientific journals, which are making a major contribution to helping us to know ourselves much better. This new approach has given rise to the discipline known as 'evolutionary psychology'. Before studying human pair selection, the most interesting aspect of sexual selection, we shall examine one of the most general predictions that arise from the theory we have studied. It may be predicted that, as with most males of other species, men will have a greater predisposition to have sexual relations with many women, whereas this promiscuous tendency will be much less marked in women. Is this prediction fulfilled? The answer is a resounding yes and many studies support it.

One of the most conclusive was an experimental study published by Russell Clark of Florida State University, USA, and Elaine Hatfield of Hawaii University, USA. They enlisted a group of attractive youths of both sexes to act as lures. Each of these young people, very smartly dressed, would approach another youngster of the opposite sex who happened to be alone.

After an opening line of 'Hello, I've been seeing you around the campus and I find you very attractive', they would ask one of the following three questions: (1) 'Would you like to go out with me?', (2) 'Would you like to come to my apartment?', or (3) 'Would you like to have sex with me?'. There were no differences between boys and girls in the replies to the first question (50% said yes in both cases). However, the responses to the other two questions were very different, in accordance with our initial prediction. Only 6% of the young women answered yes to the invitation to the apartment and none at all (0%) accepted the direct offer of sex. In contrast, 69% of boys accepted the offer of accompanying the girl to her apartment and 75% agreed, probably enthusiastically, to have sex with her (Clark & Hatfield 1989). These results clearly support the prediction that men are always more inclined than women to have sexual relations.

4.6.3.1. What do women and men choose when looking for a permanent partner?

Mate-seeking strategies are complex in human beings but in general both men and women exhibit two distinct types, those culminating in long-term relationships and those leading to brief sexual encounters. We shall deal with the former in this section, those strategies that give rise to more lasting relationships within which normally children are born and raised. Such lasting relationships may begin as a result of what we call 'falling in love', a favourite theme that has inspired poets and artists and one long regarded as among the most sublime sentiments of the human soul.

We may, however, need to lower the concept of love to a less sublime and more earthly level. First of all, what does falling in love entail? No doubt most of you have been in love and you will have your own particular answers to this question - all of which will be correct. For two people to fall in love means: attaining the seventh heaven, living in a permanent state of euphoria, unleashing a tempest that disrupts and upturns their lives, a rebirth of youth (in more mature couples), an avalanche of joy and enthusiasm, and so on. Still, let us examine it coolly from a more distant viewpoint, that is to say, without reference to ourselves but rather as we see others who are in love. We tend to say that they seem crazy and that they neither know nor care what they do, although we also tend to add that they seem very happy. How would an impartial observer describe love? Imagine an extraterrestrial scientist who sets out to observe human couples in love. After studying a sufficient number of cases over a long-enough period he would no doubt describe their state as a transitory deviation from the norm characterised by a very high frequency of copulation, a certain generalised hyperactivity and a reduced need for sleeping and eating, all worthy of psychiatric investigation.

With that I think we have lowered love from its romantic pedestal but we can lower it still further if we ask ourselves what are the physiological causes of this state of mind. Neuroendocrinology has made enormous advances in this field and without going into the details, we can say that falling in love is chiefly directed by neural pathways whose principal chemical neurotransmitter is dopamine. This is to say that the pathways involved are those of the brain's gratification systems (Tobena 2006). Hence the adaptive mechanisms of the brain are responsible for lovers feeling happy and besotted with one another.

What makes one fall in love? I doubt that anyone believes in Cupid's arrow, but when you ask people why they have fallen in love with their chosen partner they are uncertain and find it very hard to reply. If furthermore they are asked why they fell in love with this particular person and not with one of the many others whom they knew at the time when they will be unable to answer - each of you can try this exercise with respect to your partner. True love, in which one person rather than another bowls us over at a particular moment, is chiefly an instinctive response to a complex series of stimuli provided by the beloved.

We can nonetheless study pair-seeking strategies in both sexes. These are highly diverse and they vary not only between men and women but also according to whether a companion is being sought for a long-term relationship or for a casual sexual encounter. In addition, various factors influence the selective behaviour of both sexes: nationality or culture, the sex ratio (the number of women divided by the number of men who are seeking mates), the richness in resources of the area and the risk of contracting infectious diseases. None of this means however that it is impossible to generalise since many clear strategies are detectable in all human populations, independently of geography, culture and other factors.

A great deal of information exists on mate-choice in humans. The abundant published studies generally involve either circulating questionnaires with a series of questions comprising the object of study or analyses of mate-wanted advertisements in newspapers or on the Internet or statistical studies of some aspects or experimental studies such as the one in the previous section.

Box 4.7 sets out ten characteristics that stand out as the most important for mate-selection in both men and women, specifying their relative importance to either sex and the degree of their universality, i.e. whether or not they figure in all cultures. We shall then examine one of the most interesting aspects from this box.

CHARACTERISTIC	IMPORTANCE TO MEN (0-3)	IMPORTANCE TO WOMEN (0-3)	IS IT UNIVERSAL? (YES IF FOUND IN MORE THAN 95% OF CULTURES)
Wealth and resources	1	2.5	YES
Possibilities for acquiring resources	1	2.5	YES
Ambition and competitiveness	0.5	2.5	YES
Height and strength	0	2.5	YES
Beauty and physical attractiveness	2.8	1.5	YES
Youth	3	0	YES
Virginity or chastity	1.6	1.3	NO
Intelligence	2	2	YES
Likeability and understanding	2	2	YES
Being a good person	2.3	2.3	YES

Box 4.7. Characteristics used in mate-selection by women and men. The relative importance of each characteristic when choosing a mate is specified (on a scale of 0-3). The universality of that characteristic, i.e. whether or not it applies generally and arises independently of culture, is also given. Information based on diverse sources but principally on the study of 37 different cultures by Buss et al. (1990).

All the characteristics display the trends and relative importance predicted by evolutionary theory, both for males and for females. Before going into details, a general finding is that all those characteristics related to the selection of direct benefits (resource availability, possibility of acquiring resources, the ambition and competitive of a potential partner) are much more highly regarded by women than by men, whereas characteristics related to physical attractiveness are more highly valued by men than by women (Box 4.7). Dozens of published studies support these general trends, which apply to all nations and in those indigenous communities where they have been studied. By way of example we will consider a study by I. A. Greenlees of Stirling University, UK, and William McGrew of Miami University, USA, based on an analysis of the 'lonely hearts' advertisements of a newspaper. They found that women sought financial security more often than men did (33% of women v. 9% of men) and that in their own advertisements men offered financial security more often than women did (69% v. 43%). Physical attractiveness was sought by 49% of men and 33% of women but was offered by 71% of women and 50% of men (Greenlees & McGrew 1994). This study thus shows that not only are resources more important to women than to men, and physical attractiveness more important to men than to women, but also that each sex offers what the other chooses with greater frequency.

The two characteristics in the summary in Box 4.7 which differ most in the preferences of men and women are height and strength, which women clearly select (for a women the ideal mate is a man taller than herself where for a man a shorter woman is preferred), and youth, which only men select preferentially. Height and strength offer both direct and indirect benefits to women. A tall strong man would bring her more effective protection against enemies and predators but, in addition, would bring her genetic benefits since her offspring could inherit these positive attributes.

All studies also show clear differences between the two sexes regarding the preferred age of their mates. A woman prefers a man older than herself but a man chooses younger women. Both tendencies are directly predicted by evolutionary theory. Women prefer older men because these already have the experience, status and accumulated wealth that permits them to provide greater resources for their children. Men prefer younger women since these are more fertile and hence of greater reproductive value.

Several studies have supported these predictions. A recent work by Samuli Helle of Turku University, Finland, and his collaborators has produced very convincing results. They analysed the registers of weddings, births and deaths in the Lutheran churches of northern Finland, a region inhabited by the Sami, a people that lived from their reindeer herds, hunting and fishing. They were monogamous since they were prohibited by law from remarriage except after a spouse died. The researchers analysed the data for 706 couples who had only married once. Each couple produced 5.6 children on average, with a range from one to fourteen. The most fertile couples were those where the man was about 15 years older than the woman. This is a substantially greater difference than that found in other similar studies, where the range is from two to six years, probably because of the special characteristics of the Sami population. The authors concluded that 15 years was the optimum age difference since it implied that an older man, with accumulated wealth and the experience needed to be a good hunter and fisherman, who married a very young woman was able to enjoy a long reproductive life with his youthful partner (Helle *et al.* 2008).

Another noteworthy feature of the information in Box 4.7 relates to the final three characteristics. Both sexes prefer intelligent, likeable and compassionate people with a well developed moral sense; in other words, good people. These characteristics were not greatly considered by early studies on human mate choice but they have gained importance in more recent work, so that it is now suggested that both intelligence and cognitive capacity (Miller 2000) and moral virtues (Miller 2007) have evolved as a consequence of selective pressures arising from the need to find a mate.

There are two particularly enigmatic and controversial aspects of mate selection in humans. One is the fact that men choose beauty and the other that women sometimes accept (and sometimes seek) sexual relationships without a long-term commitment. We shall consider the first of these here and the second in the next chapter.

Why do men choose beautiful women? Clearly this preference is more than a whim. If it is the outcome of selective processes it implies that men who succeed in pairing with beautiful women derive reproductive benefits. And what exactly do we mean by a beautiful woman? This is hard to sum up in a few words but the fact is that all men know a beautiful woman when they see one, without any need for instruction. Diverse studies, both geographically and culturally, have shown that men need no more than a brief glance to assess the beauty of a face or a figure and they do so with a high degree of concordance. What is most remarkable is that the evaluations are highly similar irrespective of the race of either the men doing the assessing or of the women being assessed. Hence, contrary to the assertions of some anthropologists, the concept of beauty does not seem to differ significantly between cultures.

The principal features highlighted by different studies as the components of the general concept of beauty are fleshy lips, a small chin, soft and unblemished skin, lustrous hair, white teeth, firm breasts, symmetrical features, a feminine aspect and a low waist-hip ratio of about 0.7 (i.e. a narrow waist and wider hips). What do all these features have in common? They are all indicators of good health or youth, and these together imply a high reproductive value. Female beauty is thus not defined by an arbitrary collection of features but instead beautiful women are potentially more fertile and may give a man more children than would less attractive women.

These general strategies of mate-choice in humans which, as we have seen are clearly predicted by evolutionary theory, in turn explain many typical phenomena of human societies. For example, as a result of men seeking health and beauty, women spend a great deal of money on anti-wrinkle treatments, collagen injections and cosmetic surgery, among others, all these amounting to an industry worth many millions in hard currency in the industrialised countries. Men in turn have developed an instinctive ambition that drives them to accumulate wealth and resources, since these are what women have looked for in them over thousands of generations. As a general rule, men are much more ambitious and avaricious than women.

All these are general rules but it is indeed the case that there has been a recent upsurge in ambitious female executives and in those males known as ‘metrosexuals’, who also spend large sums on cosmetic treatments. It is too soon to analyse these phenomena from the point of view of mate selection but they may be currently adaptive cultural modifications in which economically independent women may be choosing male beauty instead of resources (see Section 4.6.3.4).

4.6.3.2. Casual sexual relationships

As we have already emphasised, given that males have much more to gain than females from copulating with many individuals, evolutionary theory predicts that the former should be much more promiscuous than the latter. This is indeed what occurs in the human species. For women, as for females of other animals, increasing the number of mates does not increase the number of offspring, yet casual sexual relationships are relatively frequent in our species (see Chapter 5). Such relationships were obviously advantageous for men during the Stone Age, given that raising a child is very costly (nine months of pregnancy are followed by a minimum of 12-15 years feeding and caring for it). Promiscuous males may avoid this costly investment. However, it is hard to understand why women consent to casual sex with a nonpaternal male.

Several hypotheses have been advanced to explain why women have casual sexual relationships, all of which have some substance and explain some cases. There are four principal explanations. The 'deception hypothesis' suggests that women accept a casual sexual relationship because they are tricked by men with promises of long-term commitment that are never fulfilled. The 'additional resources hypothesis' suggests that such copulations allow women to obtain additional resources from men, which occurs today in huntergatherer societies, such as the Ache, of Paraguay. The 'mate-change hypothesis' suggests that such copulations are an attempt by a woman to change her current mate for a better one. Finally, the 'good gene search hypothesis' maintains that such sporadic sexual relationships, when a women already has a mate, bring her the opportunity to have more diverse offspring of higher genetic quality, which is advantageous as we have seen.

Women give more importance to physical attractiveness for casual sexual relationships than they do when they are looking for long-term relationships (in accordance with the final hypothesis above), preferring men with more masculine features such as tall, broadshouldered, narrow-waisted and muscular. This means that such men should be more involved in such casual relationships, something that has been confirmed by other studies. For example, Gillian Rhodes and her team at the University of Western Australia studied a sample of 166 men and 196 women. They found that the more attractive men had more casual sex but not more longterm relationships. For their part, the more attractive women had more long-term relationships but not more casual ones (Rhodes et al. 2005). This shows that the women who permit casual sexual relationships are not the more attractive ones.

4.6.3.3. Human secondary sexual characteristics

As we have already mentioned, human males also participate in mate choice since they too contribute to parental care or at least provide some family resources. Secondary sexual characteristics may therefore be predicted to occur in both sexes, although they would not be expected to be as spectacular as those of males of more polygynous species.

The differences between males and females are certainly varied and important and some could be considered sexual ornaments. The principal candidates are the penis and the high waist-shoulder ratio in men, and the breasts and low waist-hip ratio in women. The existence of secondary sexual characteristics in humans is not at all clear given that the features that we have studied and which tend to be the basis of mate selection by women, such as greater height and a combination of broad shoulders and narrow waists, are neither ornamental nor still less costly but instead are indicators of strength, which have evolved through natural selection. The human penis may be a secondary sexual characteristic since it is very large relative to that of other primates -about twice as large as in the chimpanzee and four times larger than in the relatively immense gorilla. The penis might be a costly ornament since the larger the penis, the more blood needed to erect it. However, most authors do not regard the large penis as a secondary sexual characteristic given that its size and other features may be explained by the other benefits that they may bring with respect to fertilisation and sperm competition. Hence we shall defer our study of it to the next chapter where we examine those two topics.

There is more evidence for regarding the two female features mentioned as secondary sexual characteristics. The broad hips - narrow waist relationship may be considered a sexual ornament since it leads to the curvy figure and distinctly feminine walk which so appeal to men. Wide hips do not indicate easier birthing. Indeed they may be a costly attribute since they make rapid movement more difficult, making it harder to escape certain predators.

Female breasts are unanimously regarded as a secondary sexual characteristic. They are very large relative to those of females of other primate species, and they remain much the same size throughout the reproductive cycle whereas in other species they are only prominent during lactation. They do not bring any other type of advantage but rather incur a cost since they make running harder. Thus wide hips - narrow waists and prominent breasts may act as secondary sexual characteristics, indicating youth and a high reproductive potential. Is there any scientific support for this last assertion?

Several studies do indeed support this hypothesis, especially with regard to breasts. Anders M0ller of Pierre et Marie Curie University, Paris, France; Randy Thornhill of New Mexico University, USA, and myself have shown that women with more symmetrical breasts have more offspring and similar results have been obtained from two very different populations, in Granada in southern Spain and in New Mexico in the southern USA (M0ller *et al.* 1998). The relationship between symmetry and fertility indicates that breasts may serve as honest indicators of good genes. These results have been confirmed and extended in a later study by Grazyna Jasienska of the Jagiellonian University, Poland, and her collaborators, who analysed the relationship between the dimensions of various body parts and fertility. The latter was measured from the daily concentration of two hormones in the saliva, whose link to the success of pregnancy had previously been shown. They found that women who had both large breasts and slim waists had a higher concentration of both hormones, 26% and 37% higher respectively, than other women, indicating that the former are more fertile (Jasienska *et al.* 2004).

To end this section on human secondary sexual characteristics I would like to suggest one that may apply to both sexes but that I have never seen mentioned in the literature: the growth of long hair on the head by both men and women and, in addition, beard growth in men. These characters meet all the requirements of sexual ornaments. Long hair is an exaggerated and extravagant adornment that may reveal the quality of its bearer (high quality individuals have more presentable hair since they can spend more time looking after it). Furthermore, as with typical secondary sexual characteristics, it is costly to maintain. Not only does it take longer to look after but it can also amount to a handicap since it may shelter more parasites and may also prove a problem both when trying to escape predators and during fights with rivals of the same sex.

4.6.3.4. Sexual selection in modern industrialised societies

As we have already emphasised in this book, human behavioural evolution took place during the tens of thousands of years that comprised the Stone Age, during which time our ancestors lived as hunter-gatherers. The society currently typical of industrialised countries is very recent indeed in evolutionary terms and perhaps there has not been enough time for adaptations to our present living conditions to emerge. Thus the adaptive significance of the human sexual behaviour complex must be sought in the ecological environments that our ancestors lived in.

One of the adaptations that has frequently been demonstrated is the flexibility of mate-seeking strategies. When seeking a partner, males as much as females, adapt their requirements to the prevailing circumstances. For example, an individual's concept of his or her own worth as a mate has been seen to be very influential. The number of potential mates available has also been shown to be equally important. This adaptive flexibility should allow us to predict that changes ought to be detectable in pair-selection strategies in industrialised societies, which have seen enormous changes in the living conditions of both sexes, particularly with respect to the high percentage of women who are economically independent. Have any such changes been detected? They have indeed. A group of Spanish investigators, Carlos Gil-Burmann and his co-workers at the Universidad Autonoma de Madrid, have come up with some very interesting results through an analysis of 'lonely heart' advertisements in a range of Spanish periodicals. They have uncovered an age-related difference in the advertisements that are published by women looking for a mate. In keeping with the general rule, 52.3% of women over 40 seek a partner of high socioeconomic status and they attach less importance to physical attractiveness, which is specified by only

40.1%. However, 50.7% of women under 40 seek attractive men and they give less importance to financial status, required by only 46.4%.

4.7. Male-female conflict when seeking a partner

We have already highlighted that males and females do not invest equally in reproduction, it pays males to dedicate their efforts to acquiring as many mates as possible, whereas parental investment is the best strategy for females since they have little to gain from additional sexual partners. This implies that the selective pressures affecting each sex are different and thus that the evolutionary interests of males and females are highly distinct. As a result, it is increasingly evident that intersexual conflict is the norm and not the exception and that such conflict gives rise to 'antagonistic coevolution' (see Chapter 9) between males and females. This coevolution has led to the emergence in each sex of defensive evolutionary strategies against potentially harmful members of the opposite sex. As a general rule we can say that in most species the males develop strategies to deceive the females and the females develop strategies to prevent themselves being taken-in by deceptive males.

Conflicts between males and females are numerous and occur at various levels. The most widespread cause is that when it comes to finding a mate not all individuals will be able to pair with the partner of their choice. Not all males can pair with higher quality females nor can all females pair with the best males and/or those who control more resources. This conflict resolves itself in nature, in species that form lasting pairbonds, through what is termed 'assortative mating', that is to say there is a tendency for males and females to pair off with mates of similar quality, and humans are no exception here.

One of the extreme consequences that may arise from intersexual conflict is that large males may try to force smaller females to mate with them. Such attempts are quite frequent in the animal kingdom and include such behaviours as bullying, intimidation, kidnapping and forced copulation (rape). Forced copulations are comparatively rare but they occur in diverse species of ducks and geese, and in some insect, fish, amphibians and mammals, including a number of primate species in addition to humans. Undoubtedly the fullest study of rape is that by Randy Thornhill, of the University of New Mexico, USA, on scorpionflies (*Panorpa* spp.). The males of these predatory insects tend to court females with a nuptial gift, which may be a prey item or a secretion from their salivary glands. Nevertheless, a male will sometimes approach a female without offering a gift. When he is close to her he leaps on her and tries to secure her with his abdominal pincer. Female try to avoid males of this sort by fleeing when a giftless male approaches and, if held fast, they struggle violently to try and escape. If the male succeeds in holding on to his victim he will try to grip his genital pincer against the female's genitalia in order to begin copulation, which may last for several hours in some species.

Such forced copulations were observed in nearly all of the 18 scorpionfly species that Thornhill studied in the laboratory but it is not solely a phenomenon resulting from the conditions of captivity, since he also observed it in seven species under natural conditions (Thornhill 1980). The strategy of these males is clearly prejudicial to the females but it does benefit the males since their way of finding gift food consists of removing prey from spiders' webs, a very risky business since approximately 65% of males get trapped in webs. By not presenting a female with a gift the male lessens the chance of dying in a web. If therefore simply grabbing a female is much less costly to a male, why do the majority court females and only a few carry out forced copulations? Probably because forced are usually ineffective. Because females control fertilisation, they have developed defensive mechanisms to avoid or reduce the chance that a rapist's sperm will be the ones that fertilise her eggs (see Chapter 5). That being so, it may be predicted that the rapists are males of low quality, those who are incapable of providing a nuptial gift adequate to attract a female.

Rape is widespread in the human species, but more frequent in some societies than in others. For example, rape is very rare in Norway but more frequent in the United States (with 60,000 instances reported). In some ethnic groups, such as the Ache of Paraguay and the Yanomami and the Mehinaku of the Amazon jungle, rape is very common (Buss 2007). Although there are important inter-cultural differences in the frequency of rape, no culture has been found in which rape is absent. Even the Bible is laden with accounts of men raping women. Rape has been studied from many viewpoints (anthropological, psychological, sociological and biological), and various ideas have been advanced to explain why it occurs. Some have argued that rape may simply be a way in which a male obtains sexual gratification. Others claim that sexual violence enables a man to impose his will on a woman. Alternatively to those proximate hypotheses, it may be an adaptive behaviour, an outcome of biological evolution, which may improve the reproductive success of the rapist. Although rape certainly involves the sexual gratification of the rapist, and forced copulation implies considerable violence that, from a psychological viewpoint, may promote feelings of dominance in a man, much data supports the last hypothesis (extracts from Thornhill & Palmer 2000; Buss 2007).

Some data indicate that rape is adaptive for men. For example, throughout history rape has been very frequent in wartime, when the possibility of punishment is low. Most victims are in their twenties and 70% of them are between 16 and 35 years old, which seems to indicate that women are selected for rape during their most fertile ages. In addition, the frequency of pregnancy as an outcome of rape is 2% greater than recorded during consensual copulation. Other data indicate that there may be adaptations for rapeavoidance in women. In particular, studies carried out in a range of major cities have found that a high proportion of women develop strategies to reduce the risk of rape. For example they avoid going out alone at night and they avoid the most dangerous parts of town. Moreover, they take greater precautions during their fertile periods. It is also the case that some male rapists are individuals of low socioeconomic status, and are also, although to a lesser extent, unattractive, which means that such men have little success when trying to find a partner in a normal way.

Thus, rape in humans is a behaviour that may improve the reproductive success of some males in certain conditions, specially when the costs of rape are low to the rapist. As in other species, including mammals and our closest relatives the primates, rape may be an adaptive strategy. However, attempts at rape have been described in some species in which males attack young, non-breeding individuals who may not even be females. One of the best examples is a study by Christopher Somers and his co-workers of Regina University, Canada, who observed 56 attempted rapes in a colony of American white pelicans (*Pelecanus erythrorhynchos*) all of which were directed at well grown, feathered chicks whose parents were temporarily absent from the nests. They were especially frequent at a time when there was a spate of late matings within the colony, as a result of which the males were highly motivated to copulate (Somers *et al.* 2007). Examples such as this also suggest that, at least sometimes, rape may not be the outcome of a reproductive strategy but rather a consequence of the fact that males, which lack access to females, may become so highly sexually aroused that they direct their sexual impulses towards inappropriate individuals.

Anyway, even if there exists a genetic predisposition to rape under certain environmental circumstances, this is not to say (as we have already seen in Chapter 1) that rape is either good or morally acceptable. Natural selection, and hence nature, lacks a moral sense. If it did the imperatives of our current society would be very different. For natural selection something ‘good’ is any characteristic that leads to increased reproductive success, so that practices such as celibacy, chastity and contraception would be considered bad if natural selection could consider anything, which it cannot. This means that although the existence of genes that predispose men to become rapists may be demonstrated one day, in no way would this discovery provide a justification for the offence. It is undoubtedly the case that our reason and our moral virtues set us apart from all other animal species, as most philosophers have maintained throughout history (see Chapter 1), but this does not mean that we lack instincts, as they suggested, but rather that we must be capable of overcoming them.

Chapter 5. Sex, fertilisation, sperm competition and cryptic female choice

5.1. Introduction

As we saw in the previous chapter, finding a mate is highly important since failure to do so means failure to reproduce. However, there is much more to it than this. Producing descendants demands successful fertilisation, which is not at all straightforward. Although other types of fertilisation exist (external fertilisation and spermatophore transfer - passing a package of sperm), we shall concentrate on internal fertilisation, which is the most interesting in terms of its consequences for animal behaviour. Before and during copulation (see section 5.3) some forms of sexual behaviour take place that serve to stimulate the pair to prepare them for fertilisation. Even once a male has succeeded in depositing his sperm within the genital apparatus of a female he still cannot claim success since many obstacles still remain to be overcome. A second type of sexual selection may occur within the female in which sperm of different males, should they coexist within the female genital apparatus, compete to fertilise the ova ('sperm competition'), and the female or her ova may select the most suitable sperm ('selection by cryptic female choice'). This chapter considers all these aspects of fertilisation in the order in which they happen.

5.2. Sexual behavior

Not all sexually reproducing species perform sexual antics during the act of fertilisation. Not only does reproduction without sex exist but there is also sex without reproduction, as we humans well know. Among the many claims to exclusivity that we have assigned to ourselves, one of the most often made is that we are 'the only animal that has sex for pleasure'. In common with many such claims, this one too is false.

Plecia nearctica is a dipteran, a member of the order of true flies, known as the lovebug. The males perform courtship displays in flight while flying in a compact group (a lek-type pairing system, see Chapter 6). Females that approach the group to copulate provoke competition between the males as these try to grab a mate. When one succeeds the pair falls to the ground to copulate, a process that in this species - hence the name - may last for as long as three days (Thornhill & Alcock 1983).

In the prairie vole (*Microtus ochrogaster*), once a pair is formed, the male and female enter into a frenzy of sexual activity and may remain together copulating frequently for long periods, sometimes for as long as 40 hours (Carter & Getz 1993).

The California sea hare (*Aplysia californica*) is a shell-less marine mollusc. It is hermaphrodite, i.e. each individual has both male and female sexual organs. It has a curious form of reproductive behaviour that perhaps cannot be correctly described as 'sex play', particularly since its nervous system is very simple. What is undeniable though is that, to human eyes, what occurs amounts to an orgy of unbridled sex. A detailed study by Steven Pennings, of California University at Santa Barbara, USA, found that, although copulating couples do occur, more often chains of four to eight individuals (sometimes twelve or more) form. In these chains each individual is acting as a male and inseminating the animal in front and, at the same time, is acting as a female and receiving sperm from the individual behind. These copulating chains may persist for days and sometimes for over a week, although the same individuals are not always involved since some leave and others join the chain at times (Pennings 1991).

We do not know whether any of the three species described above can be said to 'enjoy sex' but we can say that they perform sexual behaviour for long periods and sometimes in company, circumstances that are not necessary for achieving fertilisation. Such sexual behaviours have probably evolved on account of their effectiveness, ensuring fertilisation by guarding of the female or through sperm competition (see below). Nevertheless, there are species apart from our own in which the practice of sex that is unrelated to fertilisation has been demonstrated. They include bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), other primates such as the white-faced capuchin (*Cebus capucinus)* as well as various species of dolphins. We shall deal with the sexual behaviour of the first two since I think it will convince even the most sceptical that we are not the only species to practice sex purely for pleasure and without a reproductive purpose.

The bonobo, or pygmy chimpanzee, is phylogeneticially very close to the chimpanzee. Both display many similarities in such diverse aspects as morphology, diet, way of life and breeding system (both are promiscuous). However, they are very different in their social organisation (see Chapter 8) and in their sexual behaviour. Regarding the latter, bonobos live in more or less large groups of males, females and juveniles of both sexes. Sexual relations are very frequent within these groups, not only in captivity but also in the wild. We shall summarise the sexual practices of bonobos briefly, mainly following De Waal (1997). The females show genital swelling when in heat but they remain sexually active not only during those fertile periods but also throughout their cycles. Sexual relations are very frequent but, in addition to typical heterosexual copulation, many other sexual practices occur involving all possible sex combinations: male-female, femalefemale and male-male. Moreover, it is not just the adults who are involved. Juveniles that have not yet reached sexual maturity also participate. For example, genital contacts between juvenile males and mature females are more common than copulation between adult males and adult females (Hashimoto 1997). Sexual practices include genital contact unrelated to copulation, genital contact using positions similar to those employed in copulation and copulation proper. Actual copulation is most frequent during the females' fertile period and the face-to-face 'missionary position' is not uncommon, despite often being cited as unique to humans. The most frequent sexual contact is genital rubbing between females, which occurs independently of the oestrous cycle. This is not seen in chimpanzees but it is typical of bonobos. Female bonobos have a highly developed clitoris shaped as a half-moon and prominently placed, which no doubt facilitates this behaviour. Genital rubbing between females plays a very important role in social relationships within the group (see Chapter 7), but clitoral stimulation almost certainly produces mutual sexual pleasure, as with other typical sexual practices of bonobos.

Sexual relations are very frequent in both bonobos and chimpanzees. In the former both males and females may perform sexual activities as often as thirty times a day. Female chimpanzees are likewise sexually promiscuous but only when in heat. For example, Jane Goodall describes how one such female copulated with eight males in just fifteen minutes and how another that she followed copulated 84 times in eight days with seven different males (Goodall 1986). To conclude, not only are we not the only species to practice sex without having an interest in procreation, but also at least one species, the bonobo, leaves us standing, not only in terms of frequency but also in terms of variety of sexual activity. Another human myth bites the dust.

5.3. Copulation

In most species with internal fertilisation, males must deposit sperm within the females' reproductive apparatus, which they do via copulation. This entails introducing a penetrative organ, or penis, into the female's genital orifice, to release sperm within. In most such species, humans included, sperm is deposited in the vagina but in others (e.g. horse, dogs, pigs and their wild relatives) penetration is deeper and sperm is deposited directly within the uterus.

Copulation is not always so conventional. In diverse animal groups, such as the platyhelminths (flatworms), leeches, molluscs and insects, there are species in which sperm is injected directly into the female through the body wall. For example, in the bedbug (*Cimex lectularius*), well-known worldwide as a parasitic feeder on human blood, a male deposits sperm inside the female but not in her genital orifice. Instead he makes a slit in her cuticle using a sickle-shaped appendage at the tip of his abdomen. Once the cuticle has been cut, his penis emerges from a penile groove and releases sperm within the female's body. The sperm then swim to find the ovaries where they fertilise the ova (Stutt & Siva-Jothy 2001).

Copulation tends to be a collaborative act between both sexes. This is especially necessary in those species that have internal fertilisation but whose males lack a penetrative organ, as in most birds. One of the most common questions that my non-scientific friends and acquaintances ask me is 'How do birds copulate if they don't have a penis?'. They are surprised by my explanation. Males and females align their cloacas, the common orifice shared by the gut and the genito-urinary apparatus. For a brief period, often less than one second, the female partly protrudes her oviduct. The male deposits his ejaculate on it and, when the oviduct is withdrawn, the sperm is carried into the female.

Nevertheless, copulation does not always imply cooperation. The exceptions are not just cases of rape, the absence of cooperation is also conspicuous in species such as the bed bug mentioned above, where the male penetrates the female's body wall with an instrument specially developed for the purpose. One of the most curious examples of this latter type of copulation has been described by Nicolaas Michiels, of the Max-Planck Institute in Germany and L. Newman, of Queensland University, Australia, in a study of an hermaphrodite marine flatworm (*Pseudoceros bifurcus*) that lacks a female genital orifice. Being hermaphrodites, all individuals possess both male and female sex organs but they prefer to perform as males, since the female role involves being penetrated through the body wall, which entails wounding and the risk of infection. When two breeding individuals meet they rear up and engage in a sort of fencing contest with their erect penises, in which each tries to penetrate the other without itself being penetrated. The loser plays the female role in the copulation (Michiels & Newman 1998).

5.4. Sex and copulation in humans: male and female orgasms

Some of you may be disappointed but this section is not dedicated to describing the sexual behaviour of human couples. More than enough has been written on that subject in an ever increasing series of publications since Alfred Kinsey published his own studies, on human male sexual behaviour, in 1948, and on that of the human female, in 1953. This is not to say that the subject is irrelevant. On the contrary it is highly important to many aspects associated with mateselection and pair-maintenance. For example, Susan Sprecher, of Illinois State University, USA, has shown that sexual satisfaction during premarital relationships is associated with the degree of love and commitment declared by both members of a couple. There is furthermore a relationship between the degree of that satisfaction and the duration of a relationship, which tends to lasts longer when premarital sexual relations are more satisfactory (Sprecher 2002).

This section will only deal with three questions of human sexual behaviour that are important from an evolutionary viewpoint: (1) 'Why does sexual desire happen?' (2) 'Why do we enjoy sex?' (with special reference to differences between men and women) and (3) 'What do the male and female orgasms signify?'.

5.4.1. Why does sexual desire happen?

Some months ago, while chatting with some nonbiologist friends, I was told that the reason why sexual desire occurs is obvious. Animals seek mates and copulate because they enjoy it, just as we do. Some species have indeed been shown to show apparent pleasure while having sex but such an answer is not completely satisfactory intellectually since what matters is why the act has evolved to be pleasurable. Why do we enjoy activities that are important for survival, such as eating, or for reproduction, such as having sex, and not scuffing our shins or being in danger? In other words, a satisfactory answer must explain why we enjoy sex but not some other experiences. The ideal is to understand what fires sexual desire and why we enjoy sexual relations. Both of these questions have two types of answers: causal and functional (see Chapter 3).

In terms of physiological causes, sexual desire is produced via a complex neurohormonal mechanism that is influenced by many factors. In brief, we can say that it arises in the brain on account of testosterone, the principal driver of sexual desire in both men and women. In women oestrogen too plays an important part, although this hormone does not heighten sexual desire but it makes women more receptive to sex and it is essential for vaginal lubrication. This is one cause for sexual activity, but what then is the functional or adaptive reason for sexual desire? (see Chapter 3). It is the same as we noted in Chapter 4 when studying pair selection and falling in love. Sexual desire is an adaptation that emerges when a suitable mate is found, whether for an enduring relationship or for a casual sexual encounter (see below).

5.4.2. Why do we enjoy sex?

The causal answer to the second question is very complex since the neurophysiological mechanisms involved are not entirely clear and the roles of different hormones are equivocal. In general, according to Panksepp (1998), oxytocin plays the major part and it is responsible for the sensations of affection and satisfaction that are felt during sexual activity. Massive doses of oxytocin are liberated at orgasm and these produce the feelings of tenderness and shared involvement that overwhelm lovers during the period of relaxation that follows moments of intense sexual pleasure. Dopamine (the substance responsible for the pleasure felt by many people when playing or drugtaking) also has an important influence in both men and women, and it drives sex-addiction in some persons.

One of the most informative studies on the roles of hormones in sexual relations was carried out by C. Sue Carter, of the University of Maryland, USA, and her coworkers. They studied the prairie vole, the species in which we earlier noted that the male and female copulate very frequently. They found that oxytocin is released during those prolonged bouts of sexual activity and it is responsible for establishing the pair's relationship (Carter & Getz 1993). They also found that in males, pair-bonding and pair-maintenance, which are very strong in this species, depend on the action of vasopressin. They were able to show experimentally that it is this latter hormone that makes a male prefer his own female, even when other females are provided to give him a choice (Winslow *et al.* 1993).

What is the functional or adaptive answer to this second question? As my friends remarked, we enjoy sex and, when all is said and done, those pleasurable feelings increase sexual desire and bring about a higher frequency of copulation. If we consider the scenario in which this behavioural trait evolved in our ancestors, those males and females (men and women) who most enjoyed sex would have had more sexual activity, increasing the possibility of pregnancies. They would thus have left more descendants than those individuals who either did not enjoy sex or enjoyed it less. The offspring of the former would have inherited the capacity to enjoy sex that would thus be passed on to following generations.

5.4.3. What do the male and female orgasms signify?

We shall now consider a phenomenon that is intimately related to sexual satisfaction: the orgasm. This topic has given rise to much controversy about whether orgasms occur in primates and other animals, the differences between the male and female orgasm and, above all, the evolutionary explanations for female orgasm.

Although sexual pleasure without orgasm exists, the orgasm is the climax of sexual pleasure. It has been defined in a number of different ways but a valid and quite simple definition is: successive waves of pleasure and of tension, increasing in intensity to a climactic point, after which there follows a marvellous sensation of relaxation.

The first interesting question is whether or not males and females of other species enjoy orgasms. We can answer this question because orgasm produces a series of observable responses, the main ones being muscular contractions and spasms, a fixed and distracted gaze and a series of specialised and characteristic vocalisations. These signals are sometimes seen in copulating animals and may be interpreted as orgasms. The evidence is clearer in primates given that such orgasms have been seen both during copulation and during masturbation. Manipulation of the genitals by males results in ejaculation and the other symptoms of orgasm mentioned above. The subject has always been more controversial where females are concerned since female orgasm is not accompanied by ejaculation nor by any other easily detectable signal. Nevertheless, it has been noted that in females of various species manipulation of the genital area and the clitoris, either by rubbing against objects or manually, produces indications of orgasm such as an increased heart rate and contractions of the uterus and peri-anal region.

One of the studies that most clearly showed the existence of the female orgasm in a non-human species was carried out by Alfonso Troisi and Monica Carosi, of Rome University, Italy, who worked with captive Japanese macaques (*Macaca fuscata*). They assumed that an orgasm occurred when a copulating female threw her neck backwards and held on to the male's fur while undergoing muscle spasms and (sometimes) emitting distinctive cries. After observing 240 copulations, involving 16 males and 26 females, they found that females 'enjoyed' an orgasm in 33% of cases. The frequency of orgasms was unrelated to the female's age or to her dominance rank but was higher when copulation lasted longer. After controlling for duration of copulation and other parameters of physical stimulation, the most striking finding was that orgasms were more frequent when copulation was between a dominant male and a low-ranking female and was less common when high-ranking females were mounted by low-ranking males (Troisi & Carosi 1998).

Such studies thus reveal that orgasms are not exclusive to humans and that both male and female orgasms exist in at least some other primates, although apparently (given the behaviour of the sexually active individuals) they are not as intense as those seen in humans.

With respect to our own species, comparisons between the male and female orgasm have changed from that promoted by male chauvinists in the past. The female orgasm was formerly considered a by-product of the male orgasm or an imperfect version of it (Sigmund Freud maintained that clitoral orgasm represented an immature state of development in the woman). It is now viewed as a highly intense neuro-physiological phenomenon that is very different from the male orgasm in both its physiological characteristics and in the duration of its various phases.

What is the evolutionary explanation for orgasms? The answer is clearer regarding the male orgasm since it is linked with ejaculation and hence with fertilisation. As we said when explaining sexual pleasure, male orgasm promotes the chances of leaving more descendants. Men whose orgasms were most intense would have a greater propensity to copulate and would leave more offspring. However, there is no direct link between fertilisation and the female orgasm. A woman may become pregnant without ever experiencing an orgasm. Moreover, a female's orgasm is most closely associated with the clitoris, which receives little stimulation during copulation since it is outside the vagina. Also, no relationship has been shown between frequency of orgasms and numbers of pregnancies or descendants. For these reasons, the female orgasm remains a controversial topic and over a dozen hypotheses have been advanced to explain its existence. The most important of these are included in Box 5.1.

1) Female orgasm plays an important role in pair bonding. It contributes to strengthening the links between a man and a woman in the monogamous long-term pairings that predominate in our species.

2) An orgasm informs a woman of a man's disposition to satisfy her desires and her needs in future. An attentive man who takes trouble to give her sexual satisfaction may be a good candidate for a longterm partner because he would also be disposed to invest his resources in her and her offspring.

3) Female orgasm favours sexual relations with males of higher genotypic quality. This hypothesis emerged when it was found that females were more likely to achieve orgasm with more symmetrical men.

4) Female orgasm increases a man's confidence in his paternity. If a woman is satisfied sexually she will not need to seek such satisfaction with other men.

5) The sexual satisfaction that it produces results in an increased frequency of copulation throughout the whole sexual cycle, leading to a higher probability of pregnancy.

6) The sexual satisfaction that female orgasm produces induces women to have promiscuous sexual relations with diverse men. In a scenario where infanticide is a possibility (see Chapter 1), female orgasm reduces the chances that other males may kill her child later on.

7) The relaxation that follows orgasm causes a female to remain lying down, which reduces sperm loss and so increases the chances of fertilisation. Given the position of the vagina, which is perpendicular to the ground when the woman stands, most of

the semen would be lost if a woman got up and started walking immediately after copulation.

8) The vaginal and uterine contractions that occur during orgasm may assist uptake of semen, increasing the chances of fertilisation.

Box 5.1. Different adaptive explanations for the human female orgasm.

As can be seen, some of the hypotheses are contradictory. Many are supported by some particular study but the methodology of some of these investigations leaves much to be desired and has often been criticised.

Which of these hypotheses are most convincing? Answering this question is not at all straightforward and certainly several of the ideas proposed have a more or less significant role in the evolution of the human female orgasm. To allow you to draw your own conclusions, we shall summarise some of the most important findings of a variety of studies based on interviewing women. The information given here is drawn from several sources but chiefly from Buss (2007): (1) Female orgasm is more frequent when sexual relations occur in the context of a stable, long-term relationship. Married women or those with a steady partner have more orgasms than unmarried ones or those without a steady partner. This is quite a reliable result since it has emerged in various studies in different parts of the world. (2) Women in a stable relationship who enjoy a higher number of orgasms claim to be happier with their marriage or relationship than those who have fewer orgasms. (3) Women who experience fewer orgasms say that they are more eager to have sexual relations with other men than do women who enjoy orgasms more frequently. (4) Women whose partners are more attractive and more symmetrical (indicators of higher genetic quality, see Chapter 4) say that they have more orgasms than do women paired with less attractive and less symmetrical men. (5) Women in stable relationships who have extramarital affairs are more than twice as likely to achieve orgasm with their lovers than with their husbands. This is also quite a reliable result that has been confirmed in a diversity of studies, perhaps because women are very selective about having extramarital affairs with men of high quality (see below).

The matter of female orgasm remains an evolutionary enigma that we are far from solving, especially when we consider two further problems to which we have not yet referred. Firstly, the frequency of orgasms differs greatly between cultures, orgasms are quite common in some and practically unknown in others (at any rate according to information gathered in interviews by anthropologists, which is not always reliable). Secondly, adaptationist theory predicts that, if the female orgasm is an adaptation, the male should have developed strategies to exploit it. For example, he should be keen to ensure that his partner reached orgasm, he should ejaculate at the same time or just after she did so, or he should have developed a capacity to detect the female orgasm so that the female could no easily fake it. The first of these predictions is only sometimes fulfilled, given that only some men are concerned about promoting orgasm in their partners, but the other two predictions are rarely met.

We have seen that orgasms also occur in other animals, at least in some primate species. Why however are orgasms more intense in humans? I wish to suggest a reason that seems quite plausible to me: it has developed as an evolutionary response to human resistance to conception. We know that diverse contraceptive methods have been developed by all people and all cultures, given that conception is costly (especially in particular circumstances such as when food is short or another small child is still being raised). Human intelligence has been used to avoid pregnancy especially by abstinence from sex and by withdrawal prior to ejaculation. This would engender significant selective pressures that may have favoured the development of more powerful orgasms, given that a higher degree of sexual satisfaction would encourage hasty and unintended encounters that would reduce the effectiveness of conscientiously employed contraceptive measures. Despite the latter, individuals with more intense orgasms would leave more descendants.

5.5. Male-female conflict in sexual relations

Conflict between the sexes is a significant phenomenon. The most widespread aspect, which has been detected in most species, relates to avoiding extra-pair mating. The motives vary a great deal according to species but in general it is not in the interest of a male for his female to copulate with other males and similarly is not in the interest of a female for her male to copulate with other females. We shall consider the sperm competition that is associated with extra-pair mating in the next section. Here we focus on conflict associated with the frequency of sexual relations.

This type of sexual conflict is very common in humans and quite rare in other animals but an example from the insects illustrates it perfectly. I speak of water-striders, aquatic hemipteran insects that walk on water surfaces. As a result of the conflict between a male and a female about when to copulate and for how long, males have developed structures for grasping females and females have developed structures to prevent males from capturing them and to make escape from grasping males more easy. In these insects, as with most other species, males are nearly always ready to copulate (see Chapter 4). They try to seize a female with their front legs and climb onto her back in order to mate. Furthermore, they try to remain on the female as long as possible since this increases the chances that their sperm will fertilize her eggs. Such pairings are costly to females since they increase the risks of predation considerably. Thus a significant conflict exists between the sexes.

Goran Arnqvist, of Uppsala University, Sweden, and Locke Rowe, of Toronto University, Canada, have shown in a study of fifteen water-strider species that both males and females have developed morphological structures for use during pairing. Males have a specialised structure within their genital apparatus for attaching to females, but females have developed abdominal spines that may be pushed downwards to interrupt copulation. Strong evidence regarding the function of these structures comes from Arnqvist and Rowe's comparative study, which showed that the more highly developed the males' attachment structures were, the more highly developed the females' anti-male spines. This is a clear demonstration that these structures have evolved in both sexes as a result of a coevolutionary arms race (see Chapter 9) between males and females for control of copulation (Arnqvist & Rowe 2002).

In human beings, as in water-striders, there also exists an important inter-sexual conflict regarding the number and duration of sexual relations, once a pair is established. In all interview-based studies, men complain that they have less sex than they would like, a finding that is repeated across all cultures. Men think about sex much more often than women do and are always more disposed than women to feel sexual desire and to indulge in sexual activity (see Chapter 4). This should come as no surprise to anybody since men not only have much higher blood testosterone levels than women (ten to 100 times higher) but also the neural centres associated with sexual activity in the male brain, located in the hypothalamus, are twice the size of those in the female brain. In contrast, women think about sex less often than men do and they tend to be much more sentimental and emotional. The prefrontal cortex, the cerebral structure that is responsible for emotions, is much more highly developed in the female brain than in that of the male (Brizendine 2006).

These physiological differences may explain the fact that men and women have different preoccupations when it comes to their feelings about their relationships. A woman is little affected when the frequency of sexual activity declines but a man will be very concerned and will think that his woman no longer loves him or has taken a lover. However, the opposite happens if communication and signs of affection decline between the man and his partner, in which case the woman tends to conclude that her mate no longer loves her. As promoters of pair stability, sex is most important to a man but to a woman what matters most is feeling loved, getting a lot of consideration and not having to worry. More than this, if such conditions are not met a woman may come to lose all interest in sex. Although the reality may seem harsh, available data suggest that a woman offers affection and sex in exchange for love, whereas a man offers affection and love for sex. Of course, we are talking about general ‘rules’, statistical averages in behaviour, for which there will always be lots of exceptions.

I think it quite probable that a coevolutionary arms race, as has occurred with the water-striders, may also have happened with human females - of course in an entirely unconscious manner given that we are speaking of evolutionary strategies. Bearing in mind that women tend to lose sexual interest when in unsatisfactory relationships, they may have succeeded in obtaining benefits, such as additional resources for the family or more care for the young, in exchange for providing greater sexual pleasure for a partner.

Anyone reading these lines may well conclude that I am a highly unromantic person. This is not so. Rather, I use an evolutionary approach because it allows us to understand the biological basis of conflict behaviour, which might even help us to resolve relationship problems in our daily lives. Just this once I am going to play the part of a sex counsellor and say that many relationship breakdowns would be avoided if both parties were aware that most such problems derive from the differences between men and women described above. These differences can generate a vicious circle in which a reduction in the frequency of sexual relations cannot be solved without increased communication and demonstrations of affection, which will not occur without an increase in sexual activity.

5.6. Male and female genitalia

Males of those species in which fertilisation is internal require an intromittent organ to release their sperm within the female's genital apparatus. This structure, the penis, is extremely variable among species, not just in size and shape but also in how it is employed. Some species with internal fertilisation lack a penis, as is true for most birds. Nevertheless, some birds do have a penis and some, such as ostriches, swans and ducks, have one of considerable size. An extreme case is the Argentine blue-bill (*Oxyura vittata*), a small duck in which males have a penis 20cm in length (McCracken 2000).

Although males with penises typically have just one, some male lizards and snakes have two penises, and certain marine platyhelminths have more than a dozen! The shape of the penis varies from species to species. In most cases, the device resembles a tub, but it may be corkscrew-shaped, as in domestic and wild pigs, or blade-shaped, as in certain squirrels. In addition, it may be accompanied by a great variety of structures including lumps, filaments, spines, hooks or even, as in most primates, a bone.

Penis size is also very variable. Some barnacles (hermaphrodite crustaceans that live permanently attached to their substrate) have penises that may be two or three times the length of their owners' bodies, allowing them to reach and fertilise neighbouring individuals. They are, however, not the record holders in terms of penis size since some slugs have extremely long penises. The champion in this respect is surely *Limax redii* whose body is some 12cm long but which has a penis longer than 80cm (Birkhead 2007), i.e. seven times longer than its body! What about primates? As a general rule, male primates have small penises that are kept permanently rigid thanks to the presence of the penis bone or baculum. This is not the case in our own species, not only in that the human penis lacks a baculum, but also because it is relatively large. The erect human penis is some 15cm long, whereas that of the chimpanzee and bonobo is 7cm long, the orangutan penis measures 4cm and the mighty gorilla has a penis only 3cm long. Such great variation between species in both the shape and size of the penis had led some evolutionary biologists to suggest that it may have other important functions apart from inserting sperm in the female genital apparatus (see below).

The female genital apparatus also varies according to species, which is to be expected since in order for copulation to be possible the penis must be adapted to penetrate the female orifice and the latter must be adapted to receive the penis of males of the same species. This much refers to the vagina but other, external, structures of the female genital apparatus are also very varied where they exist. For example, among anthropoids, female chimpanzees have a very long, straight clitoris, female bonobos also have a large clitoris but shaped like a half-moon and human females have quite a small clitoris that is some distance from the vagina. The clitoris is also very variable among other primates. In many lemur species and also in spider monkeys (American monkeys of the subfamily Atelinae), the females have enormous, pendulous clitorises.

Zoologists have known for centuries that the genital organs differ greatly among species, so much so that, in many groups of insects and other invertebrates, precise identification of individuals of closely related species is only possible by removing and examining their genitalia. Species that are so similar as to be inseparable on the basis of external morphology often possess different genitalia that allow them to be correctly and speedily identified. Why should this be? The evolutionary explanation is quite clear. The selective pressures that favour both those males who are effective at fertilising females and those females who succeed in being fertilised by the best males are so strong that they bring about rapid evolutionary change of their genitalia that gives rise to new species (divergence) that differ in their genital morphology. Goran Arnqvist, the Swedish investigator to whom we referred earlier in this chapter, carried out a comparative study of the genital apparatus and external morphology of insects. In accordance with what we have just said, he found that divergence between species was much greater in terms of genital morphology than with respect to all other morphological characters (Arnqvist 1998). These findings strongly support the idea that sexual selection (see Chapter 4) acts on the genitalia of different species in a direct manner. In the same way, among primates it has been found that males of species with promiscuous females have longer and more complex penises than do males of monogamous or polygynous species (Dixson 1987).

To return to the human penis, why should our species have evolved such a large penis relative to that of the other primates? There is no clear answer to this question although various hypotheses have been advanced. For example, it may be a visible signal that can be employed in sexual selection or it may increase the chances of women achieving orgasms. One of the most accepted ideas is that a longer penis is an aid to fertilisation since it deposits semen closer to the ova.

The key question with respect to all that we have dealt with in this section is ‘Why is there so much variability in penile structures?’ Two hypotheses attempt to answer this: the ‘lock-and-key hypothesis’ and the ‘sexual selection hypothesis’. The former suggests that the high degree of variation is because the precise match of the penis to the female genital orifice prevents interspecific mating, which would amount to a great loss of time and energy since hybrid matings rarely produce viable offspring. The sexual selection hypothesis suggests that the evolution of both the male and the female sexual apparatus is governed by two powerful influences that we studied in the previous chapter: competition by males and female choice, only that this time they operate within the female’s body (see below).

The lock-and-key hypothesis is the older of the two and is the choice of classical zoology, but the sexual selection hypothesis has received powerful support more recently, in particular Goran Arnqvist’s comparative study of insects (Arnqvist 1998), which tested some of the predictions that arise from each hypothesis. One prediction is that since the lock-and-key hypothesis is thought to prevent errors in species-choice when mating, it would be expected that monogamous species, in which females only mate with one male so that mistakes would be disastrous, would have the most complex genitalia. In contrast, the sexual selection hypothesis predicts that greater male genital complexity would be found in polyandrous species. In these a female mates with several males and competition between the sperm of these (selection by sperm competition among males) and any choice the female may make of the most adequate sperm (selection by cryptic female choice) are the decisive factors. Both these concepts are studied in detail below.

Arnqvist analysed the morphological complexity of the genitalia and other characters in monogamous and polyandrous insect species. He found no significant differences between these two groups in morphological characters other than in the genitalia, where the differences were very clear. The genitalia of males of polyandrous species were almost always much more complex than in males of monogamous species (Arnqvist 1998). These results amount to resounding support for the sexual selection theory as opposed to the lock-and-key hypothesis.

5.7. Sperm competition

In the early 1970s Geoffrey A. Parker made a fascinating scientific contribution when he proved that competition between males does not end with copulation but instead, that when a male's ejaculate coexists with that of another male within the female genital tract, competition to fertilise the ova continues between the sperm. This phenomenon is termed sperm competition and the discovery introduced a revolution in the field of reproductive biology. A multitude of studies have since revealed that sperm competition is a very significant and widespread force in evolution.

Molecular studies of paternity have revealed that females often copulate with more than one male during the same fertile period. This even happens in species, such as birds, which have previously been considered to be monogamous, a realisation that has made it necessary to distinguish between social monogamy and genetic monogamy. By definition, monogamous species are those in which a male and a female form a pair, that is to say, an association that endures throughout the breeding season. Nevertheless, genetic monogamy, in which all the offspring are those of the male and the female that comprise the pair, is very rare. This is because, as we have noted, females very frequently copulate on the side with additional males, so that some of their offspring are not those of the 'social father'.

Since males may increase their reproductive success considerably by inseminating a larger number of females (as mentioned in Chapter 4), it is unsurprising that males court females who are already paired in order to obtain extra-pair copulations. A spectacular example involves a small, beautifully coloured Australian bird, the superb fairy-wren (*Malurus cyaneus*). In this species a male and a female form a long-standing relationship that may endure for several breeding seasons. Nonetheless, a very high percentage of nests include a chick that is not the offspring of the incumbent male. Raoul Mulder, of Melbourne University, Australia, studied male behaviour and, remarkably, he found that when a male courts a female who is not his own mate he employs a different approach. After finding a female in a neighbouring territory, he presents her with a petal or a flower (Mulder 1997). On 97% of occasions when this behaviour was seen the male was courting a female that was not his. The 'wife' never gets any flowers!

Since males have most to gain from extra-pair copulations there has been a widespread belief that it is they that are principally responsible for initiating them. However, many observers feel that females do not just accept extra-pair copulations but actively seek them. Probably the most conclusive study of this is by Bart Kempenaers and his coworkers of Anwerp University, Belgium, who made detailed observations of the behaviour of male and female blue tits (*Cyanistes caeruleus*) during the fertile periods of the latter. They found that it was the females who chose males that they preferred for extra-pair copulations (Kempenaers *et al.* 1992).

If females actively seek out such copulations with other males, what benefits do they derive? As we pointed out in Chapter 4, a female cannot increase the number of chicks that she raises by increasing the number of males that she mates with, but by doing so she might increase the quality of her offspring. This is the principal hypothesis explaining extra-pair copulations: females choose the best available males to achieve offspring of higher genetic quality. Another study of blue tits by Bart Kempenaers and his team provides a good example. When they examined instances of extra-pair paternity they found that 11-14% of chicks were not offspring of the male nest-owner and paternity due to other males affected a high proportion of nests (31-47%). Paternity was established by means of highly reliable molecular analyses. They found that the most successful males, those whose nests contained only their own young but who also had fathered some young in other nests, had larger tarsi, sang longer song phrases and also survived better. Chicks who were the outcome of extra-pair copulations tended to be males and survived better than those fathered by the nest owners (Kempenaers et al. 1997). Such data thus supports the idea that females paired with males of lower biological quality seek extra-pair copulations with better males, which allows them to improve the quality of certain of their offspring.

Such extra-pair copulations are responsible for many socially monogamous species being polyandrous from a genetic viewpoint (all the young belong to the mother but they are the product of several fathers). These findings make clear that sperm competition imposes very strong selective pressures. Males must be effective not only at securing mates but also at ensuring that it is their sperm that fertilises the eggs of those females. As a result of such selective pressures males have evolved a large array of adaptations, behavioural as well as structural, to reduce the chances that the sperm of another male may fertilise the eggs and to increase the chances that it is their own sperm which succeeds. We shall consider these adaptations by classifying them according to the advantages that they confer (see Box 5.2).

1. PREVENTING THE FEMALE FROM COPULATING WITH ANOTHER MALE

a. Female guarding: In most species this involves the male remaining by the female after copulation, so delaying any possible copulation by another male.

b. Blocking the female's genital orifice: Along with the ejaculate, males of many species inject a sticky substance that forms a stopper closing the female's genital orifice after copulation.

c. Preventing the female from being attractive to other males: This is infrequent (see text).

d. Inhibition of female sexuality: The male ejaculates of some insect species contain anti-aphrodisiacal substances that reduce the propensity of the females to copulate again.

2. PREVENTING SPERM PREVIOUSLY INTRODUCED BY OTHER MALES FROM FERTILISING THE EGGS

a. Increasing copulation frequency: This is entirely a behavioural adaptation. Copulation is much more frequent in species in which a female cannot be guarded effectively and in which extra-pair copulations are common.

b. Increasing the sperm density of the ejaculate: In many species exposed to high levels of sperm competition, the testes are larger and produce more copious ejaculates, containing a larger number of sperm.

c. Removing semen that has been previously inoculated by another male. In many insect species the male genital apparatus includes structures that are used to remove semen stored within the female genital tract.

3. TAKING ADVANTAGE OF WORK DONE PREVIOUSLY BY OTHER MALES (see text)

Box 5.2. The principal sperm-competition strategies employed by males of different species

5.7.1. Preventing the female from copulating with another male

Once a male has succeeded in being accepted by a female and in copulating with her, any strategy that may contribute to reducing the chances that she can mate with another male could be adaptive, since then his sperm will not have to compete with that of others to fertilise the eggs. Four types of such strategies may be distinguished (Box 5.2 - 1), and we shall now consider them in turn.

Mate guarding is quite frequent in birds and in insects and other arthropods. Before the discovery of sperm competition, the frequent observations of male birds remaining close to their females were regarded as a way of strengthening the pair-bond. We now know that the motive is less romantic. The male stays close to his female to prevent her from copulating with other males.

More drastic evolutionary strategies have evolved in cases where the males do rather more than merely staying close to their females. For example, many male insects tend to remain on top of the female for some time after copulation has ended. For example, in many dragonflies and damselflies such as the azure damselfly (*Coenagrion puella*), the male guards the female until she has laid her eggs, and he does it by holding her thorax with a pincer at the tip of his abdomen. This strategy is costly for the females since it renders them less mobile and so more vulnerable to predation. Females have thus tended to develop mechanisms for ridding themselves of males and the latter have developed counter-adaptations that allow them to remain attached for longer.

Surely one of the most extreme strategies evolved by males to guard their females is seen in canids, both wild and domestic. The male and female remain attached after copulation by the swelling of the penis, which does not allow them to disengage. This is a highly effective mate guarding strategy. Since the female cannot copulate again until the pair separates, it gives the male's sperm an advantage over that of his rivals and increases his chances of fertilizing her eggs.

The advantages of mate guarding have been analyzed in some studies. For example, Helen Chuang- Dobbs, of New York State University and her coworkers performed an observational and experimental study of a small bird, the black-throated blue warbler (*Dendroica caerulescens*), in which molecular techniques were used to establish paternity of all chicks. They found that males who guarded their females most closely had less chance of having chicks fathered by others in their nests. Also, when a male was removed and kept isolated from his female for an hour, there was an increased chance that one of the chicks in his nest was fathered by another male (Chuang-Dobbs *et al.* 2001).

Another effective strategy for preventing a female from mating with another male is to block her genital orifice. This tactic has been described from a wide range of animal groups, including worms, spiders, insects, snakes, rodents and bats. On the face of it, such a 'chastity-belt' would seem to be a very effective way of stopping another male from mating with a female. However, it is not always so. As a result of the evolutionary mechanisms of sperm competition, males of many species have developed ways, and even structures, that allow them to remove the plug from a female's genital orifice.

Some species have evolved a truly dramatic way of producing the genital stopper. For example, in the European honey bee *Apis mellifera*, once a drone has finished copulating with the queen he explosively fire his genital apparatus into the female's genital opening, which plugs her orifice (Gary 1963). This action kills him but no matter because he has achieved his objective of inseminating her and in this way he is increasing the chances that it will be his sperm that fertilised her eggs.

Another convoluted and Machiavellian way of making use of the genital plug has been found in males of the spiny-headed worm *Moniliformis dubius*, an acanthocephalan intestinal parasite of rats. In this species, as in many others, the male's sperm forms a plug at the entrance to the female's genital orifice. What is unusual is that dominant males sometimes 'copulate' with rival males and seal their genital orifices in the same way, preventing them from transferring sperm to females (Abele & Gilchrist 1977).

As we indicated in Box 5.2, another mechanism for avoiding insemination of a female by other males is to ensure, after copulation, that she becomes unattractive to them. This is uncommon since it is not easy to achieve (except in humans, see below) but a good example is provided by the butterfly *Heliconius erato*. Gilbert (1976) found that females smelt oddly after copulation. He later found that it was not the female who produced a malodorous substance. The male deposits it during copulation and this serves as a powerful counteraphrodisiac against even the most determined males.

Another possibly way of avoiding copulation between a female and another male is to inhibit her receptiveness. This too is uncommon but in some insects it has been shown that the males' ejaculate contains anti- aphrodisiacal substances that reduce the females' disposition to copulate. A well known case involves the housefly (*Musca domestica*). Rieman *et al.* (1967) showed that a substance transferred with the sperm not only delayed searching for new males by females, but quite often led to females not copulating again for the rest of their lives.

5.7.2. Preventing sperm previously inoculated by other males from fertilizing the eggs

Despite the adaptations described above, males often cannot prevent a mate from mating again with another male. Where there is a high chance that other males have copulated previously with a given female, natural selection favours those individuals that develop mechanisms that prevent or reduce the likelihood that previous ejaculates fertilise the eggs. A wide range of strategies to achieve this adaptive goal exists in nature. One way in which a male can succeed is to ensure that his sperm are in the majority within the female's genital apparatus, simply because this increases the odds that some of his sperm will fertilise the eggs. This result can be achieved either by increasing the numbers of a male's sperm present or by removing those previously introduced by other males (see Box 5.2).

Another obvious fertilization tactic is to increase copulation frequency. Many examples demonstrate that copulations are very frequent in those species in which a female habitually mates with several males. This is also the case in those where a female cannot be guarded effectively, as happens with raptors and seabirds, where one member of the pair remains to guard the nest while the other seeks food.

One such species is the goshawk (*Accipiter gentilis*). The male cannot guard the female and copulation correspondingly occurs very frequently. According to a study by Anders M0ller, then at Aarhus University, Denmark, goshawks copulate astonishingly often for an average of 518 times per clutch. Many of these copulations take place when the male returns from a foraging trip to the nest. Males copulated within 30 minutes of their return on 20 out of 52 occasions and did so, on average, after 72.8 minutes (M0ller 1987). The high frequency of copulations on return in species in which the male cannot guard his female effectively offers evidence of the close relationship between high copulation frequency and sperm competition arising from extra-pair copulations.

Another mechanism that may confer a sperm competition advantage is to produce ejaculates with a high sperm density. Under conditions of sperm competition, the greater the number of sperm transferred by a male, the higher the chances that the offspring will be his. Numerous studies have established that the greater the level of female promiscuity, the larger the testes and the larger the number of sperm produced by the males.

Nevertheless, following a rule of 'transferring the maximum possible number of sperm' is not always adaptive because although sperm are cheap to produce their cost is not negligible. The rate of sperm production is limited in males of all species. It may thus be predicted that the number of sperm transferred would be adjusted according to the reproductive benefits that a male can obtain on each occasion, at least in species in which copulations are frequent. A series of fine studies by Tim Birkhead of Sheffield University, UK, and his co-investigators have shown that at each copulation domestic fowl cockerels (*Gallus gallus domesticus*) transfer a variable number of sperm to hens, the quantity depending as much on the male's status as on the female's quality and her level of promiscuity. Dominant cocks, which have preferential access to hens, adjust the quantity of sperm transferred according to the number of hens in their flock. On the other hand, subordinate cocks, whose copulatory activity is restricted by the dominant males, always transfer a high number of sperm (Cornwallis & Birkhead 2006). Both dominant and subordinate males reduce the number of sperm transferred to a given hen in successive copulations but, nevertheless, if they are then presented with a new hen they are capable of increasing the sperm density of their ejaculate immediately (Pizzari et al. 2003). Female quality is another factor that influences the quantity of sperm ejaculated significantly, in accordance with the idea that sperm donations are adjusted in relation to the benefits associated with the male's investment. Males ejaculate a larger quantity of sperm into higher quality females, namely those whose secondary sexual characteristics are more developed, since these hens are the ones that most invest in caring for the chicks (Pizzari *et al.* 2003).

Another strategy that would be very effective if possible would be to remove sperm that another male has previously inseminated (see Box 5.2.). A very large number of mechanisms evolved for this purpose have been described, especially in insects. Krebs and Davies (1993) give two highly instructive examples involving dragonflies, which we will now consider. Males of the black-tailed skimmer (*Orthetrum cancellatum*) have a structure consisting of a dense group of filaments that they insert into the female's genital orifice before beginning to transfer their sperm. When they withdraw the filaments these are laden with any sperm that other males may have inserted earlier. Males of the scarlet darter (*Crocothemis erythraea*) possess a type of 'inflatable horn' that they insert into the female and that, once inflated, displaces any stored sperm to the sides or to the exterior.

A fascinating example of sperm competition involving sperm withdrawal has been reported in a small bird, the dunnock (*Prunella modularis*). Females in this species are highly promiscuous (see Chapter 6) and males have developed a famous behavioural adaptation in response. Nick Davies, of Cambridge University, UK, noted that the males peck at the female's cloaca before copulating. He showed that this induces the female to expel sperm inserted during earlier copulations with other males (Davies 1983).

5.7.3. Taking advantage of work done previously by other males

We have now seen some truly surprising adaptations resulting from sperm competition. In this section we shall consider two further remarkable examples, the second of which borders on the incredible.

Fertilisation in many tailed amphibians (urodeles) is via a spermatophore that the male deposits on the ground after courtship. He then has to ensure that the female lowers her cloaca on to it and presses down until the spermatophore passes into her body. Sperm competition arises in the spotted salamander (*Ambystoma maculatum*) since some males (satellite males, see below) watch those that are courting and, when these have dropped their spermatophores, the rival males deposit their own spermatophores on top. Thus when the female lowers her cloaca she takes in not the spermatophore of the male that courted her, but that of the opportunistic satellite male (Arnold 1976).

We have already seen how fertilisation in some species does not occur via the female genital opening but through the body wall, within which sperm are liberated to swim freely to reach the ova and fertilise them. In the cave bat bug (*Xylocoris maculipennis*), a hemipteran insect, dominant males may behave in this way not only with fertile females but also with males weaker than themselves. In the latter case, sperm from the dominant male swim to the testes of the subordinate males and enter within. In this way, when a 'raped' male mates with a female, he also introduces the sperm of the dominant male (cited by Krebs & Davies 1993).

5.7.4. Human sperm competition

As a general rule, we humans belong to a species in which one male and one female form an enduring relationship within which children are born and raised. These circumstances are very like those seen in most birds, a group in which there is often a predisposition to extra-pair copulations and hence to sperm competition. The intensity of sperm competition in humans is controversial since experts disagree. Without going into detail, we shall simply quote some figures. For one thing, studies on conjugal infidelity in different populations have found that 40-50% of men and 1826% of women have had at least one extra-pair sexual adventure. In addition, paternity studies have revealed that the social father is not the genetic parent in a variable percentage of cases, ranging from 1-30% among populations with a mean of 10% of children (Buss 2007). Nevertheless, not all of the studies on conjugal infidelity and paternity reviewed by Buss employed reliable methodology. According to Simmons *et al.* (2004), if only the most rigorous studies are included, the mean percentage of people who have had extra-pair relationships varies from 2-27%, and extrapair paternity is approximately only 2%. Whereas the data in Buss (2007) imply the existence of strong sperm competition, those presented by Simmons *et al.* (2004) suggest that such competition is quite limited. In short, the argument goes on.

Criticisms of those who maintain that a high level of sperm competition exists in humans are well founded since some studies of the subject are not highly rigorous. Indeed, the famous results obtained by Baker & Bellis have not been repeated by others using the same methodology. Nevertheless, sperm competition in humans may be greater than critics maintain, for two reasons. Firstly, in hunter-gatherer communities, where effective modern contraceptive methods are not used, quite a few children are said not to belong to their 'official' fathers (about 10% according to the most conservative data in Simmons *et al.* (2004)). This suggests that sperm competition may well have been considerable during our evolutionary history. Also, if this is so, both men and women would be expected to possess adaptations related to sperm competition. The second reason why I believe that such competition is, or at any rate has been, more intense than some critics suggest has to do with the many physiological and psychological attributes of men and women that only make biological sense in the light of sperm competition. We shall consider them in the next two sections.

Another important fact supports my conclusion, the relative size of the testes in relation to male body size in our species. It is well known from a wide range of animals (insects, fish, reptiles, birds and mammals) that relative testis size is a good indicator of the intensity of sperm competition. Males in which such competition is intense have larger testes, enabling them to produce more sperm, than those in which there is little sperm competition. A. H. Harcourt of Cambridge University, UK, and his co-workers conducted a comparative study of testis size in primates. They found that males of species in which females are promiscuous and copulate with all the males in the group (which are therefore exposed to strong sperm competition) have significantly larger testes in relation to body size than do males of monogamous species (where one male pairs with one female) or polygynous ones (where one male pairs with several females). In a graph of relative testis size in the genera studied, *Homo* falls between the chimpanzee, in which males and females live in groups, and the gorilla, in which one male controls several females, which are unlikely to engage in extra-pair copulation (Harcourt et al. 1981). This finding supports the idea that sperm competition exists in our species, although to a moderate extent, and that the typical human pairing arrangement would comprise a male paired with one female with only a modest risk of extra-pair copulation occurring (see Chapter 6).

Biological and psychological adaptations to sperm competition in humans

The most important of these are given in Box 5.3, separately for men and women.

With respect to human beings, in many cultures the man makes a sizeable investment by providing the necessary resources for raising the children. It is a very costly business for a man if his woman is impregnated by another man since, from an evolutionary point of view, his investment is wasted since it does not contribute to perpetuating his genes. Natural selection may therefore be assumed to have favoured strategies that are more effective in preventing other men from fertilising one's partner. We need therefore not be surprised by the great diversity of 'anti-cuckold' strategies, both biological and cultural, which have been developed by human males. In men we can find nearly all the behavioural mechanisms of sperm competition that we earlier described for animals in general, those listed in Box 5.2.

As in many species, female guarding is widespread and takes many forms (see also the next section, on cultural 'adaptations'). In addition, some findings indicate more subtle mate guarding. For example, a man guards his partner more carefully when there is a greater risk that an extra-pair copulation may produce a pregnancy, i.e. when his wife is young and not pregnant (see Box 5.3a).

Other adaptations that were described for animals in general and that are also seen in the human species when the risk of extra-pair copulation is high include increasing copulation frequency and increasing the sperm concentration of the ejaculate (Points 3, 4 & 5 in Box 5.3a).

a) Adaptations in men

1. Guarding of mates is widespread in men.
2. Men guard their partners more closely when these are young and not pregnant than when they are older or pregnant.
3. Men increase the frequency of copulation when there is a greater risk of extra-pair copulation.
4. The longer a man is separated from his partner since their last copulation, the more attractive she becomes to him and the greater his desire to have sexual relations with her.
5. A greater number of sperm is transferred per ejaculation in relation to the length of the period that a man is separated from his woman since their last copulation.
6. Some authors have interpreted the shape of the human penis as an adaptation for displacing sperm deposited by another man during an earlier mating.
7. A man who suspects infidelity exacts significant costs from his partner, such as physical and psychological abuse, rape and divorce.
8. Men find the odour of women more agreeable when these are in their fertile period.
9. Men guard their partners more closely during their fertile periods than during the rest of the menstrual cycle.
10. Men are more attentive and more possessive towards their women during their fertile period.

b) Adaptations in women

1. Women select more attractive and more symmetrical men (with good genes) for casual sexual relations.

2. Women in stable relationships who have extramarital sexual relations are more than twice as likely to have orgasms and to become pregnant with their lovers than with their husbands.

3. A woman's interest in her partner does not increase during her fertile period but her attraction to other men does so.

4. During their fertile periods women find the odour of more symmetrical males more attractive.

5. During their fertile periods women find males with more masculine faces (indicating higher testosterone levels) more attractive than at other times.

6. During their fertile periods women prefer men whose actual or potential genetic quality is greater than that of their partner.

7. During their fertile periods women prefer men who appear more confident and competitive in the presence of other men.

8. During their fertile periods women alter their behaviour to reduce the risk of rape and thus of impregnation by an undesired male.

c) General adaptations of both sexes

1. Pair disruption strategies

2. Pair maintenance strategies: courtship

Box 5.3. Adaptations of men and women that support the existence of sperm competition. From various sources but chiefly after Gangestad et al. (2002) and Shackelford & Pound (2006).

There has also been an attempt to explain the shape of the human penis as a tool to withdraw sperm deposited by other males during recent copulations. We have noted how anatomical adaptations have quite frequently evolved for this purpose in different animal groups but no attention was given to this matter in relation to human males until Gordon Gallup, of New York State University, and his co-workers, performed an investigation. They used liquids to simulate semen of different densities and artificial vaginas and penises, such as may be obtained from sex shops. They were able to demonstrate that the shape of the human penis, in particular the widening at the base of the glans, makes it quite effective at withdrawing sperm that has previously been deposited in the vagina (Gallup *et al.* 2003).

In most species, males and females maintain sexual relations only during the breeding season, when the females are fertile. In humans, in contrast, women are potentially sexually receptive at all times. Thus, since extra-pair copulations by the woman are only costly for her man during the fertile period, selection will have favoured adaptations that enable mate guarding during that fertile period, which takes up about seven days each month (from the 7th to the 14th day of the menstrual cycle). As seen in Box 5.3a, that prediction is fulfilled. Men find their wives more attractive and find their odour more agreeable during the fertile period than at other stages of the menstrual cycle, and they guard them more intensely and behave more attentively and possessively towards them at this time (Points 8, 9 & 10 in Box 5.3a).

Two adaptations associated with long-term and short-term pair selection have been detected in women. We considered these in Chapter 4 and they comprise points 1 and 2 in Box 5.3b. There are also other adaptations that refer to changes in behaviour or strategy according to whether or not a woman is in her fertile period or at another stage of the menstrual cycle (points 3-7 in Box 5.3b). In particular, her attraction to other men increases during her fertile period, when she also finds the odour of more symmetrical men and those with more masculine faces more alluring as well as preferring men who show themselves to be more self-assured and competitive in the presence of other men. All these tendencies show that during the fertile period women prefer mates whose actual or potential genetic quality is high, as occurs with female blue tits, something that does not occur at other stages of the menstrual cycle. It is curious to see that these changes arise only with respect to casual sexual relations and no significant trends arise when a woman is selecting a long-term partner.

This data on changes in preference during the fertile period support the idea that women are particularly predisposed to selective extra-pair matings at that time, which leads to sperm competition. These changes allow women to obtain genetic benefits by means of extra-pair copulations. This is not surprising because, at least during most of our evolutionary history as hunter-gatherers, most women will have been paired with men of medium or low genetic quality. They could therefore obtain significant genetic benefits for their offspring by having occasional sexual relations with men of high genetic quality. Nowadays, at least in our industrialised western societies, this tendency may be concealed by the widespread use of effective contraception. The drive to produce better quality children through copulating with men of higher genetic quality would not have involved a conscious decision (any more than it is among female blue tits). It would be the outcome of evolved psychological mechanisms. A preference for such men during the fertile period may endure in modern societies but very often the women employ contraception, even more carefully than when having sexual relations with their regular partners, because of the risk of pregnancy or of acquiring a sexually transmitted disease. The use of contraceptive methods clearly amounts to a behavioural revolution that will do away with current adaptations and may eventually lead to the development of new ones. This though is another matter and many generations must pass before we can know what transpires.

I do not want to end this topic without making one point clear. The changes mentioned in relation to the woman's fertile period do not mean that she has a general interest for men other than her husband during this time. What happens is that when such an interest arises it is highly selective so that women tend to be attracted to men who display signs of high genetic quality.

With respect to adaptations common to both sexes, Box 5.3 notes the tendency of some to disrupt established pairs in order to acquire a partner and the role of jealousy. David Schmitt, of Bradley University, USA, and David Buss, of Texas University, USA, in the first serious study on the frequency with which people try to attract an already-paired person as a partner, revealed that such behaviour is very common. They found that 60% of men and 53% of women admitted having tried on some occasion to lure away someone's partner with a view to having a long-term relationship with them. However, when people were asked about doing so with only short-term sexual relations in mind, the percentage of men who admitted doing so remained high (60%), but the percentage of women so engaged was much lower (38%) (Schmitt & Buss 2001).

Jealousy is a much more frequent and well-studied phenomenon, and infamous for giving rise to a great deal of violence. Many men have perished across history in fights (or duels) driven by jealousy. Many women have also died for the same reason at their own husbands' hands and some men too have also been killed by their wives. For example, in Canada, of 812 women murdered by their husbands between 1974 and 1983, 195 (24%) died because of the husbands' sexual jealousy. Of 248 men killed by their wives during the same period, jealousy was the motive on 7.7% of occasions (Daly & Wilson 1988).

Jealousy has been interpreted by some evolutionary biologists as an adaptation that reduces the chances of extra-pair copulation. A jealous woman or a jealous man may be expected to keep a close eye on a partner. As evolutionary theory predicts, the motives that give rise to jealousy differ between men and women. Bearing in mind that certainty of maternity is always absolute, whereas certainty of paternity is very far from being so, suspicion of infidelity may be predicted to be the chief provoker of jealousy in men, but not in women. For women the most important matter is ensuring that a pair's resources are supplied entirely for herself and for her children, as happens with females in most other species in which males also invest in parental care (see Chapter 6). It may thus be predicted that what concerns a woman most will be the suspicion that her husband may have become involved in a longterm extramarital relationship that will oblige him to divert resources to another woman. In accordance with these predictions, David Buss and his co-workers asked interviewees to imagine that their partners were cheating them and were having sexual relations and emotional involvement with another person. When asked which of these two aspects of the relationship most concerned them, 60% of men and 13% of women responded that it was the sexual relations, whereas emotional relations were much more worrying to the women (87%) than to the men (39%) (Buss *et al.* 1999).

These results have emerged from a large number of studies carried out in different countries, sometimes with different methodologies. For example, in one experiment persons were seated in a comfortable chair and were connected to sensors measuring such parameters as heart rate and skin conductance. They were asked to imagine various scenarios related to jealousy. These sensors, and others indicating anxiety and stress, recorded maximum levels in women when emotional infidelity was raised. The sensors recorded maximum levels in men when different sexual positions employed by their wives and lovers were mentioned (Pietrzak *et al.* 2002).

Cultural ‘adaptations’

Human societies, nearly all of which are dominated by men, have promulgated a great variety of regulations and laws and have developed many taboos all with the ultimate aim of guarding women against extra-pair sex. The chastity belt, a massive iron device employed in the Middle Ages, is perhaps the method that we most associate with mate guarding. On reflection, the belt is but a crude imitation of the plugs employed by males of many species, to which we referred above. Other more subtle ‘customs’ related to sperm competition strategies are the veils, burkas and other body and facial coverings of women, whose purpose is to render them less attractive to men. It is instructive that such coverings are only obligatory for women of reproductive age. Furthermore, in countries where such customs apply, women normally seldom leave the house and are always accompanied when they do so.

Another ‘tradition’ favoured by female guarding, although a much more drastic one, is female circumcision or clitorectomy. This inhuman practice (so cruel that it is confined to our own species) succeeds in diminishing or nearly eliminating a woman’s sexual desire (something that male houseflies achieve in a much more subtle way). Another very exaggerated type of genital mutilation is infibulation, which consists of sewing up both sets of vulval labia, leaving an orifice only large enough to permit the passage of urine and menstrual flow. In this way, which is truly worthy of the script of a horror film, a woman is guaranteed to be a virgin when she marries.

Undoubtedly, the preoccupation with guarding women is most evident in the mass of laws established by nearly all cultures to punish adultery, these treating it as an offence against a man’s most valued property: his woman. Hence, adultery has often been punished by death. For example, according to Marco Schwartz, the Bible is full of stories of adultery and of edicts that forbid it. It is the seventh commandment of the ten given in the book of Deuteronomy, the punishment for both parties being death, in ancient times by burning, but later by stoning (Schwartz 2008). It is striking that nearly all known legal codes, from the code of Hammurabi (18th century BC) to the most recent, include articles condemning adultery and all consider the woman to be her husband’s property, making him the victim of the crime. In most modern societies, there are grounds for divorce if a woman is caught in adultery but if her spouse is the offender this is not necessarily the case. Of course, any case of adultery involves one woman and one man, but always along human history, women have been punished much more than men.

5.8. Sexual selection by cryptic female choice

As we have noted, the process of sexual selection that we studied in Chapter 4 continues after copulation within the female reproductive tract. Competition between males continues as sperm competition and selection by females continues in the form of sperm selection. The latter comprises not permitting just any sperm to fertilize an egg, but instead selecting the sperm most likely to generate superior development of the offspring. This process is known as sexual selection by cryptic female choice, cryptic since it is not readily detectable.

The ingenious idea that females, after copulating with several males, may be able to select the sperm with the best genes to fertilise their eggs was popularised by William Eberhard, of Costa Rica University. In his book, Eberhard (1996) highlights that insemination is no guarantee that eggs will be fertilised and he describes some 20 mechanisms by which females may control processes associated with fertilisation. Some, such as deciding when copulation ends or expelling the sperm of some males, are directly observable. Others, however, are invisible. These include whether or not sperm of a particular male is transported to sperm storage structures, selecting sperm and favouring or blocking the development of a fertilised egg. These remain speculative possibilities without direct supporting evidence, since sperm that succeed in fertilising the available ova may be those that succeeded in competition between spermatozoa, or that were selected criptically by the female, or both of these at once, so it is very difficult to know.

At any rate, there are some findings supporting the idea that a female may select between sperm in some way, even if the mechanism is unknown. For example, Mats Olsson, of Gothenburg University, Sweden, and his co-workers studied genetic similarity, an indicator of relatedness, and paternity in the sand lizard (*Lacerta agilis*). This species is highly promiscuous and females will even mate with close relatives. The researchers found that the more closely related males fathered a smaller proportion of the offspring than did more distantly related males (Olsson et al. 1996). These results show that selection of sperm was occurring within the female reproductive tract.

Another study, this time experimental, has shown the existence of cryptic selection in the small red damselfly (*Ceriagrion tenellum*), a member of the order odonata. In this insect group, males have been regarded as dominating fertilisation on account of their complex reproductive apparatus, which includes a diversity of structures adapted to withdrawing the sperm of other males that have copulated previously. Some examples of these adaptations were discussed earlier. Considerable variation is known to exist in the duration of copulation in this damselfly, which may last from 30 minutes to three hours. Jose Andres and Adolfo Cordero Rivera, of Vigo University, Spain, carried out a series of experiments under laboratory conditions to test four hypotheses that might account for this high variability. The two hypotheses that are most related to the subject of this chapter were, firstly, that the longer a male copulates the more effective he is at withdrawing the sperm of rival males that preceded him, and, secondly, that lengthy copulation favours preferential selection of the sperm by the female, i.e. cryptic selection. Both hypotheses predicted that the longer the duration of copulation, the more eggs would be fertilised, which was indeed the case. However, laboratory tests established that males only need ten minutes to withdraw rival sperm from the spermathecae, the female's sperm storage organs. Thus sperm withdrawal could not explain the lengthy duration of copulation. The conclusion reached was that prolonged copulation fertilises more eggs because cryptic selection by females favours the ejaculates of those males that have spent longest in the act (Andres & Cordero Rivera 2000).

Only one study so far has shown one of the mechanisms of cryptic selection that takes place within the female reproductive apparatus. Daniele Carre and her collaborators at Pierre et Marie Curie University of Paris, France, studied a comb jelly (*Beroe ovata*), a marine animal of the phylum Ctenophora, whose eggs are transparent and large (1mm in diameter), allowing the process of fertilisation to be observed directly in the laboratory. It was found that once several sperm have attached to the ovum a series of changes occur in the ovum membrane near each sperm leading to, among other things, gatherings of mitochondria around the pronucleus of each sperm. The pronucleus of the ovum next moves quickly straight the egg cytoplasm to visit one or more of the attached male pronuclei. Sometimes the ovum's pronucleus returns to a sperm pronucleus that it has already visited in order to fuse with it. This seems to be a clear demonstration of an ovum selecting which spermatozoan will fertilise it (Carre *et al.* 1991).

Although scant proof exists of the importance of cryptic sperm selection by females, this is not to say that this is an unlikely evolutionary phenomenon or that generalisations cannot be made. The lack of proof is the inevitable consequence of the lack of suitable techniques for investigating a process that occurs concealed within the female genital tract. In addition to what evidence we have described, other data support the idea that selection by cryptic female choice is an evolutionary phenomenon of great relevance, as is sperm competition. Firstly, the female genital apparatus shows great morphological variation and complexity in most species, especially regarding the route that sperm must travel. The female reproductive tract usually consists of a tube presenting numerous obstacles, which zoologists and doctors have considered to be a surprisingly hostile environment for the sperm. A logical explanation is that the female reproductive tract amounts to a selective medium that eliminates the less competent sperm. A second argument in favour of cryptic selection is that although many sperm, which may derive from different males, reach the ovum, only one of them actually fertilises it. Females would gain an advantage by being able to select the sperm that bear the best (or most compatible) genes to fertilise the egg since this would increase the chances that the fertilized egg would develop into an offspring of higher quality, which might itself survive to be a breeding adult.

5.9. Fertilization without courtship: alternative strategies

Before closing this chapter we shall consider a topic of great interest to behavioural ecologists, that of alternative strategies. The term refers to the fact that not all individuals of a given species behave in the same way. Each may employ different ways to solve the same problem. We could have studied this topic in other chapters since it also applies to other aspects of behaviour. However, I have decided to deal with it here since competition to fertilise eggs offers particularly abundant and peculiar examples of alternative mating behaviours.

We have seen that, as a general rule, before a male can fertilise a female he has to succeed in being selected by her and, after copulating, he must ensure that it is his sperm that fertilises her eggs. Both these stages imply competition, the former between males and the second between ejaculates. As we humans well know, to win a competition it is very important to have some sort of advantage over one's rivals. Animals do not base their behaviours on premeditated decisions but rather on evolutionary strategies, which are transmitted from generation to generation when they are effective and provide benefits to the individuals that employ them. The following example will help us to understand the topic better.

In many animal species in which the males attract females by means of sounds, as happens with frogs and other tail-less amphibians, there often exist individuals, known as 'satellite males', that do not call. These silent satellites take up positions close to singing males in order to intercept females that the latter attract. This behaviour seems sensible when we consider what the song signifies and that not all individual males are equally dominating or attractive. When a male toad or frog sings during the courting season he is sending the following message to both males and females of his species: 'Hear my song; it shows that I am a large, strong male'. The song nonetheless has different significance to either sex. To females he is saying 'come and mate with me', but to males he means 'this site is occupied and if you come near you will have to fight me'. Imagine now a small weak male who is also keen to reproduce. Would it be wise for him to take up a position and sing? In this case, as pointed out in Chapter 4, the song is an honest signal of his physical condition and all he would be doing is indicating his low quality. His song would serve to advise females not to approach him and would inform males that his site is occupied by an easily displaced rival. Clearly the best thing such a male can do is to keep quiet. This then is why satellite males keep silent, because when a male with a more attractive voice than theirs is near it pays the satellites to keep quiet and to try to intercept females that pass by headed for the singing male.

These sorts of strategies are very widespread in the animal kingdom, raising the key question ‘how can alternative strategies exist?’. It might be supposed that the less effective alternatives would be eliminated by natural selection. There are three possible answers to this question and we shall consider each in turn.

1. Often, juvenile individuals, whose development is not yet complete, are not ready to compete with the larger and more experienced adults. It is thus adaptive that they should avoid direct confrontations and instead employ alternative tactics. This may apply in the case of the satellite male frogs described above, as they could be young individuals that will engage in direct competition by song when they have grown.

Another example involving individuals that have not yet developed fully has given rise to a fascinating behavioural adaptation in the marine iguana (*Amblyrhynchus cristatus*). Martin Wikelski and Silke Baurle studied their mating system and found that males gather in groups in which each iguana defends a small territory. Females visit the group in order to mate with one of the males (an example of a lek mating system - see Chapter 6). Copulation takes about three minutes and competition between males is very strong, so that when one is mating those nearby attempts to displace him. Dominant males perform most of the copulations since the females prefer them and they are able to complete copulation successfully on 95% of all occasions, despite disturbance by other males. Smaller males initiate fewer copulations, but in addition, other males succeed in displacing them 29% of the times, before they have had time to ejaculate. In these circumstances, young male iguanas have developed a satellite behaviour, they wait around the boundaries of the territories of the dominant males and try to intercept approaching females. None of this is particularly unusual and similar satellite behaviour is common in many species. What is surprising is that, when a female appears, these satellite male iguanas masturbate to ejaculation before she approaches. They retain the viscous mass of semen at the entrance to the cloaca so that if they succeed in mounting a female they can transfer their sperm immediately, in much less than the three minutes that it normally takes. This tactic allows them a chance to fertilise the female before the dominant males intervene to separate them. This behavioural option increased the reproductive success of the satellite males by up to 41% (Wikelski & Baurle 1996).

2. Two or more evolutionary strategies may coexist because each is effective depending on local environmental conditions. The American cricket story described in Chapter 10 is a good example. Something similar applies in the case described above of amphibians in which some males are vocal but other, satellite males, keep silent. Here the short-term reproductive success of vocal males is greatly superior to that of the silent ones but the former also run a high risk of being parasitized by a fly that kills them (see Chapter 10). Which of these two strategies will be favoured by natural selection? It depends. If flies are scarce, the vocal males mate the most. However, if

there are many flies, the best tactic is that of the silent males because as they may attract fewer females they do not attract the killer flies.

3. Two or more strategies may coexist if they are in an evolutionary equilibrium, and this is the commonest explanation for the alternative tactics that we observe in nature. For example, there are many fish species in which the males defend a small territory, build a nest and care for the eggs and later for the young. Males of such species court females to induce them to lay their eggs in the nests that the males built. At that instant the male fertilises the eggs and from then on he dedicates himself to his charges. As it happens, however, an alternative strategy has been described in over 100 fish species that have this reproductive arrangement; the alternative is employed by smaller males known as 'sneaks'. The sneaks do not compete for territories but instead hide near territory holders. When they see a territorial male courting a female they wait until the moment when she lays her eggs. They then rush out of hiding and release their sperm over the eggs at the same time as the nest owner.

The issue is complicated further by a second alternative strategy in some species. For example, in the bluegill (*Lepomis macrochirus*), a freshwater fish, in addition to sneaks there are also males that have the size and morphology of females (employing the 'transvestite male strategy'. See Chapter 10 for a detailed treatment). Given that males using different strategies all release sperm at the same time, sperm competition must be intense and natural selection will have favoured those individuals capable of producing a larger quantity of sperm. The enormous sexual dimorphism that exists between territorial males and sneaky males in the marine toadfish (*Porichthys notatus*) is surely the result of such sperm competition. According to a study by R. Brantley and A. Bass of Cornell University, USA, territorial males are eight times larger than the sneaks but the sneaks have enormous testes, seven times bigger than those of the territory holders (Brantley & Bass 1994). Indeed, the sneaks could be called swimming testes.

A different tactic, the 'pirate' male, has been described in other species. Pirates are larger than territorial males and their strategy consists of attacking males when these are guarding their nests, fertilising the eggs and then leaving so as to return the nest to the care of its proprietor (van den Berghe 1988).

Two or more of these strategies (sneaks, transvestites and pirates) can coexist in a population if they are in an evolutionary equilibrium, in which case the reproductive success of each kind of male will be about the same. This outcome results from 'frequencydependent selection', which favours the strategy that has relatively fewer practitioners. For example, in a population in which territorial males and sneaky males coexist, both strategies will have similar reproductive success if they are in evolutionary equilibrium. This equilibrium persists because if for some reason the proportion of territorial males increases, the sneaks will have more chances to fertilise eggs and so will leave more (sneaky) descendants, which restores the proportions to equilibrium. If, in contrast, the proportion of sneaks increases, there will be more competition between them and territorial males will become more vigilant, leading to the sneaks leaving fewer descendants and returning their numbers to a proportion that allows an approximately equal reproductive success to both strategies. This then is frequency-dependent selection, which is responsible for maintaining evolutionary equilibrium.

Chapter 6. Parental care and mating systems

6.1. Introduction

We have previously studied problems associated with mate seeking (Chapter 4) and fertilisation (Chapter 5). This third chapter on the theme of reproduction examines the strategies associated with parental care and goes on to consider different mating systems, which differ according to the number and sex of individuals that make up a reproductive unit. These two topics are closely related but we shall study parental care first since it is then easier to understand the evolution of mating systems.

Robert Trivers (1972) pointed out the inverse relationship between effort devoted to mating and that devoted to parental care. His ‘parental investment theory’ rests on some of the arguments that we considered in Chapter 4, for example that males have much higher reproductive potential than females and tend to invest less than their mates do on parental care. The theory is also based on the idea that while a female (or pair) is caring for a group of offspring, further offspring cannot be produced.

In terms of evolution, reproduction is one of the most important activities of any living being. However, the time and resources available for this task are limited and must be employed effectively. The sum of the time and resources that an individual dedicates to reproduction is its ‘reproductive effort’. This, in accordance with parental investment theory, has two components, ‘mating effort’ (an individual’s lifelong investment in seeking mates), and ‘parental effort’ (its investment in caring for its descendants). Reproductive effort is thus the sum of mating effort and parental effort. Hence, if an individual devotes a great deal of time to parental care, it will spend little time on mateseeking, and vice-versa. In this respect the sexes differ because females devote most of their reproductive effort to parental care and males mainly invest in mating. Here lies the key to the link between parental care and mating system. Both sexes in monogamous species invest highly in parental care and little in mating. However, in polygynous species, in which a male mates with several females, the typical male invests very little in parental care and devotes practically all his reproductive effort to mating with as many females as possible.

6.2. Parental care

Parental care comprises behaviour that parents undertake, at some cost to themselves, which contributes to increasing the survival chances and reproduction of their offspring. Parental care is very lengthy and costly in our own species, as in most mammals, but this is not the general rule. Most species are concerned only with laying as many eggs as possible and these are then abandoned to their fate. Parental care is characteristic of mammals and birds, but it is also observed in a diversity of other groups. These do not just include fish, amphibians, reptiles and insects, but also, much more rarely, some molluscs, polychaete worms, echinoderms and even sponges.

Parental care is highly varied both in the degree of development that it attains in different groups and in the range of care provided. The main types and the animal groups in which they occur are summarised in Box 6.1.

The great diversity of types of parental care in groups often thought to be non-parental is striking. Box 6.1 is only a general summary and does not go into details but some of the ways in which parental care has evolved deserve particular attention. For example, the classic scenarios of a bird carrying food to its chicks in its beak, or of a carnivorous mammal carrying prey home in its mouth, have only rare equivalents among other animal groups. Much more unusual adaptations have developed in some cases. For example, parental care is common among frogs of the genus *Dendrobates* and after the females have laid their eggs in the grass the adults care for the young and carry them to pools of water. In one species, the strawberry poison frog (*D. pumilio*), the female feeds the tadpoles when they hatch, but what is unusual is that she uses unfertilised eggs to do so. In other words, she produces special eggs that have no reproductive purpose and uses them to nourish her young (Weygoldt 1980). Another example of feeding the young goes a good deal further. The female of the spider *Stegodyphus lineatus* opens the egg capsule thirty days after the eggs have been laid and helps her young to emerge. These are not yet completely developed and depend entirely on her care. She feeds them for two weeks by regurgitating a liquid feed. Thereafter she allows them to feed off her own body and, before long, the young have devoured their mother entirely, leaving only her empty husk (Schneider 1995).

Development of the young within the mother's body, as is typical of mammals, is a highly complex type of parental care that keeps the young secure from all types of external dangers during their development, which is when they are most vulnerable. The mammalian arrangement is not unique and many variations of this adaptation have been described (see Box 6.1). For example, there are several frog species in which development occurs within skin folds or within the males' mouth, but there is a still more unusual case. In the southern gastric-brooding frog *Rheobatrachus silus*, the female swallows fertilised eggs or recently hatched tadpoles, whose development occurs entirely within her stomach. She eats nothing throughout this period and the stomach stops producing gastric secretions, until the well-developed young emerge through her mouth after several days (Tyler & Carter 1981).

Even more extreme parental adaptations exist. In the mite *Acarophenax mahunkai*, a parasitoid of the eggs of a certain beetle, the young females remain inside the mother. The mite's life cycle is quite complex, as is often the case with parasites. Steinkraus & Cross (1993) found that a female mite that get to introduce into a beetle egg starts to eat it and grows fatter. Within her

body some 30 of her own eggs develop, most of them giving rise to females (27.2 females and 1.7 males on average). Once the eggs hatch inside the mother, the females are fertilised by their brothers. The whole process takes four days during which the mother's body swells to twenty times its original size. She then bursts, releasing the young. The male young then die, but the females set off to find a female beetle laden with eggs, in order to repeat the process.

Main category	**Specific types**	**Occurrence**
Provision of chemical energy, nutrients and/or food	Direct provision of food (prey) and/or water	Some arthropods and fish. Many birds and mammals.
External provision of epidermal or other glandular secretions. Delivered via the mouth or anus.	Some arthropods, fish and birds. All mammals.	
Internal delivery of secretions of the ovary, reproductive apparatus or special cells	Some sponges. Some arthropods, fish, amphibians and reptiles.	
A placenta or similar system connected to the maternal circulation	Some arthropods, fish, amphibians and reptiles. Most mammals.	
Nutrients delivered directly by the maternal circulation	Some insects	
Supply of maternal or sibling tissue	Some molluscs, arthropods, fish and amphibians.	
Supply of warmth that favours the growth and survival of offspring	Directly from the parental body (nearly always by the mother)	Some reptiles. Many birds and mammals.
By means of nests that the parents build of decomposing vegetation	Some crocodiles and a few birds.	
Protection of offspring from predators and inclement weather.	Keeping offspring in hidden places or constructing or making use of refuges (nests, holes and burrows).	Some polychaete annelids, octopuses and arthropods. Many vertebrates.
Carrying offspring externally on the parents' bodies	Some rotifers, arthropods, echinoderms, fish, amphibians, birds and mammals.	
Carrying offspring within the reproductive system, the gut, the ovaries, within special sacs or within other spaces inside the parents' bodies	Many invertebrates and vertebrates.	
Guarding and defending offspring	Some octopuses, arthropods and echinoderms. Many vertebrates.	
Retrieving lost young	Some arthropods, fish and reptiles. Many birds and mammals.	
Care of nest or offspring	Fanning or irrigating offspring to aid thermoregulation, respiration, removal of excreta and to reduce infection risk.	Some leeches, insects, octopuses and fish

Box 6.1. The chief types of parental care and the animal groups in which they occur. After Glazier (2002).

Nearly all of these examples relate to parental care by females. However, it is not always so and males in some groups often perform the task. Among fish, for example, it is common for males to guard, defend and irrigate the eggs, and care continues after the fry hatch in many species. In the well-known case of seahorses (and their close relatives) females lay their eggs in the males' abdominal brood pouch, where they hatch and the young develop. There are other less familiar examples that are no less fascinating.

I was surprised by a television documentary that I saw some time ago. It showed the process of laying and egg fertilisation in a small, freshwater fish. The male and female leapt out of the water almost in unison, the female then laying her eggs on a leaf of some overhanging plant and the male brushing them with his sperm to fertilise them. These leaps went on for quite some time, given that the female could lay up to 300 eggs. I noted the species' name, the splash tetra (*Copeina arnoldi*), and sought further information. I discovered that apart from this being very rare behaviour among fish (which the documentary was highlighting), males also perform unusual parental care in this species. After laying they remain near the eggs for three days and keeps on leaping, to brush them with water and prevent them from drying out (Krekorian 1976).

By way of a final example of parental care performed by males we have the case of a frugivorous bat, the dyak fruit-bat (*Dyacopterus spadiceus*). This is perhaps the most unusual of all, at least from our point of view as mammals, since here the males help to suckle the young by producing milk of similar quality to that of the females. This seems to result from their eating plants that contain chemicals that stimulate milk production (Francis *et al.* 1994), but this proximate explanation leaves unanswered why males in this species have evolved the ability to be stimulated to produce milk.

6.2.1. Evolution of parental care

We have seen that parental care presumably increases the chances that offspring will survive to breed successfully. The key question, therefore, is 'why has parental care evolved in some species and not in others?'. We can only give a very general answer: not all species are subject to the same selective pressures. We cannot really be more precise but evolutionary theory allows us to say that in species where parental care has evolved, the benefits obtained by the parents and the offspring must be greater than the costs incurred by the parents. That said, it is the case that the amount of parental investment is very variable among species in which it occurs and is also dependent on the relationship between the costs borne by parents and the benefits obtained by offspring.

The selective pressures favouring the evolution of parental care are also very variable. The most important are surely associated with life in a hostile environment in which the living conditions are very difficult. The outcome of such influences as adverse climate and the presence of numerous predators and/or parasites, for example. There are also other pressures associated with the biology and evolutionary history of species, which may act at the same time as the environmental ones. In any event, the chief compromise is between the number of descendants produced and the degree of parental care. If the environment is favourable for the independent development of the young, parental care declines.

6.2.2. Parental care by males: the importance of paternity certainty

Before addressing the conflict that exists between males and females with respect to parental care, it is worth highlighting a very important matter when it comes to the evolution of male parental care: their certainty of paternity (see Chapter 5). Given that parental duties are costly to males, the behaviour will only evolve if care is actually directed at their own offspring (i.e., their own genes). It may therefore be predicted that the level of parental care offered by a male will be related to his certainty of paternity. This idea has been tested both in comparative studies and by means of experimental investigations with many species in which the males' confidence in paternity has been manipulated.

In one of these latter studies, Bryan Neff, of West Ontario University, Canada, carried out a brilliant study of a freshwater fish, the bluegill (*Lepomis macrochirus*), whose males care for and defend the eggs and young. In this species, in addition to males that court females, there are 'sneaky' males (those that fertilise eggs laid by a female who is being courted by another male; see Chapter 5), so that absolute certainty of paternity is impossible. In one of Neff's experiments, the presence of a sneaky male near to an experimental nest was simulated. In the another experiment, a third of the eggs were exchanged with those from other nests, bearing in mind that male bluegills can distinguish eggs by smell. Both experiments also employed unmanipulated nests as control groups. In order to quantify parental care, a live predator was presented within a transparent bag and the nest owners' behaviour was observed in order to produce an index of their investment in defence. As predicted, both types of manipulation significantly affected the intensity of the parental care performed. Males were less defensive when they had observed a rival male near the nest when the eggs were laid and also when they had detected strange eggs in the nest.

6.2.3. Which sex provides parental care? The conflict between males and females

By definition, parental care can help offspring survive to reproduce, and thus contributes to the genetic success of both parents, the male as much as the female. However, such success arises independently of who provides the care. Natural selection does not favour the most successful pair, but rather the individual who leaves most descendants. It is therefore unsurprising that there is significant conflict between males and females, given that selection will favour the individual who is capable of getting its mate to invest more in parental care than it does itself. That individual can then invest more in seeking more mates and thus will leave more descendants.

A review of different animal groups reveals enormous variation regarding which sex cares for the young. For example, it is usually provided by the male in those fish in which there is parental care. In birds usually both sexes participate, whereas in mammals it is nearly always just the female who cares. This variation is the outcome of the evolutionary conflict between males and females in which each sex tries to ensure that it is the other that provides parental care. Why have males won this conflict in most species? Perhaps because biological, physiological and other factors predispose females to be the carers (see Box 6.2).

Why is parental care in birds provided by both sexes but solely by males in fish? Several factors may be involved and these give rise to various hypotheses. Where birds are concerned there is a particular hypothesis that applies quite generally although not to all species. The situation in fish is less clear (See Box 6.3).

In general, we can say that parental care is provided by only one sex when it is not essential that both should participate. In this circumstance, when one sex has the opportunity of finding another mate and of deserting, it will leave the other sex to care for the offspring.

1. Biological and physiological factors predisposing females to be carers

a. Males have the possibility of deserting earlier in species with internal fertilisation.

b. Where gestation is internal, as in mammals, females are predisposed to provide parental care since the young develop within them. This makes it easier for the male to abandon one partner to seek other mates.

2. Other factors

c. Males are much less certain of their paternity than females are of their maternity.

d. Males have more opportunities than females to pair again and they have more to gain from doing so.

e. The costs and benefits of parental care are not equal for males and females. The costs are typically higher for males and the benefits higher for females.

Box 6.2. Factors that favour the evolution of exclusive female parental care in most species.

Matteo Griggio, of the Konrad Lorenz Institute of Ethology, Austria, and Andrea Pilastro, of Padova University, Italy, have published several studies of parental care in the rock sparrow (*Petronia petronia*). Both sexes in this species apparently have opportunities to desert their partners because some nests are attended by the male only, others by the female only, and still others by both sexes jointly. This species thus provides an interesting model for trying to understand how the division of parental care between both sexes evolves.

Why is parental care in birds provided by both sexes?

- **Influencing factors**: Parental care in birds is highly elaborate and costly. It involves building a nest, incubating the eggs for 24 hours a day and then feeding the chicks, which grow very rapidly and thus have voracious appetites.

- **Conclusion**: The most widely accepted hypothesis is that biparental care has evolved in birds because the investment required by the offspring is so large that both parents are needed to provide it.

Why is parental care in fish provided by the male?

- **Influencing factors**:

o Fertilisation is external, not internal, so the female has the first opportunity to desert, leaving the male holding the eggs.

o The female lays her eggs in a nest built by the male in his territory. The male continues to defend the territory and the nest while trying to attract more females so performing parental duties that only consist of defending and oxygenating the eggs is less costly for the male than for the female.

- **Conclusion**: Three explanatory hypotheses have been suggested. The carers are the males because (i) they have a high certainty of paternity, (ii) they release their gametes after the females do, and (iii) they are physically more closely related to the embryos. The third hypothesis has attracted most support.

Box 6.3. Influencing factors and hypotheses explaining the distribution of parental care in birds and fish. After Krebs & Davies (1993).

In the rock sparrow, as with most species, males desert more often than females. The investigators identified the principal reasons why. The females incubate the eggs and brood the chicks during their earliest days, so the males are the first to have an opportunity to desert (Griggio & Pilastro 2007). When either sex deserts, a new breeding attempt with another partner begins. Thus the benefits of desertion are limited by the availability of individuals of the opposite sex with which to pair. The investigators found that females desert more often when there are more available males (Pilastro *et al.* 2001). Finally, they found that desertion is costlier for females than for males since, when a male deserts the female compensates for his absence by increasing the number of feeds brought to the young, so favouring the survival of the entire brood. However, when a female deserts the male only partly compensates for her absence and therefore some of the chicks are likely to die (Griggio & Pilastro 2007).

6.2.4. Parent-offspring conflict and sibling conflict

The 'parent-offspring conflict theory' that Robert Trivers (1974) proposed, maintains that although survival is what matters to offspring and that offspring survival is vital to their parents, the interests of both parties do not completely coincide. Trivers argued that the optimal strategy for parents is to invest equally in all their offspring, including those that have yet to be born, since all of them share 50% of the parental genes. On the other hand, the optimal strategy for each of the offspring is to receive more parental investment than their siblings, given that an individual is obviously 100% related to itself, but shares only 50% of its genes with its brothers and sisters. This implies that natural selection can favours offspring that demand and receive greater parental investment from their parents than the latter are disposed to provide. It also implies that selection will have favoured those parents that have developed counter-adaptations to avoid blackmail by selfish offspring, given that parents who give in to individual offspring at the expense of the others will leave fewer descendants than those that distribute resources equally. In other words, offspring have evolved to demand more from their parents than these have been selected to provide; and parents have developed counter-adaptations to resist such demands so as not to endanger the survival of the remainder of their young as well as not harming their own reproductive future.

One of the best-studied aspects of this conflict concerns the duration of the period of parental care. Offspring prefer to prolong this period as much as possible, but it is in the interests of parents to cut short their investment in offspring as soon as these are capable of fending adequately themselves, with a view to beginning investment in further offspring. This strategy allows parents to increase the number of breeding attempts that they can make throughout their lives, thus leaving more descendants. A typical example of the conflict associated with the duration of parental care arises from the timing of weaning in mammals. Most of you who have bred dogs or cats will have noted that once the puppies or kittens have grown, they nevertheless keep trying to suckle, while their mother makes it harder for them and allows them to do so for progressively less time, until at last she stops altogether

(although if only one offspring has been left with its mother the latter is much more indulgent).

This independence conflict of offspring is not confined to mammals, but is widespread throughout the animal kingdom. Another good example comes from a study of a predatory bird, Montagu's harrier (*Circus pygargus*) by Beatriz Arroyo (then of the Centre for Ecology and Hydrology at Banchory, UK), and her coworkers. In this species, as with other birds in which the chicks develop within a nest, the young are attended by their parents for a more or less prolonged period after they have fledged, until they become independent. The investigators found that the young attempted to prolong the period of dependence on their parents, especially when the food supply was scarce. As time went on the young improved their flying and hunting ability, but kept on soliciting food from their parents. Nevertheless, the parents eventually reduced the frequency of feeds, provoking more aggressive demands for food from the young, even though their parents had stopped feeding them some days later (Arroyo *et al.* 2002).

Given that for each offspring the optimum situation is to receive more resources than its siblings, parent-offspring conflict predicts that the latter will have to compete among themselves in order to secure a larger share of what the parents provide. This conflict is seen very clearly in birds, especially in those in which hatching is asynchronous because the female begins incubation before the clutch is complete. In such species some chicks hatch earlier than others and, being larger, have an advantage when competing for food. Such competition often leads to the death of one or more of the smallest chicks. Sibling conflict is most severe in some species with asynchronous hatching where the older sibling itself often kills the younger one.

Sibling conflict has been studied in other animal groups, particularly in mammals. Fritz Trillmich and Jochen Wolf, respectively of Bielefeld and Cologne Universities, Germany, carried out an exemplary study of this conflict in two marine mammal species, the Galapagos fur seal (*Arctocephalus galapagoensis*) and the Galapagos sea lion (*Zalophus wollebaeki*). The females of both species do not wean their young until these are two years old, by which time they themselves may have given birth again. In about 23% of cases a female finds herself caring for a two-year-old as well as for a newborn offspring. In such cases sibling conflict reveals itself in various ways. For example, the younger sibling weighs less at birth and grows more slowly than those whose mothers are not also feeding a larger brother or sister. Younger pups with siblings also suffer higher mortality, either through competing unsuccessfully for food or as a result of being attacked by the larger sibling. This was especially so when food availability was lower and also when the larger sibling was a brother and not a sister (Trillmich & Wolf 2008).

The same study also revealed the conflict between the mother and her offspring. As parent-offspring theory predicts, the mother served her own interests, by defending the smaller pup against aggression by the larger one and, if the latter was sufficiently developed, by ceasing to feed it and forcing it to become independent. On the other hand, if the larger pup was not yet capable of independence, the mother might abandon the smaller one, leaving it to die (Trillmich & Wolf 2008).

6.2.5. Human parental care

All of you will acknowledge that we humans care for our own young, as do other animals. However, if I maintain that Trivers' parental investment theory also applies to human parental care, I am sure that not all of you will agree. We shall return to this matter at the end of this section.

Let us start by asking ourselves a question: ‘why do we care for our children?’ Most parents will immediately reply ‘because we love them’. However, this does not resolve the matter from a scientific point of view since we need to consider the deeper significance of ‘we love them’. Before answering the question I will put another that is fundamental to assessing the relationship between human behaviour and that of other animals: ‘Is it a conscious decision, made because we are inclined that way by our intellect and by our most sublime rationality, or is it in some way instinctive as in other animals?’ We shall examine the neurohormonal changes that result from the birth of a child, in order to answer these two questions. The principal changes are given in Box 6.4. If we look at these carefully we can see that many of the changes that take place in mothers prepare them for enjoying the experience while they perform the heavy onerous tasks that caring for their babies involve. To illustrate the latter I can supply a little-known fact: first-time mothers lose 700 hours of sleep on average during the baby’s first year.

Moreover, bearing in mind the neuro-hormonal changes given in Box 6.4, it is not surprising that having and caring for a baby is so gratifying to mothers, since maternal love has much in common with romantic love (both activate the same parts of the brain). Andreas Bartels and Semir Zekiof, of University College London, UK, studied mothers who had recently given birth, using a modern scanner to record cerebral activity. They presented the mothers in turn with photographs of their own babies, of their romantic partners, and of other babies and of friends, in order to compare their responses. They found that both photos of own babies and of partners activated different parts of the brain but both of these, and not the control photos, activated the same reward zones that comprise areas rich in oxytocin receptors, this being the hormone that produces intense feelings of satisfaction (Bartels and Zeki 2004).

Neurohormonal changes in fathers also increase their willingness to care for and defend the baby (see Box 6.4). It appears that in men such changes are brought about by pheromones produced by pregnant women.

Box 6.4. provides the answers to our two earlier questions. We certainly care for our children because we love them but that ‘love’ is the outcome of an evolutionary process that has favoured both mothers and fathers with the proximate neurohormonal systems that encourage parents to take care of their offspring. For example, the baby’s cry provokes an immediate physiological response in its mother that alerts her to the need to attend to it. Such a response depends on a complex interaction between external stimuli, the nervous system and hormonal influences and may thus be very flexible. That response may also operate in the father if he is conditioned to the need and may not do so in the mother if she thus feels liberated from that need. A personal anecdote may illustrate this flexibility clearly. My second child was born thirteen months after the first. Since my wife had to return to work after her maternity leave we agreed that, at night, she would get up if the younger child cried and I would do so for the elder one. My wife had to wake me for the first few nights but, to our surprise, only two weeks later on most occasions each of us only woke up when 'our' baby cried and not when the 'other one' did so.

Changes in mothers

1. Dopamine (the substance responsible for pleasure and reward) levels rise due to the effect of oestrogen and oxytocin (this is the same reward circuit activated during intimate communication and by female orgasm).

2. Oxytocin is released in great quantities during lactation (as it is during orgasm) and causes the sensations of love that all mothers feel towards their babies and triggers protection and care of the young.

3. Breast-feeding reinforces maternal behaviour. When the baby starts suckling, great quantities of oxytocin, dopamine and prolactin are released in the mother. The first two make her feel loved, link her physically to her child and make her emotionally satisfied, so that sexual desire declines. Many of the emotional benefits that sexual relations used to provide are now provided by motherhood.

4. Breast-feeding lowers blood pressure, tranquilises the mother, makes her feel relaxed and stimulates an intense feeling of love for the baby.

Changes in fathers

1. Levels of prolactin (the child-raising and lactation hormone) increase by 20% during the weeks preceding the birth, stimulating strong sensations of love for the child even before it is born.

2. Levels of cortisol (a stress-related hormone) may double, stimulating sensitivity, alertness and concern for the baby's security.

3. Testosterone levels fall by a third and oestrogen levels rise above normal during the first few weeks after the birth. (Testosterone increases sexual drive and represses maternal behaviour). This reduces the need to have sexual relations and increases concern and affection for the baby.

Box 6.4. Neurohormonal changes that occur in the female and male brain towards the end of pregnancy and after birth. Chiefly after Brizendine (2006) and Goleman (2006).

The hormonal basis and the flexibility of the parental behaviour that we have studied indicate that, as in all other animals, parental care in humans is the result of natural selection. It thus supports the initial assertion, that human parental care may also be analysed from the evolutionary approach of Trivers' parental investment theory.

The evolution of human parental care

We shall now consider various matters arising from Trivers' theory that we studied earlier in other animals. In the first instance, we highlighted the importance of paternity certainty on the evolution of parental care. Evidence suggests that certainty of paternity influences decisions on parental care by we humans. A man invests less in parental care when he believes that his children are not his genetic offspring. For example, many studies have revealed that men invest less in their stepchildren than in their own children and that children living with an adoptive father are more likely to suffer maltreatment and to die than those who live with their biological father (see a detailed account in Chapter 1).

These are cases in which certainty of paternity is absolute and thus the behaviour may derive from a conscious decision. However, as in other animals, positive or negative indicators of paternity have been found to be influential. A study by Coren Apicella and Frank Marlowe, Harvard University, USA, provides a good example. They investigated the influence on parental care on two factors associated with probability of paternity. These were a man's perception of how much his children resemble him and also his perception of his wife's fidelity. A group of 144 men was presented with a questionnaire designed to evaluate each man's view of three aspects important to the study: his resemblance to his children, his wife's fidelity and his investment in parental care. Each man was presented with a series of statements to which a value of 1 to 5 had to be assigned, on a scale ranging from 'totally agree' to 'totally disagree'. An example of the statements, relating to the man's resemblance to his children, was: (a) 'I think my children resemble me more than their mother', (b) 'I think my children have some of my personality traits', and (c) 'many people think my children resemble me'.

The predictions based on Trivers' theory were also met in this study. Men invested more in parental care, by paying more attention to the children and spending more time with them, when these men thought that the children resembled them and that their investment was lower when they thought that there was not much resemblance. The second prediction was also fulfilled, men who were more confident of their wife's fidelity dedicated more time to their children than did those who were less certain (Apicella & Marlowe 2004).

We have also previously studied the relationship that should exist between parental effort and effort to secure mates, according to the parental investment theory. This too has been demonstrated in humans, both in modern developed societies and in hunter-gatherer societies, where investment by men in parental duties is influenced by the availability of women as potential partners (as happens with the rock sparrow). Men who consider themselves to be very attractive invest less in caring for their children and instead invest more in seeking more partners, than do men who think themselves less attractive. A good example was provided by Frank Marlowe, one of the investigators in the previous study, who worked with the Hadza, a hunter-gatherer people in Tanzania. He found that adopted children received less care than biological children, a finding confirmed by many other studies. He also found that the more women of fertile age there were in a village, the less time fathers spent with their children (Marlowe 1999). This result shows that there exists conflict between paired men and women (fathers and mothers) regarding care for their children, and it supports Triver's general prediction that there should be a negative correlation between parental effort and mating effort.

Human parent-offspring conflict

In humans, as in other animal species, both parents and offspring derive important evolutionary benefits from parental care. The offspring benefit since parental care improves their chances of survival to breeding age, whereas the parents benefit since they increase the chances of producing successful descendants. One might therefore expect both parties to facilitate parental care; the offspring should cooperate with their parents and should look after them in a way that would be optimal for both. Nevertheless, this cooperation does not happen in humans any more than it does in other animals. We shall consider what does occur in our own species since I believe that it is a most important topic and a highly topical one.

As we all know, raising children properly is very difficult. If we over-protect them they may become spoilt, demanding and impossible to satisfy. At the opposite extreme, if we neglect them they may even die for lack of love and companionship as has occurred in orphanages set up for foundlings and other abandoned children. For example, there is very clear and reliable data that reveals that in the United States, during the early 20th century, nearly all children taken in by such orphanages died before they were two years old.

Why is raising children so hard? The simple answer, without going into details, is because this activity is fraught with conflict. There is conflict between the father and the mother (as in the case of the Hadza above), conflict between siblings and, most important of all, between parents and offspring.

Does the parent-offspring conflict that we have described for other animals also exist in humans? Some may not see this clearly but the answer is a resounding 'Yes'. It begins at the moment of conception and continues throughout life (see Box 6.5).

By way of example, Box 6.5 presents some apparent examples of conflict between mother and foetus. This information, the fruit of modern medical investigations, should convince the most sceptical of the existence of such conflict. They reveal that the foetus has evolved mechanisms to secure the greatest possible supply of resources from its mother, who in turn has developed mechanisms to avoid excessive exploitation by the foetus.

Mother-child conflict continues after birth. For example, babies attempt to obtain as much milk as possible from their mother. In the face of excessive demand she secretes benzodiazepine in her milk, a substance that has a sedative effect.

Babies have been shaped by natural selection to obtain what they need. On the one hand, their cry is highly effective in gaining the attention of the mother and father. On the other, their smiles and cuddling give great pleasure to their parents, which help insure that the joys of parenthood exceed the disadvantages. In other words, babies possess suitable adaptations for making themselves loved, which are clearly worthwhile since only babies whose parents love and care for them are likely to reach adulthood.

A warning about the parent-offspring conflict

There is a very worrying side to parent-offspring relations in modern western societies. To explain this we shall first consider what may have been the relationship between mothers and suckling babies during the Stone Age, based on what we know of the Bushmen and other modern hunter-gatherers. Mothers, with babies in arms, spent many hours searching for and collecting food. The babies often cried and would be immediately suckled when they did so, three or four times an hour for one or two minutes at a time. Mothers did not have large food reserves but rather depended on what they gathered daily. Moreover, mothers with babies very often also had an older child, some four years old, to care for. Life was very hard and there would have been periods of scarcity during which the children would have gone hungry and been otherwise in need. The adaptations that babies possess to make themselves loved and to secure the greatest parental investment possible evolved in such circumstances. Mothers (and fathers) were also adapted to respond quickly to their baby's begging cries since, in times of scarcity, descendants were only produced by those parents who were capable of meeting their children's needs quickly and effectively.

A. Conflict in the mother

1. Defective embryos are aborted (from 30% to 75% of embryos are aborted spontaneously). Genetic studies of foetuses that abort have shown that a high proportion have genetic defects. It is thus best for the mother to abort rather than to continue investing in an embryo with little chance of survival.

2. The greater the maternal blood flow to the placenta, the more nutrients available to the foetus. The mother tends to reduce her blood pressure, which prevents the foetus securing too great a share of resources and so prejudicing her health.

3. When a non-pregnant woman consumes a carbohydrate-rich meal her blood sugar level rises rapidly, and then falls on account of insulin, which stimulates the conversion of sugar to glycogen, which is stored in the liver. Pregnant women are less sensitive to insulin and have to increase its levels in their blood.

4. Some 70% of pregnant women suffer nausea and vomiting during the first three months of pregnancy. This happens precisely during the period when a foetus is most vulnerable and, especially, in response to substances most likely to be toxic to it (meat, eggs, strong-flavoured vegetables, coffee and alcohol).

B. Conflict in the foetus

1. High maternal blood progesterone levels help to sustain the pregnancy. When the foetus is sufficiently developed it releases gonadotropin, a hormone that stimulates maternal progesterone production, and so contributes to this process.

2. From the moment of implantation, the foetus stimulates a dilation of the maternal arteries and an increase in maternal blood pressure, enabling it to secure a greater supply of resources.

3. The placenta produces a hormone that reduces the mother's sensitivity to insulin, thus ensuring a larger supply of glucose to the foetus.

Box 6.5. Conflict between mother and foetus. The first three points in both sections are matching adaptations and counter-adaptations. Point 4 in section A may not be a case of conflict since it may not be instigated by the foetus, as it could be a response of the mother since it increases the chances of a successful pregnancy. After Cartwright (2000) and Barret et al. (2002).

Things are very different in modern societies. Women go out to work and can neither take their baby with them nor can they keep stopping to suckle it. Other profound changes have also occurred. Abundant food resources are available. Women often wait until they are 30 years old before having their first child and the number of children born per woman has declined sharply (it is currently 1.3 per woman in Spain). We live under completely different conditions from those of our ancestors, in which parents need not be overly concerned with the survival of previous or future offspring, nor with their own. This change between primitive and current living conditions may explain differences between the parental care strategies of our ancestors and those seen in modern industrialised societies. Human parents nowadays are inclined to invest much more in their offspring than was the case in Prehistory, when limited resources had to be stretched to keep themselves alive and to feed several children. There will often have been times when there was insufficient food and breast-feeding mothers would have had trouble producing sufficient milk.

The problem to which I drew attention in the section heading is that, although modern parents have changed their parental care strategies since they often no longer face limits to investing more, children have not changed their begging strategies and continue to be very demanding. Parents tend to respond to all signals of need (cries) from their children but the latter have evolved to beg and demand, which means that they will continue to do so even after their basic needs have been met. They may be neither hungry nor ill or cold, the basic causes that made them cry in the Stone Age, but they have other needs that come to acquire more importance for them, such as being picked up, being fed certain favourite foods or getting more toys, and they cry to obtain these. Parents may give in to all these whims but the children do not necessarily stop crying but rather cry to demand less important 'needs'. The conclusion is that children will never stop crying however much some parents respond by satisfying all their children's demands. Children have evolved to be effective at begging and they will continue crying and to be more demanding with each passing day.

Parent-offspring conflict, with respect to the period during which children remain dependent on their parents, also arises as a consequence of modern living circumstances in our opulent western societies. Numerous studies have revealed that children become independent much later than used to be the case. For example, according to the Youth Institute ('Instituto de la Juventud') in Spain, now only 23% of young people have left home at the age of thirty. This dramatic statistic reveals an enormous change since only thirty or forty years ago children became independent to start their own families soon after they reached the age of twenty. The reasons are various, but perhaps the most important change is the same as we mentioned earlier: parents are disposed to invest more in their children. They give them every opportunity to stay and so it is much more convenient for them to do so instead of becoming independent, especially considering the difficulties mature offspring face in securing employment in today's economic environment.

Human sibling conflict

As we have noted, Trivers' parent-offspring conflict theory also predicts conflicts between siblings, given that each may try to secure more than its fair share of resources. Humans are no exception and conflict between human siblings is widespread. The history books record numerous instances of competition between siblings for rights of primogeniture, these even ending in murder. Psychologists are also well familiar with problems of jealousy between small siblings. Offspring also sometimes feud over the distribution of their inheritance. This is not to say, however, that the general rule is for human siblings to get on badly. On the contrary, they often collaborate and help each other for reasons that we shall discuss in Chapter 8.

Quite a few studies reveal the existence of sibling conflict at various levels, although the topic has been less studied that parent-offspring conflict. We shall examine an example that meets one of the most drastic predictions of the theory, that having insufficient time between successive births increases the chances that one of the children will die. Noval Alam, of the Indian Centre for Population Studies, followed the lives of nearly 4,000 children who were born in a rural part of Bangladesh between 1983 and 1984. He found that if two children were born less than 15 months apart, the survival of the elder child increased the chance that the younger would die. However, if the elder died, the interval between births did not influence the survival of the younger. These findings were significant after controlling statistically for gender, the mothers' age and familial economic status, so the conclusion was that the mortality was due to competition between the siblings for the available resources (Alam 1995).

6.3. Mating systems

Different mating systems are defined in terms of the number of individuals of each sex that comprise them. Box 6.6 gives the most usual classification, which is followed with minor variations by all textbooks. It is undoubtedly useful but it must be emphasised from the start that the limits between different systems are not at all clear-cut, and there may be considerable variation even within a particular species. This is unsurprising since mating systems may be seen as the evolutionary outcome of conflict between the sexes in specific ecological scenarios. The particular ecological conditions in each scenario will determine what sex wins the conflict in those circumstances. In other words, the evolution of mating systems is determined by ecological conditions because they directly affect the opportunities for males or females to manipulate the opposite sex or to escape manipulation by a partner.

- Monogamy: One male and one female. Both sexes share parental care. May be annual (a new pair forms each breeding season) or permanent (pairing is lifelong). Relatively infrequent and only predominant in birds.

- Polygamy: One member of one sex with several of the opposite sex.

- Polygyny: One male and several females. Females deliver parental care. May be successive (one female follows another) or simultaneous (several females at a time). This is the optimal system for the reproductive success of the male. Occurs when males have the chance to monopolise several females. May involve pair formation but more usually the female is left alone after mating.

- Polyandry: One female and several males. Males deliver parental care. May also be successive or simultaneous. This is the optimal system for the reproductive success of the female. Occurs when females are able to control access to themselves by males. This is the most uncommon mating system and occurs only in a few species of birds as well as a few species in other groups.

- Polygynandry: Several females and several males. Both sexes share parental care but in mammals this is chiefly delivered by the females. A mixture of polygyny and polyandry. Also quite rare but less so in mammals, especially among primates.

- Promiscuity: Males and females may mate with multiple partners without bestowing parental care on offspring. No parental care. Common in fish and in marine invertebrates.

Box 6.6. Classification and definitions of animal mating systems.

6.3.1. Mating system conflict between males and females

The key to understanding the evolution of mating systems is conflict between the sexes. We will thus begin by recalling some general aspects of that conflict (see Chapter 4 for a more detailed account). Males have higher reproductive potential than females so their optimal reproductive strategy is generally to fertilise as many females as possible and to leave them in charge of the offspring (polygyny). In contrast, females have a limited number of ova that require considerable investment, and they can only increase their reproductive success by getting males to care for the young, or at least to help with raising them. The ideal mating system for females is generally that in which males remain to deliver parental care, allowing the females to devote all their effort entirely to producing and laying more eggs, thus leaving a greater number of descendants (polyandry).

The study that best highlights the role of intersexual conflict in determining mating systems is that by Nick Davies, of Cambridge University, UK, on the dunnock (*Prunella modularis*), a contemporary classic of behavioural ecology. This small bird does not have a fixed mating system. It is possible to find pairs, polygynous or polyandrous trios and polygynandrous groups (usually two males with two females), all within the same population. Nick Davies and his co-workers employed molecular analyses to establish the father and mother of each chick. They found that reproductive success was identical for both sexes in monogamous pairs (the male and female were each parents of an average of 5 offspring). In the polygynous trios each female was the mother of 3.8 chicks on average, whereas the male was the father of all of them, an average of 7.8 offspring. In polyandrous trios the reproductive success of the males depended on their dominance status (3.7 offspring for dominants and 3.0 for subordinates), and the female was the mother of all of them, an average of 6.7 offspring. Finally, in the polygynandrous groups the two females had the same reproductive success of 3.6 offspring each whereas that of the males once again depended on their dominance (5.0 for dominants and 2.2 for subordinates). Thus, as we noted earlier, a male achieved maximum reproductive success in polygyny whereas a female did so in polyandry. Bearing the above differences in mind, intersexual conflict is revealed to be the consequence of females trying to be polyandrous whereas males strive to be polygynous.

Indeed, Nick Davies and his co-workers proved that once males have acquired their first female they are not content to remain monogamous, but continue to court other females in order to become polygynous males. Much the same occurs with females, who also are not satisfied with just one male and try to attract others to mate with them in order to become polyandrous. There is also significant conflict between same-sex individuals, given that it is better for a male to be monogamous than polyandrous and also better for a female to be monogamous than polygynous. Thus if a male attracts another female, the first female will try to drive her away. Similarly, if a female succeeds in attracting another male, the first male will attack him with a view to chasing him off. The resulting mating system depends on the aggression and degree of dominance of the females and males making up the group but it is also related to resource availability. A male with a food-rich territory has a good chance of attracting a second female and becoming polygynous. However, if the territory is poor there is more chance that the female will acquire a second male, who will also help to feed the chicks (Davies 1992).

In general and as seen in the dunnock, polygyny is the outcome of a male's victory in the inter-sexual conflict and polyandry represents the same for a female. Monogamy and polygynandry occur when neither sex proves capable of manipulating the other to its own advantage.

What we have seen so far allows us to predict that in polygynous species the reproductive success of the most successful males will be greater than that of the most successful females, whereas the opposite applies to polyandrous species, where the success of the most successful females will be greater than that of the most successful males. Reproductive success will be similar in both sexes in monogamous and polygynandrous species. It is important to emphasise that reproductive success here refers to the success of individuals. At the population level, the number of descendants left by males is obviously exactly the same as that left by females. However, in polygynous species where a few males monopolise a larger number of females, the weaker males fail to reproduce. The same applies in the case of polyandrous females. Thus, polygyny and polyandry, the most successful systems for males and females respectively, are advantageous only for the stronger individuals since competition is fierce: the weaker leave few or no descendants.

The lifetime reproductive success of males and females has been recorded for few species but what data exist support what we have just concluded. As evident in Box 6.7, in the kittiwake, a monogamous species, both sexes produce approximately equal numbers of young. The maximum number of young produced by a stag with a harem of hinds at his disposal is nearly twice that produced by each female (even though he is shorter- lived). The maximum number of young produced by a male elephant seal, a highly polygynous species in which only a few males reproduce and these have large harems, is much greater than the output of any one female. The data on the human species refer to Moulay Ismael the bloodthirsty, emperor of Morocco, who had a harem of 500 women at his disposal and to Madalena Carnauba, a Brazilian woman, who gave birth to 24 sons and 8 daughters. The Guinness book of records cites a 19th century Russian peasant who is said to have had 69 children from 27 births (Krebs & Davies 1993), but the claim is regarded as unreliable by various experts.

Common name	**Scientific name**	**Maximum lifetime reproductive output**	
Male	Female		
Black-legged Kittiwake	*Rissa tridactyla*	26	28
Red Deer	*Cervus elaphus*	24	14
Elephant Seal	*Mirounga augustirostris*	100	8
Man	*Homo sapiens*	888	32

Box 6.7. Maximum known lifetime production of offspring in several species according to their mating system. Modified from Krebs & Davies (1993).

6.3.2. Monogamy

Monogamy is more typical of birds than of any other animal group. Up to 90% of bird species were thought to be monogamous prior to the employment of molecular analyses to determine paternity. However, as noted in Chapter 5, such monogamy is not so clear-cut when examined at a genetic level. Extra-pair copulations mean that some of the young in a nest have been fathered by a male other than the female's social partner. Prior to drawing conclusions regarding the characteristics of monogamy we shall consider the case of the barn swallow (*Hirundo rustica*), a species that has been regarded as typically monogamous. This swallow is very well known thanks to the work of Anders M0ller, of Pierre et Marie Curie University of Paris, France. The following account derives from M0ller (1994).

Early each spring, the swallows return to Europe from their African winter quarters to breed. As we noted in Chapter 4, the males have somewhat longer tail streamers than the females and these ornaments serve as indicators of their quality. The longer-tailed males arrive and find mates earlier. The early-arriving females are also of higher quality than those that follow. The longer- tailed males pair with the earlier females, which tend to be larger and are often capable of producing two broods per season. Long-tailed males tend to invest less on parental care and females paired with them tend to invest more on parental duties than do those paired with shorter-tailed males.

Swallows are monogamous but this is not to say that they are faithful. Both males and females may mate with other than their regular partners, although not all individuals are equally successful in obtaining extra-pair copulations. Longer-tailed males are more successful in mating with other females but short-tailed males never do. Among females, those paired with short-tailed males are most likely to take part in extra-pair copulations but those paired with long-tailed mates hardly ever do so. In other words, the tail length of their males determines whether or not females have extra-pair copulations. This apart, instances of intraspecific nest parasitism sometimes occur, generally when there is a high density of breeding pairs. Here females lay some of their eggs in the nests of neighbours that have started laying at about the same time.

The swallow example, which may be typical of most monogamous passerine birds, reveals some important matters, notably that avian monogamy is not based on mutual collaboration and fidelity, as some people used to like to believe. In accordance with intersexual conflict theory, the male and female do not have identical interests and individuals of each sex try to maximise its own reproductive success. This explains the existence of extra-pair copulations in males as a strategy for increasing the number of their offspring. Females take part in such copulations because, by mating with males of higher quality than their own, they too improve their reproductive success, not by producing more young but by raising young of higher quality. Females of many species have also developed intraspecific nest parasitism as a strategy that allows them to increase the number of offspring that they contribute to the next generation.

Bearing in mind that a male's own nest often holds young fathered by other males, we can also draw another conclusion, which we highlighted in Chapter 5, that it is necessary to distinguish between social monogamy (pair formation to raise progeny) and genetic monogamy (where all offspring are fathered by the incumbent male). The latter is much less common than was thought to be the case twenty years ago, given the frequency of extra-pair copulations (see Chapter 5). Social monogamy is easily revealed but detecting genetic monogamy —which furthermore may be highly variable in occurrence between different populations of the same species— requires molecular analyses. Thus, throughout this chapter, references to monogamy mean social monogamy, except where otherwise specified.

The rarity of genetic monogamy is unsurprising given that each member of a pair strives to increase its own individual reproductive success and not that of the pair. When all is said and done, what may seem strange is that genetically monogamous species should exist at all, and they do! There are indeed species in which the partners pair for life and in which both males and females remain faithful to each other. This is seen particularly among some raptors, corvids and seabirds.

A number of hypotheses have been offered to explain the evolutionary persistence of monogamy. In the above-mentioned groups, where such monogamy is widespread, the species tend to be long-lived and the males are considered to be indispensable for the care and feeding of the young. The males incubate, or feed the female while she does so, and later they bring about half of the food needed by the chicks during their development. Monogamy makes sense in species such as these where the needs of the young cannot be met by just one member of the pair and the collaboration of both is essential. This idea is supported by the fact that reproductive success in many of these species has been shown to increase over time, as the partners gain in experience.

Another group of birds in which extreme parental care is necessary is the hornbills (family Bucerotidae), large-billed, often frugivorous, birds whose reproductive behaviour is unique. The female seals herself into a cleft in a tree trunk using mud initially and later faeces and food residues, leaving only a small hole for ventilation and for receiving food from the male. She lays her eggs and does not leave the hole until the fully-developed chicks are ready to fledge. She takes advantage of the opportunity to moult becoming naked and flightless during this time. Parental care is thus almost entirely the concern of the male and it is especially costly since he must feed the female throughout and after incubation as well as the chicks during the fledgling period. It is hard to understand why male hornbills are prepared to perform such an arduous task, but we can imagine two evolutionary scenarios that may explain it. Firstly, despite being incarcerated, the females must play an important part in ensuring the survival of the chicks. Also, monogamy in such species must be genetic, not just social, since natural selection would only favour such enormous investment in parental care by the male if it was for the benefit of his own young. Both predictions are fulfilled. The narrowing of the access hole by the female is highly effective defence against predation. Also, in some species at least, molecular investigation of paternity confirms that the females are entirely faithful and none of the chicks in hornbill nests are fathered by other males (Stanback *et al.* 2002).

The earlier idea provided for explaining monogamy in hornbills would not be valid for many bird species in which the female alone is capable of raising at least part of her brood, nor does it apply to most species of other animal groups. We shall go on to consider two examples of monogamous mammals, members of a group in which monogamy is very rare. These will assist us in examining other possible hypotheses that explain monogamy and will pave the way for studying human mating systems.

Campbell's dwarf hamster (*Phodopus campbelli*) is a small monogamous rodent of the Russian steppes. Males take great interest in their offspring and offer all kinds of parental care, other than providing milk, which they cannot do. They even assist at birth, helping the young to emerge, cleaning them and eating the placentas (this is the only known mammal to do this). The male spends a great deal of time with the young in the burrow, which is very important since this hamster inhabits a very cold, dry habitat. They keep the young warm while the female emerges to find moist food. Monogamy and parental care by males are very rare in rodents. Even congeneric species, such as the Djungarian hamster (*Phodopus sungorus*) do not behave like Campbell's dwarf hamster. The Djungarian hamster lives in less cold and dry areas, so that the female alone is capable of caring for the young (Wynne-Edwards 1995; Jones & Wynne-Edwards 2000).

Marmosets and tamarins are very small American monkeys, many species of which are monogamous. The common marmoset (*Callithrix jacchus*), one of the best- studied species (Evans & Poole 1983; Albuquerque *et al.* 2001), lives in family groups composed of a male, a female and one or more young of various ages. The females generally give birth to twins, which are quite large at birth, around 23% of their mother's weight. The males play an active role in caring for the young, watching over them and, especially, carrying them. In this species monogamy once again seems to be based on the need for the male's collaboration in raising the young but there are other factors that contribute to its maintenance. Females live widely separated, so there are few opportunities for males to meet other females. Also the females reproduce very rapidly (they can become pregnant again only 20 days after giving birth). In these circumstances, when a male finds a female, he probably benefits by staying with her in order to guard her against rival males. Monogamy is also favoured by the fact that both males and females are very aggressive towards any same-sex individuals who approach their group. In other words, both sexes enforce monogamy on their partner.

These mammalian examples reveal that monogamy may evolve under specific ecological conditions. As in birds, it is important that there should be major benefits from parental care. Natural selection may favour monogamy if either sex cannot raise the young unaided. The latter example also allows us to offer another hypothesis that explains why monogamy exists. It may evolve when it is very hard for males to find females, either because these are widely separated from each other or because they are very well guarded by their males. Under such conditions the best option for a male is to remain with the first female he can acquire.

6.3.3. Polygyny

This mating system in which one male pairs with several females (see Box 6.6) is the commonest in nature. It predominates in mammals, 97% of which are polygynous, but also in the great majority of other animal species. As we have observed, this is generally the most successful system for males but it is less ideal for females, so that inter-sexual conflict tends to be significant. Polygyny only occurs in species in which resource distribution enables a dominant male to monopolise several females. Its occurrence is thus chiefly determined by the distribution of resources and of the females themselves. If resources are patchily distributed, it becomes possible for a male to defend a rich patch and thereafter to mate with those females that come to use the resources that he owns. In contrast, it is much harder for males to be polygynous if resources are highly scattered or are uniformly dispersed. The same applies to the distribution of females. If these live in groups, whether in a particular territory or tending to use predictable routes, it may become possible for a male to succeed in mating with several females. Such behaviour becomes much more difficult where females are widely dispersed.

There are no grounds for believing that females will make polygynous mating easy for the males, since this mating system is less productive for females. We might rather predict that females will distribute themselves according to resource distribution, risks of predation and their own gregarious tendencies, without giving too much regard to where the males are located. In contrast, males will decide their movements and distribution on the basis of female location. This prediction has been established for several mammal species. For example, Johan Nelson, of Lund University, Sweden, performed a detailed experimental investigation into the effect of female distribution and density in the field vole (*Microtus agrestis*).

Female voles were placed in individual cages with supplies of food and water. Each cage had a hole so that males could enter but the females were prevented from escaping by a plastic collar. This arrangement permitted the investigator to modify both the distribution and density of females within fenced circular enclosures of 1,000 m^2. Four males, fitted with radio-transmitters so that they could easily be located, were released into each enclosure. As predicted, males distributed themselves according to the distribution of females. Also when female density was high the males maintained smaller home ranges (Nelson 1995).

The vole example serves to illustrate the most common arrangement seen with poygyny. The females conduct their lives without any regard for the males, but the males distribute themselves according to the disposition of females. No pairs form and males do not offer any parental care. Variations on this pattern are widespread. For example, in polygynous birds a more or less enduring seasonal pairing may occur between a male and a female, with or without parental care by the male. When males do not help to care for the young, it is all the same to the female whether the mating arrangement is monogamous or polygamous as far as reproductive effort is concerned. However, where a male does assist with parental care he tends to dedicate all his efforts towards his first female while leaving any other mates to fend for themselves. In this case we must assume that being polygynous is costly for all but the favoured females. Why then, in species where males help with parental care, do some females pair with already paired males when bachelor males are available? Two answers to this question have been proposed (see Box 6.8).

By way of an answer Verner (1964) proposed a model, later popularised by Orians (1969), known as the ‘‘polygyny threshold model’. It proposes that when a female chooses to pair with an already paired male instead of with an unpaired one, it is because the polygynous male has a high quality territory. This will enable her to raise more offspring than she would have done in the territory of the monogamous male despite her not receiving any assistance with parental care, which the latter male would provide. This model has not been found to have as wide an application as was first believed, but it has played an important role in our understanding of the evolution of polygyny and it has received considerable support from some studies on birds.

Polygyny with males providing parental care

- Based on resource defence: the ‘polygyny threshold model’
- Based on deception of females

Polygyny without males providing parental care

- Based on resource defence
- Based on defence of females
- Based on leks

Box 6.8. Models explaining the existence of polygyny in species in which the males provide parental care, and mechanisms used by them to achieve polygyny in species in which they do not contribute to parental care. See text for more details.

One of the best of these was an experimental study of the red-winged blackbird (*Agelaius phoeniceus*) by Stanislav Pribil and William Searcy, of Miami University, USA. Nesting success in this species generally depends on nests being sited over water, those over dry land usually being less successful. The quality of two adjacent territories was manipulated experimentally during the breeding season, in order to test the polygyny threshold model. In one territory of each pair, chosen at random, nest platforms were placed over water (the high quality territory) and a female was allowed to remain, so that the incumbent male remained paired. Nest platforms were placed over dry land in the other territory (the low quality territory) and any females paired with the territory owner were removed, so that he was now unpaired. Fourteen such territory pairs were studied. As the model predicted, in twelve cases (86%) the first female to arrive settled in the high quality territory of an already paired male. Only two females (14%) chose to settle in the low quality territory of an unpaired male (Pribil & Searcy 2001).

Another reason why a female may prefer to pair with a polygynous male has to do with deception by the already paired male, which convinces the second or third female into believing that he is actually unpaired. Such deception has been reported in several species, but the best example remains the classic study of the pied flycatcher (*Ficedula hypoleuca*) by Rauno Alatalo and his co-workers of Uppsala University, Sweden. Courting males defend a suitable nest-cavity (a nestbox in the study population) and sing to attract females. Very often, once a male has paired and the female has laid her clutch, the male finds another suitable cavity and sings to attract a second female. The observers noted that these males did not choose a cavity near the first nest, but rather chose one some way off, some 200m away on average but over 3km away on occasion. Once the second female had completed her clutch, the male abandoned her to return to his first mate, whom he assisted in raising the chicks. The deceived second female was left to raise and feed her chicks all on her own and, as a result, she fledged fewer than a monogamous female would have done. However, the first polygamous female, given her mate's assistance, fledged about the same number of chicks as did monogamous females (Alatalo *et al.* 1981).

Male deception is sometimes more blatant. The hen harrier (*Circus cyaneus*) is a polygynous raptor in which males may pair with up to five females. Deception by the males here consists of bringing frequent and significant nuptial gifts (prey items) to all the females that they court, indicating to them that they are good hunters and will bring much prey to the chicks (see Chapter 4). However, once the chicks have hatched the males no longer bring the same amount of food to each female. They mainly assist the first female with whom they paired. The second female gets less help and any others receive very little assistance (Simmons 1988).

Three types of polygyny figure among those mating systems in which the males do not deliver parental care (see Box 6.8). The polygyny may be based on resource defence, on direct defense of group of females or via defense of a display territory at a lek, although the boundaries between these are not always sharp, as we shall see.

A good strategy for mating with females, if the males are not going to help with parental care, is to defend some resource that the females need in order to breed successfully. This may be a territory, food or a breeding site, for example. A male who is capable of securing possession of such a resource will be able to mate with females that come to exploit it. Resourcebased polygyny is particularly common in the many mammal species in which males play no part in parental care. For example, in the puku (*Kobus vardoni*) and the topi (*Damaliscus lunatus*), two medium-sized antelopes, the distribution of females within the territories of various males is explicable in terms of grass quality, although there are two other influencing factors: the males' physical characteristics and protection from predators (Balmford *et al.* 1992).

Polygyny based on defending females is also very common in mammals. The gorilla (*Gorilla gorilla*) provides a typical example. It lives in by groups that contain one male, usually three or four females, and their offspring (Gatti *et al.* 2004). Male gorillas defend their females and this strategy is easily understood since they all feed on leaves and other abundant plant material, so that resource defence is pointless whereas females do live together in defendable units.

It is not always so easy to decide whether or not an instance of polygyny is due to resource defence or to female defence. For example, in the northern elephant seal (*Mirounga angustirostris*) the males arrive at the breeding colony beaches ahead of the females and the largest of them defend stretches of beach, i.e. territories. Once the females arrive, these spread out across the area and territory-holding dominant males mate with them, while keeping other males away, i.e. they defend the females. This is one of the most polygynous species known, some males acquiring harems of up to 100 females (Baldi *et al.* 1996).

The females' role in polygynous mating systems has traditionally been seen as insignificant and the striking and often noisy competition between males has always been regarded as deciding who pairs with whom. It is important to realise that this need not be the case. Females often have a chance to choose the male with whom they mate. Moreover, in many species females may often move from one harem into another. In addition, it has been found that in the grey seal (*Halichoerus grypus*), a polygynous species in which males are much larger than females and compete for harems between themselves, in 30% of cases the young born to a particular mother in successive years have all been fathered by the same male, who is not necessarily the harem master (Amos *et al.* 1995). This means that despite a dominant male controlling his harem, a female may give preference to another male, the father of her pups in earlier years.

The third polygynous system in situations where males do not offer parental care is neither based on resource defence nor on female defence. This is lek polygyny (see Box 6.9) in which groups of sexually active males await visits from sexually receptive females.

Definition: A lek is a gathering of males that perform courtship displays to females that visit the lek seeking males with whom to mate. Lek polygyny is a rare but widespread mating system that has been described in groups as diverse as birds, mammals, insects, lizards, amphibians (where they are known as choruses) and fish.

Characteristics:

1. Males defend small territories that do not contain any of the resources that the females need.

2. Males do not deliver any form of parental care.

3. Males only provide females with their gene-containing sperm.

4. Females have free access and may mate with whichever male they choose.

5. Lek males have enormously variable reproductive success. A few males fertilise nearly all the females and many males do not fertilise any at all.

Evolution:

Various models have been proposed to explain lekking. The chief ones are:

1. The hot-spot model: males gather at places that females very often visit.

2. The hotshot of supermale model: males gather around a very attractive male who may entice many females to come to or near his territory.

3. Female choice model: males are obliged to gather since females need to make comparisons between them. Males outside the lek are not visited by females.

4. Kin selection model (see Chapter 8): if males are related, the less attractive individuals will also join a lek since it helps to increase the number of females that visit and hence increases the reproductive success of relatives.

Problems:

1 It is very hard to identify which male characteristics influence female choice. The characteristics responsible have not been identified at all for some species and there are disagreements regarding others.

a. Female choice is highly complex and based on multiple male characteristics.

b. Potentially the most important of such characteristics are: morphology (size, colour and other adornments such as tail length), intensity of display (comprising sounds and movements mainly), position and size of territory within the lek, dominance status and previous experience.

2 ‘The lek paradox’ is a theoretical problem based on the following argument: if females always choose those males with the best developed features, natural selection will favour the alleles that increase success and will eliminate those that reduce it. The point comes when there will be no genetic variation for those characters among males and then selection by females would confer little or no genetic benefit.

Box 6.9. Lek polygyny. Definition, evolution and associated theoretical problems.

The first lek species to have been studied in detail was the sage grouse (*Centrocercus urophasianus*). Male sage grouse have extremely showy plumage and other ornamentation and they perform highly elaborate displays. They gather at dawn and dusk during the breeding season in groups of sometimes more than 15 birds. Each defends a small territory aggressively preventing its neighbours from coming too close. Females visit the lek for two or three days before deciding to copulate with one of the males (they only choose one for each breeding event). They very often pick the same male given that only a few males perform most of the fertilisations. One study observed 105 copulations and nearly half of these were performed by the same male. The next two males in the females' order of preference were responsible for around 20% of the copulations each and the fourth male accounted for 10%. The remaining 5% of copulations were shared between the remaining males, six of whom did not mate at all (Wiley 1973).

Clear distinctions between the three types of polygyny do not always exist. For example, some males of lek species instead defend larger territories away from the lek and others may not display any type of territoriality. Topis, the antelopes to which we referred above, sometimes defend very small territories and in that case constitute a lek. In several species males of different populations have been found to employ different strategies. For example, males of most populations of red deer (*Cervus elaphus*) defend harems of females but in some parts of Spain they defend food resources for females, whereas they have been known to form leks in Italy. Manipulating the environmental conditions experimentally has been shown to bring about a change from defending harems to defending resource-containing territories. Juan Carranza and his co-workers of Extremadura University, Spain, provided food in areas in which red deer stags defend harems. The change was immediate. That same day the hinds remained near the food for most of the time and two of the stags switched to defending those areas. Five other stags also switched to defending territories rather than groups of female during the next few days (Carranza *et al.* 1995).

6.3.4. Polyandry

This mating system, in which a female pairs sexually with several males, either at the same time or sequentially, is regarded the rarest in nature. Social polyandry, in which a female associates with several males, has been reported in very few species. Although genetic polyandry, in which a female's offspring have more than one father, is quite common (see Chapter 5), social polyandry is only known for a few bird species, and in a few mammals, such as the saddle-backed tamarin (*Saguinus fuscicollis*), whose family groups most often contain one female, two males and their offspring (Goldizen *et al.* 1999).

Sequential polyandry is most usual in polyandrous birds, in which the male alone provides parental care. The female mates with one male, lays her clutch and leaves it in the care of that male while she departs to repeat the process with another male. Such classic polyandry is typical among several shorebird species of the family Charadriidae. In this group when one member of a pair deserts it is usually the female. In the spotted sandpiper (*Actitis macularia*), females may mate with up to four males in succession. This species, as with jacanas, shows 'sex-role reversal' (see Chapter 4); the females are larger and compete for males among themselves.

An alternative termed ‘cooperative polyandry’ also occurs in birds but even less often. Here the females pair with several males at one time and the latter perform most parental care. An interesting example is the eclectus parrot (*Eclectus roratus*), in which each female may mate with up to seven males. Robert Heinsohn and his co-workers from the Australian National University have studied this species for several years. They found that the female defends a nest hole where she and the chicks are fed by the males. Males compete aggressively for females but sometimes successive copulations by different males occur without any squabbling between them. An eight-year molecular genetic analysis of eclectus broods has shown that the two young that normally comprise a brood usually share the same father, but different broods involving the same female are fathered by different males. Some males never get to be fathers at all (Heinsohn *et al.* 2007).

The rarity of social polyandry has always been explained on the grounds of basic considerations that we have noted several times (see Chapter 4). In this case they are that females have little to gain by mating with more than one male and also that, in mammals and birds, the males always have the first opportunity to desert and so to leave the female caring for the young. Nevertheless, as indicated in Box 6.10, although copulating with several males does not increase a female’s reproductive success, she may obtain both direct benefits (to herself) and indirect ones (for her offspring).

Social polyandry is certainly rare. Nevertheless, as noted earlier and in Chapter 5, studies based on genetic analyses reveal that genetic polyandry is much more frequent. A further good example of this is provided by two Australian workers, Phillip Byrne of Monash University and J. Scott Keogh of the Australian National University, with their work on a small amphibian, the brown toadlet (*Pseudophryne bibronii*). As often happens with fish, male toadlets build and defend nests in which females lay their eggs. Observation and genetic analysis has shown that the female toadlet distributes her eggs between the nests of up to eight males. This means that the mating system is polygynous from the males’ standpoint, but is polyandrous from that of the females (Byrne & Keogh 2009).

1. Direct benefits: those obtained by the female herself

a. Fertilisation is assured. Copulating with more than one male avoids the risk that a male might be sterile.

b. Extra food is obtained. Mating sometimes involves receiving nuptial gifts or nutrient-rich ejaculates. Either may help a female to produce more descendants.

c. Obtaining more parental care by the male. Exchanging sex with males for parental duties may benefit the female since the additional help may allow her to raise more offspring.

d. Avoiding harassment by males. Where such harassment is common (as in some ducks where a female may even be drowned as a result), it may be a good strategy to copulate with another male who may protect her, or even to accept the aggressor male rather than to resist futilely.

2. Indirect (genetic) benefits: those obtained for her descendants

a. Increasing the genetic diversity of the offspring. This increases the chances that some at least may survive.

b. Achieving genetic complementarity. The availability of sperm from several males makes possible selection by cryptic female choice (selecting the best sperm, see Chapter 5) in which females may select the sperm that best complements their own genetic constitution.

c. Obtaining genes that render the offspring more attractive, in accordance with Fisher's runaway selection model (see Box 4.6).

d. Obtaining the best genes for increasing the chances that the offspring will be good at surviving, competing and leaving descendants.

Box 6.10. Possible benefits that females may derive from mating with several males. After Birkhead (2007).

6.3.5. Polygynandry and promiscuity

As defined in Box 6.6, these mating systems are characterised by individuals of both sexes mating with several or many of the opposite sex. Polygynandry involves parental care but promiscuity does not. In polygynandry not all individuals are involved in copulation at the same time but this is more usual in promiscuous systems, which tend to occur among species with external fertilisation. In many fish and in marine invertebrates, males and females may assemble in very large groups and when the time comes they all release their gametes into the water at the same time, so that fertilisation happens on a vast scale.

Polygynandry is very rare. It is somewhat more frequent in mammals, especially among primates and rodents, but it is very uncommon in other groups. Smith's longspur (*Calcarius pictus*) is one of the very few bird species that employs polygynandry, in which females copulate with various males in turn during their fertile period, and a male may copulate with several females. Subsequently, the male longspurs collaborate in bringing food to the nests owned by females with whom they copulated. Interestingly, male longspurs have been shown to be capable of 'calculating' how many chicks in a nest may be theirs and they bring food to the nest in accordance with this estimate. What is truly remarkable is that the feeds brought by a male to a nest are more closely correlated with the number of chicks he has fathered (established by molecular analyses of paternity) than with the time he spent with the female during her fertile period (Briskie *et al.* 1998). On what can Smith's longspur males base such an exact calculation? We have yet to find out.

Conclusions on classifying mating systems

Box 6.6 presents a traditional classification of mating systems and we have seen that polygyny has always been regarded as the most frequent arrangement. Nevertheless, evidence has been accumulating over recent years that females play a much greater part in mate choice than has normally been attributed to them. Most previous investigators were men and this is still the case, so it is not surprising that the issue has always been studied from a male viewpoint.

We noted in Chapter 5 that extra-pair copulations are most often initiated by the females and also that they happen in most monogamous species. Thus, although 90% of bird species are considered monogamous, on a genetic level and from the females' point of view they may be considered polyandrous, since several males may have fathered the young in a nest. Also, in polyandrous species, where the female is the sex that benefits from multiple mating, females have several males to help them care for their young. They are not necessarily satisfied with just a few partners and sometimes continue seeking more-attractive males who also will father some of their offspring. The superb fairy-wren (*Malurus cyaneus*) provides an extreme example. This small Australian passerine does form pairs but the commonest reproductive unit comprises a female, a dominant male and several subordinate males. Nevertheless, despite possessing a harem of males that will later collaborate in raising the chicks, the female often also copulates with the most attractive neighbouring male (see Chapter 5), so much so that on average 76% of the chicks in the nest have not been fathered by any of the males in her family (Mulder *et al.* 1994).

What then happens in polygynous species, in which the prejudiced sex is supposed to be the female? A brief summary of an outstanding study of the great reed warbler (*Acrocephalus arundinaceus*) by Dennis Hasselquist and his co-workers of Lund University, Sweden, will help to provide an answer. This is a polygynous species in which females choose those males with the most diverse vocal repertoires (an honest indicator of male quality as noted in Chapter 4) and whose territories are most rich in resources. It is certainly the case that the male provides little help in caring for the young, but, does this mean that he is taking advantage of the females? Molecular analyses of paternity revealed that females have extra-pair copulations with males whose song is more elaborate than that of their own partner. Moreover, the survival of the chicks after fledging is related to the size of their father's repertoire (Hasselquist *et al.* 2002). In short, females choose the male who can best provide a foodrich territory. If he is not one of the highest genetic quality, the female will copulate with others of higher quality who will pass their good genes on to her offspring —see also the blue tit (*Cyanistes caeruleus*) study in Chapter 5. From a genetic viewpoint, polygyny becomes polyandry if there is a high rate of extra-pair copulations by females.

Evidently some of the concepts relating to mating systems need modifying. I agree with Marlene Zuk (2002) that nowadays we have more than enough information to know that what is observed on a social level rarely matches what is going on at a genetic level. The high frequency of extra-pair copulations means that the commonest mating system is in fact polyandry. The Australian toadlet mentioned above provided an example of a species thought to be typically polygynous, since each male pairs with several females that lay the eggs in his nest, but that has been found to be polyandrous from the females' standpoint on the basis of the more precise information supplied by molecular analyses. However, we may still have to wait a while before revising the classification of mating systems on the basis of genetic analyses of paternity. This is because such analyses have as yet been performed on few species and also because significant differences sometimes exist between different populations of the same species.

6.3.7. Human mating systems

This section heading is not an error. I have written 'systems' since one cannot speak of a sole mating system in the human species. Although monogamy predominates in our western industrialised societies, this is not the case among other cultures. As with other primates, our mating system is variable and flexible since, as we have seen, ecological conditions have very direct influences on such systems. The human species is no exception and, since we inhabit a great diversity of habitats across nearly the entire planet, instances of practically all possible mating systems have been described (see Box 6.6). Despite this diversity, we shall end the chapter by trying to determine which mating system may be considered more widespread among our species.

According to an analysis of a large number of ethnicities and non-western cultures, i.e. those not under the strong religious or state influences that so characterise our own civilisation, the majority of societies are polygynous (83.4%), although monogamy is also well represented (16.1%) while polyandry is quite unusual (0.5%) (Cartwright 2000). We shall consider the different mating systems in the reverse order to our earlier review, with a view to dealing last with the most interesting, monogamy.

Polygynandry and polyandry

Polygynandry (see Box 6.6) is extremely rare in humans. Setting aside the social experiments of the hippie communes of the mid 20th century, it can only really be found among the Inuit, and then in a very particular form unlike that which we described for some bird and mammal species. Two Inuit couples may have a mutual arrangement to share hospitality and help that extends to sexual favours. When a man needs to leave his wife for a time and visits the igloo of the other couple they will not only provide accommodation and assistance, but also he will be allowed to have sex with the woman, a favour that is reciprocated. Long absences of this type are uncommon which means that cross-copulation between such 'associated' couples is also uncommon and the risk of extra-pair paternity is not very high. On the other hand, the arrangement confers very important benefits since under the harsh living conditions of the Arctic a spell of poor hunting could mean death and being able to count upon the help of another couple (and a second set of relatives) is of inestimable value in times of scarcity.

Polyandry (see Box 6.6) is also very uncommon. It is only frequent among several Himalayan peoples. Interestingly, instances of polyandry have two points in common in all cultures where they occur: the land is resource-poor and the men who share a spouse are often brothers. These circumstances favour polyandry. On the one hand, polyandry occurs where living conditions are so poor that it is hard for one man alone to provide the resources needed to support a family and so collaboration between two men is what makes raising a child possible. Also, the fact that the two men are brothers diminishes the inevitable conflict associated with sharing the same woman. For example, in a Sri Lankan population in which such husbands were not always brothers, it was shown that the marriages were more stable and lasting when they were brothers than when they were not (Birkhead 2007). The older brother enjoys more frequent sexual relations so it is unsurprising that the younger one leaves to find a wife for himself when conditions permit. The joint occurrence of the above two circumstances in all cultures in which polyandry is practised supports the idea that it is an adaptation that strengthens social alliances that enhance reproductive success under difficult conditions. This adaptive conclusion has been criticised by some anthropologists but the evidence in favour of the hypothesis continues to accumulate (Smith 1998).

Kim Hill and Magdalena Hurtado, of the University of New Mexico, USA, have described a special form of polyandry among the Ache, a huntergatherer people from Paraguay (Hill & Hurtado 1996). The men in this society are very violent and resolve problems by fighting with sticks, as a result of which some of them die. As a result, many children are orphaned and this considerably reduces their chances of survival, from 86% for children with a father to 50% for those without. The investigators found that Ache women tend to live with two men, one as the primary partner and another with whom sporadic sexual relations also occur, so that he too has a chance of fathering her children. They interpreted this hierarchical polyandry as an adaptive strategy that allows women to achieve protection for their children in the event that their first spouse dies.

Polygyny

Polygyny, as we have seen, is the most frequent mating system in cultures outside western influences. There is strong evidence that it has always been widespread. For example, numerous passages in the Bible make it clear that the Israelites, together with all other peoples of the region, allowed a man to have as many wives and concubines as he could support. The custom is so ancient that the first polygynous man mentioned is Lamec, son of a great-great-grandson of Cam, one of the sons of Adam and Eve (Schwartz 2008).

As happens in other species and also in polyandry, polygyny is influenced by environmental factors (see Box 6.6). The relationship is a complex one. According to a review by Bobbi Low (2000), the factors that most influence polygyny are the risk of parasites, the seasonality of the rains, irrigated agriculture and hunting. Together these explain 46% of instances of human polygyny. The most surprising and interesting finding is that parasite abundance has the clearest effect. It has been often maintained that polygyny is chiefly determined by resource availability, as happens in other animals (see Box 6.8). The thinking is that monogamy would predominate when resources were scarce and polygyny would do so when they were abundant, for example in agricultural communities. However, the situation is far more complex and parasites instead appear to be especially important because, for example, monogamy is practically non-existent in areas with a high incidence of pathogens nor does polygyny involving marrying two sisters occur in those circumstances, unlike in other places where there are lower risks of contagion. According to Low (2000), both findings suggest that polygyny increases the genetic variability of offspring and would thus increase their resistance to parasites. However, the main advantage of polygyny is that it allows females to choose resistant mates (see Chapter 4).

Low's review did not take account of another factor that has been shown to influence the spread of polygyny in humans: a shortage of men. It has been shown that polygynous trios often form after a war and these comprise a man and two sisters. The explanation is the same as that offered for polyandrous trios involving a woman and two brothers. The fact that the women are sisters reduces possible conflict among them. An interesting anecdote may help us to understand this situation. During our study of the black wheatear (*Oenanthe leucura*), which is covered fully in Chapter 2, we colour-ringed the adults at 200 nests but found only a single case of polygyny. Here there were two nests, ten metres apart, in one male's territory, a rare event in what is usually a totally monogamous species. We noted that the two females were ringed and when we re-trapped them we found that they were sisters from the same nest. This helped explain the polygynous trio because normally one female would not tolerate a competitor for her partner. Normally one of the factors that impedes a male mating with two females is competition between the latter. Instead, as we saw in the case of the dunnock, each female will try to drive away the other so as not to have to share the parental care offered by the male. In this case, by being sisters the conflict was less and both accepted the situation. The same may happen among humans when few men are available. A woman might not accept her husband taking a second wife but, where that wife is her sister, it is less out of the question given the many genes shared by the two women.

When speaking of human polygyny it is obligatory to give special attention to the famous harems that were a common feature of the palaces of sultans, emirs, kings, emperors and other rich and powerful leaders. Such extreme harems comprise a very recent phenomenon in human evolution. Until the development of agriculture made possible the accumulation of resources, it simply was impossible for a man to dispose of sufficient resources to be able to support several wives and their offspring. A review by Laura Betzig has revealed that harems were common among the great empires of antiquity such as Babylon, Egypt, India, China, the Incas and the Aztecs, and among all peoples ruled by powerful kings. The harems of King David and King Solomon are particularly renowned. All these men acquired great riches and so were able to collect many spouses, who provided them with a large number of children (Betzig 1986). We have already mentioned Moulay Ismael, emperor of Morocco from the late 17th century into the early 18th century, who had 888 children from his harem of some 500 wives (Box 6.7). Very probably the potentates of antiquity did even better since their harems were ever larger. The largest of all was perhaps that of King Solomon who, according to several sources, had 1,200 wives.

Returning to the more usual type of polygyny, involving a man with two or just a few women, just as we did for animals in general we need to ask ourselves why a woman should pair with an already paired man. In our species, in which the man contributes to parental care, two models may serve to explain this, the polygyny threshold model and the mate deception model (Box 6.8).

Does it benefit a women to be polygynous if the man disposes of abundant resources, as proposed by the polygyny threshold model? The answer is sometimes yes. A recent study by Mhairi Gibson and Ruth Mace, of Bristol University, UK, provides a good comparison between the reproductive success of a monogamous woman and that of a polygynous one. The number of children borne by a polygynous woman depends on her ranking within the man's spouses, as happens in birds. The first wife of a polygynous man has greater reproductive success than a monogamous woman but the second and third wives do less well, and this is reflected not so much in terms of the quantity of offspring but of their quality. The children of the second and third wives tend to be thinner, weighing less relative to their height, and so, probably having less chance of long life and high competitive ability (Gibson & Mace 2007).

There are no detailed studies of the deception model but this mating system may have been quite common in situations where men had to travel in a regular fashion as in sailors having a wife in every port. Cases are still reported from time to time, especially now that information technology allows all those involved to keep in touch. For example, a recent news bulletin told of a lorry driver who was arrested for keeping two wives, each in a different Spanish city.

Box 6.8 also gives three models that may explain polygyny in species in which the males do not participate in parental care, based on resource defence and female defence. Two possibilities are offered to explain why a woman might pair with an already-paired man in such circumstances: because she has decided that it is to her benefit or because she is obliged to do so, either by her own family or by the man himself. In both cases the men involved would probably have resources with which to pay the woman's family.

The other model of polygyny given in Box 6.8 is the lek model, in which males display to attract females. Does anything similar occur in humans? If you think about it, a discotheque offers certain similarities to a lek. Various women interact with various men and an exchange of information takes place via a diversity of displays. Instances of violence between the men in question are not unusual. However, two differences from leks proper arise. Copulation is not always being sought, some of the participants are seeking a pair-bonded partner. Also the females as well as the males advertise their attributes. This last is unsurprising since, as we noted in Chapter 4, since the human male also invests in parental care, he too is selective.

Monogamy

This is the mating system of modern industrialised societies and, as we have seen, of 16.1% of traditional cultures. It is also always present among ethnicities in which polygyny or polyandry exist. Nevertheless, we must stress that monogamy in humans, as in other animals, does not imply fidelity. As we saw in Chapter 5, extra-pair copulations are also common in our species and these may result in children by other than the ‘official’ father. In other words, in the human species too, social monogamy does not always mean genetic monogamy.

Monogamy may seem entirely normal to us, particularly if we live in a country where it is the only legal option, but in comparison with other species it is less usual. Only 3% of mammals are monogamous, so why are we among them? We have seen that one of the circumstances driving the evolution of monogamy is that the offspring require such demanding parental care that it is very hard for one parent to raise them alone. This situation applies to humans. Our babies are born highly dependent and incapable of doing anything for themselves. Their long period of dependency on their parents makes severe demands of the mother that make it almost indispensable for her to be able to count on the father’s assistance in order to raise them successfully. This is undoubtedly an important factor but it does not explain the differences that exist between ourselves and other primates since the females of our closest relatives also give birth to offspring that require a great deal of parental care, but they are not monogamous.

The most widely accepted explanation (see the review by Buss 2007) is that the emergence of concealed ovulation in the human species is responsible for monogamy having become the most appropriate mating system for our species, since it allows the woman to obtain more help with parental care and it provides the man with greater paternity certainty. The reasoning is as follows. Most female primates signal when they are in heat by changes in colour (and smell) and by swelling around the genital area. When males detect that females are in heat they can guard them and copulate with them during that period, deriving certain guarantees of paternity. At other times they can seek other females. When the females in one of our ancestral species ceased to signal when they were fertile and became potentially sexually available at all times, it became impossible for a man to guard a woman effectively, which thus enormously reduced his certainty of paternity. This left the man with two options. He could continue being polygynous, with the risk that when he was with one woman, another man could be with another of his wives, thus reducing his assurance of paternity. Alternatively, he could become monogamous and remain together with one woman, thus blocking access to her by other men and so increasing his paternity certainty. His chances of mating with other women would be reduced but he would have a greater chance of being the father of the children borne by his wife. It is also the case that the monogamous tendency would have been favoured by custom at a social and cultural level. Such rites have existed in all known cultures and they served to convert the union of a man and a woman into a publicly acknowledged and respected partnership. The impact of social norms, latterly including religion, became progressively stronger to the extent that monogamy is now imposed by law in many cultures.

The idea that monogamy in the human species is an adaptive strategy that evolved long ago is supported by the fact that a mechanism exists that favours pair maintenance, and reduces the chances of extra-pair copulations: jealousy. This is a well established human adaptation, not only because it is common to all cultures, but also because it occurs in both males and females. Moreover, the factors that provoke jealously differ between the sexes in accordance with the predictions of evolutionary theory (see Chapter 5 for a detailed account of jealousy).

Is monogamy the typical mating system of industrialised countries?

Having more than one spouse at a time is prohibited by law in western industrialised countries. This constitutes monogamy, from a social standpoint. However, from a biological point of view it is not so for two reasons. Firstly, the existence of extra-pair copulations implies a degree of polyandry. Secondly, monogamous unions are frequently broken by separation and divorce.

Taking data supplied by the National Spanish Statistical Institute by way of example, 95,000-150,000 marriage dissolutions have occurred in my country annually over the past ten years, taking divorces and separations together. In total nearly 1,200,000 couples separated or divorced between 1998 and 2007, a very high number even without including the ever increasing but un-quantified number of unmarried couples that have separated unofficially. This high rate of relationship breakdown, which tends to be followed by the establishment of a new relationship (more often in men than in women) does not permit us to consider monogamy as typical of modern human societies. It is more accurate to speak of successive polygyny from the man's point of view or of successive polyandry from that of the woman. This phenomenon is also known as serial monogamy.

What is the typical human mating system from a biological viewpoint?

This question can only be answered by reference to biological characteristics that are outside cultural influences. Two meet this requirement: sexual size dimorphism and relative testis size. With respect to the former, a number of comparative studies have shown a direct relationship between the degree of polygyny and sexual size dimorphism (the size difference between males and females of the same species). The more polygynous the species, the greater the sexual size dimorphism. The explanation lies in that a high level of polygyny implies greater competition between males so that sexual selection would favour the larger males. Sexual size dimorphism is moderate in humans, where a man is 8-10% taller and 20-40% heavier on average than a woman. This indicates that a moderate degree of polygyny would be typical of our species. Comparative studies support this conclusion. For example, according to data on anthropoid primates gathered by Cartwright (2000), sexual size dimorphism in polygynous species is greater than in other species. Thus, sexual size dimorphism expressed as male weight divided by female weight is 1.8 in the gorilla *(Gorilla gorilla)* and 2.2 in the orangoutan (*Pongo pygmaeus*), both of which are polygynous. In the polygynandrous chimpanzee (*Pan troglodytes*) it is 1.3 and in humans (*Homo sapiens*) it is 1.1.

With respect to relative testis size, as we saw in Chapter 5, comparative studies have demonstrated that the greater the amount of sperm competition, the larger the testes. Harcourt *et al.* (1981) showed that human males fall between polygynous species such as the gorilla and polygynandrous ones such as the chimpanzee. In the gorilla, one male has several females and there is much inter-male competition but no sperm competition, whereas in the chimpanzee males and females live in groups so there is much sperm competition, but less direct inter-male competition. The data thus suggest that according to relative testis size the human mating system would be moderate polygyny with an also moderate level of sperm competition.

Barret *et al.* (2002) provide additional evidence that supports the conclusion that moderate polygyny is the standard mating system of our own species. Monogamy has to be imposed by law in modern western societies in order to be maintained, although serial monogamy and other strategies can circumvent the law.

Chapter 7. Gregariousness, groups and societies

7.1. Introduction

Nearly all animal taxa include some species whose individuals are solitary, pairing up only to reproduce, and others that form more or less substantial stable groups. These groups may simply be seasonal gatherings to achieve some objectives, such as attracting mates, or they may be permanent congregations within which all activities, such as food-seeking and reproduction, are performed. Gregarious species are those in which individuals form temporary groups in which they may or may not remain for long according to their interests. This in turn will depend on the balance between the costs and benefits of being in a group. In social species the relationship between individuals is generally tighter, social groups often being composed of relatives.

Edward Wilson published his famous book 'Sociobiology' over 30 years ago. In it he defended the need to apply biological methods to the study of social behaviour in all species, including our own (Wilson 1975). The book stirred up enormous controversy, particular on account of its final chapter, which was devoted to the human species. Wilson was criticised not only as an inadequate scientist but also as an ideologue who was in effect defending racism, male dominance, social inequalities, genocide and rape, among other unpleasantnesses. These criticisms were rebutted in Chapter 1 of this book, precisely because I wish to justify, from a biological viewpoint, the joint study of human behaviour alongside that of all other animals.

In the year's after Willson's book was published, and although critics headed by Stephen Jay Gould did not cease their attacks, sociobiologists continued their evolutionary work, which helped explain a great many behavioural phenomena. After three decades of turmoil, history has pronounced its verdict: sociobiology has triumphed (see the book by John Alcock (2001) in which he applies lucid argument and crushing logic to justify this conclusion).

Alcock (2001) highlights that whereas criticism did not impede the advance of sociobiology, it did harm the development of other social sciences, which have generally resisted the application of the theory of natural selection to an analysis of human behaviour, thanks to the criticisms of Gould and others. Sociobiologists on the other hand have made notable progress, not only in explaining the social behaviour of many species but also by discovering a great variety of strategies and behaviours that imply coordinated action by individuals in groups in species in which this had never been suspected. Thus, it has been shown that many microorganisms have quite complex social behaviour, which not only includes cooperation between individuals but also involves networks of communication that help them seek, reproduce and disperse (see a review by Crespi 2001). For example, *Pseudomonas* and other pathogenic bacteria have been shown to be capable of responding in unison in a coordinated way when it is necessary. They are able to communicate via certain molecules that they use as indicators of population density. This enables them to attack their hosts at the ideal moment, precisely when their population density has reached a level likely to maximize the success of individuals in reproducing or dispersing (Juhas *et al.* 2005).

7.2. The costs and benefits of living in a group

Why are some species solitary and others gregarious or social? Before answering this question we shall examine what happens among spiders, a group that includes gregarious and solitary species, taking advantage of a review by Mary Whitehouse and Yael Lubin, of Ben Gurion University, Israel. There are approximately 38,000 known species of spiders and the great majority are solitary. Group living has been described for only some sixty species, 23 of which form fairly complex societies. In some cases gregarious species form large groups in which each spider builds its own web, captures its own prey and reproduces independently. New arrivals are accepted readily, but there is no chance of cooperation between the group members since each maintains its own web. The colonies derive a clear advantage when it comes to prey capture but social behaviour yields no other reproductive benefit. Maternal parental care is poorly developed in such species. More highly social spiders on the other hand spend their entire lives in communal webs and nests that, depending on the species, may include from a few individuals to thousands. For example, in *Anelosimus eximius* webs up to 7.5m long, 2m wide and 1.5m high have been found, containing up to 50,000 spiders. These extraordinarily social spiders cooperate in capturing prey that is frequently much larger than is caught by non-social spiders of the same size. They feed together, reproduce within the same web and may care for the young communally. Each individual's success increases as more spiders join the web since the larger it is the more effective prey capture becomes and the greater the number of offspring produced (Whitehouse & Lubin 2005).

Let us now return to our earlier question, but in a different form. Bearing in mind the advantages we have mentioned, why are social spiders so uncommon? The answer is because living communally not only confers advantages, but also has its downside (see Box 7.1). The 23 species of social spiders belong to seven different families and spider sociability has evolved independently at least 12 times (Aviles 1997). This means that it must not be too difficult for sociability to emerge when the benefits outweigh the costs but usually the costs must exceed the benefits. Communal living in social species is favoured by two factors: firstly, when all the individuals involved are related, which reduces the costs of competition; and, secondly, when they exhibit parental care, so that looking after the young provides an additional benefit (see Chapter 8).

Box 7.1 summaries the principal costs and benefits of living in groups. The benefits clearly predominate for some species and the costs for others, but usually any form of gregariousness is the evolutionary outcome of the cost-benefit relationship. For example, in the familiar case of African lions (*Panthera leo*) no single benefit can be held as responsible for the social habits of this feline; instead, several are involved. Among other benefits, living in a relatively large pride lows lions to defend their territory against other prides and their cubs against intruder males, makes hunting more effective since it enables the group to encircle and surprise their prey, and makes it possible for large aggressive prey, such as Cape buffaloes (*Syncerus caffer*), to be tackled.

1. BENEFITS

a. Obtaining food

i. Greater efficiency in finding food. Where the food sought is localised but hard to find (e.g. carrion, seeds etc.) it is easier to find it as a group so that when one individual locates it all are able to feed. Fish, birds and mammals.

ii. Information centres. Grouping allows those who may be hungry, for example, to follow or join those who have already found richer feeding areas. Known chiefly among birds. Enabling the capture of large or difficult prey. Predators often come together to tackle prey that would be impossible or very costly to tackle unaided. Fish, terrestrial and marine mammals.

iii. Defending resources against other groups of individuals of the same species.

b. Predator avoidance

i. The dilution effect. The fact that individuals are gathered in a group reduces the chance that any one of them will be captured. Insects, fish, birds and mammals.

ii. The confusion effect. Members of group are harder to single out by an attacking predator. Alarm calls provoke generalised fleeing making prey capture harder. Fish, birds and mammals.

iii. Vigilance is increased at a lower cost to each individual because any one member of a group need not look around as often given that flight by one vigilant individual will trigger escape by all. Occurs very widely in many animal groups.

iv. Group defence. Individuals combine forces to defeat predators. Social insects, birds and mammals.

c. Others

i. Taking advantage of scarce refuges. Large groups of pairs or breeding females may form when few suitable, predator-free breeding sites are available. Seabirds, bats and marine mammals.

ii. Group modification of the environment. Typical of many social insects, which together may construct large, secure and comfortable nests.

iii. Defence of resources from other groups of the same species. Social insects and mammals.

iv. Defence against infanticide. Groups of females may be able to defend their offspring against infanticide by males. Lions, primates and other mammals.

v. Thermoregulation. Coming together favours body temperature maintenance at lower individual cost. Social insects, penguins and communal roosts of some birds and mammals.

2. COSTS

a. Food requirements are increased. The general rule is that once optimum group size has been reached the food ingestion rate per capita decreases as additional individuals arrive. Occurs generally.

b. Competition increases. This is not just for food but also for mates. Occurs generally.

c. Risks of extra-pair copulation and intraspecific brood parasitism increase (see Chapters 5 and 6 respectively). Seen in birds.

d. Risks of transmission of infections, diseases and parasites increase. Occurs generally.

e. Groups are more conspicuous to predators. Applies generally.

f. The risks of cannibalism and infanticide increase. Birds and mammals.

Box 7.1. Costs and benefits of living in groups. Information chiefly after Alcock (1993), Krebs & Davies (1993) and Dockery & Reiss (1999).

Individuals of different species sometimes form mixed- species groups as in large African herbivores and in some bird groups, including crows, waders and finches. Such mixed groups benefit from the different capabilities of their component species. A well-known example is the association between impalas (*Aepyceros melampus*), antelopes with superb senses of hearing and smell, and olive baboons (*Papio anubis*), which have good eyesight. Both species are gregarious and they quite often form mixed groups that allow them to detect and hence avoid predators at long range.

7.3. Adaptations to living in a group

Given that group living involves significant costs (see Box 7.1), it may be predicted that as colonial living evolves from solitary existence adaptations will arise that will smooth the transition. To illustrate such adaptations we will consider in detail one of the most universal costs that group living incurs: the greater risk of transmission of infectious diseases and parasites. This effect has been demonstrated in many species, not just by observation but also experimentally. A comparative study by Jose Luis Telia, of the Estacion Biologica de Donana, Sevilla, Spain is convincing in this regard. He compared the quantity and diversity of blood parasites between closely related species-pairs usually members of the same genus, each comprising a solitary and a gregarious species. His results showed that the gregarious species ran a higher risk of transmitting blood parasites to one another and they were attacked by a greater variety of these pathogens. By comparing closely-related species-pairs it is possible to conclude that the evolutionary transition from solitary life to group living was accompanied by a high risk of infection by blood parasites (Tella 2002).

Some blood parasites are quite virulent and bring increased risk of host mortality. As the earlier example shows, living in groups does not only increase the numbers of parasites per individual but also their diversity, making it more likely that a particularly dangerous one will be acquired. What adaptations might colonial birds be expected to develop in order to combat blood parasites? M0ller & Erritz0e (1996) proposed that colonial birds should have a more highly developed immune system than solitary species and they showed that indeed the colonial species have larger organs associated with the immune response (the spleen and the bursa of Fabricius) than do solitary bird species.

Parasites exert strong selective pressures on their hosts that it is unsurprising that our earlier prediction has been confirmed in many species. One of the best demonstrations is provided by a study by Kenneth Wilson, of Stirling University, UK, and his co-workers on the desert locust (*Schistocerca gregaria*). This is an acridid grasshopper that occurs in two phases: a green solitary phase when the population density is low, whose individuals match their background, and a striking yellow and black gregarious phase when densities are high and the locusts gather in swarms. As the investigators predicted, despite belonging to the same species, solitary phase individuals should have a less developed immune system than gregarious phase insects, given that investing in an improved immune system is costly. In contrast, the gregarious insects should invest more in immune defences to counteract the higher risk of infection associated with living in close proximity to each other. The hypothesis was tested experimentally on two groups, each of forty insects, all of which were infected with a fungus that regularly parasitizes these locusts. A group of solitary phase individuals was kept under low-density conditions and gregarious phase individuals were kept in dense groups of many individuals. As predicted, gregarious phase locusts kept at high density proved more resistant to the fungus than were the solitary phase insects (Wilson *et al.* 2002).

If the risk of infection is so significant as to oblige gregarious or colonial species to invest a great deal in strengthening their immune systems, what is the situation with social species such as ants and termites, which live in great agglomerations within enclosed nests? They provide ideal conditions for parasite transmission by living at high density with frequent interactions between individuals of close kinship. However, it is also the case that such insect societies evolved many millions of years ago and therefore ought to have developed special adaptations to mitigate the costs of living in crowded confinement. In fact it has been shown that the relationship between population density and parasite transmission in social insects is the converse of what we described for birds and desert locusts. William Hughes, of Copenhagen University, Denmark, and his co-workers have shown that leafcutter ants of the genus *Acromyrmex* that are infected with a parasitic fungus have a better chance of surviving if they are with their companions than if they are alone. The investigators also showed that the effectiveness of disease transmission declines as the ant population density increases. How can we explain these paradoxical findings? They are actually the result of effective antiinfection adaptations that have evolved in these highly specialised ant societies. Two of the most important are mutual grooming, an activity in which a caste of small worker ants plays an important role, and the production of antibiotic substances (see Chapter 8) that are used to destroy pathogens.

7.4. Group structure: there are not always dominants and subordinates

Whenever a group of animals feeding together is observed closely it is evident that not all the individuals behave in the same way. Some, the dominant members of the band behave as if they have priority of access to valuable resources, and others, the subordinates, often give way to them. High ranking individuals in some species behave quite aggressively to maintain their dominance and they often threaten or attack the subordinates. However, this behaviour does not occur in other species where the dominant individuals, having battled to win their status, use psychological intimidation to maintain it. A glance or a gesture suffices for a subordinate to give way at once. Group life in all such species is based on a dominance hierarchy that, once established, contributes to the avoidance of contests between group members, each individual having previously learnt whom it can threaten and from whom it should withdraw. Dominants thus impose their wishes on the subordinates and enjoy priority of access to females, food and the safest positions within the group. Such cases are termed 'despotic' societies and it is assumed that group members enjoy the advantage that comes from resolving disagreements through simple threat signals, thus avoiding costly contests or other violent interactions and permitting a more effective exploitation of resources to the benefit of all (see review in Piper 1997).

Many studies have shown that high ranking individuals have priority access to resources. A good example is an experimental study under natural conditions by Julia Stahl and her colleagues at Groningen University, Holland. They set up four small areas of high quality grass, previously fertilised and fenced against other herbivores, in a pasture used for feeding by barnacle geese (*Branta leucopsis*). Many of the geese were colour-ringed and recognisable as individuals. The observers recorded what took place when the geese approached the high quality feeding areas. The first arrival tended to be a subordinate individual but it was rapidly displaced upon the arrival of a dominant bird (Stahl *et al.* 2001).

Dominants not only have priority access to resources but also often punish subordinate individuals when the latter behave in some way that is prejudicial to the former (Clutton-Brock & Parker 1995). These punishments compel the victims to avoid such behaviour and instead to act in ways that benefit the dominants, for example by remaining at the group periphery where the risk of predation is higher and the need for vigilance is greater.

A curious study of keas (*Nestor notabilis*) shows how a dominant individual may force a subordinate to behave in a way that benefits the former. The kea is a parrot of the New Zealand mountains, where it lives in social groups. The bird is renowned for its manipulative abilities, so much so that a favourite entertainment of visitors is to leave a closed backpack in reach of the birds. Having learnt that there is often food inside a backpack, the keas cooperate in working it over until they succeed in opening the pack.

The study was carried out by Sabine Tebbich and her co-workers at the Konrad Lorenz Institute, Austria, using seven captive keas. They designed an ingenious apparatus that required two individuals to cooperate in order to obtain food. However, the operator of a lever necessary to open the apparatus did not itself have access to the food, which the other individual received instead. Tebbich's team established several pairs of birds and it was always the case that the dominant individual aggressively forced the subordinate to operate the lever, so that the former got the food. The subordinate got nothing, its only reward being avoidance of punishment (Tebbich *et al.* 1996).

This inequality in resource exploitation raises a couple of questions. Firstly, why do subordinates form groups with dominant individuals? We can predict that they should have evolved mechanisms allowing them to minimise the negative effects of being close to dominants. Indeed, subordinates in various fish, bird and mammal species simply move away from dominants when foraging for food.

The second question concerns recognition of status. Many bird species form large flocks in winter and these combine individuals from many distant areas, so that they cannot possibly know each other. How then does a hierarchy arise? We can discard the possibility that it is established through confrontations between all the individuals, since then they would do nothing but fight. In reality, fighting rarely occurs in these flocks. A number of studies published over the past thirty years have shown that many gregarious species have certain markings that may act as indicators of dominance status. Nonetheless, it remained uncertain whether the birds responded solely to these signals or to the more or less aggressive behaviour of the individuals they met. An experiment was needed to test which of these alternatives is correct, in which the markings indicating dominance could be manipulated. This is precisely what was done by Juan Carlos Senar and Montse Camerino, of Barcelona Zoological Museum, Spain. Two smaller cages, each containing a siskin (*Carduelis spinus*) were placed within a 2m x 1m aviary. The dominance markings of the siskins (bib size) were enlarged, removed or left untouched, according to the test involved. Some seeds were placed in the aviary adjacent to the small cages, such that a third bird released into the aviary could feed either close to one caged individual or to the other. In general, the third bird preferred to feed from the seeds nearest to the individual with the smallest dominance marking, irrespective of its true status (as revealed by the size of its marking before manipulation). These findings demonstrate convincingly that it was the dominance indicator and not the actions of the caged individual that indicated its dominance (Senar & Camerino 1998).

Dominance is sometimes decided not on an individual basis but through competition between pairs or families (or allied groups, see below). This is typical of many birds of the order Anseriformes, especially among swans and geese, in which pairs are normally dominant over solitary individuals and families (a male, a female and their young) are dominant over pairs. Such family groups, as is true for many primate species, have a very marked tendency to defend their offspring.

Not all animal groups, however, are organised on a despotic basis. Sometimes, in 'egalitarian' societies, resources are distributed fairly equally among individuals. These groups are much less common than despotic societies but there are some genuine examples of equitable sharing and peaceful coexistence. One of the best known of these involves lionesses. As Craig Packer and his co-workers of Minnesota University, USA, have shown, prides of lionesses are entirely egalitarian, both regarding access to food and when it comes to reproduction (Packer *et al.* 2001). When a kill is made the order of arrival is respected, that is to say once a lioness has taken her place at the carcass she will snarl at any others who approach and the latter will have to find another place at the kill or wait until a space becomes free. This 'respect for property' is also shown by males with respect to females on heat. The first male to discover that a lioness is entering her fertile period will remain next to her and other males will respect his right to mate repeatedly with her. When it comes to reproduction in lions, all the lionesses in a pride produce approximately the same number of cubs during their lifetimes. Moreover, lionesses with cubs cooperate in caring for those of other group members.

Reproduction involving the collaboration of group members is known as 'cooperative breeding' (see Chapter 8). In most mammal species, societies of this type are despotic and the dominant female (or dominant pair) somehow prevents or reduces reproduction by other females so that these instead cooperate in caring for the young of the dominant female. Why do lions breed cooperatively but within an egalitarian society? Packer and his co-workers (2001) offer at least two convincing suggestions. The first, is because a lioness cannot control the reproduction of the others. The second is that because those lionesses that do not have cubs do not take part in caring for those of other females. Hence it benefits a lioness that others should be raising cubs at the same time as herself since this will increase the survival chances of her own young.

Egalitarian societies are relatively common among primates. As it happens, among the macaques (genus *Macaca*) there are species with despotic societies (*M. mulatta*, *M. fuscata* and *M. fascicularis*) and those with egalitarian ones (*M. tonkeana*, *M. arctoides* and *M. sylvanus*). Comparing the two species-groups may reveal why differences exist between these two types of social organisation, which was the goal of Charlotte Hemelrijk of Zurich University, Switzerland. The most important factors are given in Box 7.2, which reveals that group-life in despotic species is very different from that in egalitarian species. The differences are because aggression and nepotism (a tendency to favour offspring) by females are much more intense in despotic species (Hemelrijk 1999). Aggressive confrontations also occur in egalitarian societies but they are less violent and less frequent. Moreover, they are more evenly distributed in that all individuals take part in such confrontations more or less equally.

1) Individuals in despotic societies keep further apart and interact less frequently than those in egalitarian societies.

2) The dominant males of despotic species tend to keep a central location within the group, unlike those in egalitarian species.

3) Low-ranking individuals in the hierarchy may attempt to change group, so emigration is more often observed in despotic species than in egalitarian ones.

4) Adolescents in despotic societies take longer to raise their status to the level of adult females than do those in egalitarian ones, the outcome of point 5 below.

5) There is a higher degree of nepotism by females in despotic societies than in egalitarian ones.

Box 7.2. The principal differences between macaque species that organise themselves as despotic societies and those that have egalitarian societies. After Hemelrijk (1999).

7.5. How are group decisions made?

The animals that comprise a group must make many decisions that involve all its members. For example, whether to go or stay, what direction to move in, what to do and when to do it. In African elephants (*Loxodonta africana*), family groups comprising females and all the young are led by the matriarch, the dominant female who is normally also the eldest. She makes all the decisions and leads the group relying on her memory and experience, a pattern that differs from that in jackdaws (*Corvus monedula*) and most other gregarious birds. Many jackdaws from different and distant foraging sites gather together to roost communally at night. They begin to aggregate at a place where they can make use of the last of the light to feed until the moment when they all fly to the roost. Who decides when that moment comes? Individuals that are ready to roost take flight making a rallying call, which is taken up by others willing to roost. This is taken up by others who are also ready to roost and who also take flight. However, if these birds constitute a minority, the call fades away and the birds settle again. These events are repeated several times as the evening progresses until at last those who call and take flight comprise a majority. Only then, when the majority view is clear, does the entire gathering take off and head to the roost to spend the night (Soler 2006). Thus jackdaws provide a clear example of a democratic society in which decisions are taken by a majority.

To summarise, there are two ways of decisionmaking within a group: imposition by one or a few dominant individuals (despotism), or decision-making by the majority (democracy), (see Box 7.3).

IMPOSED DECISIONS (DESPOTISM): The decision is imposed on others by one or a few dominant individuals in the group.

SHARED DECISIONS (DEMOCRACY): The decision is made by a majority. It may be totally or partly shared, depending on whether all group individuals take part or whether only some do so.

- Shared decisions are generally more advantageous for a group (and for each individual) than imposed ones since (1) they tend to be less extreme, and (2) they combine information derived from different individuals.

- Shared decisions may be implemented without any need for individuals to possess complex cognitive abilities.

- **Combined decisions**: Each individual makes its decision depending on what the other group members do but without the need for a preceding consensus.

- Some examples: (1) Joining or leaving a non-permanent group, (2) deciding on individual tasks in social insects (see Chapter 8), and (3) deciding whether to reproduce or be a helper, in species with cooperative breeding.

- **Consensual decisions**: Decisions made jointly by the group to arrive at a consensus that is accepted by all its individuals.

- Some examples: (1) Choosing the direction and destination of movements, (2) deciding when to perform an activity, and (3) prey selection by cooperative hunters such as lions.

Box 7.3. Different types of decision-taking in animal groups. After Conradt & Roper (2005).

Decisions imposed by a leader are not always as clear as those described for elephants or those that occur in mountain gorillas (*Gorilla gorilla beringei*), a species in which the male nearly always initiates movements of the whole group. For example, the green wood-hoopoe (*Phoeniculus purpureus*), is a bird that displays cooperative breeding (see Chapter 8) and in which feeding groups comprise the breeding pair and up to ten helpers, who help to raise the young but do not themselves reproduce. Andrew Radford, of Cambridge University, UK, was able to demonstrate that the breeding individuals (the dominants) were the ones that initiated most movements to new feeding areas. The male and female did not differ in this respect and, moreover, movements initiated by either of them were more likely to be followed than those started by one of the helpers (Radford 2004).

Often decisions are not imposed by a despotic leader but are taken by the group, as occurred with the jackdaws. We shall examine how displacements are started in the common zebra (*Equus burchellii*), an example that allows us to draw some interesting conclusions. Zebra groups may be small harems composed of a stallion, his mares and their offspring, or large herds formed by the union of several or many harems. Ilya Fischhoff, of Princeton University, USA, and his co-workers studied which individuals were most influential in taking decisions. They found that in the harems it was the lactating mares that habitually started movements to new zones followed by other females, the stallion and the foals. Similarly, in herds, those harems that included mares with suckling foals were those that initiated movements and the rest followed them. Lactating mares, as is true for all mammals, have a greater need for water and nutrients. The study concluded that the individuals with the greatest needs are the first to change sites in order to go to a waterhole or more nutritious pastures, and thus it was they who initiated moving to a new area (Fischhof *et al.* 2007).

The zebra example allows us to distinguish between two quite different situations. When a group is small and permanent (a harem may persist over months or years), its individuals know each other and a decision may be taken by direct communication with each other. When a group is large and unstable each individual can only communicate with its neighbours. Decisions within a herd need not always be unanimous and, for example, when one harem with lactating females decides to move off other harems may decide not to follow. However, within a harem the decision is consensual. If the first female to move off is not followed by the others she will return, to wait and try again later. This is a fine example of a consensual decision, although by a small group (see Box 7.3).

7.5.1. Consensual decisions

We have previously described how jackdaws decide when to fly to roost, a typical example of a decision made by consensus in a very large group, often numbering thousands of individuals. This observation raises many interesting questions. Which individuals start the process? Are the 'proposals' of some individuals more likely to succeed than those of others? Above all, how is a consensus reached? This topic has not received much attention from investigators until recently, but there have been important advances during the past few years. Newer theoretical models now permit us to make some generalisations about consensual decision-making (see Box 7.4 and the zebra example above).

- Decisions of this sort not only occur in humans but are also frequent among other animals.
- Cooperation when making decisions is normal, even when not all the individuals in the group have the same interests.
- Consensual decisions fall into distinct categories depending on whether or not there is a conflict of interests between individuals and on whether or not communication within the group can be global (between all group members) or is only local, between near neighbours.
- Consensual decisions are achieved in two main ways: by a system of self-organisation or by voting-type behaviour.
- The more individuals involved, the more information available to the members of the group, and the lower the chance of error, allowing a decision more beneficial to all to be made.
- There is a trade-off between how effective a decision is (based on how many individuals participate) and how quickly action is taken (when many individuals are involved, the time costs of decisionmaking increase).

Box 7.4. The most important general characteristics of consensual decisions. After Conradt & Roper (2005).

The jackdaw case involves a very simple decision. When to start moving to a roost known to all and where the birds sleep every night. For a more complex and utterly fascinating case, consider how swarming bees decide where they will construct their new hive. When a hive becomes overpopulated it is abandoned by the queen and thousands of her workers in order to found a new colony. Once the swarm has moved sufficiently far away from its original hive, all the individuals settle together somewhere, normally on a branch, forming a football-sized ball around the queen. Some of the workers then fly off to explore their surroundings to find a suitable place to set up the new hive. These scout bees return to the swarm and perform their figure-of-eight dance to inform others of what they have found (see Chapter 10). The scouts are numerous. There may be several hundred, some 5%, in the swarm; collectively, they may discover several dozen different sites to advertise with their dances. How are they able to reach a consensus and decide unanimously in favour of one of the proposed sites? Thomas Seeley of Cornell University, USA, and his co-workers, have devoted many years to studying this matter by marking individuals, positioning potential hive sites of greater or lesser suitability at variable distances and using cameras to record the scouts' dances when they return to their swarms. These procedures have allowed them to make some important discoveries. For example, according to Seeley & Buhrman (1999) and Seeley (2003), when a scout returns its dance is more energetic the better the site it has found. Scouts that have found mediocre hivesites dance with little enthusiasm on their return and may eventually stop dancing altogether, the equivalent to withdrawing their 'proposal'. Some of them will then visit one of the sites advertised by a more animated dancer and when they return they may announce the location of the new site via an altered dance. In this way, progressively fewer of the initial proposals remain until a point is reached when one site has majority support. Then, although there may still be scouts supporting other 'proposals', some of those who favour the majority decision begin to introduce into the swarm, which soon stimulates the group to fly to the chosen site.

Various conclusions emerge from this description. Note that only some 5% of the individuals shape a decision that affects the whole group; furthermore, communication between all the scouts is not general because each bee can only communicate its discovery to a small group near it upon its return to the hive. The eventual decision is made without comparing different sites directly. It is based on the 'proposals' made and although no one individual compares and makes the decision, all 'proposals' are taken into account. In conclusion, the decision is the outcome of a selforganising system through which the scouts, operating on very simple rules, progressively reject the inferior options while the better ones attract more support. In this way all the available information is integrated, permitting the most suitable decision to be taken. The investigators were able to demonstrate this by making available potential hive sites of different quality and seeing how the bees chose the best option.

7.6. Coalitions alliances and superalliances

It is quite normal among many group living species, individuals, most often males, form alliances to seek food, to defend their territory or other resources or to defend themselves against predators. These types of alliances are found in mammals such as primates, carnivores and cetaceans, but they are also common in other groups, such as insects and birds and even among some fish. Such alliances are an integral part of group life and so will not be considered in this section. We shall deal instead with more temporary associations (coalitions) and more lasting ones (alliances proper) that enable some members of a group to compete against other members of the same group (see Box 7.5).

These types of coalitions or alliances are much less common. Among birds, pairs or family groups may form alliances that endure outside the breeding season (see Box 7.4). In mammals, however, such alliances have only been seen among cetaceans and primates. The formation of coalitions in primate bands is quite frequent and is thought to be related to the evolution of primate social organisation (Silk *et al.* 2004). Such coalitions or alliances demand high cognitive ability (see Chapter 11), given that they require an ability to distinguish between opponents and allies and to remember who is whom.

Coalitions: Temporary unions of two or more individuals that join forces to attack one or more opponents from the same group.

Alliances: Lasting associations of two or more individuals who collaborate during aggressive encounters with opponents from within the same group.

GENERAL FEATURES

1. Coalitions are commoner than alliances and, in general, the supported individual is the victorious attacker in a confrontation.
2. Coalitions are commoner among relatives but may also arise among unrelated individuals.
3. Alliances are commoner among relatives and chiefly arise between females.
4. Alliances are highly variable: (1) Although they may be common among the males in a population, there may exist males who participate in none of them. (2) The size of alliances varies as much within coalitions as between regions. (3) Alliances may occur commonly in some populations and not at all in others of the same species.

Functions:

5. Two or more males may associate to displace another male from a female on heat in order to mate with her.

6. Two or three males may form an alliance to guard their own females as reported among chimpanzees. Two or three high ranking males form an alliance to prevent other males from copulating with the females that they defend. The allies allow each other sexual access to any of the females under their control.

7. Two or more males may form a coalition that may allow one or all of their number to improve their ranking in the group hierarchy. This type of coalition may form among adults and also among young animals.

8. Coalitions may arise between females, or between a female and a male, to defend a juvenile against attack by another adult. Such cases nearly always involve defending an offspring or a near relative (nepotism).

9. Two or more females may form a coalition to defend one of their number against attack by an adult male.

Possible explanations: kin selection, reciprocity or obtaining of direct benefits by the helpers (see Chapter 8).

Box 7.5. Definitions and chief characteristics of coalitions and alliances between members of the same group. Chiefly after Hemelrijk & Steinhauser (2007).

The functions of coalitions or alliances are varied (see Box 7.5). Coalitionary attacks tend to be brief and to end when the victim flees. However, prolonged and violent attacks by allied male chimpanzees (*Pan troglodytes*), have been reported. For example, David Watts, of Yale University, USA, describes how in Kibale National Park in Uganda, where groups of male chimpanzees are particularly numerous, a fatal attack against a male took place, involving seven other males of the same group. The attackers held the victim down to immobilise him (as they do with males of other groups when they catch them. See below). They then hit him and bit him for five minutes producing wounds from which the victim died several hours later (Watts 2004). The motive was not a dominance struggle since the attacked male was of medium rank and the attackers included both higher- and lower-ranking individuals. The dominant male also took part although he was not the most vehement assailant. The victim was an unsociable male who was not well integrated into the group, given that he only practised mutual delousing with a few males. Watts (2004) suggests two factors that may have influenced this attack: the large number of males in the group (making competition for females very severe), and the fact that the victim was not well integrated into male society in the group.

Superalliances, that is to say the alliances formed by union of several groups, which are so characteristic of our own species, have only been reported for the Indian Ocean bottlenose dolphin (*Tursiops aduncus*). In this cetacean, two or three males frequently form alliances with the object of forcing females to mate with them. Richard Connor, of the University of Massachusetts, USA, and his co-workers, in a study over several years, found that superalliances existed within which alliances between individuals were unstable each individual could vary its habitual alliance partners but these were always males who belonged to the superalliance. Connor's team observed four conflicts between one of the male alliances with groups of males who were alien to the superalliance. They found that in some cases other male members of the superalliance travelled up to three kilometres at top speed to reach the area of conflict. The superalliance groups emerged victorious in all instances (Connor *et al.* 1999).

7.7. How are conflicts avoided and resolved?

Life in a group brings many advantages but there is a significant downside: the emergence of intragroup conflicts. Each individual has its own interests and when these conflict with those of other group members, competition arises between them and may lead to a confrontation. Some conflicts end quickly while others may become more and more aggressive until it leads to violence. Confrontations are obviously costly, not only physically but also socially, since they bring about a tense situation that may endure and affect social relationships, which diminishes the advantages of group living, especially for the loser. It may thus be expected that mechanisms will have evolved that serve both to avoid conflict and to lessen the social costs of aggression. This is indeed the case and we have described some of them earlier. For example, the hierarchical organisation that is so widespread in many groups favours a reduction in aggression. The respect for 'private property', seen in lions, is even more effective. Other specific mechanisms appear in some cases. For example, in various primate species adult females have sometimes been seen to form a coalition to prevent attack by a male.

Perhaps the most curious mechanism for avoiding aggression to have been described involves bonobos (*Pan paniscus*), a species in which, as we have seen (see Chapter 5), sexual relations are very frequent, not only heterosexual ones but especially homosexual ones involving females. Genital rubbing between females is the commonest sexual activity and it has been shown to play a very important role in social relationships within the group. Female homosexuality contributes to the formation of coalitions that allow them to dominate the males. In bonobo societies it is the females who rule and sex is used to resolve all sorts of conflicts. This close relative of ours, quite unlike our other equally close relative, the common chimpanzee, has evidently adopted the old hippy mantra: make love not war.

The most important mechanisms used in conflict resolution are given in Box 7.6.

1. **Avoidance:** A mechanism used by the aggressee that consists of keeping out of areas frequented by the aggressor.

2. **Submission:** A mechanism used by subordinates, which comprises recognition of the aggressor's dominance and adoption of appeasement postures.

3. **Comforting:** A behaviour adopted by third parties, which approach the aggressee (mainly) and interact with it in some way, according to species, providing him emotional support. Comforting is more common when there is no reconciliation.

4. **Reconciliation:** Occurs when the two contenders come together after conflict. Is a demonstration of friendship between two previous opponents that serves to end a conflict, reduce tension, and enable the individuals involved to resume a peaceful relationship. More effective the sooner it happens. Commonest between individuals who shared a close relationship before the conflict.

Box 7.6. Post-aggression behavioural strategies developed to reduce the social costs of an aggressive confrontation between members of the same group.

Conflict resolution mechanisms post-aggression have been extensively studied in primates but little work on this subject has been done with other animal groups. However, Nobuyuki Kutsukake and Tim Clutton-Brock, of Cambridge University, UK, have recently published an analysis of these mechanisms in meerkats (*Suricata suricatta*), small carnivorous mammals that live in groups of up to 40, including a dominant pair that produces around 80% of the pups in the band. The other group members help to raise those pups and to keep watch against predators. Post-aggression behaviour was studied after more than 50 confrontations between group members. In this species, reconciliation did not occur, despite the negative effect that such conflicts had on social relationships. The opponents almost never come together in the minutes following an aggressive encounter. The post-aggression mechanisms employed were submission (which did not reduce the chance of another aggressive encounter) and avoidance (Kutsukake & Clutton-Brock 2008).

Although comforting behaviour has not been reported for meerkats, the behaviour has been found in one of the few studies on this topic involving birds. Amanda Seed and her co-workers at Cambridge University, UK, studied a captive group of rooks (*Corvus frugilegus*), markedly gregarious members of the crow family. They found that there were no reconciliatory encounters between opponents following an aggressive encounter but instead both the aggressor and the loser might contact a third individual. Then, the one who is contacted and the third individual behaved in a peculiar manner with the newcomer. They entwined their beaks while moving their wings and tails rhythmically and making special vocalizations. The authors of this study emphasise that despite the great phylogenetic distance between rooks and primates, the consolatory ceremonies in both groups are very similar (Seed *et al.* 2007).

Many studies have been published on reconciliation in primates, especially in various macaque species and in chimpanzees. A study by Matthew Cooper, of Georgia State University, USA, is particularly interesting since he considered the effects of both the sex of the contenders and their state of anxiety on acts of reconciliation. His study of the bonnet macaque (*Macaca radiata*) demonstrated that the degree of reconciliation was greater when aggression occurred between females than when it occurred between a male and a female and it was shown that this was related to anxiety levels. When behaviour associated with anxiety was quantified it was found that after a conflict between females both showed signs of high anxiety, which diminished considerably after reconciliation, and moreover that such anxiety was higher in cases where reconciliation followed than when it did not occur. These and other results thus showed that the greater the level of post-conflict anxiety the greater the chance that reconciliation would take place (Cooper *et al.* 2007).

7.8. Human societies

Without a shadow of a doubt, of all animal species it is the human one that has the most complex societies. We live in huge groups (there are already five capital cities that together with their satellite towns, exceed 20 million inhabitants). Human societies also exhibit much division of labour, a great diversity of regulations and laws, and enormous cultural variation that exists between different societies, not only according to countries or cultures, but also within particular countries and the occurrence of multiple societies actually within other societies. In the following sections we will study human societies, first analysing whether they are despotic or egalitarian, then examining how they function and finally describing the 'social intelligence hypothesis', which proposes that the principal driving force behind the evolution of human intelligence has been our social way of life.

7.8.1. Despotism or egalitarianism?

Which predominates in human societies, despotism or egalitarianism? There is no easy answer to this question. Indeed, the history books are full of examples of both types of human societies. Nevertheless, there are two ways of trying to arrive at an objective answer. Firstly events throughout history, and especially during the dawn of the human species in the Stone Age, may be analysed. Secondly the despotic or egalitarian behaviour of children during their development offers another kind of information relevant to the issue.

The most important generalisations about human history are presented in box 7.7. Nowadays experts agree that our forefathers in the Stone Stage lived in societies that were basically egalitarian. They shared resources and very probably made decisions by common agreement. Democracy, then, did not begin in classical Greece, as most history books would have it. Although the Greeks formalized democracy, similar practices began considerably earlier with our distant ancestors.

There is also unanimity of opinion that despotism emerged with the development of agriculture, which produced surplus food that could be stored, so that the owners of these resources could benefit and could also control those who were most in need, namely the poorest in the population. In support of this position, note that the most stratified and most despotic societies have developed in regions where resources were distributed very unequally, i.e., where resource-rich and resourcepoor areas lay side by side. The clearest example is that of ancient Egypt, one of the first nation states to appear after the discovery of agriculture. The difference between the extraordinarily fertile Nile valley and the desert lands that nearby is extreme, which led to the population to settle populous cities within the valley that made it easier for the dominant classes to control their inhabitants and to extract substantial taxes from them. These favourable conditions surely contributed to the development of this highly despotic and long enduring society dominated by the pharaohs (Allen 1997).

The Stone Age

- Hunter-gatherer societies were quite egalitarian, judging from the fact that existing hunter-gatherers form relatively egalitarian societies.
- This egalitarianism, which would have started at least 100,000 years ago, would have been based on mutually beneficial relationships in which resources, especially meat from the large prey animals that they hunted, would have shared more or less equally.
- Egalitarianism would have been favoured by the nomadic lifestyle, since nomadism impedes the accumulation of riches, and by the non-existence of food preservation technologies.
- There would have been psychological mechanisms that contributed to the maintenance of equality. First a ‘moral sense’, to encourage those who behaved well, and second, a ‘sense of justice’, which would have led to the imposition of sanctions on those who did not behave well.

From the Neolithic revolution to the industrial revolution

- The discovery of agriculture and domestic herding some 10,000 years ago resulted in food surpluses that could be stored. This brought about sedentary living and a fundamental change to a society in which people, instead of sharing resources, devoted themselves to accumulating resources and riches, which were passed from parents to offspring (inheritance).
- These changes brought about inequalities and the emergence of social stratification, the basis for the first truly complex human societies (villages, tribes, chiefdoms, states and, later on, kingdoms and empires) that arose independently in many geographical regions.
- Sexual discrimination began with the appearance of these complex societies since resources (and weapons) were under male control.
- The possibility of storing food and riches, and the emergence of more complex societies, favoured wealth accumulation and resource control by chieftains, allowing them to train and equip soldiers with whom to suppress opponents. Despotism thus emerged.
- Powerful families competed for land. In order to conserve power it was important than inheritances should not be divided, which led to the institution of primogeniture in which only the eldest son inherited the wealth of his parents.
- Dominant individuals controlled weapons whereas peasants and the rest of the populace were denied access to them. There were practically no revolutions during the period when this control was effective.

- The more complex the social system - the more stratified it was - the stronger the repression and despotism, since the dominant classes numbered more individuals.

- There has normally been a very clear relationship between despotism and differential reproduction. Dominant chiefs used their power and riches to favour their reproductive success and that of their relatives.

From the industrial revolution to the present

- During modern times, principally since the discovery of firearms, despotism has been declining in human societies.

- The manufacture of large quantities of firearms, which required no special training to use, made repression of the populace harder and revolutions became more frequent.

Box 7.7. Some generalisations regarding the emergence and development of human societies across history. There are of course many exceptions but the general trends are given here. Chiefly after Betzig (1986), Summers (2005) and Harris (2006).

The most important aspect of despotic societies, from a biological viewpoint, is the fact that the control of resources by dominant men led to control of reproduction. The men used their power to obtain more women and thus to have more offspring. Harems were born under despotism. Men who belonged to the highest echelons of the hierarchy had multiple wives in direct proportion to their social status. The fact that some men acquired many women implies that many low status men went without any wives at all. Laura Betzig, of Michigan University, USA, showed in her now famous study of more than a hundred pre-industrial societies that levels in the social hierarchy were also expressed in a reproductive hierarchy who controlled the most resources also controlled the most women, acquiring larger number of spouses and concubines (Betzig 1986).

The fact that best explains the decline of despotism in modern times is a general rule that has often been repeated throughout history: despotism has been most severe the bigger the difference between the despots' capacity for struggle. An army paid for and equipped thanks to the riches accumulated by the despots, and that of the dominated populace, nearly always landless peasants. For example, in various societies in antiquity, the discovery of armour and other protective measures, such as shields and helmets, led to an increase in despotism. On the other hand, the discovery of bows that could drive arrows through such armour led to greater levels of equality (see review by Summers 2005). In modern times the large-scale manufacture of firearms, which smugglers can sell all over the world, has made the fighting capabilities of despots and their subjects more equal, and may have contributed to the greater equality within many modern states. As I see it, another important factor has been the enormous increase in the human population since the industrial revolution, which has strengthened the standing of the populace against that of the despots. Nonetheless, despotism endures today in many countries thanks to the complicity of a privileged upper-middle class that includes, in addition to people with considerable economic resources and the upper levels of religious hierarchies, the military and the police who control access to firearms.

With respect to the behaviour of children, a superb study by Ernst Fehr, of Zurich University, Switzerland, and his co-workers has studied child behaviour in experimental games offering two mutually-exclusive choices. Among other things, the experimental results show that three- to four-year-olds tend to behave selfishly but gradually, between the ages of three and eight, they come to play in a more egalitarian way, not only when they personally benefit from their actions but also when they do not (Fehr *et al.* 2008). The fact that a tendency towards egalitarianism emerges so widely at such a young age raises the possibility that a hereditary basis for the behaviour exists (Wallace *et al.* 2007).

Another important trend in the evolution of human societies is the tendency of people to favour their relatives, mates and friends whenever possible. All readers will surely agree since they have probably suffered, or know someone who has suffered, discrimination derived from this tendency (although when we ourselves are the beneficiaries we are less aware of any unfairness and think that any benefit we have received is our just desserts). Favouritism towards those closest to us is very widespread and may sometimes be extended to include other members of our group, society or culture. We all know, because history reveals it, that people tend to favour members of their own society and may regard other groups or cultures with indifference, hostility or, at times of conflict, with aggression that may culminate in the most irrational violence.

The tendency to favour members of one's own group, which in turn is one of the advantages of belonging to different groups or societies, has been extensively documented. For example, in the study mentioned above, Fehr and his colleagues (2008) also found that children made decisions that tended to favour members of their own circle of friends and acquaintances. Likewise, a recent study by Charles Efferson of Zurich University, Switzerland, and his collaborators has shown in an experiment that promotes the creation of societies that not only are group members favoured but also the identifying symbols of each society (clothing, linguistic jargon or bodily adornments) play such an important role in generating group solidarity that they become highly reliable indicators of the behaviour of those who display them (Efferson *et al.* 2008).

7.8.2. How do human societies function?

As we have already mentioned, human societies are enormously variable and making generalisations on how they function is not easy. In this section we will highlight some of their characteristics that relate to our earlier analyses of other gregarious animal species.

When it comes to decisions, these are taken in a more or less egalitarian manner in most 'voluntary' human societies, that is to say those to which an individual may choose or decline to belong. However, there is a great deal of variation in 'obligatory' societies, those to which one is compelled to belong through having been born in a particular community. With respect to political organisation, an individual may be born in a country governed by a dictator, who makes all the important decisions more or less discreetly. On the other hand, he or she may be born in a fully democratic country, where decisions are made by persons elected by the citizens, after these have examined the candidates' proposed programmes. Such elections may be egalitarian to the extent that just a few votes may make the differences between victory or defeat for a given candidate. In religious societies, which traditionally have been 'obligatory' (nowadays they no longer are, at least in states where there is religious freedom), decisions tend to be taken despotically. There tends to be a formal leader, or leadership group, making the decisions.

Throughout history there have been instances in which certain human groups, such as armies or colonists, have found themselves in a situation similar to the swarm of bees mentioned above (7.5.1), and it is intriguing to note that they have resolved their problem in a very similar fashion. When armies had to travel far across unknown lands they sent scouts in all directions. These later returned to report on what they had found. As with the bees, the decision was based on the information brought by the scouts but here there is a fundamental difference, the scouts themselves did not decide after comparing the advantages and disadvantages of particular routes. Instead the highest ranking individual made the decision after having received reports from all the scouts and having asked pertinent questions.

Coalitions and alliances are a constant finding among human societies and they emerge at all levels. Even within a family group there may be members with shared interests who act together to achieve a common goal. More frequently, there have been alliances throughout history between related family groups to defend their interests against other families, at least until the emergence of tribes. From that moment, alliances between societies that agreed on mutual defence gained importance and prominence. Our present-day society has a great diversity of alliances at the level of nation states, which may be highly complex. Nevertheless, however structured and complex human societies may become, the underlying relationships are characterised by what we may term human social capacities, which are based on feelings and emotions such as culpability, loyalty, vengeance, gratitude and the sense of justice (see next section), to which we must add a moral sense and religious belief.

As societies became more complex it became harder to avoid conflict between their members. However, for a society to work well it is necessary to reduce internal conflict to a minimum. Hence, from time immemorial, all societies have passed laws that favour coexistence and avoid social conflict. For example, the Code of Hammurabi, which existed as early as the 18th century BC, was a highly complex body of law that regulated coexistence in that epoch.

As a general rule, most individuals in a society respect its norms. This is the outcome of three main factors. Firstly, when infringements are not serious there is a tendency for those who breach social norms to be chastised or reproached. Other people will remonstrate publicly against those responsible for antisocial or unneighbourly behaviour; for example, parking where traffic is obstructed or failing to dispose of rubbish according to the community rules. This is what some psychologists call ‘altruistic punishment’ and it tends to bring a more or less intense feeling of satisfaction to those who employ it.

Secondly, there are the severe punishments imposed by law on the perpetrators of more serious offences. In all societies such punishments are imposed by persons appointed by the society itself and these are invested with the authority and power to ensure that they are carried out. This arrangement has proved highly effective in reducing conflict or, at least, avoiding that conflict should be violent. There is abundant evidence throughout history that the number of violent deaths is much higher in societies that do not have this formal system of imposing justice.

Finally, the third factor that contributes to compliance with social norms is that human beings are predisposed to comply with those norms. Such a predisposition should not surprise us since if social norms benefit individuals, these will have developed adaptive psychological mechanisms that favour normacceptance and that penalise their infringement (see Chapter 8). Respect for property is one of the most important principles within the laws of all cultures. This is the same principle that regulated the lives of lion prides, as described above. Ever since the emergence of nation states, when a family owns a house and goods, their right of ownership has been respected under law. Society would be reduced to chaos if a family that was powerful enough could deprive another of its property. Respect for property operates constantly on a day-to-day basis in our modern cities: a ticket guarantees a seat in the cinema, a number decides the order in which we are served at the supermarket, we can occupy a vacant table in a bar, and so on. Usually no one would consider taking our cinema seat, our place in the supermarket queue or our table in the bar.

Mechanisms for conflict-resolution also exist among humans and these are similar to those that we have found in other animals as they involve comforting and reconciliation, albeit in a more complex form. As in other species, there may be acts of reconciliation between adult human beings that restore relations between the confronting individuals. At times, conflicts are more complex and the contenders each consider themselves to be in the right. There then appears a new reconciliation mechanism, evolutionarily speaking, which has never been found in other animals: mediation by third parties. The intercession of a shared acquaintance may sometimes suffice but where necessary this is performed by a judge and it is regulated by the society’s laws to which we referred earlier.

Among children, however, such mechanisms are very similar to those described for other primates. For example a study of pre-school Japanese children aged three to five years by Keiko Fujisawa and her coworkers at Tokyo University, Japan, revealed that reconciliation is less common among the under-threes but increases in both frequency and complexity with age. When one of those involved in a confrontation offered reconciliation to make up with the other and this was accepted, signs of aggression diminished and a return to play was promoted. As in other primates, comforting was offered more often by other companions when reconciliation did not occur, which supports the idea that comforting acts as a substitute for reconciliation and that it contributes to reducing the stress experienced by the victim of aggression (Fujisawa *et al.* 2006).

7.8.3. The social intelligence hypothesis

Our brain gives us extraordinary cognitive capabilities (see Chapter 11). The development of our great mental abilities has traditionally been explained as a mechanism for resolving the ecological problems that have confronted the human species, for example, foraging for food and hunting, which led to the making and use of tools, the processing and preservation of the food obtained, and the adaptation to hostile and unstable environments. Nevertheless, these explanations do not seem to be sufficient. The social intelligence hypothesis suggests that life in a society is the principal factor that has influenced the evolution of human intelligence and that of other primates. Coexistence in a society imposes very significant selective pressures on individuals, favouring those capable of processing large quantities of social information. They benefit by knowing all those with whom they have frequent interactions and from being able to distinguish friends from enemies and, furthermore, to remember all this information for a considerable period. Such knowledge allows decisions about whom to cooperate with and whom to avoid. Moreover, competition with the other group members also demands significant cognitive abilities including deceiving and uncovering possible deception, setting up worthwhile alliances and, in general, anticipating the social scheming of others.

Such complex social relations favour a need for obtaining and storing an enormous quantity of data. For example, in various macaque species that live in large troops, each individual has been shown to be able to recognise the cries of all its companions, and there may be 80 of these! We humans cannot only remember enormous numbers of people but also we are capable of interpreting their states of mind rapidly and almost unconsciously. Sometimes, too, we can decipher individuals intentions' based on their faces, a highly complex matter if we bear in mind that some 200 muscles participate in creating the facial expressions that signal emotional states.

The idea that the primate brain is an adaptation for resolving the problems of social living has received considerable support in recent years. For example, a key prediction has been validated, namely that brain size should be correlated with group size in different species. However, this prediction was not fulfilled in all taxonomic groups so it has been suggested that the types of social relationships and their stability may be more important than the numbers of individuals in a group. A recent comparative study by Susanne Shultz and Robin Dunbar, of Liverpool University, UK, which has analysed data on brain size and social organisation in birds and four mammalian orders, including the primates, found that relative brain size is associated with stable and enduring social relationships in primates but not in three other mammalian groups nor in birds. In these, brain size is linked to the system of pair formation with larger brains occurring in species whose males and females form long-lasting monogamous relationships (Shultz and Dunbar 2007).

Are human relationships so much more complex than those of other primates that they explain our greater brain size relative to theirs? Apparently so. Esther Herrmann of the Max Planck Institute of Evolutionary Anthropology in Leipzig, Germany, and her co-workers designed an experiment to see if there was any clear fundamental difference between human social abilities and those of other anthropoid primates. They set up a series of tests including ten of physical ability (related for example to spatial memory, judging quantities and using a small stick to reach objects) and some of social skills (including some aspects of social learning, understanding instructions, communicating intentions and the like). The same tests were given to 106 chimpanzees, 32 orangutans (*Pongo pygmaeus*) and 105 human babies aged 30 months. The researchers found that with respect to the physical abilities, the human babies and chimpanzees scored very similarly, the orangutans somewhat less well. However, in tests of social ability the babies achieved a much higher percentage of correct responses than the other two species managed (Herrmann *et al.* 2007).

Social relationships are so important to our species that we have evolved many associated psychological adaptations for social life, including a dependence on living and interacting with others. We descended from other hominid species that were already social creatures several million years ago, and this long evolutionary history makes us dependent on our social networks. Thanks to several studies during the 1980s, psychologists nowadays assume that, compared to others, loners have more social and psychological problems (a tendency to depression), they feel dissatisfied and they seldom enjoy success in life.

Here is a specific example. Daniel Kahneman, of Princeton University, USA, and his co-workers interviewed a large number of people on their activities of the previous day. They found that social relationships were rated the second most gratifying, second only to intimate relations. Another very striking result was that the company of friends gave most satisfaction, ahead of that of family members or partners (Kahneman *et al.* 2004). Results such as these suggest that to feel well it is important to improve social relationships and to devote more time to them. Widening the circle of 'us' and reducing the number of 'them' may be essential for feeling happier.

In any event, although the social intelligence hypothesis has received much support, in my opinion this does not mean that the selective pressures imposed by social relationships alone explain the great development of the brain and of the cognitive capabilities of the human species. As we saw in Chapter 4, a complementary hypothesis is that the cognitive abilities of the human mind have evolved as a result of selective pressures arising from the need to find a mate, an idea that is also well supported (Miller 2000). It is surely the case that human cognitive abilities are the evolutionary outcome of selective pressures operating at multiple levels, not only at a social level but also at a sexual level and at others, including the ecological levels to which we have referred earlier and that were considered the most important several decades ago.

In this chapter we have studied the most important aspects of group living, except for one, which is possibly the most important of all -the evolutionary mechanisms responsible for the origin and maintenance of the most complex modern societies. An impermanent gathering of individuals or groups may have a simple explanation, that the benefits of staying in a group are greater than the costs. But what occurs in the permanent associations that exist in many species, including our own, which involve close relationships between group members who may help others at a cost to themselves. Altruistic behaviour is the theme of the following chapter.

Chapter 8. Altruistic behaviour

8.1. Introduction

Ants, bees, termites and many other insects characteristically form collections of individuals most of whom leave no descendants. Instead they work to benefit the queens, the males that fertilise them and the resulting offspring, which they care for, guard and feed with great dedication and determination. Such social insects provide the most familiar but striking example of altruism. The workers' behaviour is enormously costly for them since they dedicate their whole lives to their labours on behalf of others. It is also highly beneficial to the queen who, thanks to the efforts of the workers, may leave thousands of descendants, many of them males and females that will have a chance to establish new reproductive colonies in their turn.

You may have noted that the previous paragraph runs counter to the rest of the book, in particular to Chapter 2, in which we studied the 'theory of evolution by natural selection'. The basis of this theory, and surely the point made most frequently throughout this text, is that natural selection penalises those individuals that fail to maximise the number of descendants that they contribute to the next generation. How then can the behaviour of worker ants, bees and termites be interpreted? This question is not easily answered and Darwin himself recognised that the behaviour of social insects seems to pose an insuperable obstacle to his theory.

Altruistic behaviour is moreover not exclusive to social insects. It is also frequent among other species. Despite appearing contrary to natural selection, the act of helping other individuals, despite the costs incurred by the helpers, is not uncommon in nature and even our own species provides many complex examples (see Section 8.5). However, it needs to be made clear that although altruistic behaviours may be hard to explain, their existence is not contrary to the predictions of evolutionary theory. The fact that genes are selfish (metaphorically-speaking) does not mean that individuals must be selfish too. Natural selection favours the transmission to succeeding generations of those genes that enable their bearers to leave the largest number of high quality descendants possible. Not all of the strategies employed in achieving this need be selfish, some of them may be cooperative. For example, we saw in Chapter 7 that coalitions and alliances may increase the survival and reproductive success of the individuals that participate in them. Thus what most benefits the selfish interests of the genes that favour such cooperative behaviours is that an individual should cooperate with and help others since these will help it in turn, so increasing the chances that its genes will be perpetuated in the next generation.

Altruistic behaviour is generally defined as that which acts to benefit other individuals at some cost to the provider (see Box 8.1). To address the problem of altruism from an evolutionary viewpoint we must start on the basis that altruistic acts imply costs and benefits that affect survival or reproductive success, given that evolution acts on genetically determined characters that pass from generation to generation.

8.2. How may the existence of altruism be explained?

As we have noted, finding an evolutionary explanation for altruism is not easy, although several proposed models offer various solutions to the problem (see Box 8.1). The first two, kin selection and reciprocity, are based on benefits being obtained in exchange for an altruistic act. Such altruism would then be apparent rather than real since, strictly speaking, a true altruistic act confers no benefit on the provider. The third model, group selection, may be able to explain acts of genuine altruism, as we shall see.

Definition: An altruistic behaviour is an act that incurs a cost for the individual that performs it (the donor) but that benefits one or more other individuals (the recipients). A genuine altruistic act confers no benefit upon the donor. From an evolutionary standpoint, such costs and benefits need to be considered in terms of survival or reproductive success.

Models

1. Kin selection: Many examples of altruistic behaviour occur between close relatives, which share a high proportion of their genes. The alleles responsible for altruistic acts would pass to the next generation not only via direct descendants (offspring) but also via close relatives that are helped to breed by altruistic assistance (see Box 8.2). Thus, according to this model, altruistic acts that benefit relatives are altruistic from a behavioural viewpoint but they are selfish from a genetic viewpoint.

2. Reciprocity (reciprocal altruism): This model has the broadest application when the cooperating individuals are not closely related. It implies an exchange of benefits in which an individual that helps another will be helped in turn in future. This is not altruistic behaviour, since the individuals involved obtain direct benefits, so it is better termed reciprocity. It is much more frequent in humans than among other animals and may take various forms (see Box 8.4).

3. Group selection: If groups include a mix of altruistic and selfish individuals, those groups that have a higher proportion of altruists will leave more descendants and will ‘export’ more altruists to other groups. Although more and more authors accept this suggestion, it is a possibility that remains without any clear empirical support.

Box 8.1. Altruism defined and the chief models proposed to explain its existence.

8.2.1. Kin selection

It is characteristic of many bee, ant and termite societies that all their members are close relatives, given that, as a rule, all the workers are daughters of the same queen. Hence they are sisters of each other and of the fertile males and females that the queen also produces, which will found new colonies. This relatedness is the key that inspired William D. Hamilton to propose his 'kin selection theory'. He suggested that an individual may increase its fitness not only by investing in its own offspring but also by investing in close relatives, with whom it shares genes to a greater or lesser extent (see Box 8.2).

Hamilton's idea is that fitness is better understood by considering the number of copies of genes transmitted to the next generation instead of just the number of offspring produced. From this standpoint, an individual may improve its fitness by transmitting its genes to the next generation, whether directly by investing in its own offspring or indirectly by investing in the reproduction of relatives that share those genes (Box 8.2). This is what can happen among ants, bees and termites and we shall return to social insects in section 8.4.

Kin selection: Favours investment in close relatives (see Box 8.1). Based on analysis of fitness founded on genes.

Coefficient of relatedness: The probability that two individuals may share a particular gene on account of shared ancestry. In normal sexual reproduction by diploid organisms the offspring receive half their genes from their father and the other half from their mother. Thus the probability that a father or mother will share a particular allele with one of their offspring is 0.5. The probability is also 0.5 between full siblings. Between grandparents and offspring, between half-siblings, between uncles/aunts and between nephews/nieces it is 0.25. Between first cousins it is 0.125.

Hamilton's rule: The basis of the kin selection theory, by means of which Hamilton established the conditions that must be met for an altruistic allele to be successful. The rule is that an altruistic allele will pass to succeeding generations when the benefit (B) of the altruistic act to the recipient, multiplied by the coefficient of relatedness (r) between the donor and recipient, is greater than the cost (C) to the donor, i.e. when **rB - C >0**.

The concept of 'inclusive fitness': Direct fitness is that achieved by producing offspring. Indirect fitness is achieved by contributing to the production of offspring by a close relative. The inclusive fitness of an individual is the sum of its direct fitness (number of own offspring) and its indirect fitness (number of additional offspring raised by a relative thanks to the help the individual provided).

Box 8.2. Key concepts of 'kin selection theory' (Hamilton 1964).

'Cooperative breeding' is another phenomenon in which kin selection is manifested through investment in the reproduction of close relatives. It has been described in several hundred bird species, in some mammals and, more sporadically, in other animal groups. Cooperative breeding consists of parents raising their offspring with the assistance of one or more additional individuals. The most common finding is that these helpers are recent offspring of the breeding pair, which have remained in the parental territory instead of dispersing to breed themselves. These individuals help raise the next generation. However, this is not always the case and helpers that are not related to the breeding pair are also frequently involved. For this reason the importance of kin selection has been called into question, especially in relation to the evolution of cooperative breeding.

We have, for example, the carrion crow (*Corvus corone*), in which cooperative breeding exists in some populations but not in others. Moreover, the helpers are not always the offspring from previous years that have not dispersed, but are sometimes immigrants from more or less distant territories. Environmental conditions have been shown to play a very important role in juvenile dispersal. Vittorio Baglione, then at Uppsala University, Sweden, and his co-workers carried out an experiment in which they transported crow eggs from a Swiss population in which cooperative breeding was unknown to a northern Spanish population in which cooperative breeding existed. They found that most of the young from the translocated eggs delayed their dispersal and some of them remained as helpers in the following season, as did those of the Spanish population (Baglione *et al.* 2002). It was thus shown that remaining to help is not genetically determined, at least in this species.

How far then is kin selection important in the evolution of cooperative breeding? Although kin selection has been questioned in the past, recent studies have once again vindicated its importance. One of these also employed the carrion crow. Vittorio Baglione and his co-workers carried out molecular analyses to determine the degree of relatedness between breeders and helpers, and they found that immigrant helpers showed a high degree of genetic relatedness to the nest owner of their own sex. This shows that crows that return to their natal area after moving away and spending some time elsewhere help those breeding pairs with whom they are closely related (Baglione et al. 2003).

Kin selection theory does not only explain altruistic acts involving direct help to breeding relatives, but also most other altruistic behaviours, since these are commonest between related individuals. This theory predicts that the higher the 'coefficient of relatedness' (see Box 8.2) between two individuals, the higher the frequency of cooperative behaviour between them and the lower the frequency of aggression. A good example is provided by instances of nepotism (preferential assistance of an offspring or close relative), which are very common in most social species, our own included (see Chapter 7).

The Siberian jay (*Perisoreus infaustus*) is a corvid that has been studied intensively by Jan Ekman, of Uppsala University, Sweden, and his collaborators. They have shown that adults favour independent offspring in various ways. For example, they allow them preferential access to food, a most important advantage in winter, when living conditions are hard within the species' range in northern Eurasia. In addition, when their offspring form part of a flock, their parents invest more and take greater risks in the face of any predators that may approach (Griesser & Ekman 2005). Such ‘altruism’ proves highly beneficial to the offspring and it has been shown that young birds that winter with their parents have a greater chance of surviving to the following spring than do those that disperse to winter elsewhere (Ekman *et al.* 2000).

Some animal species live in much more complex societies than do Siberian jays. For example, spotted hyenas (*Crocuta crocuta*) live in clans, permanent social groups in which relationships between individuals are quite complicated. A clan is comprised by females born within the group, their own offspring and various males that were not born in the group, but that may stay in the clan for many years. Bearing in mind that males and females mate promiscuously and that females usually produce twins, the kin relationships between the females in a clan may be very varied. They may be step-sisters, sibling, more distant relatives or, in some circumstances, barely related at all. All individuals in a clan are hardly ever together and spotted hyenas perform most of their activities in smaller groups, whose composition frequently changes. Sofia Wahaj, of Michigan State University, USA, and her co-workers studied these small group associations and aggression between individuals in hyena clans, employing molecular analyses to establish the coefficients of relatedness between different individuals. They found that although aggression did not differ according to relatedness, it directly influenced small group membership. The commonest association was between sibling sisters that had been raised together, followed by step-sisters that also had been raised together, and, in third place, stepsisters that had not been raised together, i.e. that were the offspring from different births. The study also revealed that associations between sisters that shared a mother were preferred over those where sisters shared a father (Wahaj *et al.* 2004).

These results clearly show that spotted hyenas are capable of recognising their relatives, something that is essential for kin selection to operate. Numerous studies have shown such a capability in diverse animal species. A notable study is that by Jason Buchan of Duke University, USA, and his collaborators, who employed molecular analyses to establish the paternity of 75 young members of a population of the yellow baboon (*Papio cynocephalus*). The females of this species are promiscuous and they copulate with many males before they become pregnant, so it seemed improbable that a male would be able to recognise the young that he had fathered. Nevertheless, observations of aggressive encounters between juveniles, and of which adults intervened to help either contender, revealed that males significantly favoured their own offspring. Such support is very important since it contributes to improving a youngster’s hierarchical status and to protecting it from possible injury (Buchan *et al.* 2003).

These findings, and those of the hyena study, show that individuals of at least some species are capable of recognising relatives. The key question concerns the mechanism that permits them to do so. This is the subject of the next section.

How relatives are recognised

Most studies that offer evidence of a capacity for kin recognition discuss the mechanism that makes such recognition possible. For example, the authors of the hyena study above suggested that it is achieved by ‘phenotypic similarity’ (see Box 8.3) and those of the baboon study propose that a number of clues permit a male to judge his probability of paternity, mainly the fertility of the female at the time when he copulated with her, phenotypic similarity and the female’s behaviour towards other potential fathers.

Very few such studies have actually established which mechanism is involved in kin recognition. Four theoretical possibilities have been proposed (Box 8.3). The first is general among bird species that raise their young in nests, most of which are unable to recognise their chicks individually, to the extent that if a chick of another species is placed in a nest it will be fed by the owners as one of their own offspring.

The classification presented in Box 8.3 is useful since each mechanism may generate different predictions as well as helping our understanding of the concepts. However, it also poses difficulties since the differences between the four mechanisms are not entirely clear-cut. For example, both associative learning and phenotypic similarity involve learning one’s own phenotype and recognising it in others. The phenotypic similarity mechanism may also imply the existence of recognition alleles.

Associative learning and phenotypic similarity may also frequently operate together in the same species. This is the case in Belding’s ground squirrel (*Spermophilus beldingi*), a terrestrial squirrel that lives in quite large social groups, as described by Holmes & Sherman (1982) in their famous experimental study that nearly all textbooks mention. They concluded that kin recognition in this species involves two mechanisms. There is associative learning between litter-mates, allowing them to be recognised as kin. Phenotypic similarity is also involved in which individuals learn their own phenotypes and those of their parents and siblings, thus establishing a generalised model of family that serves them in the future to distinguish those that fit the model (kin) from those that do not (non-kin). In connection with this, a good study by Jill Mateo, of Cornell University, USA, has shown that Belding’s ground squirrels produce odours that act as kin indicators. Experiments involving odour discrimination showed that individual odour enables quite precise determination of the relatedness of unfamiliar individuals (Mateo 2002). A similar arrangement quite probably also occurs among other species, i.e. the associative learning mechanism is used to recognise relatives encountered during an individual’s development, and the phenotypic similarity mechanism is used to determine the degree of kinship of unfamiliar individuals.

1. **Site-based recognition**: The simplest mechanism and well known in birds, the group in which it is most frequent. Where offspring are located in a specific place, as happens with bird chicks that develop within a nest, a form of ensuring investment in one’s own offspring is to follow the ‘feed the chicks that are in my nest’ rule.

2. **Associative learning**: A mechanism based on the interactions of developing individuals with each other and with their parents, in which they learn that those raised with them are their brothers or sisters and those providing care are their parents. This mechanism is independent of genetic kinship.

3. **Phenotypic similarity**: Based on learning a character or a group of characters that identifies the familial group. When individuals meet strangers comparing such characters will allow them to evaluate the degree of similarity with themselves and will serve to indicate the degree of kinship.

4. **Recognition alleles**: This mechanism does not involve learning but relies on the existence of a genetic marker that confers a characteristic phenotype on its bearers that will serve as an indicator of kinship and induces a tendency to favour individuals with such a characteristic.

Box 8.3. Proposed mechanisms to explain kin recognition. Mainly after Komdeur & Hatchwell (1999).

It is very hard to differentiate between mechanisms 2, 3 and 4 in Box 8.3 and harder still to demonstrate an effect of any one of them that is independent of any interaction with the other two. However, Anne Lize, of Rennes University, France, and her collaborators have shown the operation of the phenotypic similarity mechanism by controlling experimentally for any possible effect of associative learning. They worked with Aleochara bilineata, a species of rove beetle whose larvae are parasitic. In most insects with similar lifestyles the females lay their eggs directly on the larvae or eggs of larger insects, so that the parasitic larvae feed within the host to complete their development. A. bilineata is unusual in that the females do not lay directly on the host but instead do so somewhere where there is a high probability that the larvae will find hosts after they have hatched. The larvae thus have to seek out their prey. Sometimes two larvae attack the same host, an instance of multi-parasitism that proves very costly since there tends not to be enough food for two and one of them will die. The larvae are capable of detecting not only whether a potential host has already been parasitized but also if it has been invaded by a sibling larva or by a stranger, given that they avoid invading hosts already parasitized by siblings.

An experiment was designed to make it possible to distinguish between phenotype similarity and associative learning in this species. The eggs laid by females were collected and kept isolated from each other until the larvae hatched. Associative learning was thus ruled out by preventing any type of familial contact. Despite this, once the larvae were presented with hosts, some of which had previously been parasitised by related larvae and others by unrelated larvae, hosts parasitised by nonkin larvae were selected preferentially (Lize *et al.* 2006).

The recognition alleles mechanism (see Box 8.3) is considered least probable in theory and has attracted least support. Nevertheless, evidence for it is clearly provided in a study by Laurent Keller, of Lausanne University, Switzerland, and Kenneth Ross, of Georgia University, USA. They solved a previously intractable enigma by invoking the recognition alleles mechanism. Each nest of the red imported fire ant (*Solenopsis* *invicta*) normally houses several reproductive queens and it was known that none are ever homozygous for the gene locus *GP-9*; all queens were heterozygous (*Bb*). The non-existence of homozygous *bb* queens was understood, because it was known that they die before reaching maturity. However, it was not known why homozygous *BB* queens also did not exist. Keller & Ross discovered why. Homozygous *BB* queens are killed by the workers when they start to lay eggs. What is most interesting is that not all workers take part in this. The ones mainly responsible are *Bb* workers (the *BB* workers, which are the closest kin to such queens, do not participate in the executions). This shows that the *GP-9* allele is associated with another recognition allele that induces the workers that possess it to kill those queens that do not (Keller & Ross 1998).

8.2.2. Reciprocity: general features and direct reciprocity

Hamilton's kin selection theory resolved the enigma of altruistic behaviour between relatives but such behaviour is also common between unrelated individuals. Robert Trivers (1971) proposed a brilliant idea that he called 'reciprocal altruism' to explain instances of cooperation between non-kin individuals (see Box 8.1). Some of us nevertheless believe that such cases are better termed 'reciprocity' since they are not truly altruistic, given that there is mutual benefit. Humans apart, altruistic acts between non-kin are considerably scarcer in most species than those involving relatives (the opposite applies in our species. See Section 8.5).

In birds, for example, when a predator approaches a nest site, the nest owners fly towards it and mob it while giving noisy alarm calls. Very often nearby pairs will join in this mobbing behaviour until the predator is driven away. Theirs is an altruistic act since the neighbours help even though their own nest is not under threat and the behaviour is costly for them, not just in terms of time and energy involved but also because there is a risk that the predator will capture one of them.

Is the assistance of neighbours in expelling predators really beneficial and necessary? We can answer this by referring to a study of the jackdaw (*Corvus monedula*) that we carried out some years ago. The jackdaws in our study area in Guadix district, Granada province, Spain, build their nests in holes in clay cliffs. Their principal predator is another, but much larger, member of the crow family, the raven (*Corvus corax*). We noted that mobbing was effective when five or more jackdaws took part, but not when there were only two or three. Nest holes with narrow entrances were safe, but all those with wider entrances lost the eggs or chicks to the ravens. As a result of our experimental treatment, in which supplementary food was provided for a month before nesting began, there was an increase in colony size in our two experimental study colonies. This increase in pairs brought about a reduction in predation by ravens, so much so that none of the nests in these colonies were lost. Increasing the number of pairs that nested close together in the same cliff ensured that there were always enough jackdaws present to drive away the raven before it approached (Soler & Soler 1996). This example is not a case of reciprocity since all the nests were close to each other and thus all were in danger (it is an example of mutualism; see Chapter 9). However, it helps us to conclude, in response to our earlier question, that predator mobbing behaviour is highly beneficial and may be highly effective when performed by a large number of individuals.

Why should in other species the owners of more distant, unthreatened nests cooperate in such behaviour? This is the key question. The answer offered by reciprocity is that since collaboration is important to achieving success, helping a neighbour is beneficial because that neighbour will return the favour in the future. Indrikis Krams, of Daugavpils University (Latvia) and his co-workers showed experimentally that individual pied flycatchers (*Ficedula hypoleuca*) collaborate in mobbing behaviour with individuals that have previously collaborated with them, confirming that this is an instance of reciprocity (Krams et al. 2006).

The existence of reciprocity poses a fundamental theoretical problem. The best strategy for an individual that has already received help is not to pay its helper back (see Box 8.4). The problem is solved if we bear in mind that under natural conditions the animals inhabiting an area have a high probability of meeting again and of needing to cooperate on other occasions. In time, neighbours and, especially, members of the same social group get to know each other. This allows them to identify selfish individuals and to avoid helping them. Hence, the selfish strategy of the non-reciprocator is not beneficial in the long term, so the best strategy is collaboration.

Reciprocal collaboration based on repeated encounters is a very complex topic. On the one hand, as we have commented already, failure to cooperate is a poor strategy but, on the other, always cooperating is also not a good strategy because it allows other individuals to take advantage of an individual that is known always to be cooperative. What then might be a good strategy? In a contest between strategies designed by Axelrod (1984), the best proved to be the so-called 'tit for tat' strategy, which consists of always collaborating during the first encounter and thereafter always doing what the opponent did in his or her preceding decision (see Box 8.4).

Definition: Reciprocity is a form of mutual collaboration in which an individual helps another, unrelated individual and, in turn, receives the same or another favour in the future.

The theoretical problem: If two individuals collaborate both obtain a benefit. However, since the first individual to receive help has already benefited all that it gets from returning the favour is that it incurs a cost. Why then return thefavour? (This situation is known as 'the prisoner's dilemma'). If this argument is applied to a reproductive scenario, natural selection would favour individuals that, having been helped, do not return the help, since they would leave more descendants through having incurred lower costs. How then may the evolution of cooperation be explained?

The solution: The answer to the above question considers the likelihood of those two individuals meeting again. If there is little chance that they will do so the best strategy is not to return any help received. However, if there will be frequent opportunities for future cooperation, this will allow selfish individuals to be identified and excluded from cooperation, which will be highly prejudicial to the selfish ones. The best strategy in the latter situation is to cooperate.

If cooperation is seen in terms of reproduction, some strategies will be more effective than others since they increase benefits and reduce costs in different proportion. Some also will result in more descendants and hence natural selection will favour the most effective and those that are not will disappear.

The 'tit for tat' strategy: This cooperative strategy is the most famous in biological circles and one of the most effective. Axelrod (1984) designed a computer program that matched different strategies against each other in a prisoner's dilemma game played repeatedly. He organised a tournament that matched 62 strategies proposed by different scientists against each other. The winner was one of the simplest, the so-called 'tit for tat' strategy. It involves always collaborating during the first encounter and thereafter always doing what the opponent did in his or her preceding decision, i.e. collaborate if the opponent collaborated and vice- versa.

Types of reciprocity

a. Direct reciprocity: A helps B because B has previously helped A.

b. Indirect reciprocity: A helps B because B has previously helped C.

c. Generalised reciprocity: A helps B because previously C has helped A. d. Enforced reciprocity: A predisposition to cooperate with others and to punish those that violate the norms of cooperation (exclusive to the human species).

Box 8.4. Reciprocity. Definition, models and types of reciprocity

Indrikis Krams and his research group designed a second, and ingenious, experimental study of the pied flycatcher that allowed them to put some of the most important predictions of reciprocity and the 'tit for tat' strategy to the test. They erected nestboxes in groups of three (A, B and C), arranged in a triangle so that each box was about 50m apart from the others. The experiment was conducted in two stages once there were chicks in the nestboxes. In the first stage pair B was captured and held in captivity. Immediately thereafter a stuffed owl was set up on a stick near to box A. This provoked mobbing of the owl by the pair in box A and, in every case, both the male and female of box C came to assist with the mobbing (pair B could not do so since they were caged). The second stage of the experiment took place an hour later, after pair B had been released. Now a stuffed owl was set up next to box B and another stuffed owl was set up simultaneously next to box C. The pairs in boxes B and C began mobbing the respective owls and pair A was confronted with having to decide which pair to assist. The results were conclusive. The pair in box A came to the aid of that in box C (the pair that had previously helped them) on 30 occasions, but never helped the pair in box B (the pair that had been prevented from helping). These results show very clearly that pair A helped the pair that had earlier helped them whereas they 'punished' the pair that had not collaborated. This supports the belief that reciprocity may explain the origin and evolution of mobbing behaviour. They also show that the 'tit for tat' strategy may operate in nature since these previously acquainted individuals follow the second rule of that strategy (see Box 8.4), because they showed the same behaviour - cooperation or non-cooperation - towards an opponent that this individual previously showed towards them.

Reciprocity is not always direct or obvious. For example, a strange form of cooperation is exhibited by the long-tailed manakin (*Chiroxiphia linearis*), a small bird whose males are brightly coloured and have very long central tail feathers. When a female appears, male manakins perform a showy and acrobatic display, always using the same perches for this purpose. Females, however, only approach males that are accompanied in their display by a second male, so that 'dominant' males have an 'apprentice' male with whom the display is performed as a dual ballet. The subordinate male apparently gains no benefit since the dominant one mates with all the females and, furthermore, the two males are unrelated, so that their cooperation cannot be explained by kin selection. Why then cooperate in a dance that expends much time and energy? When David McDonald and Wayne Potts, of Florida University, USA, investigated, they found the answer. They found that the apprentice derives important long-term benefits. Several years later he may become the dominant male and inherits the display site as well as benefiting from the fidelity to that site that females show each breeding season (McDonald & Potts 1994).

8.2.2. Indirect, generalised and enforced reciprocity

Reciprocity may also take more sophisticated forms. Examples are known in which reciprocity is indirect, acting via a third party, or even generalised, offered to any unfamiliar individual although always after help has previously been received from other unfamiliar individuals (see Box 8.4). Such types of reciprocity are very rare in non-human animals. Indirect reciprocity has only been demonstrated in an interspecific interaction between fish (see Chapter 9), and generalised reciprocity is only known from an experiment with brown rats (*Rattus norvegicus*; see below). In our species, although generalised reciprocity has not been studied much, indirect reciprocity is known to be of great importance (see Section 8.5).

Claudia Rutte and Michael Taborsky, of Berne University, Switzerland, have obtained evidence that generalised reciprocity exists in rats, at least under laboratory conditions. They trained a group of rats so that, when one pressed a lever, food was supplied to the others, but not to the operator of the lever since the food remained out of its reach. They found that the rats cooperated most often in pressing the lever in the presence of unfamiliar individuals when on a previous occasion another rat had operated the lever so that they could eat (Rutte &Taborsky 2007). Enforced reciprocity is a mechanism only described in humans (see Section 8.5.4).

8.2.3. Group selection

As we saw in Chapter 2, the notion that behaviour evolves for the good of the group or the species is unsustainable and was seriously discredited during the 1960s. Nevertheless, some less naive versions of group selection could work. In theory a group may be an adaptive unit should selection at group level act more strongly than at an individual level. It is thus possible that group selection may have influenced the evolution of altruism, but it seems improbable that it has played an important role since individual selection is normally strongest.

A form of group selection distinct from the classical version proposes that, although within a given group selfish individuals rather than altruists will leave more descendants, groups with a higher proportion of altruists disposed to work for the common good will leave more descendants in total than less altruistic groups. Taking all groups together, this results in altruists rather than egoists leaving more descendants. This idea is again current thanks mainly to studies of cooperative behaviour among microorganisms. The two best-studied genera are *Myxococcus* and *Dictyostelium*. The genus *Myxococcus* includes a group of bacteria that live sociably and collaborate throughout their life cycles. When food is scarce they group together into multicellular structures (fruiting bodies) in which some individuals die to form the structure and others are transformed into resistant spores, which lie dormant until environmental conditions improve and food is once more available (Travisano & Velicer 2004). The genus *Dictyostelium* includes different slime-mould species whose individuals live terrestrially as solitary, unicellular amoebae, feeding on bacteria and other organisms. As in myxobacteria, they group together under conditions of food shortage, forming a pseudoplasmodium that moves towards the light. It forms a stalked fruiting body with a spherical spore mass at one end. Eventually the cells comprising the stalk die and the spores are dispersed, to begin a new life cycle (Travisano & Velicer 2004).

Some authors consider these examples to be clear instances of group selection, given that some individuals die so that others may survive. Selfish individuals are common in these microorganism societies and these do not cooperate but take advantage of the others. Their strategy is beneficial to them since as they do not expend resources in collaborating they have more chance of converting into spores and surviving to reproduce. The activities of these opportunists may prove harmful to the society and when they come to constitute a majority the whole group may die out. As modern group selection models predict, this selective pressure is so strong that altruistic individuals have evolved defensive strategies against the selfish ones (given that group selection may work if the cost of imposing cooperation is less than its benefits). Michael Travisano, of Houston University, USA, and Gregory Velicer, of the Max-Planck Institute, Germany, have reviewed the strategies developed by altruistic individuals to prevent exploitation by egoists. Without going into too much detail, such strategies fall into two broad groups: (1) those that prevent egoists from access to the benefits that result from the activity of the altruists, and (2) those that actively punish noncollaborating individuals. The fact that cooperators may produce bactericidal substances that act exclusively against egoists is well documented (Travisano & Velicer 2004).

Before accepting such instances as examples of group selection, however, we should consider the possibility that their cooperative behaviour may be due to kin selection (see section 8.2.1). No convincing proof has been offered that the individuals are not closely related; indeed they may even be clones! There are indications of kinship in *Myxococcus*, whose individuals are very similar genetically. Nevertheless, in the case of *Dictyostelium* it seems less likely that the individuals are close relatives given that the slime mould groups form from a grouping of previously solitary and independent individuals.

8.3. The importance of social punishment in the evolution of altruistic behavior

In accordance with theoretical models, penalising individuals that seek only to benefit themselves negates the advantages of non-cooperation and favours altruistic collaboration. Such action is known as social punishment and it is used to dissuade the recipients from behaving selfishly in future. Such behaviour is seen, for example, in the superb fairy-wren (*Malurus cyaneus*), a small bird referred to previously that is a cooperative breeder, several individuals helping a breeding pair to raise their brood. If one of the helpers is removed temporarily during the period in which helpers are feeding nestlings, on its return it is attacked by the dominant male, seemingly as a punishment for not carrying out its duties (Mulder & Langmore 1993).

An even more striking example concerns the naked mole-rat (*Heterocephalus glaber*). This permanently subterranean species forms colonies in which most individuals are worker females but also include soldier males, a breeding male and a breeding female or queen. The organisation is quite similar to that of ants and other social insects. In this case, the queen aggressively pushes around the most idle of the workers, which tend to those that are largest and least closely related to the queen (Reeve 1992).

The idea that social punishment plays a very important role in the evolution of altruistic behaviours has currently gained prominence. As we saw in the kin selection section, until recently all altruism between relatives was explained by kin selection and social punishment was thought to operate only in cases of reciprocity, which are frequent in humans but rare in other animals. Nevertheless, many recent studies highlight the importance of social punishment in explaining altruism, including that exhibited by the social insects (Ratnieks & Wenseleers 2007). We shall consider social punishment in the following two sections, which deal with the two most fascinating instances of altruism: in social insects and in the human species.

8.4. Altruism in eusocial insects

We have so far used the term social insects to describe those that live in more or less numerous groups or societies. Here we introduce a new term, eusocial insects, which refers to species that form more complex societies, characterised by division of labour, with some individuals concerned with reproduction and others taking charge of other tasks (see Box 8.5).

Nearly 15,000 species of eusocial insects are known and the variation in colony organisation is enormous. We shall start by considering the life cycles of two species, one considered a primitive eusocial species and the other advanced (see Box 8.5). Both will serve to illustrate the topic and will allow us to draw pertinent conclusions.

Colonies of the common paper wasp (*Polistes fuscatus*) are founded by small groups of females that, after winter is past, cooperate to build and defend the nest and to feed the larvae. The queens are organised in a hierarchy and the dominant one lays most of the eggs, but not all. The first larval generation develops into females, some of which remain to help and others that depart and become breeders the following spring. All collaborating females can lay eggs, but the dominant queen controls the reproduction of her subordinates and she eats about a third of the eggs that they lay. Subordinate queens have the advantage of being able to replace the dominant queen should she die. H. Kern Reeve, of Cornell University, USA, and his collaborators precisely determined, by means of genetic analysis, the degree of relatedness between the queens and the number of offspring that each produced. The results were striking regarding the proportion of offspring produced by the dominant queen. For example, that proportion was greater the larger the number of larvae produced by a colony and the greater the degree of relatedness between the queens. Also, in nests in which the dominant queen laid a high proportion of the eggs, the aggression showed towards her by the other queens was greater than in nests in which reproduction was distributed more equally between the queens (Reeve 2000).

Definition: Social groups comprising at least two types (castes) of individuals, reproducers and workers. The latter are females in most cases and they perform the various tasks necessary for the former to reproduce.

Eusociality in insects takes two forms. Primitive eusocial species are those in which castes are not morphologically differentiated. These species form small colonies and workers have some chance of replacing the reproducers. The opposite characteristics are shown by advanced eusocial species.

Characteristics:

- Eusocial species have been discovered in five insect orders. Most occur in the Hymenoptera (ants, bees and wasps; 12,000 species), but also in the Isoptera (termites; 2,000 species), Homoptera (aphids: 40 species), Thysanoptera (thrips: 6 species) and Coleoptera (beetles: in a sole species of the weevil family Curculionidae).

- In nearly all groups, the breeding individuals that live in the interior of colonies are always females (queens). The exception is the termites, whose termitaries house both fertile males and females. The number of queens per colony varies. Most often there is only one but there may be a few or even more.

- Workers perform diverse tasks. In advanced eusocial species they make up different castes that may be morphologically specialized for different kinds of work.

- In general, caste differentiation is not genetically determined.

Box 8.5. Eusociality defined and general characteristics of eusocial insects.

The situation is very different in advanced eusocial species (see Box 8.5), such as the leaf-cutter or fungusfarming ants, of which 200 species belonging to several genera have been described. These ants live in enormous colonies, sometimes exceeding ten million individuals. They construct complex nests with a multiplicity of tunnels and small chambers and, in addition, larger spaces in which they cultivate their fungal orchards and a deep chamber that they use as a rubbish tip. The workers cut large pieces of leaves that they then carry to the nest. Here smaller workers cut them into smaller fragments and clean them meticulously to avoid introducing some parasitic organisms that might infect the ants or their fungi. When the leaf fragments are ready they are carried to the orchards and 'seeded' with the fungus that, once grown, provides the food supply for the whole colony.

Marked division of labour occurs among leafcutter ants, with workers of different sizes suited to carrying out each of the various tasks. The size range is enormous, so much so that the largest workers may be two hundred times larger than the smallest ones. The most demanding task is cutting leaves and carrying them to the nest and numerous large or medium-sized workers perform it. Other smaller workers carry out diverse jobs within the nest. Some care for the larvae, others cultivate the fungi and others take charge of the rubbish tip. In some species too there exist much smaller workers adapted to perform a highly specialised task, the bodyguard role. Each of these minuscule workers rides back to the nest on top of the leaf fragment carried by a larger worker and its mission is to protect the leaf-bearer from attack by any small parasites that may try to lay eggs on the large workers' bodies (Roces & Holldobler 1995).

Although significant morphological differences between workers in charge of different tasks exist in leaf-cutter ants, such differences may be even more marked in other advanced eusocial ant species in which different castes do not just differ in size but may look completely different. For example, some species have workers with enormous, armoured heads that they use as doors, i.e. they use them to block entrances to the nest. In others that inhabit arid zones some workers act as 'reservoirs' and spend their entire lives hanging within nests while storing fluid in their spherical abdomens, which may swell to many times their original volumes. The soldier caste is the most common and is formed by large workers whose mandibles are highly developed and whose chief task is colony defence.

To return to the leaf-cutter ants, these are also known as fungus-farming ants because their survival depends entirely on fungal cultivation. They cannot digest cellulose and so cannot feed directly on leaves, but they do eat the fungi that develop on those leaves. They perform systematic and meticulous work in seeding and harvesting the fungi and in cleaning their gardens before re-use. Moreover, they have specific sites on their own bodies, whose location varies between species, in which they maintain suitable conditions for the development of filamentous bacteria that produce antibiotics capable of killing pathogenic bacteria and fungi. These substances are used as a chemical treatment for their crops. The fungus that they grow lives only within ant nests and is so important that when the young queens leave their natal colony to found a new one each carries a small piece of fungus in her mouth to start cultivation in her new nest.

Leaf-cutter ant workers have poorly developed ovaries that hardly ever produce viable eggs (the exceptions are some species that may, in the queen's absence, produce eggs that give rise to males). Nevertheless, some workers produce eggs that are used to feed the queen or the larvae, according to species. Michiel B. Dijkstra and his colleagues at Copenhagen University, Denmark, dissected worker ovaries to study the eggs produced by ants of various leaf-cutter species of the genera *Acromyrmex* and *Atta*. They found that many *Acromyrmex* workers lay eggs of similar size to those of the queen but with less yolk and no reproductive purpose, using them instead to feed the larvae. Most *Atta* workers do not lay eggs but a few that live in proximity to the queen lay large eggs, also with little yolk, which in this case they use to feed the queen. With respect to fertile eggs, the study concluded that *Atta* workers are sterile but that *Acromyrmex* workers do have the ability to produce viable eggs, although this capability is restricted (Dijkstra *et al.* 2005).

8.4.1. Evolution of eusociality

As noted earlier, this type of social organisation has evolved independently in the various insect groups in which altruistic behaviour predominates. Comparative studies have revealed that eusociality originated in species in which a female cared for its descendants, some of which began helping, as we have seen occurs in the common paper wasp and in some cooperativebreeding birds.

What factors have influenced the evolution of eusociality? The three most important are considered in the following sections. They are the kin relationship between helpers and the descendants produced by a breeding female, the environmental conditions that influence the cost/benefit relationship of helping versus reproducing, and coercion, which contributes to the predominance of altruistic behaviours through the punishment of non-cooperative individuals.

Kin relationships

As we have seen, helping relatives can increase an altruistic individual's 'inclusive fitness' since it is collaborating in the production of offspring by a close relative and thus transmitting its own genes to the next generation (see Box 8.2). Hamilton was also the first to notice that this might be especially relevant in the case of Hymenopterans since these have a type of reproduction known as 'haplodiploidy', whose outcome is that a female is more closely related to her sisters (r = 0.75) than to her own offspring (r= 0.5) (see Box 8.6). In other words, from a selfish viewpoint it is a better option to help sisters to breed than to breed oneself (Hamilton 1964). For some years the haplodiploidy argument provided the major theoretical basis for understanding altruism in eusocial insects.

Haplodiploidy: A reproductive mechanism in which males originate from unfertilised eggs and hence are haploid, whereas females originate from fertilised eggs and so are diploid.

Coefficients of relatedness: Since males are haploid their sperm are not formed by meiosis and hence are all identical. This means that all daughters of the same male receive an identical genetic contribution from him, comprising half of their genomes. The other half is derived from the diploid mother and so two sisters have a 50% chance of sharing any of the mother's alleles. In other words, in haplodiploid organisms, sibling full sisters have a 75% chance of sharing the same gene.

- The coefficient of relatedness between close relatives in haplodiploid species is: mother-daughter 0.5; mother-son 0.5; father-daughter 1; father-son 0; sister-sister 0.75; sister-brother 0.25.

Box 8.6. Haplodiploidy defined and coefficients of relatedness in haplodiploid species.

However, it was soon pointed out that the high degree of relatedness between sisters (r = 0.75), which would presumably predispose workers to help, was countered by the low degree of relatedness that such workers have with their brothers (0.25). Given that the reproductive success of a colony is measured in terms of the number of breeding individuals that it produces, namely queens that found new colonies and the males that fertilise them, the mean genetic relatedness of the workers to those descendants is 0.5. This is the same as they would have with their own offspring and hence haplodiploidy should not lead to a special tendency to help for this reason alone. Moreover, other factors were discovered that restored the importance of the genetic relatedness between sisters as being the primary explanation of altruism in eusocial insects. For example, queens are quite often fertilised by several males and in many species there is more than one queen in each colony. Both factors contribute to the kinship between workers and the sexual individuals that they help to breed often being considerably lower than previously thought.

None of this means that kinship no longer matters in explaining altruistic behaviours in eusocial insects. It is just not as central as formerly believed. Kin selection theory remains current and allows us to predict that workers will show a greater predisposition to help the more closely they are related to the queen's offspring (see Hamilton's rule, Box 8.2). It also predicts that the workers, being responsible for caring for the eggs and feeding the larvae, will favour those offspring to whom they are most closely related genetically.

A good demonstration that supported the prediction about kin-based worker care was provided by Minttumaaria Hannonen and Liselotte Sundstrom, of Helsinki University, Finland, in their work on the black ant (*Formica fusca*), whose nests often contain more than one queen. They determined the kinship between individuals in ten different colonies by taking DNA samples from eight workers in each, chosen at random, and a considerable number of offspring (some 50 eggs and nearly 100 pupae). They found that the workers favoured those eggs and pupae to which they were most closely genetically related. The results show that, as predicted, workers behave selfishly from a genetic viewpoint and that, in addition, they are capable of detecting the degree of relatedness between themselves and the young ants in the nest (Hannonen & Sundstrom 2003).

Environmental conditions

Kinship has been the chief driver of studies of altruism. However, if we recall Hamilton's rule (see Box 8.2), it also includes two other factors: the benefit that an altruistic act confers to the recipient and the cost incurred by the donor. These two factors are also important and they may be strongly influenced by environmental conditions. A key element in the origin and evolution of eusocial societies is the costs and benefits that arise from the two options that, at least in theory, are available to individuals: to stay and help or to leave familiar ground to become a breeding individual (as happens in the common paper wasp). Environmental conditions may influence this choice directly since they determine the reproductive success of either option.

By way of example we shall consider the influence of environmental factors in termites (Isoptera). Haplodiploidy does not exist in termites but they have still achieved levels of organisation as complex as those seen in Hymenopterans. A review by Barbara Thorne of Maryland University, USA, (Thorne 1997) highlights that for a juvenile termite the option of changing into a sexual winged adult and of dispersing to reproduce on its own would have the advantage of saving the time and energy demanded by helping. However, such dispersal carries a high risk of predation and has a highly uncertain outcome. The possible reproductive success of a dispersing individual is very low, given that it must first find a suitable site in which to establish a colony, and once there it will need to wait a long time before that society produces fertile males and females.

In contrast, the other option of staying to help the natal group not only avoids the risks of dispersal but has important advantages that favour the evolutionary origin of eusociality. The chief one of these is that important benefits are available to termites at hatching (they find themselves in a secure place with an abundant food supply). For example, termitaries are often located within dead trees whose wood serves them as food. Other inherent advantages are that an individual might inherit the opportunity to become a breeder and that it therefore can benefit directly from group defence of the nest and its resources.

Coercion

Francis Ratnieks, of Sheffield University, UK, and Tom Wenseleers, of the Catholic University of Leuven, Belgium, have reviewed the role of coercion in altruistic behaviour of eusocial insects (Ratnieks & Wenseleers 2007). They found that the degree of kinship that exists within colonies is too low to explain the extreme altruism observed in many such societies. One of their conclusions is that although coercion was certainly not an important factor in the origin of eusociality, it is the principal mechanism responsible for maintaining it.

The workers of many wasp, bee and ant species have ovaries and could lay unfertilised eggs, which would give rise to males. Why do they not do so given that they would then produce direct descendants of their own? Numerous studies have tried to answer this question, and these have revealed the great importance of coercion. It has been shown that in many species workers do not lay eggs because of the risk that they will be destroyed or that they themselves will be killed by the queen or by the other workers (Ratnieks & Wenseleers 2007).

The benefit to the queen of arresting the reproductive efforts of her workers is clear since these would amount to direct competition that would reduce her reproductive success. But what about the workers? Why should they penalise egg laying by their sisters? Kin selection offers an answer to this question, one that is valid for all cases in which the queen is fertilised by several males: the workers do not necessarily share the same mother and father and so are less related to their sisters' offspring than to those of their mother. Kin selection thus favours investing in the male-producing eggs laid by the queen rather than in the male eggs laid by other workers. Workers, as has been shown by Wim Bonckaert, also of the Catholic University of Leuven, Belgium, and his collaborators. They studied the German wasp (*Vespula germanica*), a species in which each queen mates with an average of 2.9 males. They observed that the workers laid over half of the male eggs in the colony (58%), and that these were as viable as those of the queen. Video recordings established that it was the workers and not the queen that destroyed the male eggs laid by other workers. The outcome was that nearly all surviving males were sons of the queen and only 0.44% were sons of the workers (Bonckaert *et al.* 2008).

The importance of coercion in preventing selfish reproduction by workers has been revealed not only in investigations of particular species but also in comparative studies. For example, Tom Wenseleers and Francis Ratnieks, whom we mentioned previously, analysed data from diverse species for which all the necessary information was available. They found that the percentage of workers that lay eggs increases the greater their relatedness to each other. It declines the more effective the control of egg laying by workers (Wenseleers & Ratnieks 2006).

8.4.2. Conflict in eusocial insects

Kin selection theory not only predicts the emergence of more complex eusociality, but also the existence of conflict. Given that individuals in a colony are not genetically identical their reproductive interests need not also coincide. Hence, when an individual has a chance of increasing its fitness through a selfish strategy, it may be assumed that the individual will use the selfish strategy. We have already seen, in fact, that egg laying by workers is frequent among many eusocial insects but has little success, since the eggs are found and destroyed either by the queen or by other workers. Sometimes, however, the workers too have ways of imposing their genetic interests on others. We noted that in the common paper wasp all females have a chance to reproduce, but that the dominant female controls reproduction by eating some of the eggs laid by other females. Excessive egg consumption by the dominant female (simulated by removing eggs experimentally) brings about an increase in aggression directed by the workers towards the dominant female (Reeve 2000). The conflict between workers and the queen sometimes goes further such that workers of various bees and wasp genera may even kill their queen (Bourke 1994).

In advanced eusocial species, such as leaf-cutter ants, there are thousands or even millions of individuals all working for the common good. They have traditionally been viewed as societies in which all individuals live in perfect harmony, so much so that some authors have regarded such societies as ‘superorganisms’, comparing them to a multicellular being in which all cells cooperate, each carrying out its function so that the individual survives and reproduces. However, the evidence is ever stronger that conflict exists within eusocial colonies because individuals are not acting solely for the good of the society but also to serve their own ends. A good example that confirms this is an experimental, laboratory study of nests of the ant *Temnothorax unifasciatus* by Natalie Stroeymeyt and her co-workers at Regensburg University, Germany. They first divided each colony into two halves, one including the queen and the other composed only of workers. In the latter cases the strongest workers began to attack each other and the most dominant ones soon laid eggs. The two half-colonies were now recombined into a single colony and it was found that the workerbreeders were not attacked either by the queen or by the workers in general, only by a few particular workers that were the ones that went on to become reproducers when the queen was removed afterwards.

In other words, worker-reproduction was only impeded by a few high- ranking workers that had a chance of becoming breeders themselves. In other words, these high-ranking workers were behaving selfishly to increase their chances of reproducing in the future (Stroeymeyt *et al.* 2007).

8.5. Human altruism

As pointed out in Chapter 7, human societies display certain characteristics that are unknown in any other animal species. By far the most important of these relate to altruistic behaviour. Cooperation with relatives and with companions whom we often meet is frequent in humans, but it is very striking that we even often help complete strangers, whom we are very unlikely to encounter again. Thus, although cooperation in other primate species occurs only between relatives or between a few individual members of the same group, in our own species it is normal to help whoever needs assistance, even if it is an unknown individual in a city of millions. Not always, but quite often, the help given may prove fairly costly. We share food with the needy, care for the sick, donate blood, donate to charities, signup as volunteers, and so forth. It is even the case that, where necessary, many people are prepared to risk their lives to save that of another person, even though he or she may be a total stranger. Such self-sacrificing cooperation, in which the donor pays a high cost, constitutes an evolutionary enigma since the models that explain altruistic behaviour in other animals (chiefly kin selection and reciprocity) cannot apply to such cases. These instead at least appear to be instances of genuine altruism; that is, they have costs but no direct or indirect benefits.

However, let us take one step at a time. We will first consider whether human altruistic behaviour fits the general models proposed to explain altruistic acts in general (see Box 8.1). We shall then consider those distinctive characteristics of human altruism that cannot be explained by those models. Finally we shall examine some of the most important proposals advanced to explain the puzzles of human altruism.

8.5.1. The application of general models to human altruism

The models given in Box 8.1 may be applied to human altruistic behaviour. Kin selection is widely applicable to humans given that the tendency to favour our relatives is highly developed in all cultures. Reciprocity too is much more important in humans than in other animals, as noted previously.

A study by Yoshi Shavit of Haifa University, Israel, and his collaborators reveals the human tendency to favour relatives. They interviewed many inhabitants of Haifa, a city that was attacked by Iraqi Scud missiles during the first Gulf War in 1991, and they analysed cooperation between relatives and non-relatives during a situation of universal danger. The interviews took place during and soon after the war, and the questions were designed to discover what help was offered, who offered it, and who received it during the missile attacks. The results showed that psychological help came chiefly from friends and acquaintances who were habitual companions during the run-up to the war. However, concern, in the form of telephone calls after the missile strikes, and direct help, such as offering more secure refuge, was most frequent between relatives. Some 83% of telephone calls after the missile strikes had ended came from family members and 80% of offers of shelter came from relatives (Shavit *et al.* 1994). Thus, during a situation of mortal danger, help was chiefly sought and received from relatives, in accordance with the predictions of kin selection theory.

We have already noted that direct reciprocity is widespread in human societies though quite uncommon in other animals. No examples are needed given that we are all perfectly aware of how often cooperation occurs between friends, neighbours, acquaintances and indeed also between relatives. We shall consider other types of reciprocity below, in particular the two most important types in humans: indirect and enforced reciprocity.

8.5.2. Differentiating characteristics of human altruism

The fact that humans often provide assistance to strangers who they will almost certainly never meet again is regarded as one of the chief enigmas of evolutionary behaviour. This is because this type of altruistic behaviour reveals that humans are predisposed to cooperate and to reject antisocial attitudes, something that seemingly cannot be explained by any benefit received by the donors, as evolutionary theory would predict. However, we must not overlook the existence of persons who tend not to help others, but who try to get as much help from other people as possible.

Blood donation is a highly typical example of human altruistic behaviour. It does not favour relatives nor is there any reciprocity with the recipient of the donated blood, since when a person needs a transfusion it is not necessary that he or she should previously have been a donor. Hence blood donation tends to be seen as an example of true altruism in which a donation is made that incurs a cost but for which nothing is received in return. It is also very widespread; 20-35% of the inhabitants of industrialised countries have given blood at least once in their lives.

We shall examine blood donation in a little more detail since it serves as an example on which to base certain conclusions. Box 8.7 sets out the most relevant information and we shall highlight several aspects. In the first instance, most of those who give blood have been induced to do so by friends or relatives who are already blood donors. Secondly, most blood donors claim to do so for idealistic motives, such as altruism, social responsibility or moral obligation. Thirdly, there are some factors that reduce a predisposition to give blood, all of which would tend to increase the costs involved in donation. Finally, the benefits received are also important when deciding whether or not to give blood. For example, a high proportion of blood donors in centres that offer payment say that they would stop giving blood if they were not paid. Furthermore, in the United States, many lower middle-class donors say that they give blood in order to get information about their health, which is provided to them along with an analysis of their blood. Many donors also say that giving blood makes them feel worthy, although they say that this is not their main reason for doing so.

We shall go into the subject in a little more depth by describing a study that followed the infamous terrorist incidents of 11 September in the United States. Simone Glynn and her co-workers of the Retrovirus Epidemiology Donor Study Group (REDS) in the USA analysed blood donations during the four weeks before and the four weeks following the incidents and found that there was a considerable increase. Mean weekly donations averaged 20,000 during the four weeks preceding 11September, but more than doubled, to 49,000, in the week following the events. They fell once more to 26,000-28,000 during the following three weeks. Donations given by people who had previously donated blood increased by a factor of 1.5, but those by persons who had never ever given blood increased by a factor of 5.2. In other words, the increase in donations in that critical situation was brought about by the response of people who previously had never been donors (Glynn *et al.* 2003).

These blood donation studies highlight that although those who take part declare idealistic motives, such as pure altruism and social reasons, other factors also play an important role, since increasing the costs of giving blood reduces the predisposition to donate and increasing the benefits increases that predisposition as we shall see below.

Reasons for becoming blood donors

1. Conversations with friends or family members who are themselves donors. This is the most important reason given.

2. Requests from priests and other religious authorities, which invoke moral obligations.

3. Blood donation campaigns. These are very common and involve face-to-face contacts, telephone calls and e-mails. Face-to-face contacts are the most effective.

Reasons offered by donors for giving blood

1. Altruism. The most frequent reason given, although to a highly variable extent. From 40-80% of studies highlight this as the chief motive of blood donors.
2. Awareness of society's need for blood donations.
3. Moral obligation.
4. Social responsibility or obligation.
5. The influence of friends.
6. Personal satisfaction.
7. Boosting self-esteem.
8. Concern that blood should be available for the donor and his or her family.

Factors with a negative effect on the decision to donate blood

1. The discomfort of the process. It is important to ensure that donors enjoy the most comfortable circumstances possible since the number of donations otherwise falls drastically.

2. The time involved. Many donors stop giving should waiting times be longer than strictly necessary for any reason.

3. The travel involved. If the donor centre is far away, donors are less disposed to donate.

4. Fear of needles or pain, which tends to be the main reason given in self-justification by non-donors.

Personal benefits received

1. Economic incentives. Many centres in some countries pay for donations.

2. Medical check-ups. Some countries, including the USA, offer medical services to blood donors, chiefly an analysis informing donors of their general health.

3. Boosting personal satisfaction and self-esteem. Most donors claim that the experience does this.

Box 8.7. Blood donation. Reasons offered for giving blood, factors with a negative influence on blood donation and the benefits of giving blood. Data from various sources but chiefly from a review by Gillespie & Hillyer (2002). Most of the information was obtained through interviews.

8.5.3. Factors that favor human altruistic behavior

We shall highlight the three most important of these. First we shall consider self-satisfaction and other psychological adaptations that favour cooperation. These are causal mechanisms that do not explain altruism from a functional point of view that focuses on possible benefits related to survival or reproduction (see Chapter 3). The other two do involve adaptive explanations, for example, the social benefit that being altruistic may bring in the form of getting a good reputation and, in contrast, the cost of suffering social punishment for not being altruistic.

Self-satisfaction and other causal explanations for altruism

As we pointed out in the blood donor example, many people who give blood declare that it makes them feel good and that they enjoy greater self-esteem as a result of their sacrifice. This feeling may extend to all altruistic acts and some authors have proposed it as one of the causes of altruism (the causal explanation; see Chapter 3).

The neurological basis for the satisfaction triggered by performing an altruistic act has been shown in studies of 'social punishment' (see below). Dominique de Quervain and his collaborators, who work at several research centres in Zurich, Switzerland, scanned the brains of various people while they carried out the punishment of an individual who had behaved selfishly. They found that the decision to punish activated a brain region related to reward pathways (de Quervain *et al.* 2004).

Self-satisfaction apart, we humans possess other psychological adaptations that favour cooperation, including the emotions, our sense of justice, our moral sense and religion. The emotions play a dominant role in decision making (see Chapter 11). Some of them, such as gratitude, loyalty, shame and remorse, favour cooperation. Others, such as vengeance, disgust and anger, promote the punishment of those who fail to cooperate. The sense of right and wrong (the moral sense; see Chapter 11) and the sense of justice, in addition to promoting the return of favours, are particularly involved in promoting social reproach and the tendency to punish those who do not fulfil their social obligations. With respect to religion, all existing forms prescribe codes of conduct in favour of cooperation and against those who do not obey those rules, often by promising supernatural rewards and punishments. In other words, our emotions, the sense of justice and religion may all be considered to be mental mechanisms that favour altruism and reciprocity in human relationships (see Chapter 11).

In the next two sections we shall examine two factors that provide benefits for cooperative individuals, who may therefore enjoy reproductive advantages or improved survival prospects (the functional explanation; see Chapter 3).

Getting a good reputation: indirect reciprocity

As a result of the emotions to which we referred earlier, human societies tend to reward altruists. Persons who risk their lives to save others may receive honours and decorations. Such honours come to relatively few but another form of social recognition is much more widely distributed: reputation. Cooperative individuals who often help others enjoy a good reputation as altruists, which can bring them social benefits. They and their offspring may receive help more often than those without such a reputation leading to enhanced reproductive success. As we saw in Chapter 4, being thought a good person may help in acquiring a mate with whom to reproduce.

Such a reputation is the basis of indirect reciprocity (see Box 8.4). Cooperative persons who help others are performing a behaviour that is costly to themselves, but they are acquiring a good reputation that may allow them to recover what they invested with interest. Such indirect reciprocity may explain many cases of ‘pure altruism’ in humans, such as blood donation. Various studies support the belief that blood donors do tend to acquire a good reputation. For example, the subject gets talked about: most people become donors thanks to conversations with friends who are themselves donors (see Box 8.7). Moreover, the largest numbers of donations occur at places of work, such as universities or large businesses, where not only are the costs of donation reduced by not having to travel but also social recognition is facilitated, since there is an increased chance of being observed by others. Blood donation centres may supply a badge allowing a donor to be identified (it was shown years ago that having such an identifying mark leads to an increase in donations). Regular donors also receive a donor card that provides due acknowledgment and that may confer certain rights, chiefly within hospital-based centres.

None of this means that people need be consciously aware of the benefits of blood donation nor do they offer their blood solely to get a reputation for altruism. Decisions to collaborate (as with many others that result from adaptive strategies, see Chapter 2) are taken subconsciously in large measure and are based on the emotion-related psychological adaptations to which we referred earlier. For example, Melissa Bateson and her collaborators in the psychology department at Newcastle upon Tyne University, UK, studied the departmental drinks service in which payment made use of an honesty box next to the drinks dispenser. A notice listed the various charges. The position of the box meant that the person paying could not be observed and hence all contributions were anonymous. The investigators carried out an experiment that simply involved putting a picture next to the price list. The picture, which was changed each week, showed either some flowers or a pair of eyes looking towards the person paying. The money collected for the drinks consumed each week was related to the picture used. They found that people paid more (three times more!) when the eyes were on show than when the flowers were presented. These results support the idea that seeing eyes provides a psychological suggestion that one is being watched and hence that one's behaviour may affect one's reputation, leading to the observed increase in payments (Bateson *et al.* 2006).

We have considered evidence supporting the idea that people who demonstrate altruism (e.g. blood donors) acquire a good reputation that is communicated to others. There is, though, another key question. Does good reputation benefit the altruist, in either the short- or long-term? I believe we all know that it does but, furthermore, there are studies showing that a good reputation increases the chances of receiving help from others. Most of them are experimental investigations based on a methodology termed 'common goods games'. These consist of a number of participants playing a fixed number of matches following some specific rules that they have previously studied in detail. At the start each player has a number of tokens with which to play and those acquired at the end are exchanged for real money. The basis of the game is that each player has to decide how many tokens to assign to a 'shared account' and how many to retain in a 'personal account'. The balance of the shared account is increased at the end and divided equally between the players irrespective of their contribution to it. The experimental design of common goods games is highly variable, depending on the hypothesis being tested, but two results consistently tend to emerge. In general, all players contribute to the shared account, in contradiction of the selfishness model that suggests that not contributing anything is the best strategy. Secondly, contributions decline as the matches proceed.

Dirk Semmann and his collaborators at the MaxPlank Institute of Limnology, Germany, have supplied a useful demonstration that a good reputation brings benefits. They designed a complex common goods game with twelve players divided into two groups of six. This allowed them to conclude that acquiring a good reputation by means of cooperative behaviour that benefits members of one's own group is rewarded in the future, not only within one's own social group but even among others (Semmann *et al.* 2005). Results such as this support the idea that the benefits obtained from acquiring a good reputation can make it adaptive for otherwise selfish individuals to contribute to the common good.

Social punishment

We have noted in this chapter that social punishment of non-cooperative individuals is effective in encouraging cooperative behaviour in other animals, especially in social insects. We humans are no exception and numerous studies, both theoretical and experimental, demonstrate its importance. The subject is highly topical and over thirty scientific papers have been published in prestigious scientific journals since the 1990s highlighting the key role that punishment of selfish individuals plays and has played in the evolution of cooperative behaviour in human societies. It is considered so important that many authors maintain that cooperation in humans could not be sustained (from an evolutionary point of view) in the absence of the social punishment provoked by the negative emotions aroused by non-cooperative opportunists.

One of the studies that has shown this best is by Ernst Fehr, of Zurich University, and Simon Gachter, of St. Gallen University, both in Switzerland. They designed a common goods experiment in which participants had first to participate in six games in which there was no opportunity to punish the non-cooperative players. They then played a further six games in which that possibility existed, although it involved a cost for the punisher. Although player-group membership changed after every game, such that no two persons confronted each other more than once, the percentage of resources assigned to the shared account fell during the six games in which no punishment was possible, but rose during those in which punishing was an option, despite the resulting fall in mean winnings for each player (Fehr & Gachter 2002). These results indicate that people will take advantage of others in the absence of punishment, but that 'learning' to cooperate is stimulated when non-cooperators can be sanctioned.

The act of punishing a non-cooperative individual often involves a cost to the punisher, both in real life and under experimental conditions. The fact that many individuals are prepared to invest time and resources to punish a selfish individual seems paradoxical since the punisher incurs a cost and receives nothing in return, a situation termed 'altruistic punishment'. Two principal explanations have been offered for this behaviour. In the first instance, long-term benefit may result since the egoist may learn to behave well towards the punisher and may cooperate from then on. Secondly, punishing someone who does not behave cooperatively may improve the reputation of the punisher.

Altruistic punishment is a much more complex subject than used to be thought. Important differences have been shown to exist between countries. Moreover it may also happen that the non-cooperators may retaliate by punishing the cooperators, because it is the latter who impose altruistic punishment. A recent study by Benedikt Herrmann, of Nottingham University, UK, and his collaborators used a common goods experiment to compare the effect of altruistic punishment in sixteen different countries and they found significant differences. In those countries where social norms and laws are less strictly applied, non-cooperators punish cooperators just as often as the latter do the former, thus cancelling out the positive effect that altruistic punishment may have on cooperation. The most important conclusion of this study was that altruistic punishment is only beneficial to society if it is accompanied by strict norms of social cooperation (Herrmann *et al.* (2008).

8.5.4. Reinforced reciprocity

The fact that humans are predisposed to be cooperative, as well as the numerous experimental demonstrations that many people are willing to punish non-cooperative or antisocial behaviour even at some cost to themselves, led some to argue that enforced reciprocity is the answer to the evolutionary enigma offered by human cooperative behaviour. Models based on obtaining direct benefits (reciprocity) or indirect ones (genetic benefits; when help is directed at kin) do not apply in such cases, so altruistic punishment of those who do not contribute to the social good may be chiefly responsible for cooperative behaviour in our own species. This idea has attracted some criticism but there is evidence that enforced reciprocity is an adaptation that has evolved through a process of coevolution (see Chapter 9) in which both genetic and cultural factors have interacted. Here, as is so often the case, culture may have provided more rapid and effective solutions to the problems of cooperation within social groups than has natural selection.

8.5.5. Group selection in humans

Nevertheless, the problem posed by human altruism is far from being totally resolved. Models based on the individual benefits of cooperation do not supply a completely satisfactory explanation of the phenomenon, although enforced reciprocity may provide a big step forward. Many authors believe that human altruistic behaviour can only be understood by invoking group selection arguments. We have noted above that group selection might work provided that selection among groups is stronger than individual selection between group members. Darwin was first to put forward one of these arguments namely, that tribes composed of cooperative, loyal and grateful individuals who were always disposed to help and defend their companions would emerge victorious from confrontations with neighbouring tribes. He concludes saying '... and that would be natural selection' (Darwin 1871).

Groups clearly work better when individuals help each other. The problem is that such help may be exploited by non-cooperative individuals, who stand to gain the most. These egoists would be able to devote all their resources, in addition to those provided by the others, to reproducing. They would leave more descendants and so the proportion of cooperative individuals in groups would gradually decline. Darwin was aware of this difficulty and concluded that tribes formed by cooperative individuals would have to exterminate others if they were to persist.

Samuel Bowles, of the Santa Fe Institute, USA, has proposed a scenario in which group selection might have the necessary power to play a major role in human evolution (Bowles 2006). It is based on four characteristics that he considers apply to human behaviour and history: (1) altruistic behaviour is most frequent towards fellow group members, (2) strangers provoke hostility, (3) social mechanisms, such as foodsharing and monogamy, have evolved to reduce competition within groups, and (4) there is a high level of inter-group competition. We shall consider these four characteristics to see whether or not they typically apply to human societies.

We have already examined the first two attributes in Chapter 7 (see Section 7.8.1) where we found that both data and the outcome of experiments confirm that they are indeed characteristic of human societies. The third is an original and very interesting contribution by Bowles. It suggests that many of the cultural norms than pass from generation to generation and that differ between cultures serve to reduce inequality between individuals. This is the case with food-sharing, which is known to be widespread among many existing huntergatherer peoples, who share especially the meat of hunted animals with other group members. The social institution of monogamy also helps to equalise reproductive opportunities among male group members, such that most of them will have quite similar reproductive success. These two factors combine in the fact that both primitive and existing hunter-gatherer societies were and are quite egalitarian when it comes to making decisions and allowing access to resources (see Chapter 7), resulting in a considerable decline in intragroup competition. Such factors act as levellers, according to Bowles, as do redistributive taxes in our own western societies to some extent, reducing the disadvantage of taking part in costly behaviour for the good of the society.

Regarding the fourth characteristic (that there is a high level of inter-group competition), there is also abundant evidence that inter-group conflict has been very frequent throughout the course of human evolutionary history. According to data gathered by Bowles, different investigations reveal very high percentages of violent deaths in a diversity of human societies. Some 13% of skeletons from Stone Age deposits show evidence that death involved a weapon. Similarly 15% of deaths among existing huntergatherers are violent. These are very high rates when we consider that fewer than 1% of persons died violently during the 20th century, notwithstanding the two world wars and numerous other bellicose conflicts. For example, Diamond (1992) records 29 massive instances of genocide between 1492 and1990, each involving the killing of at least

10,000 people and of over a million in eight cases. Some of these genocides brought about the extermination of an ethnic group.

The importance of inter-group competition in the evolution of altruistic behaviour has also been shown via common goods experiments. Mikael Puurtinen and Tapio Mappes, of Jyvaskyla University, Finland, analysed what players contributed to the shared account according to whether or not inter-group competition existed. They found that contributions were much higher when there was such competition than when there was not. The difference was very clear even though the experiment was designed in such a way that the level of inter-group competition was not very high, since it was equalised to the intra-group competition level (Puurtinen & Mappes 2008).

Bowles' four characteristics, that is to say the conditions necessary for group selection to shape human evolution, are thus met. There is reduced competition between individuals within groups and hence a reduction in selective pressures between group members. At the same time there is a high degree of inter-group confrontation, which implies strong selective pressures on groups, given that the most effective groups - those with the most cooperative individuals - will survive and the less effective ones will become extinct. A curious conclusion emerges from all this. The altruistic behaviour that we are so proud of is due in large measure to our belligerence, not something of which we can feel too proud.

Group selection need not be seen as a model that replaces kin selection or reciprocity. All surely have contributed to the evolution of human cooperation in its current form. It seems logical to think that early in human evolution, when small family groups predominated, kin selection may have acted alone. Reciprocity will have gained importance later, as groups became larger and included unrelated individuals, although kin selection will still have operated. Finally, enforced reciprocity and group selection will have begun to play a part as the complexity of human societies increased as groups became very large, although kin selection and both direct and indirect reciprocity have endured. The factors that most influenced the progressive increase in the complexity of human societies were probably the advantages of division of labour and the need to suppress thieves and looters.

8.5.6. Is human behavior genuinely altruistic?

A genuinely altruistic act brings no benefit to the donor, as highlighted in Box 8.1. Nevertheless, we have seen that much behaviour is altruistic only in appearance since the donor gets some future benefit, whether direct or indirect. To answer 'Yes' to the above question, an act must be entirely voluntary and confer no benefit to the donor.

Most persons would offer a resounding 'Yes' to such a question. They would do so not only regarding activities of religious societies, or of those that aim to help a particular group, but also those of scientific societies, sports groups or neighbourhood associations. However, in accordance with the predictions of evolutionary theory, a truly altruistic act cannot spread through a species because it would be costly without providing any benefit. The sole possible alternative is that it might benefit the group to which the altruist belongs (group selection, see Section 8.5.5). However, ultimately, except on the exceptional occasions in which the altruist dies as a result of his altruism, the benefit of the group is also a benefit for the donor and his relatives since they gain if their group does well. Even such behaviour as blood donation, which has been held up as an example of true altruism, turns out to provide a benefit since being known to be an altruist improves one's social reputation.

An important point must be clarified. The above does not imply that a person who gives blood, belongs to an NGO or who leaps into the water to save a drowning child behaves in that way in a conscious attempt to secure the benefits that will come to him or her. As we have often said, we almost always make decisions without being aware of the evolutionary basis for our actions. Within sporting clubs and neighbourhood groups, those individuals who take up committee posts and who work for their society are probably convinced that they are doing so for the good of others. Nevertheless, there is only one evolutionary explanation for why such behaviour persists and is widespread throughout the population: because it brings benefits, or has brought them across evolutionary history, to the individuals that behave in that way or to their relatives, whether directly or indirectly, within the society to which they belong.

Chapter 9. Interspecific relationships

9.1. Introduction

The most common relationships among individuals are those that occur between members of the same species, especially gregarious ones that live in more or less large groups. Nevertheless, individuals of different species may also interact in a diversity of ways and to a highly variable extent. Interspecific interactions range from simple coexistence in the same habitat without mutual interference to an intimate, permanent relationship in which individuals of one species live within the body of another. Two species may even combine to form a single organism such that it may be very difficult or impossible to tell them apart (as occurs in lichens, which are formed by a fungus and an alga).

An interspecific interaction between two species may benefit both of them ('mutualism'), may benefit one of them but have no effect on the other ('commensalism') or may benefit one and be harmful for the other ('parasitism'). This classification on the basis of costs and benefits has been used for decades. More recently, however, the list of interactions in which one species benefits at the cost of another has been expanded and the term 'antagonistic species' is now used to encompass them (see Box 9.1). Such classifications are always helpful and instructive since they assist our understanding of the concepts involved. However, the boundaries between different types of interspecific interactions are highly diffuse. For example, the interaction between two particular species may range from mutualistic to commensal to antagonistic. Moreover, some concepts, mutualism in particular, remain unclear. There is clear evidence that mutualists may on occasion harm their guests, sometimes considerably, questioning if they really are mutualistic. For example, those ants that, in theory, care for aphids in exchange for the chance to feed on their honeydew (the liquid feces produced by aphids), quite often kill and eat the aphids themselves. The oxpeckers, birds of the genus *Buphagus*, which remove ticks and other external parasites from the hides of medium-sized and large African mammals, may also peck at any wounds they find, impairing the healing process or even making the injury more serious because that facilitates consumption of blood produced by the mammal. A final example of this type concerns one of the most noteworthy of mutualistic relationships, that between flowering plants and their pollinators. Such plants may devote up to 40% of the energy they acquire to make nectar. Rather than mutualism this resembles a form of exploitation in which payment for service is obligatory.

We shall first consider an example that confirms what we have just stated and that establishes some of the most important theoretical bases of this chapter.

9.2. The relationship between a plant and its principal pollinator: coevolution

The prairie star (*Lithophragma parviflorum*) is a North American saxifrage whose chief pollinator is the moth *Greya politella*. Pollination by these moths does not involve inserting the head into the flower to take nectar or pollen, as usually happens with most insect pollinators. Instead, it occurs when female moths insert their abdomens in order to lay their eggs inside the flowers. When the caterpillars hatch they feed on the developing seeds, devouring some of the hundreds that develop in each capsule. In other words, these moths both benefit and harm the plant by pollinating it. It is likely that the interaction between these two species probably began as parasitism by the moths, but as these lay their eggs they pick up pollen on their abdomens, which is then transferred to other flowers visited. Thus flowers with suitable morphology for this kind of pollination to occur derived a benefit from the parasite. In due course natural selection would have favoured those plants whose floral structure facilitated effective pollination instead of those whose morphology did not do so. Thus a coevolutionary process leading towards mutualism took place (Box 9.2). However, there would also be selection for those plants that defended themselves from being parasitised. They may have done this, for example, by selectively aborting those capsules that contained seed-eating caterpillars, quite a common event in plants subject to this type of parasitism. This would allow the plant to avoid investing resources in seeds that caterpillars would eat. Such a situation would also lead to a coevolutionary process but one that resulted in antagonism (if a plant develops defences, parasites may produce counter-defences). A process of this kind is known as a ‘coevolutionary arms race’ (see Box 9.2).

INTERACTIONS	SYSTEMS
Indifference: two species coexist in the same habitat without interfering in each other's lives	
Mutualism: Both species benefit from interacting with each other	Pollinator-flowering plant Seed/fruit disperser-plant
Commensalism: One species benefits without having either a positive or a negative effect on the other	
Antagonism: One species benefits from the interaction but at some cost to the other species	Coevolution between competitors Predator-prey Plant-herbivore Plant-pathogen Kleptoparasite-host External parasite-host Internal parasite-host Parasitoid-host Brood parasite-host

Box 9.1. Classification of interspecific interactions on the basis of their outcomes for the two parties involved | It is important to understand that an evolutionary arms race always depends on the characteristics of the other individuals in the population. For example, in a predator-prey relationship in which the success of the hunt or the getaway depends on speed, the arms race operates since predators capture the slowest prey, which favours breeding by the fastest individuals. In this way, the speed of flight from predators increases generation after generation. The same argument applies to the predators given that only the fastest get to leave descendants, which also leads to increasing speed on the part of the predator. What matters is the relative biological efficiency of the individuals concerned, given that the quality of each must be judged against that of all the others. This idea may not seem obvious so in order to explain it to my students I tell them a story that I read somewhere many years ago, which makes it very clear. Two hunters are out of ammunition when a wounded bear goes for them. Straightaway one of the hunters bends down to do up his bootlace. The other hunter, astonished, asks 'Why are you wasting time? That bear can run faster than you'. The other hunter replied: 'That may be so but I don't need to be able to outrun that bear, I just need to run faster than you'.

Coevolution: The development of reciprocal changes in interacting species brought about by natural selection. It is insufficient that changes should occur in only one of the species. To be considered coevolutionary, changes must occur in both, in response to the selective pressure exerted by each species upon the other.

Arms race: The most important coevolutionary model and the commonest between antagonistic species. It is characterised by the evolution of successive adaptations and counter-adaptations in the interacting species, which give rise to an escalation that may have different evolutionary outcomes, including the disappearance of one of the species.

Other important models of coevolution:

(1) Coevolutionary alternation.
(2) Competitive character displacement.
(3) Expansion of mutualistic relationships leading to the formation of new species.
(4) Coevolutionary diversification.
(5) Escape-and-radiate coevolution.

Box 9.2. Coevolution and arms races. After Soler (2002)

John Thompson and Bradley Cunningham, respectively of the Universities of California and Washington, USA, carried out an excellent study of the plant/moth interaction referred to above, involving 12 different populations in the United States (Thompson & Cunnigham 2002). The moth is quite specialised and depends almost entirely on the prairie star in order to feed and reproduce. The plant, however, is less dependent on the moth since it may also be pollinated by other insects, which do not eat its seeds and so would seem to benefit it more. Thus, in populations where other pollinators are more frequent, the plant is less dependent on this particular moth species (*G. politella*) and, depending on the relative abundance of the two distinct types of pollinator, the interaction between plant and pollinator may be mutualistic, commensal or antagonistic.

The investigators determined to what extent the prairie star depends on *G. politella* for pollination, after studying nearly 20,000 flowers. They examined the flowers and determined the probability that their seed capsules developed seeds or were aborted, according to whether or not they contained moth eggs. In four of the 12 regions, pollination and egg-deposition by the moth had no effect on floral development, i.e. there was a commensal relationship in those four populations that benefited the moth without hurting the plant. In four other populations, the plant depended entirely on the moth for pollination, and the moth depended on the plant for food and for deposition of its eggs. Here the capsules that developed seeds were twenty times more likely to contain moth eggs than to be aborted (although the plants aborted up to 60% of their flowers, they 'respected' those that contained moth eggs and only aborted 3% of them). These four populations may be considered coevolutionary hotspots (see Box 9.3) since they had a mutualistic relationship with the moth in which the interaction was direct and very powerful. There was clearly an antagonistic relationship between the plants and the moth in the four other prairie star populations. Here the plants selectively aborted flowers that contained moth eggs. These populations too may be considered coevolutionary hotspots, in this case antagonistic ones.

The study thus showed that populations subjected to distinct selective pressures may give rise to different coevolutionary outcomes - commensalism, parasitism or mutualism - resulting in geographical variation in both the intensity and in the direction of the coevolutionary process, which has given rise to what is termed the 'geographic mosaic theory of coevolution' (Thompson 2005; see Box 9.3).

Geographic mosaic theory of coevolution is based on three points:

(6) The selective pressures affecting a particular interaction will not be the same in different geographical zones. The characteristics of the interacting species may dif-

fer between zones and different evolutionary outcomes may result depending on the strength of the selective pressures acting in each zone.

(7) Due to (1), there will be zones in which coevolution is marked (hotspots) and zones in which it is scarcely perceptible (coldspots).

(8) Gene flow resulting from movements of individuals between populations has an important influence on theoutcome of interactions.

Conclusion: species coevolve within a mosaic of coevolutionary hotspots and coldspots. This results in complex spatial or geographical patterns of phenotype selection that are directly influenced by gene flow.

Box 9.3. The basis and key points of the geographic mosaic theory of coevolution. After Thompson (2005).

9.3. The origin and evolution of interspecific interactions

Although many kinds of interspecific interactions exist, Darwinian logic suggests the hypothesis that all of them may have had a similar origin, the relationship being initiated by one species that derives some benefit from the other. It would be incomprehensible for a species to begin a relationship favouring another species without obtaining anything in return, since incurring a cost without a corresponding benefit would be eliminated by natural selection. A pollinator visits flowers to obtain food, not to benefit the plant. The general rule then is that interspecific interactions began as an attempt by one species to take advantage of individuals of another. How then is it possible for an interaction that began as an exploitation to evolve towards such different situations as mutualism or parasitism? It is now accepted that the evolution of coevolutionary interactions depends on the factors that influence it, affecting both virulence (the damage done by a parasite to its host) and infectiveness. The first of these factors is the mechanism of transmission, which may be vertical or horizontal. The second is the duration and/or the intensity of the interaction (Futuyma 1998).

A mutualistic or parasitic organism, or its descendants according to its life cycle features, needs to be able to transfer to another host. Its reproductive success will not depend on the number of eggs that it lays within its host, but on the success that the descendants of those eggs have in reaching other hosts. Such transmission may be vertical (direct transfer to all the host's descendants) or horizontal ('jumping' to other individuals in the population of the host species). When transmission is vertical, given that the organism's reproductive success is directly dependent on that of the host, natural selection may be predicted to favour those individuals that least prejudice their hosts' growth or reproductive success, a situation that favours mutualism. In contrast, where transmission is horizontal, the interaction may involve greater virulence, since the organism's reproductive success is not directly dependent on that of the host and instead will increase the more resources it derives from the host, causing it more harm; a situation that favours parasitism.

The intensity and duration of interspecific interactions also play an important part. Where it is lifelong, we can predict that a viable strategy for a parasite will be to exploit its host only moderately and even to help it where possible (mutualism). On the other hand, it may be that the interaction is less intense and involves only sporadic visits by the parasitic or mutualistic organism to its host. In such circumstances the reproductive success of a parasitic organism depends neither on the host's survival nor on the host's own reproductive success, so the parasite will tend to extract as many resources as possible from the host for the lowest cost possible (parasitism).

9.4. Mutualism

Mutualistic interactions are very common. In fact, it may be said that nearly every species on earth is involved in at least one such interaction. For example, most multicellular organisms, and especially the vertebrates, shelter a multitude of microorganisms in their guts and these give the host access to certain essential nutrients that it could not otherwise obtain.

Mutualistic species may also obtain three other kinds of benefits, always in exchange for food. They may achieve the transport of something essential to them, as seen when pollinators convey pollen from one flower to another or when animal species disperse plant seeds. They may also receive protection from predators, as occurs in those hermit crabs that place one or two sea anemones on their shells. Lastly, they may benefit from having their body surfaces and mouths cleaned, as done by certain cleaner organisms to larger animals, both on land and in the sea.

It is evident in all these cases that the basis of mutualistic interactions is the benefits that are obtained. Nevertheless, given that getting benefits is the object, such interactions are open to deception and exploitation, since natural selection will favour those individuals that succeed in obtaining the greatest benefit at the lowest cost. For example, some pollinator hummingbirds may cut through flowers in order to access their nectar more easily, although the plant does not then benefit from pollination. Some plants have evolved strategies that allow them to deceive pollinating insects by offering them nothing in return. For example, numerous orchid species imitate the olfactory or visual cues of the females of certain bees or wasps in order to attract the males, which pollinate the flowers when they try to copulate with them. For this reason they are known as bee orchids. Deception is costly since it requires an expenditure of time and energy. Flowers have apparently not evolved any defensive mechanisms against the flower-piercing beaks of hummingbirds, but male bees deceived by bee orchids have developed a defence. Manfred Ayasse, of Vienna University, Austria, and his collaborators have shown that this defence happens with males of the solitary bee (*Andrena nigroaenea*) that are deceived by the early spider orchid (*Ophrys sphegodes*), a species whose flowers produce a complex scent with more than a hundred chemical components. The males are capable of learning each flower's scent during their pseudocopulation and they recognise them when they revisit the plants. In this way, they avoid wasting more time by copulating with the deceiving orchids (Ayasse *et al.* 2000). Thus, due to the frequency of attempted deception in mutualistic systems, mutualism may also be defined as reciprocal exploitation (Futuyma 1998).

A curious example of deception merits detailed consideration. The bluestreak cleaner wrasse (*Labroides dimidiatus*) is a coral reef fish that removes and eats parasites from the bodies of other fish. Client fish come to the wrasses' cleaning stations, when they need their services, but the relationship is not straightforward since the cleaners may also deceive the clients by consuming their protective surface mucus instead of their parasites, doing more harm than good. Natural selection might thus be predicted to have favoured some defensive mechanism against this deception. Redouan Bshary, of Neuchatel University, Switzerland, and Alexandra Grutter, of Queensland University, Australia, have shown by experiment that indirect reciprocity (see Chapter 8) exists between this wrasse and its clients, something very common in humans, but not otherwise known in any other animals. They created situations in which a client was serviced by a wrasse either on its own or in the presence of another watching client, with some fascinating results. Clients often waited and watched while the wrasse attended to other fish. It was found that they waited longer for their turn next to a known cooperative wrasse than next to one whose degree of cooperativeness was unknown because they had not previously watched it. Furthermore, wrasse ate parasites rather than mucus more often when they were being watched by other clients. These results show that the cleaners behave as do humans (see Chapter 8): they are less selfish mainly when other clients are watching, which confers the wrasse with a good reputation that will allow it to get more clients (Bshary & Grutter 2006).

We humans are no exception to the universality of mutualism as demonstrated by the abundant microorganisms in our guts that help us to digest our food. Among other associations involving humans, many authors have long regarded our relationship with the animals that we have domesticated and the plants that we cultivate also to be mutualistic. They are indeed so from a coevolutionary point of view since such species gain enormous reproductive success whereas we have benefited to such an extent that the abundant resources resulting from the relationships permitted the enormous geographical expansion of our species and the emergence of the most important civilisations of Antiquity (see Chapter 7). However, some authors who take an ethical stand do not regard these relationships as mutualistic since although we have certainly favoured the reproduction of domesticated species, for the most part we have done so in order to eat them and hence the relationships are exploitative. Nevertheless, we must regard the relationships as mutualism from a coevolutionary viewpoint, given that the interacting species reproduce more effectively thanks to their relationship. The situation of our domesticated species is very similar to what occurs between leaf-cutter ants and the fungi that they cultivate for food (see Chapter 8 for a detailed account), and that relationship is regarded as an outstanding example of mutualism.

Our relationship with dogs and cats is generally acknowledged to be mutualistic. By and large we do not eat these carnivores, but we have had a mutualistic relationship with them throughout our history. We provide them with food and shelter. In turn, dogs provide a great variety of services, including assistance with hunting, defence and livestock herding and also companionship. Cats have helped us to control rats and mice effectively, species that have caused serious damage to our food stores since time immemorial.

There is another, behaviour-based, mutualistic relationship in which our species takes part. The greater honeyguide (*Indicator indicator*) is a small bird that feeds largely on honeycombs, consuming the honey, bee larvae and wax. However, it has difficulty in gaining access to many of the hives that it finds and so needs help from other species that can extract the honeycombs from their hiding places. An interaction with this purpose has been described involving the bird and either of two mammal species, the ratel or honey badger (*Mellivora capensis*) and human beings. When the honeyguide finds a hive that it cannot access, it searches for a ratel or a person and, when it finds one, it makes a characteristic sound. This indicates that the mammal should follow the bird. When the ratel or person extracts the honeycomb, the honeyguide eats the remains. There has been no serious study of the interaction between the honeyguide and the ratel, but its interaction with human beings has been examined in detail. H. A. Isaac, of the National Museums of Kenya, and H.-U. Reyer, of the Max Planck Institute for Behavioral Physiology, Germany, found that both species benefit. When humans look for honeycomb without the birds' assistance, they take 8.9 hours on average to find a hive, but only 3.2 hours on average when guided by the bird. The honeyguide benefits greatly from human assistance since 96% (178 of 186) of the honeycombs that they showed to humans would not have been accessible to the birds without help from human tools (Isack &Reyer 1989).

9.5. Commensalism

It is rare that two species interact such that one benefits without prejudice to the other, most probably because the system is less stable. If the interaction is truly innocuous for the non-benefiting partner, it will not develop any defensive mechanisms and the benefiting party may then tend to increase what it takes at minimum cost to itself, making it likely that the relationship will develop into a parasitic one. Basically, it is hard to imagine that a species may benefit from another without some cost to the latter, since mere disturbance may be harmfull. For example, consider the numerous cases in which small tropical spiders live on the webs of larger species (sometimes 100 times larger) and eat tiny prey items that the large spiders do not notice. This may well be a case of commensalisms, but very often the little spiders also 'help' to eat the larger prey captured.

Another often-mentioned example of commensalism involves small bird species that place their nests within the nests of much larger birds. Very often species such as house sparrows (*Passer domesticus*) and starlings (*Sturnus* sp.) build their nests within the massive stick nests of eagles, vultures and other large birds, such as white storks (*Ciconia ciconia*). I saw a large stork nest some years ago that was also inhabited by several pairs of sparrows, several pairs of starlings and a pair of jackdaws (*Corvus monedula*). The benefits to the small birds in these situations are considerable since a large stork or raptor nest offers considerable shelter and the tenants also benefit from the protection of the owners of the large nest, which will drive away any medium-sized predators that may approach.

9.6. Antagonism

Antagonistic relationships are the commonest and most varied of interspecific interactions. They are characterised as such since only one species benefits whereas the other is damaged. These relationships favour coevolutionary arms races since the victim species tends to develop adaptations that prevent exploitation whereas the exploiter species tends to develop counter-adaptations that overcome the victims' escape or defence strategies. What thus most often happens is that the escape and defence abilities of the interacting species improve over successive generations (arms races; see Box 9.2). The clearest example involves predators that chase down their prey. The fossil record plainly shows how anatomical adaptations have enabled increased speed in both predators and prey throughout the course of their evolution.

Antagonistic relationships have also led to the development of unusual and surprising defensive adaptations by the exploited species. We shall consider two examples: another predator-prey system involving hornets (genus *Vespa*) and their prey, the honeybees (genus *Apis*), and also some plant-herbivore interactions.

Hornets are immune to attack by bees since they are much larger and their chitinous exoskeleton provides effective protection against bee stingers. Hence a few dozen hornets may attack a hive and kill thousands of bees with impunity. Such a situation might be seen as an arms race that the hornets have won and that, in time, will lead to the disappearance of the bees. Nevertheless, some bee populations have evolved defence mechanisms that even the most imaginative investigators could not have predicted. For example, Masato Ono and his collaborators at Tamagawa University, Japan, (Ono *et al.* 1995), discovered that the Japanese honeybee (*Apis cerana japonica*) has developed an effective defence against its formidable predator, the Japanese giant hornet (*Vespa mandarinia japonica*). When the hornets attack, many bees gather at the hive entrance. Once a bee succeeds in getting hold of a hornet, hundreds of other bees cluster around the invader to form a ball, using their body heat to increase the temperature to as much as 47°C. This proves lethal to the hornet but not to the bees. In short, the bees, being unable to injure their enemy with their stings or mandibles, have developed a way of 'roasting' them alive. More recently, Alexandros Papachristoforou, of the Aristotle University, Greece, and his collaborators (Papachristoforou *et al.* 2007) have discovered that their study population of the Cyprian honeybee (*A. mellifera cypria*) kills oriental hornets (*V. orientalis*) in another way. They also enclose hornets in a ball of bees but they asphyxiate them, rather than 'roast' them.

Where plant-herbivore systems are concerned, plants cannot move and thus cannot flee or hide from their enemies. This is very probably why collectively they have developed over 10,000 chemical compounds that serve as poisons or repellents against attack by herbivores or pathogens. Some of these compounds form part of some quite ingenious defence mechanisms. For example, when certain plants are under attack by insect larvae, they release particular substances that attract the predators or parasites that attack those larvae (Turlings *et al.* 1995).

Stranger still is the finding that certain plants produce defensive substances that make those herbivores that feed on them become infertile. For example, cotton plants (genus *Gossypium*) produce gossypol, a substance that causes infertility in such diverse groups as insects and mammals. It even has a significant effect on humans, as was found in China, where the birth rate dropped drastically across entire regions when cotton oil was used for cooking, and rose again when the oil was no longer used. The effect of gossypol is to prevent sperm manufacture (Coutinho 2002).

As noted in Box 9.1, antagonistic interactions are highly diverse and occur in a great variety of systems. This chapter would be overlong were we to consider them all. Therefore we shall next focus on some of the most interesting aspects of parasitism, the type of interspecific interaction that most affects the human species.

9.6.1. Parasitism

Most of the species that inhabit the Earth have parasites and even parasitic species are themselves parasitised in turn by other species. In fact, it has been estimated that over half of all living species are parasitic. For example, the tomato plant (*Lycopersicon esculentum*) is attacked by over 100 different fungal species, as well as by a good number of bacteria and plant-eating insects. We humans are again no exception as we are home for a great many parasitic species, including 30 that are sexually-transmitted from one person to another. Some parasites, such as the mites *Demodex folliculorum* and *Demodex brevis* that inhabit the eyelash follicles and sebaceous glands respectively, are largely inoffensive. Others though, such as the infamous HIV, the cause of AIDS, are highly virulent and may kill us.

Obtaining resources at a cost to others is a highly beneficial strategy, particularly if the exploited individuals lack defence mechanisms, so we may suppose that parasites are nearly as ancient as the first living beings. It is unsurprising, therefore, that some fascinating adaptations have evolved over such a long period, including complex life cycles that require several changes of host species before the reproductive stage is reached (see the example of the fluke *Dicrocoelium dendriticum* described below).

Parasites live and reproduce at their hosts' expense and are then transmitted to other individuals whose ability to survive and reproduce may or may not be greatly reduced to a variable extent, ranging from a negligible effect to death. As in all other living beings, natural selection has also favoured those strategies and behaviours that prove most effective when it comes to leaving descendants. Where parasites are concerned, succeeding in securing hosts for their des descendants is even more important than laying many eggs or producing many offspring. As we have noted, such transmission may be vertical or horizontal, and it is the latter that is usually more damaging to hosts.

It may be expected that when a parasite is at a stage when its life depends on that of the host, it should not harm the host more than absolutely necessary, and may even act to protect its the host. A case in point involves a mite (*Dichrocheles phalaenodectes*) that lives inside the ears of some moth species (Treat 1975). The female mites distribute themselves among flowers where they wait for a moth to come and feed. At that moment the mite climbs up the moth's proboscis and onto its head. After inspecting both ears, the mite installs itself in one of them, breaks the tympanic membrane (destroying that ear) before laying some 80 eggs. Most of these eggs hatch into females that are fertilised by their own brothers soon after they reach adulthood. The males then die in the ear, but the females leave the moth by descending the proboscis when the moth is feeding. The mites then wait on the flower for a new moth in whose ear the cycle may be repeated. The survival of the mites depends on their moths not being eaten by bats, their chief enemies. Natural selection has thus favoured the development of a strategy based on absolute respect for the still-functioning moth ear, since having one operative ear enables the moth to detect the ultrasounds emitted by bats. A second female never settles in the sound ear. If she finds that one ear is already infested the mite will abandon the moth and descend to another flower, to await another host with two intact ears.

Infections are costly to hosts. Even blood parasites, thought by some investigators not to have a significant negative effect since they infect only a small percentage of blood cells, have been found to do real damage that may even affect reproductive success. Santiago Merino and his collaborators at the National Natural History Museum in Madrid, Spain, showed this experimentally in the blue tit (*Cyanistes caeruleus*). Half the females in the study population were injected with an effective medication against blood parasite infections, the other half receiving an equal volume of saline solution as a control. The females were recaptured shortly before the young fledged in order to determine infection levels and the reproductive success of each nest. They found that the treatment had been effective in that the experimental females had significantly fewer blood parasites than the controls. Moreover, more chicks died in the nests of control females than in those of treated females, so that the latter produced a larger number of descendants. The fact that the costs of infection were paid by the chicks indicates that the less- parasitised females were able to devote more time and/or resources to feeding their chicks (Merino *et al.* 2000).

The costs arising from infections have led to natural selection favouring individuals who happened to be able to reduce the negative effects of parasites. Undoubtedly the most widespread of these adaptations is the immune system found in all animals. The 'innate' immune system is activated when a body is invaded by a bacterium, virus or other pathogen, at which time the immune mechanism responds to the threat in a predetermined fashion. However, should the infection persist, a second phase known as the ‘adaptive immune system’ is activated and this develops a specific attack against the pathogen, whose effectiveness improves gradually and establishes a ‘memory’ of the pathogen’s characteristics that is employed in any future encounters.

Infectious diseases in humans

Infectious diseases are caused by pathogenic organisms, which grow and reproduce within living hosts and are transmitted from ill individuals to healthy ones. Most diseases have an infectious origin, the exceptions being those whose origin is hereditary as well as most cancers and those due to vitamins deficiencies or other dietary shortfalls. Even some diseases that were not thought to be infectious have proved to be so. For example, gastric ulcers were attributed to acid build-up in the stomach provoked by stress, but most are now known to be caused by the bacterium *Helicobacter pylori.*

We have already noted that a multitude of parasitic species affect humans. This great diversity has surely been favoured by our gregarious habits, which facilitate horizontal transmission of parasites, but also by the close contact that we have kept with domesticated species. Many of the diseases from which we suffer originated in domestic animals, the various types of influenza derived from domestic fowl being a well- known example. In fact, our diseases are known to include 50 that originated from cattle, 46 from sheep and goats, 42 from pigs and 26 from domestic fowl (McNeill 1976).

The coevolutionary process that has affected the relationships between pathogens and their hosts has given rise to a broad range of infective mechanisms in the pathogens that, in one way or another, counteract the resistance strategies developed by hosts during the course of the interaction. An infectious disease causes symptoms that may allow it to be diagnosed. However, not all symptoms are the result of the pathogens’ attack. Some are instigated by the infectious agent to favour its transmission and others result from the deployment of the hosts’ defences.

Most of the symptoms of infectious diseases provoke discomfort and so medical practice, in addition to trying to overcome the infection, most often by using antibiotics, also attempts to relieve the symptoms, without considering whether these may be adaptive responses to pathogen attack. True, some common symptoms such as fever, lack of appetite, iron deficiency and listlessness may be damaging to the host. Nevertheless, from an evolutionary standpoint we should consider the possibility that they evolved in response to infection because the benefits conferred outweigh the costs. This approach makes sense given that fever is known to inhibit the reproduction of most pathogens, iron deficiency slows bacterial growth, and lack of appetite may ultimately deprive pathogens of resources. In general, these defensive mechanisms may help reduce the reproductive rate of pathogens, which helps the immune system to be more effective in eliminating the infection. Hence, the advocates of the so- called ‘evolutionary medicine’ (or ‘Darwinian medicine’), in which evolutionary theory is applied to the study and treatment of diseases, maintains that it is necessary to keep in mind the long coevolutionary relationship of pathogens and hosts when deciding the best strategy for treating a disease (Nesse & Williams 2000).

The coevolutionary arms race between pathogens and their hosts means that when an effective resistance mechanism spreads within a host population, those pathogens that have some way of overcoming the novel defence will reproduce more and become more and more common over time. When this happens, hosts will once again be under strong selective pressure favouring new defensive mechanisms. This process is of great medical significance since pharmacologists do not generally succeed in eliminating pathogens completely from hosts and so mutants resistant to the drugs used regularly appear. Infection of other hosts by such resistant mutants renders drugs ineffective and enables such pathogens to spread rapidly through the host population. Antibiotic resistance in many pathogenic bacteria has spread in this way. Microorganisms have very high reproductive rates that allow them to produce hundreds of generation within a few hours. Moreover, they are capable of exchanging genes horizontally at random and they have an enormous capacity for mutation, increasing the chances that mutants resistant to particular drugs may emerge quickly.

The development of antibiotic resistance by bacteria is one of the clearest demonstrations of biological evolution and one of the best examples is the evolution of resistance to penicillin by staphylococci (Nesse & Williams 2000). Staphylococci are the bacteria that were responsible in the past for the extremely high mortality rate of persons who suffered severe injury or who underwent surgery. The discovery of penicillin was one of the most important in human history since it was highly effective in destroying staphylococci and so saved the lives of very many people who would otherwise have died. Penicillin was effective against all staphylococci in 1941, but only three years later there emerged some strains of the bacteria that produced enzymes which broke-up penicillin and rendered it ineffective. Nowadays, nearly all staphylococci possess some resistance to penicillin. A new antibiotic, ciproflaxin, which was effective towards penicillin- resistant staphylococci, was developed in the 1980s, but nowadays over 80% of *Staphylococcus* strains are resistant to this antibiotic as well (at least in New York, where the investigation was done). Antibiotic resistance by pathogenic bacteria is now widespread and, given that no new efficient antibiotics have been discovered during the past 20 years, we must accept that this is one of the most serious medical problems.

The brood parasite-host system

Brood parasites practice a peculiar form of parasitism in which the host suffers no direct harm. Such parasites lay eggs alongside those of the host species, thus tricking it into incubating, defending and feeding the young as soon as they hatch. Intraspecific brood parasitism between females of the same species is known, but strictly speaking brood parasites are species that never care for their own offspring but instead always leave them in the charge of other species, the hosts.

This type of interspecific parasitism is rare and only relatively frequent in hymenopterans (chiefly in social species) and in birds. A great diversity of such strategies has been described for different wasp, bee and ant species and these differ greatly in complexity. A typical example involves the cuckoo bees, of which several thousand species have been described. These bees do not build any form of nest or hive. Instead they enter the hives of pollen-gathering species and lay their eggs within cells that the host female (or workers in social species) has already provisioned with pollen. When the parasitic larva hatches it feeds on that pollen and on the larva for which the cell was constructed.

Quite a few ant species are also brood parasites and these make use of very varied strategies. Some behave like the cuckoo bees, but others have more sophisticated and remarkable strategies. For example, the slave-making ants, as their name suggests, enslave the host species to work in the parasites' own nests. This happens with *Rossomyrmex minuchae*, a slave-making ant studied by Francisca Ruano and Alberto Tinaut, of Granada University, Spain. *Rossomyrmex* workers attack nests of *Proformica longiseta* and, after killing most of the defenders, they carry back the larvae and pupae to their own nest. When these develop into adults within the parasite's nest they follow their usual instinct and act as workers in the nest in which they find themselves, thus becoming lifelong slaves of their capturers. They clean and guard the *Rossomyrmex* nest, feed the queen and her workers and look after, guard and feed the queen's descendants (Ruano & Tinaut 1999).

With respect to birds, over 100 brood parasites are known and these belong to five families, although over half are from the cuckoo family, Cuculidae (Davies 2000). This brood parasite-host system provides excellent opportunities for the study of coevolution, particularly in those cases in which the parasites use only one, or very few, host species.

Brood parasitism imposes significant costs on hosts given that, as a rule, only the parasite chick survives in a parasitised nest, a fact that strongly favours of the evolution of effective defence mechanisms by the hosts. In turn, the host defences are costly to parasites so that there is also selection for counter-defences to overcome them. These strong selective pressures have brought about the emergence of adaptations and counteradaptations in all stages of the breeding cycle (before, during and after the laying of the parasite egg and also during the period when the chicks are in the nest).

Prior to laying, the first challenge for a female brood parasite is to find a suitable nest in which to lay her egg, whereas the first line of defence for the host species is to prevent her from doing so. Active nest defence is an effective strategy only when the host species is larger than the parasite, as happens with the great spotted cuckoo (*Clamator glandarius*) and its host the magpie (*Pica pica*), which will chase any cuckoos found near the nest. The cuckoos have responded to this adaptation by developing a more complex laying strategy in which, unlike in other brood parasites, both the male and female cuckoo collaborate. First the female approaches the target nest discretely. The male then approaches the nest conspicuously until the female magpie, or the magpie pair, try to drive it away from the area, providing an opportunity for the female cuckoo to emerge from hiding and lay her egg in the magpie's nest (Alvarez & Arias de Reyna 1974).

Once a parasite egg has been laid in a nest, the most effective way of avoiding the costly effects of parasitism is for the egg to be recognised and expelled. Once such an ability develops, it soon spreads throughout the host population, since the reproductive success of parasitised pairs that can do this is much greater than that of pairs that cannot. Expelling the parasite egg is simple for large hosts, who only have to pick it up in their beaks, but it is a bigger problem for small species whose nests contain the large eggs of a large parasite. When the egg is not too large, they may peck it until they pierce it after which they can then lift the egg and throw it out. Those small species that can recognise a parasitic egg, but cannot remove it, may respond by covering the parasitized clutch with nest material and laying a new clutch on top, or by abandoning the nest and building a new one.

Once a host species has acquired the ability to expel parasite eggs, it may be expected that it will expel those that are most readily recognisable, those most different from its own eggs, whereas those most similar to the host eggs will survive. Mimicry by parasite eggs is thus favoured and in some cases parasite eggs have become very similar in size and colouration to those of the host species (Davies 2000).

Until recently this was thought to be the extent of the arms race between brood parasites and their hosts, something very well documented during the egg stage. Scientists never considered the chick stage since only one case was known in which parasite chicks are recognised (some African waxbills are able to recognise parasitic indigobirds of the genus *Vidua*). In that case, as predicted, the parasite chicks have developed excellent mimicry and are quite difficult to distinguish from host chicks. Nevertheless, there was no known case of a host species that was capable of recognising a cuckoo chick and of expelling it from the nest, even though most cuckoo chicks look nothing like those of their hosts and are often much larger, so that towards the end of their growth period their adoptive parents may have to perch on their shoulders to feed them.

Two recent and fascinating discoveries have revealed that an arms race may also occur during the chick-in-nest stage. Naomi Langmore, of the Australian National University, and her co-workers have shown that one host species, the superb fairy-wren (*Malurus cyaneus*), a small passerine, can recognise and abandon chicks of its specialist parasite, Horsfield's bronzecuckoo (*Chrysococcyx basalis*). Eleven females, out of 29 parasitised nests, stopped feeding the cuckoo chick when it was between three and six days old and abandoned it in the nest. Although the cuckoo chick carried on begging for food in desperation, the females began a new nest and solicited copulations to lay a replacement clutch (Langmore *et al.* 2003).

A discovery by Tomas Grim and his collaborators at the Palacky University, Czech Republic, was even more surprising, given that they worked with the reed warbler (*Acrocephalus scirpaceus*), one of the best- studied hosts of the common cuckoo (*Cucu-*

lus canorus). Their study-area was distinguished by having a much higher percentage of parasitised nests than is usual, and they found that the cuckoo chick was abandoned by the warblers in about 15% of parasitised nests, when it was about 14 days old. They explained this previously undescribed behaviour as a consequence of the cuckoo chick staying in the nest much longer than the warbler chicks do. The most significant and novel aspect of this discovery is that it does not imply visual recognition of the parasitic chick. The warblers simply stop feeding a chick that spends too many days in the nest. Such 'discrimination without recognition' probably helps the warblers since the rule of thumb 'stop feeding chicks after 14 days' reduces the cost of being parasitized.

The manipulation of host behaviour by parasites

Among the most extraordinary adaptations of parasites are those that help them manipulate host behaviour for the parasites' own benefit. These adaptations evolved as ways to help parasites gain access to other hosts, especially by those parasite species with complex life cycles that include at least two hosts, an intermediate host and a final one. As might be expected, in such cases natural selection favours efficient transmission mechanisms. An example involving totally abnormal behaviour by one species involves ants that are parasitised by the fluke *Dicrocoelium dendriticum.* Ants are the intermediate host, the definitive hosts being sheep. The only way in which the parasite can pass from an ant to a sheep is for the sheep to eat the ant. This is normally improbable since sheep are not insectivorous, and ants normally avoid being accidentally ingested by sheep because they keep close to the ground. Remarkably, ants parasitised by *D. dendriticum* change their behaviour and tend to climb to the highest tips of grasses (Spindler et al. 1986). How do the parasites make the ants behave in this way? A parasitised ant contains some 50 flukes and one of these travels to the ant's brain and, by some unknown means, induces the ant to climb up to the top of the grass where it grips the stem strongly with its mandibles. In this way the ant remains anchored until it is eaten by an herbivore. If the latter is a sheep, the parasite will have fulfilled its objective.

Another remarkable example involves the parasitic barnacle *Sacculina granifera*, which uses the blue swimming crab (*Portunus pelagicus*) as its host. Jeffrey Shields and Fiona Wood, of the University of Queensland, Australia, found that if the parasitised crab is a female the changes occasioned by the parasite are not very striking. However, should the crab be a male those changes are enormous. As the parasite grows it destroys the male crab's gonads and thus reduces its androgen levels. This results in the male crab's body taking a female form. Moreover, as the parasite continues to grow, hanging between the crab's cephalothorax and abdomen, the host progressively resembles a female laden with eggs. Furthermore, the parasite also secretes a feminising hormone that induces maternal behaviour. The male crab's behaviour changes radically as a result of these changes. It becomes less aggressive and more tranquil, and it avoids confrontations with other males. It also cleans itself more often, as do female crabs that are looking after eggs. These changes help both the crab and the parasite to survive. The parasitised male crab digs a shallow depression in the sand, similar to that dug by females to favour the development of their young. In this case the male crab clearly cannot lay any eggs (not only is it not a female but also it has been castrated), instead the depression favours the reproduction of the parasite, and the male crab takes charge of caring for the parasite's offspring (Shields & Wood 1993).

A less subtle but more direct way of manipulating host behaviour exists, explained by what is known as 'the mafia hypothesis'. As happens with human gangsters, the behaviour involves compelling individuals of the same species or of another to do what benefits the mafioso. Such behaviour was first demonstrated in great spotted cuckoos as they exploited their chief host species, the magpie. In our study area in Guadix, Granada, Spain, we found that when the cuckoos parasitize a nest, they revisit it some time afterwards. If they then find that the magpies have expelled the cuckoo egg, the cuckoos take reprisals and smash the magpie eggs, or kill any magpie chicks that have hatched (Soler *et al.* 1995). We experimented by removing cuckoo eggs from a number of parasitized nests, with the result that these suffered more predation than did control nests from which cuckoo eggs were not removed. By replacing some of the magpie eggs by plasticine models we were able to prove that they were pecked by cuckoos. These results together strongly support the mafia hypothesis. The cuckoos' behaviour, despite having already lost their eggs, is beneficial to them since when magpies lose a clutch at the start of the breeding season, they often lay a replacement clutch, thus providing the cuckoos with a second chance for parasitism. Also, if the reprisals are effective, they may make the affected magpies learn the lesson of the mafia behaviour: it is better to accept the cuckoo egg and try to raise some magpie chicks at the same time, than to remove the parasite egg and lose the whole clutch once again.

Mafia-type behaviour has been identified in other types of interspecific relationships, chiefly in hostparasite ones, but also in a mutualistic relationship, specifically that in which ants care for and defend aphids in exchange for their sugary secretions. It has been known for some time that aphid-tending ants sometimes kill and eat some of the aphids. Sakata (1994) discovered that the ants do not kill aphids at random, but instead selectively eliminate the ones that produce sugary secretions in lower quantities and of lesser quality. Their behaviour in penalising the less collaborative aphids allows the ants to succeed in improving the production of the sugary juices on which they feed. This is quite similar to the way in which humans, since ancestral times, have selected breeding animals for their domesticated livestock.

Regarding host-parasite relationships, a good example of mafia behaviour is the amply demonstrated fact that many of the bacteria that cause infectious disease in humans become more virulent in the face of the host's defensive mechanisms. In particular, the decline in blood iron levels that normally accompanies fever provokes such bacteria as *Escherichia coli*, *Vibrio cholerae* and *Pseudomonas aeruginosa* to produce harmful toxins and they increase their production as iron levels fall (Nesse and Williams 2000). This penalty makes the host's defence mechanism less effective.

Chapter 10. Animal communication and human language

10.1. Introduction

Communication is a fundamental feature of animal behaviour. It is naturally of greatest significance in social species but it is also very important to all other animals. Courtship of females by males, confrontations between rivals, territorial advertising, begging behaviour of young animals, and, indeed, most of the other behaviours described in this book all involve communication. Because many of the factors that influence survival and reproduction involve communication, it is not surprising that it plays an important and often striking role in animal behaviour and in the adaptations of most living things.

Contrary to what many believe, communication is not confined to animals, but also occurs in many other organisms. For example, plants have been shown to emit signals by which they are able to communicate with other plants and with other organisms associated with themselves, such as pollinators, herbivores and some of the enemies of those herbivores. An interesting demonstration of this has been provided by Genichiro Arimura, of the Bio-oriented Technology Research Advancement Institution of Tokyo, Japan, and his coworkers, who showed that communication occurs between plants of the same species. When the Lima bean (*Phaseolus lunatus*) is attacked by the two-spot spidermite (*Tetranychus urticae*), the plant emits volatile compounds into the air that elicit an anti-herbivore response in neighbouring plants. They showed this experimentally by infecting some plants with 100 spider-mites over several days. When plants detected the compounds liberated by infected neighbours, they activated five defensive genes that swiftly brought about an effective anti-mite response, since from that point the plants were less susceptible to spider-mite attack. The response was quite specific because volatile compounds liberated during the control treatment, involving physical damage to the plants, did not activate the defensive genes (Arimura *et al.* 2000).

The best studied plant communication system is that involving plants and the enemies of their herbivores. For example, Consuelo De Moraes, of University of George, USA, and her co-workers showed that plants as different as tobacco, cotton and maize emit different volatile compounds according to whether they are attacked by caterpillars of the tobacco budworm (*Heliothis virescens*) or those of the corn earworm (*Helicoverpa zea*). The fact that the signal emitted differs according to which moth species is attacking allows a parasitoid species, the red-tailed wasp (*Cardiochiles nigriceps*), to detect when the attacker is the species (*H. virescens*) in which it lays its eggs. The specificity of these signals, and the fact that they are produced by very different plants, shows that communication between plants and their herbivore enemies is quite complex (De Moraes *et al.* 1998).

A capacity for communication is also possessed by many microorganisms. For example, many bacteria detect changes in their population densities and they respond by releasing certain substances that act as signals to neighbouring bacteria. Such 'behaviour in unison' regulates much microbial activity. For example, it allows pathogenic bacteria to coordinate attacks on their hosts (see review by Crespi 2001).

10.2. What is meant by communication?

Consider the following scene, which is based on studies by William Cade, of Brock University, Canada. We are observing an overgrown field in North America in which a field cricket (*Gryllus integer*) abounds. During the courtship season, we can hear the loud chirps (stridulations) of the males. Closer observation reveals that some chirping crickets are moving about, others are stationary but chirping and yet others are making no noise but are positioned near the stridulating males. As we continue to watch, as well as noticing some flies overflying the crickets, we notice that when a male stops chirping another previously silent one may start up.

Among other things, this scenario reveals a process of communication. The stridulating crickets (senders) are emitting signals (chirps) that are heard by other individuals (recipients) that change their behaviour on receiving the signals. If we observe the silent individuals closely we see that some of them are females, which approach the chirping males, but others are males that remain stationary near to the chirpers in order to intercept and copulate with some of the females attracted by the stridulations (satellite males; see Chapter 5). Thus, the sounds crickets make bring about behavioural changes in the individuals that receive the signals.

Communication always involves transmission of information. What information is transmitted by stridulating male crickets? As we saw when we considered mate-seeking and courtship (see Chapter 4), in such situations the males are offering information on their physical condition. In this particular case, the fittest males emit louder, more frequent chirps than do those that are in poorer physical condition. The former tend to attract more females but they also attract more satellite males, which try to copulate with the females that the stridulators attract (Cade 1979).

Bearing this in mind, how may communication be defined? It might simply be said to be the transfer of information between individuals but such a definition is inadequate. Not only is it far too broad but also it does not lend itself to an evolutionary perspective. For example, when a mouse or a lizard moves through the leaf litter it makes a rustle that informs where it is and that may allow a predator to find it. This clearly cannot be termed communication, since such a sound happens simply as a result of the animal's movement and not because it has evolved to provide information that may cost it its life. A better definition then is that communication is a transfer of information by means of signals that have evolved to that end (see Box 10.1).

The above definition may seem excessively 'selfish'. As a rule, we humans are unaware of the manipulative nature of communication, i.e. that when we are speaking to someone we are constantly trying to manipulate his or her behaviour to our advantage. Of course it is not as simple as that because cooperative communication also exists (see below) and is frequent between friends and, above all, between close relatives or mates. Nevertheless, in most cases, our communication complies with the proposed definition, even if we are unconscious of it. I ask incredulous readers the following question: 'Do we tell everybody everything we know?' Clearly, we do not. We tell some people some things and other people other things. It is all very complicated since it depends on the type of relationship that we have with each person and his or her association with the information being given. Furthermore, when we are dealing with something personal that we want to keep private, we will only tell it to those with whom we are most intimate. On the other hand, when it is something that we want widely known, because it helps a friend (or ourselves, whether directly or indirectly), or because it disparages an enemy, we are happy to tell it to the biggest gossips we know, precisely because we know that they will tell everybody. Moreover, we relate things differently according to whom we are speaking and according to the effect that our story is having.

- **Components of communication**: signals, senders and recipients.
- **Interaction between components**: sender ^ signal ^ recipient.
- The process is often more complex since (1) several individuals may be involved, and (2) the same individual may be both a sender and a recipient, either simultaneously or in turn.
- All communication involves a transfer of **information**.
- **Definition of communication**: The process by which senders use signals developed through natural selection to modify the behaviour of recipients.

Box 10.1. Fundamental concepts and definition of communication. Chiefly after Krebs & Davies (1993).

10.3. Signal types in relation to the dominant senses

Any type of sensory system may be used for communication provided the sender is capable of generating the signal and the recipient can receive it. Signals with very different characteristics are produced according to the systems involved (see Box 10.2). For example, auditory signals have a high ability to pass around physical barriers but they cost a great deal of energy to produce. Visual signals convey information very quickly but are obstructed by obstacles and, as is also true for auditory signals, they have the disadvantage of possibly attracting predators. Chemical signals may be highly persistent and, as a rule, they are very cheap to produce, but they cannot readily be changed. Finally, tactile signals have the advantages of being cheap to produce and not attracting predators, but they have only very short transmission distances, and they are blocked by obstacles (see Box 10.2 for more details).

Signals are shaped by the sensory equipment of organisms and by the medium that they inhabit. For example, most birds are diurnal and hence have very good eyesight, so they have evolved numerous signals that rely on showy, colourful adornments. In contrast, most small mammals are nocturnal and have an excellent sense of smell, so scent is most important to them.

10.4. Signal transmission and environmental conditions: acoustic signals in birds and mammals

Signal effectiveness often depends on environmental conditions, both atmospheric and those of the habitat in which a species lives. The best-studied examples of how environmental characteristics influence signals relate to acoustic communication, the type most used for longdistance communication (reaching over 3 km in some bird species, 2 km in some grasshoppers and over 100 km in certain whales). Classic studies in the 1970s revealed that environmental characteristics strongly influence the evolution of acoustic signals. Such signals become attenuated and degraded to varying degrees over long distances and hence natural selection favours those that are easiest to detect and to recognise, i.e. the most resistant to such changes. In accordance with this adaptive hypothesis (see Chapter 2), it has been shown, not only in birds but also in mammals (especially primates) and some insects, that different species produce sounds with a structure that is optimal for transmitting information in the habitats that they inhabit. Various predictions arising from this hypothesis have been confirmed in numerous studies involving many different species. For example, the acoustic signals of different species travel better in their typical habitats than in other places, i.e. they are most effective in the environment in which they evolved.

Another observation that supports the adaptive hypothesis is that some species have two or more different call types that they use for long-distance or short-distance communication, each being best structured for effective transmission. For example, the pygmy marmoset (*Cebuella pygmaea*) is a tiny South American primate that has three different contact calls used for short-, medium- or long-distance communication. The structure of each of these calls has been found to be optimum for effective transmission at each of these distances within the species' habitat (De la Torre & Snowdon 2002).

Long-distance acoustic communication is, in general, quite costly, not only because it requires a lot of energy but also because it may attract predators. Thus, an adaptive hypothesis lead us to predict that animals should have evolved the ability to optimise signal efficiency by modifying sound intensity according to how far away the recipient is. We humans reduce the volume when the recipient is not too far away, thus saving energy and reducing the chances of being heard by a predator or a competitor. The possibility that other animals too might do this had not been considered because it was thought to derive from the high cognitive ability of our own species. Nevertheless, Henrik Brumm and Peter Slater, of St Andrews University, UK, have shown that a small bird, the zebra finch (*Taeniopygia guttata*), is capable of adjusting its song to its distance from its recipient. They performed a laboratory experiment in which a caged male was presented with a caged female at four different distances. The male increased its song volume, and hence the effort involved in sound production, in accordance with the increase in distance to the female (Brumm & Slater 2006).

One of the best examples supporting the hypothesis that the signals used for acoustic communication have been selected according to their effectiveness in transmission involves a peculiar language system evolved by humans, namely whistling languages that have arisen independently in various parts of the world. According to a recent review by Julien Meyer, of the French Human Sciences Institute, although only twelve such languages have been studied in depth, the descriptions of anthropologists and travellers show that there were very many more, although most have disappeared or are in danger of doing so (and no doubt mobile phones will contribute directly to the disappearance of the remaining ones, unless effective conservation measures are taken). Such whistling languages have developed in parts of the world where steep mountainsides make moving around difficult. Under these conditions, one cannot communicate by speech with a friend or other person who is on an opposite mountainside. However, this can be done by whistling that concentrates all the sound energy into a narrow frequency band of 1-3 kHz that can travel far (Meyer 2004). Indeed, in one of the best- studied examples, the silbo gomero, typical of La Gomera, one of the Canary Islands, sound transmission has been shown to reach 10 km (Meyer 2004). These whistles constitute true languages that allow practically any type of information to be transmitted. In fact, Manuel Carreiras and his co-workers at La Laguna University, Tenerife, Canary Islands, have shown that when two people are communicating in the Gomeran language, the same brain areas usually associated with normal speech are also activated (Carreiras *et al.* 2005).

CHARACTERISTIC	SIGNAL TYPE			
	Auditory	Visual	Chemical	Tactile
Transmission distance	long	medium	long	Short
Speed of propagation	rapid	instant	slow	Instant
Speed of change	rapid	rapid	slow	Rapid
Ability to cross obstacles	high	low	high	Low
Persistence	poor	poor	good	Poor
Ease of location	medium	high	variable	High
Energy cost	high	low	very low	Low
Risk of predation	medium	high	variable	Low

Box 10.2. Characteristics of different signal types in relation to the sensory systems used to detect them.

10.5. The cost of signals

Signals are often costly. They may require time to produce and/or demand large amounts of energy. Furthermore, signals may be used by predators or parasites to locate their victims. In the cricket example at the start of this chapter, the flies to which we referred are parasitoids that locate their hosts by sound, i.e. they are attracted by the males' stridulations. When the parasitoids find a male cricket they deposit their already hatched larvae on it. These penetrate the cricket and feed off its internal organs until they are large enough to become adults, when they burst through the cricket's body wall, killing it (Cade 1979). Natural selection thus favours signals that confer the least risk and are cheapest to produce, always presuming that they retain their effectiveness. In other words, a trade-off exists between the efficacy and the cost of signals.

There are other cases in which unwanted receivers exploit signals produce by others. Predators very often attack prey when these are signalling because this makes them easier to locate. However, there are also some much more subtle examples. One of these was provided by my own study group when we investigated how great spotted cuckoos (*Clamator glandarius*) select the nests of magpies (*Pica pica*) in which they lay their eggs. As previously described, this cuckoo is a brood parasite that prefers to lay its eggs in magpie nests. We showed in an earlier study that the cuckoos do not choose magpie nests at random. Instead, the female cuckoos select the best parents, i.e. the parasitised magpies were those that could raise more young than the unparasitised ones (Soler *et al.* 1994). This posed an interesting question. How do cuckoo females know which magpies are best for raising their chicks? Our initial hypothesis was that the cuckoos would choose a larger magpie nests, because we were aware that in some monogamous species nest size may serve as a signal employed in sexual selection (see Chapter 4), by means of which the members of a pair inform each other of their physical condition. The relationship on which this idea is based is quite straightforward. When two magpies form a pair, they begin to build a nest. If they are fit they work more assiduously and make a larger nest than they would if they were weak or sick. Thus magpie pairs in good condition build larger nests than do less physically fit magpies (see the experiment described in Chapter 4). Female cuckoos need only use this signal when choosing nests. Clearly, cuckoo chicks have better survival prospects when left in charge of good parents (builders of large nests) than when left with lower quality ones (builders of smaller nests). Because this means that female cuckoos will choose large magpie nests in which to lay their eggs, magpies may be expected to respond to this evolutionary arms race by reducing the size of their nests in areas where they are parasitised by cuckoos. We tested this in a comparative study and found that, indeed, magpie nests in areas with great spotted cuckoos are significantly smaller than those in areas where the cuckoos are absent (Soler *et al.* 1999).

10.6. The origin and evolution of signals

Signals may have their origins in a diversity of sources, the most important of which are given in Box 10.3.

1. **Intention movements**: movements that must precede some activity, e.g. flexing the legs before jumping.

2. **Displacement activities**: behaviour carried out when nervous or under stress.

3. **Autonomic responses**. E.g. scent marking territories using urine as an olfactory signal.

4. **Self-protective responses**: those that may give rise to appeasement signals.

5. **Ambivalent behaviour** (when there is uncertainty over what to do): gives rise to low intensity signals.

Box 10.3. Origins of behavioural signals. Chiefly after Krebs & Davies (1993). to evolve into the complex signal that it has become (an endless and unvarying, very loud sound). In short, it has become ritualised (see Box 10.4).

Why do signals become ritualised? Why do signals always evolve to become more exaggerated and more stereotyped, that is to say more repetitive and unvarying? We shall answer these questions by addressing the three hypotheses offered in Box 10.4 and we shall once again use the familiar example of the threat signal of wolves and dogs, in which they stand stiffly upright, with bared teeth and erected back fur.

THE EVOLUTION OF SIGNALS: Signals tend to change from their ancestral simple and variable forms to become more repetitive, exaggerated and stereotyped. Such changes are often accompanied by the development of striking colours or structures. This process is termed **ritualisation.**

WHY DO SIGNALS BECOME RITUALISED? There are three main hypotheses, which are not mutually exclusive.

1. **The reduction of ambiguity hypothesis**: Ritualisation results from the selective advantage to senders of reducing the risk that their signals may be confused or misinterpreted.

2. **The manipulation hypothesis**: Ritualisation results from the resistance of receivers to being manipulated by a particular signal.

3. **The honesty hypothesis**: Receivers are selected for their ability to distinguish between honest and deceptive signals.

Box 10.4. Hypotheses explaining the mechanism of signal evolution. After Krebs & Davies 1993.

Konrad Lorenz and Niko Tinbergen proposed that many signals have developed from incidental movements or responses that just happened to provide information to receivers. It makes sense to believe that natural selection would favour those receivers that could anticipate the future conduct of a sender by responding to slight movements that allowed them to predict some important future action. Krebs & Davies (1993) provide a good example of this. Imagine an ancestral scenario in which the typical threat signal of wolves, baring the teeth and especially the canines, has not yet evolved. An ancestral wolf, when attacking, would have to draw back its lips, uncovering the teeth, before its mouth made contact (otherwise the lips would be damaged by the impact). Hence, receivers that were capable of anticipating and escaping an attack through detecting the teeth-baring movement that preceded it would be favoured by selection. Once this occurred, selection would also favour senders who bared their teeth as a way of dissuading receivers, with the result that bared teeth would begin to serve as a threat signal.

As in this example, the movements and responses from which signals have evolved are those that originally provided information on future actions, such as intention movements. This has also been demonstrated in many studies of sexual and threat displays in birds, fish and mammals. The responses of the autonomic nervous system of vertebrates to stressful conditions, such as blushing, hair raising, urination and so forth, have also been the starting point for the development of many signals.

Signals may originally have been simple and variable. In the cricket example considered above, stridulation consists of rubbing the leg against the wing, producing a complex sound. It may have originated from accidental rubbing of the wings that made some vague noise. Once it proved effective in attracting other individuals, however, the stridulations will have started The original explanation, employed by classical ethologists in the 1960s, was that signals became ritualised to avoid ambiguity, i.e. so that there was no confusion about their significance. Support for this idea comes from the observation that very different signals often have opposite meanings. In the canine example, the bared-teeth threat signal is utterly different from the appeasement signal. As every dog owner knows, a scolded dog tends to crouch down, sometimes lying flat on the ground.

If, however, we keep in mind the definition of communication given in Box 10.1, according to which the point of signals is to affect the behaviour of receivers, the interpretation of ritualisation becomes very different. Imagine that a sender has reached a point in which it succeeds in manipulating receiver behaviour. In such a situation, selection will favour resistance to manipulation by the receiver. This in turn will favour senders with more effective signals that will overcome such resistance, and it will also have favoured the signal becoming more exaggerated and repetitive. Something similar is the basis of those interviews in which judges or police interrogate a suspect to establish whether or not he or she is lying: they repeat their questions over and over again in case any contradictions emerge.

The third hypothesis was proposed by Amotz Zahavi, of Tel Aviv University, Israel. He suggested that signals become ritualised because receivers are selected to be able to distinguish between honest and deceptive ones. Taking the canine threat signal, given that the sender could employ it deceptively, selection favours those receivers who can distinguish between honest signals (those made by individuals that are really going to attack versus threats made by individuals that are bluffing). In these circumstances, the threat signal will have become ritualised because receivers will have obliged senders to exaggerate and repeat the signal, making it more costly, in order to better evaluate its trustworthiness. According to the honesty hypothesis, the only signals that persist over evolutionary time are those so costly to produce that they could only be made by individuals in good physical condition.

10.7. The conflict of interests between actors and receivers: an arms race

As our definition of communication (Box 10.1) and the above hypotheses assume, the interests of senders and receivers often do not coincide since each has been selected to derive the greatest possible benefit from an exchange of information. In order to benefit, a sender must succeed in making a receiver modify its behaviour to the sender's advantage, whereas the receiver must use the information supplied by the sender to further its own ends. This gives rise to a coevolutionary arms race (see Chapter 9) but here there is an important difference. The arms race is not between species nor even between different individuals, but instead between the different roles that the same individual may play. In the cricket example, the stridulating male obtains significant benefits if it succeeds in attracting females and warning off other males. However, for the receivers, both males and females, what matters is to be able to evaluate the quality of the sender precisely and without being deluded by first impressions. As the manipulation hypothesis suggests, receivers are selected to resist misleading signals. The honesty hypothesis, however, offers another interpretation, which is especially applicable in the context of sexual selection, which is that signals may become ritualised simply because receivers select the most exaggerated ones that can only be produced by individuals in top physical condition.

Possibly one of the clearest examples of the arms race between senders and receivers emerges from the human advertising industry. As potential purchasers, we are all receivers and we are subjected to so much publicity material that we have developed resistance. Indeed, many of us have reached the point where we feel that advertisements do not influence us, and that we do not buy products just because we have seen or heard them advertised. We are certainly resistant (and the invention of the TV remote control that allows us to switch channels during the advertisements represents a great advance in the arms race against publicity), and that is why advertising techniques have greatly increased their effectiveness by changing their strategies frequently. The aim is to exploit the psychological susceptibilities of the target audience, especially by invoking the emotions, given that much of the information provided is not true. For example, when a man sees a car advertisement in which the car is driven by a handsome, muscular youth while attractive girls look on impressed, he does not really believe that buying the car will improve his appearance, but he is being manipulated psychologically into believing that having such a car would enhance his sex appeal. Another example of the scant information supplied in advertisements concerns a recent car advertisement that asserts that your money will be returned if the car fails to make you happier. Nobody really believes such a promise, but it may work by persuading us that buying the car will make us happier.

Although we may think ourselves immune to publicity, this is not actually the case. Advertisements are the product of intensive studies and of strategies that are very well designed to achieve their objective. Good advertisements may increase sales enormously, which is why the best advertising executives are among the best- paid professionals. Clearly if companies invest enormous sums on publicity, it is because this pays off. We, the consumers, are being manipulated despite our resistance. The receivers are losing this arms race, perhaps because we are influenced by something novel in our evolutionary history as we receive the same message hundreds or thousands of times, and the communication media ensure that it always reaches us in exactly the same form. Although we are aware that this repetition is only made possible by technology, we subconsciously may interpret the messages as honest signals (see the honesty hypothesis, Box 10.4).

10.8. Honest communication and deceptive communication

As we all know, deception is a common feature of human communication, but is it also frequent in other animals? The answer is 'yes' when the exchange is between different species. For example, predators and parasites employ a great diversity of deceptive strategies in order to attract their victims. In contrast, deceptive communication between conspecifics is much rarer, probably because the same individuals sometimes act as senders and sometimes as receivers. A highly effective deceptive signal would spread through the population and the deceivers would themselves be fooled very often.

There are nevertheless plenty of examples of deceptive communication that might be regarded as permanently established. They originate in individuals that disguise themselves in order to deceive and that therefore always act as the senders and never as the receivers of the deceptive signals. Well known and frequent examples occur in many fish species in which so-called 'sneaky males' exist (see Chapter 5). The latter are much smaller than normal males and, instead of competing with other males to attract females, a sneaky male lays in wait, and when a normal male has succeeded in getting a female to lay her eggs, the sneaky male dash out and fertilises the eggs until driven away by the other male. In such cases the deception relies chiefly on being small and so going unnoticed. However, Wallace Dominey, of Cornell University, USA, found that the bluegill sunfish (*Lepomis macrochirus*), an inhabitant of freshwater lakes and rivers in North America, truly employs deceptive signals. In this species there exist males that mimic females in size, colour, and behaviour. When a typical male is courting a female, the disguised male approaches the couple and behaves like a second female, leading the male to court both of them with additional enthusiasm. Once the seduced female lays her eggs the disguised male releases his sperm at the same time as the large male, so that he ends up fertilising about half of the eggs (Dominey 1980).

There are also infrequent instances of undisguised deceptive communication. i.e. where the same individual acts as both the sender and receiver of signals. One of the most remarkable cases has been described by Anders M0ller, of Pierre et Marie Curie University, Paris, France. During his study of the breeding ecology of the barn swallow (*Hirundo rustica*), M0ller (1990) noted that during the laying period the females spend most of the mornings on their nests and that the males visit them frequently, on average 12.6 times per hour, as part of their mate guarding strategy (see Chapter 4). What was unusual was that if the female was absent when the male visited, he reacted by giving loud alarm calls for several minutes. This occurred on 96.8% of 112 observed occasions.

On five of these occasions the absent female was seen to be with another male, who sang intensely and attempted to copulate with her. When these couples heard the alarm calls of the first male they took flight and so the courtship was interrupted. These observations made Anders M0ller conclude that the alarm calls made when a female was absent were deceptive signals that induced the female to 'escape' from a non-existent predator, reducing the chance of her mating with another male. This hypothesis was supported by an experiment in which M0ller startled the female and then recorded the male's behaviour. He found that the alarm calls that were given so readily during the laying period were much less frequent during the nest-building stage (given in only 6% of cases) or during the incubation period (none at all given). Moreover, alarm calls were more often given when the nest was near other nests than when the nest was isolated, as predicted by the deception hypothesis.

Why do honest signals persist given the evolutionary advantages of lying? It may be because they cannot be faked, or are very costly to produce, or both of these (see Box 10.5). A signal that cannot be faked requires something that is scarce. A good example is the visual signals that rely on striking colours due to carotenoid pigments. These cannot be synthesised by any animal species and instead must be obtained from the diet. Hence, an individual that cannot obtain the carotenoids will be unable to produce the signals dependent on the biochemical. In the same way, if a signal is very costly to produce only individuals that are in very good physical condition will be capable of generating and sustaining that signal ('the honesty hypothesis', Box 10.4). In addition, the cost may be a social one, that is to say, the deceit may be limited or punished by the sender's companions as has been shown in various group-living bird species and also in primates. For an example we turn to a study of rhesus macaques (*Macaca mulata*) by Marc Hauser, of the University of California, Davis, USA. These primates roam in large groups and when an individual finds food, it tends to call out to announce its discovery - at least it does so 45% of the time. Such calls benefit nearby individuals since they will come and share part of the food. Marc Hauser found that individuals that did not call to others, and were instead seen eating by other monkeys, were the object of more aggression from other group members than those that made it known when they found food. Other results of this study, both observational and experimental, supported the interpretation that aggression of this sort punished individuals that did not advertise the location of food (Hauser 1992).

Why deceptive signals exist, as we have noted in the swallow example, from an evolutionary viewpoint may be because the signal is only produced for the few days of the laying period. At other times, the signal is an honest one. Another reason that allows for the evolution of deceptive signals is that the benefits of responding to an honest signal can be much greater than the costs of responding to that signal when it is intended to deceive.

The alarm calls provide a good example. Swallows that did not respond to a genuine alarm call could be killed by a predator and thus would pay an enormous cost. However, the cost of fleeing when the signal is a false alarm is nowhere near as great, because all that is lost is a mating opportunity that may be reattempted later.

Why do honest signals persist?

- Because they may be impossible to fake.

- Because they may be very costly for competing communicators to produce

- Because of the social costs of unsuccessful deception.

Why do deceptive signals exist?

- Because they are only employed sporadically.

- Because the benefits of responding to an honest signal are much greater than the costs of responding to a deceptive one.

Box 10.5. The evolution of signals. Why most are honest and why some deceptive ones exist.

10.9. Complex communication in animals

As a general rule, communication in animals other than man is relatively simple. Most other animals can only communicate information on matters directly related to the sender, for example making known territory ownership, the approach of a predator or a predisposition to mate. Others animals cannot communicate abstract ideas or anything about objects outside their environments. Other animal species have a limited repertoire of signals that in no way compares with the enormous complexity of human speech. Nevertheless, animal communication is not always entirely simple and we shall consider some of the more complex forms in this section.

For example, although many bird species have very simple, repetitive songs, the songs of passerines (songbirds) may be extraordinarily complex and in some species the repertoire may continue to increase throughout life, as happens with the island canary (*Serinus canaria*). Birdsong has also been shown to be culturally transmitted in some species, as Rosemary and Peter Grant, of Princeton University, USA, have shown in two species of Darwin's finches (the medium groundfinch *Geospiza fortis* and the cactus ground-finch *G. scandens*). In these birds, songs are very similar between brothers; singers also sing like their paternal grandparent, but not their maternal grandparent. This means that the song is not hereditary, but instead is transmitted culturally from fathers to sons (Grant & Grant 1996).

Thomas Struhsaker suggested that vervet monkeys (*Cercopithecus aethiops*) use different alarm calls according to the type of predator that they discover. Experiments by Robert Seyfarth, Dorothy Cheney and their co-workers, of Pennsylvania University, USA, showed that this is indeed the case. They played-back previously recorded alarm calls and observed the reactions of a group of vervet monkeys. The three chief alarm calls led to different behaviour. When the alarm call corresponding to 'leopard' was heard, all the monkeys rushed up the nearest trees. The call signifying 'eagle' caused the vervets to look upwards and to hide among the vegetation. Finally, the 'snake' call made the monkeys stand erect on their hind legs and survey the ground in front of them (Seyfarth *et al.*1980). The vervet monkey repertoire is even more extensive because there

are at least three other types of alarm call; for 'mandrill', 'minor mammalian predator' and 'unfamiliar human'. They are also able to recognise and signal 'dominant individual', 'subordinate individual' and 'rival group'. Such communication is indeed abstract because different reactions are made to different sounds without necessarily seeing the enemy that provoked the alarm call.

The vervet monkey communication system has been rated the most complex among all non-human animals. Nevertheless, Michael Griesser, of Uppsala University, Sweden, has shown by experiment that the Siberian jay (*Perisoreus infaustus*), a corvid that lives in family groups, uses different alarm calls according to the behaviour of its most frequent predator, the northern goshawk (*Accipiter gentilis*). Goshawk hunting behaviour has three distinct phases: searching for prey while perched, prey-seeking in flight between perches, and once prey has been located launching an attack. The alarm call of a jay that detects a goshawk differs according to whether the hawk is perched, in searching flight, or attacking, and each of these alarm calls leads to different escape and defensive responses (Griesser 2008).

Another curious example that shows how complex animal communication can be involves the bottlenosed dolphin (*Tursiops truncatus*). Each individual has been shown to have its own particular call, equivalent in a sense to its 'name', which develops during its first few months of life. The call is used in different situations, particularly when the dolphin wants to maintain group cohesion. Vincent Janik and Peter Slater, of St. Andrews University, UK, have shown with captive animals that a dolphin calls its 'name' repeatedly when it is separated from its group members (Janik & Slater 1998). The call is a way of identifying itself and signalling its location. These observations thus support the idea that this call is used to maintain group cohesion. It has also been shown that bottlenosed dolphins are capable of 'discovering' and using new sounds as a result of interacting with other individuals (Janik & Slater 1998).

It is definitely the case that, as animals go, dolphins have a more complex system of communication than most, but it is not as exceptional as some people seem to believe. I have always been struck by the popular belief that dolphins have a language that is almost as complex as that of humans, but that has yet to be deciphered. Such belief may stem from sensationalist TV documentaries. In reality, there is no evidence that dolphins have a language that allows them to 'converse' as we humans do.

It is remarkable that the most outstanding example of non-human abstract communication involves not a primate nor a dolphin, but an insect, the honeybee (*Apis mellifera*). The classic study by Carl von Frisch, one of the founding fathers of ethology and a joint winner of the Nobel Prize along with Konrad Lorenz and Niko Tinbergen in 1974, showed that when bees find a foodrich area they return to the hive and are able to communicate to their companions not only the direction to the sometimes faraway food, but also the distance and the food's nutritional value (Frisch 1976). The information is communicated via a set of movements, the 'waggle dance', in which they trace a figure of eight while vibrating their abdomens. The direction to the food is given by the angle relative to the sun of the axis separating the two halves of the figure eight. The waggle frequency indicates the distance to the food, being higher when the food is nearer. Food quality is communicated by floral scents released by the dancer. Von Frisch also showed that even if a foraging bee has to make a detour around a hill on its return journey it will still signal the direction to the food correctly when it dances, as if it had not been diverted. Such a communication system incorporates two features that were believed to be exclusive to humans. Firstly, the language is symbolic as distance and direction are expressed during the dance in coded form. Secondly, the bees are capable of providing information about something that is not taking place at that moment or at the site of the dance. This means that the bee communication system is one of the most complex known because those two aspects of the dance are only otherwise known to be shared by human language. However, the bee system should not be overrated. When all is said and done, the bees only provide information on food location and cannot give a full account of all that they encountered on their travels.

10.10. Human language

The ability to speak is arguably the most distinctive feature of the human race. Language is not just a communication system. It is much more than that because it is a mechanism that allows us to express what we think. Although language is comprised by a finite number of elements, it permits us to convey an infinity of ideas. In evolutionary terms, language is a new form of transmitting information and its graphic version, the written word, made the emergence of our great civilisations possible. Seen in this way, human language is completely distinct from the communication systems of all other animals.

But is human language so different from animal communication, and what characteristics distinguish the two? There are two major distinctions, the use of 'symbols' that allow us to refer to abstract ideas, and the employment of 'syntax', the tool that makes it possible for us to combine and coordinate words to converse and to express judgments. These two elements make it possible for humans to attain communicative achievements beyond the reach of other animals, such as speaking about that which is neither present nor current or speaking with the intention to communicate.

10.10.1. Is there anything resembling human language among other animals?

Some animals undoubtedly do use symbols in order to communicate, as discussed above in the vervet monkey and honeybee examples. Whether or not any employ syntax is more debatable. Some primates have been shown to have certain rules for combining sounds when communicating, but these have never been related to changes that may occur in what the signals mean, with one exception that we shall consider in detail below.

A commonly used method to compare the resemblance between animal communication and human language is to try and teach an artificial language designed by the investigators to various animals, chiefly to our closest relatives the anthropoid apes. This approach has involved techniques such as sign language and use of computer keyboards. The results obtained have differed widely and have also been severely criticised in some cases. Nevertheless, some recent attempts have produced quite convincing results. The most informative of these has been that of Kanzi, a bonobo (*Pan paniscus*) who, as a baby, learnt a great number of symbols that were being used by Sue Savage-Rumbaugh and her co-workers at the University of Georgia, USA, to try and teach a language to Kanzi's adoptive mother. The language employed signals that the animal had to select using a computer keyboard. The mother proved incapable of learning it and so the investigators then started to teach the baby. They were enormously surprised to find that Kanzi had already adquired knowledge of many symbols. The instructors communicated with him by speaking to him while they employed the computer keys. When Kanzi grew up he carried the keyboard around with him in order to communicate with his trainers. He was able to signal his intentions prior to carrying them out and he could sometimes refer to distant places. Kanzi was also able to understand spoken instructions such as 'put the apple in the fridge', even when he could not see his trainer (Savage-Rumbaugh & Lewin 1994).

Studies of this type have revealed several interesting facts. Chimpanzees and bonobos are capable of learning quite a wide vocabulary of 150 to 250 words, and they are apparently able to acquire some ability to understand and employ rules of syntax. However, although these abilities are much greater than had been expected, they are very poor in comparison to the capacity that we humans have for understanding our own language. This is not surprising because one species cannot be expected to learn the complex language of another species of higher mental ability. It would surely have been the case that, contrary to what the cinema has led us to think, Tarzan would also have failed to learn chimpanzee language - had they had one - despite having lived with them since infancy.

In any event, such discoveries using captive animals trained to use an artificial language are hard to evaluate because nothing similar was done to employ their natural communication systems, operating outside human influence. However, a quite recent field study of two primate species, the Diana monkey (*Cercopithecus diana*) and Campbell's monkey (*C. campbelli*) have shown their ability to understand and employ simple syntactical rules associated with the meaning of some of their calls.

Both species have different alarm calls for 'leopard' and 'eagle', as do the vervet monkeys. The two species often coexist and sometimes even form mixed groups. The Diana monkeys understand the alarm calls of the Campbell's monkeys and when they hear them they make their own, different alarm calls. In addition to the above, male Campbell's monkeys make another type of sound, two 'boom' calls a few seconds apart, which sometimes immediately precede an alarm call. When Campbell's monkeys discover an approaching predator they only give the alarm call. However, when danger is not imminent, as when they see a distant predator or when something such as a snapping twig startles them, they give the boom-boom call followed by the alarm call. Diana monkeys do not give their own alarm call when they hear the Campbell's call preceded by 'boom-boom'. Klaus Zuberbuhler, of the Max Planck Institute of Evolutionary Anthropology, Germany, performed playback experiments with wild groups of Diana monkeys. He broadcast alarm calls of both species, both preceded or not preceded by the 'boom-boom' call, and noted the animals' responses. As expected, the Diana monkeys did not respond to Campbell's monkey alarm calls preceded by 'boom-boom' but they did respond to their own alarm call even if it too was preceded by the

Campbell's 'boom-boom' (Zuberbuhler 2002). It is thus evident that the 'boomboom' modifies the significance to the Diana monkeys of the Campbell's monkey alarm calls, changing it from meaning imminent danger requiring a rapid response to a signal of some disturbance that does not require any immediate precautions. In other words, the 'boomboom' is simply a modifier that inhibits the Diana monkeys' response to the signal that follows it. However, it is no longer inhibitory when it precedes the Diana monkeys' own alarm call. These results show that Diana monkeys are able to understand the semantic changes brought about by a syntactic rule, the insertion of another sound, which is a feature of the natural communication of another primate species.

In any event, although evidence is gradually accumulating that the communication system of some animals is more language-like than had been thought, the conclusion remains that animals do not represent their world linguistically. For most experts, therefore, language marks a discontinuity between human mental capacities and those of other animal species.

10.10.2. The origin and evolution of human language

Psychologists and linguists have traditionally maintained that human language is a cultural acquisition that developed gradually from a primitive protolanguage to reach its present forms. In the mid 20th century, Noam Chomsky, a famous linguist at the Massachusetts Institute of Technology, USA, published an influential book in which he asserted that the ease with which children learn a language cannot be explained in terms of simple, all purpose learning mechanisms, but instead indicates that we humans have an innate capacity to develop language (Chomsky 1957). This book gave rise to a heated debate, which continues to this day. Psychology and linguistics are two disciplines that have virtually no tradition of thinking in terms of evolution. Nevertheless, although there still are some psychologists and linguists who believe that language is simply the outcome of an increase in brain size linked to an increase in associative learning ability, very few continue to make this argument.

There are many indicators supporting Chomsky's idea, the most important of which are given in Box 10.6. For example, there is the fact that over 100 Creole languages exist, each developed from a lingua franca, a common language created when native speakers of several different languages end up living together, usually for work reasons. A fascinating example derives from Papua-New Guinea, a country in which over 700 native languages coexisted within an area smaller than Spain. The current official language is Neomelanesian, a Creole or pidgin language that developed from a lingua franca of the early 19th century when, after the arrival of English-speaking traders, the need arose to communicate between the different local ethnicities in order to establish common trading arrangements (Diamond 1992).

Another convincing proof that language has a significant hereditary or instinctive component arose from the discovery of an English family whose members, despite being entirely normal in all cognitive matters unrelated to language, shared a linguistic anomaly that led them to make syntactic errors that they were unable to overcome despite intensive training. The problem affected sixteen of the thirty family members across three generations. The case was studied by Simon Fisher, of Oxford University and his collaborators, who demonstrated that the gene FOXP2 that was responsible for this anomaly. All sixteen affected individuals had a mutation of FOXP2, the others all possessing the normal version (Fisher *et al.* 1998).

1. The complex human vocal apparatus is very well suited to producing the enormous variety of sounds that comprise speech.

2. The sense of hearing is also excellently suited to decodifying a great variety of sounds following each otherin quick succession.

3. Language is largely, though not entirely, associated with two specific brain regions: Broca's area and Wernicke's area.

4. The capacity for learning a language is centred on a very specific period during development. This reliance on a critical period also occurs with most instinctive behaviours.

5. Some persons are born with an inability to employ grammatical rules correctly. These disabilities run in families and may thus be considered heritable.

6. Children learn to speak extraordinarily quickly, despite not being taught any rules (they infer these automatically).

7. Children, such as the famous wolf-child of Aveyron, that are raised in social isolation neither develop the ability to speak nor do they invent a language of their own. This shows that an adequate social environmentis needed in addition to the genetic capacity to learn language.

8. When adults that speak different languages come into contact they create a **lingua franca**, a very simple language with hardly any grammar.

9. The offspring of adults that created a lingua franca automatically transform it into a true **Creole** language, with fully developed grammar.

10. Indigenous languages are neither less complex nor more primitive than those of developed countries. Even the first written languages, from 5,000 years ago, were already as complex as current ones.

Box 10.6. Some generally agreed findings on human language.

The debate has centred in recent years on whether or not an innate capacity for language has evolved by natural selection. Strange to say, the same Noam Chomsky who originally proposed an innate universal capacity for language that was not acquired by cultural transmission suggested that our linguistic capabilities were simply the outcome of the progressive increase in mental capacity of our ancestors, without there being any need to invoke adaptive advantages. One of the chief arguments used to support the idea that the evolution of language was not adaptive (apart from the philosophical and metaphysical ones which we shall not consider) is that if language had evolved by natural selection, there should exist important differences between different ethnicities in the structure of their languages and in their capacities to learn them, given that such languages would have evolved independently in different human populations as they adapted to different environmental circumstances. This prediction is not met since an Inuit or San Bushman child is perfectly capable of learning English, just as an English child can learn any other language. However, the uniformity of the 'language instinct' does not rule out the evolution of language by natural selection. It merely shows that such a capacity originated before the first *Homo sapiens* dispersed throughout the world. This assertion is supported by a diversity of studies that, despite using different methodologies, have all led to a similar conclusion, that all modern humans are descended from a small group that left its natal home in eastern Africa to begin the colonisation of the whole planet.

Chomsky's standpoint is illogical and contradicts his original idea that linguistic capacity is instinctive, particularly because he accepts that language brought significant advantages to its users. Most of what is known about language (see Box 10.6) directly or indirectly supports the opposing view, that linguistic capacity was acquired through natural selection and that it favours those individuals that possess it, because it confers clear reproductive benefits. It is this opposing viewpoint that is taken by Chomsky's disciple, Steven Pinker, who is also at M.I.T.

The adaptive hypothesis is well supported and Chomsky's proposal has attracted much criticism. Pinker (1994) sets out several quite conclusive arguments. Two of the most important of these are that, firstly, if language is a product of culture, there should be a correlation between cultural complexity and linguistic complexity, which is not the case. Even the languages of hunter-gatherers are as complex grammatically as those of more developed societies (for example, in the Iyan language spoken by a tribe of the marshy plains of Papua-New Guinea a single vowel may have eight meanings according to the tone used; Diamond 1992). The second argument is that it is hard to accept that language is just the outcome of having a large brain because our quite primitive ancestors already had big brains, whereas language emerged much more recently. What then was the large brain used for previously?

Language is far too complex for us to imagine that it could have evolved without being favoured by natural selection, because it confers so many advantages to individuals who have it. Following Pinker's well argued defence of the adaptive viewpoint (Pinker 1994), many psychologists have come to support his evolutionary focus and several adaptive hypotheses have emerged regarding how natural selection may have favoured the evolution of human language. The chief ones are given in Box 10.7. All the proposed adaptive advantages are important and together they provide more than enough reason to believe that natural selection played a significant part throughout human evolution in favouring ever more effective linguistic capabilities for communication.

11. Mother-offspring communication would be favoured, allowing the young to be alerted to potential dangers.

12. In a social context it would give an advantage over rivals within the group.

13. It could provide a big advantage when seeking a suitable mate.

14. It would improve the ability to convey information on food sources.

15. It would increase the efficiency of cultural transmission of information.

16. It would help to sustain social cohesion.

17. It would assist dispersion and range expansion, given that a single individual could explore and then relate what it had found when it returned.

18. It would be an advantage during inter-group confrontations, making it possible to organise coordinated responses to rival bands.

Box 10.7. Potential adaptive advantages supporting the evolution of human language by natural selection.

The first three of these advantages operate at the individual level and the remainder would be promoted by kin selection, given that groups were probably composed of related individuals, or would enable group selection, which as we have noted may have played an important role in human evolution (see Chapter 8).

The third point in Box 10.7 was proposed by Geoffrey Miller, of New Mexico University, USA, who suggests that the working vocabulary of any language, perhaps some 50,000 words, far exceeds the requirements of communication but that this excess can be explained in the context of mate seeking and pair selection. Miller (2000) points out that, for example, an artificial language called Basic English has been created with just 850 words, and these are more than enough for transmitting any kind of information (it has even been used for whole books on biology and astronomy). He concludes that most of the vocabulary is redundant and that the hypothesis that best explains its diversity is that it is a way of displaying an individual's cognitive capacity, which could be advantageous when seeking a mate. Because conversation has an important influence on mate selection in humans (see Chapter 4), sexual selection may have had a strong influence on the evolution of language.

Although no existing languages are more highly developed than others and although, as we have noted, all human beings are descended from a group of individuals that already had as complex a language as any that exist today, human language must have evolved gradually under natural selection. Although there is disagreement regarding when language emerged (between 50,000 and 200,000 years ago), and which adaptive advantages favoured its evolution, most experts agree that what first appeared would have been a protolanguage. This would have been characterised by its limited vocabulary and lack of syntax, because it would have been used only to identify concepts. Gesturing would have played a big role. A true language with well-defined syntax would have developed subsequently, via a process whose mechanism is also a source of controversy. Some maintain that it could have evolved directly, but others suggest that it would have done so gradually, simple syntactic rules gradually giving rise to other, more complex ones.

10.10.3. Might some animals possess a poorly developed language?

You may be puzzled by this question because it was answered with a resounding 'No' earlier in the chapter. However, I would like to present an idea of mine on this theme, one that differs from the prevailing scientific consensus. For many years I have thought that at least some animals of higher cognitive ability may possess some mechanisms permitting them to 'speak', that is that they may be capable of communicating on some simple matters in a more complex way than we imagine. This idea derives from my many years experience of working with corvids, birds of considerable cognitive ability (see Chapter 11). Many of my feelings may derive from the admiration and affection that one has for the animals one works with, but there are also some less subjective reasons for thinking that these birds are very inteligent.

We captured magpies over several years employing an experienced person who used baited spring traps large enough to catch the birds unharmed. The traps were set from early March until the end of June. The trapping effort was the same each week but, nevertheless, the same thing happened every year. After two or three quite successful weeks the number of captures dropped steadily, even though the trapping effort remained the same. I cannot pretend that the only possible explanation for this is that the magpies 'told' each other of the risks of taking a mealworm found twisting on a hook in a particular location. There may well be other explanations and the correct one may have escaped me but, nonetheless, the observations are enough to sow some doubt.

In any event, given that it would be highly advantageous to be able to communicate certain basic matters relating to survival, for example regarding food sources and risks of predation or parasitism, I ask myself why the beginnings of language should not have evolved in animals of sufficient cognitive ability. Perhaps it exists but we have yet to detect this trait. Most conclusions in this field are based on what investigators understand about what is being transmitted, For example, it is accepted that cercopithecine monkeys have quite a complex communication system because investigators have succeeded in deciphering it, but the existence of such a system in gorillas and chimpanzees has been queried even though the latter are known to have more highly developed cognitive powers. For example, the trained captive bonobo Kanzi, described above, was able to learn a vocabulary of up to 250 words and could even understand the spoken phrases of a species of much higher cognitive ability. Perhaps the possibility that such animals may have an elementary language is denied simply because investigators have not yet deciphered anything resembling a language.

In order to test the existence of a capacity for complex communication it is unnecessary to decipher the system's components. A different experimental approach is required. I do not believe that the method used so far for such studies, which rely on understanding the significance of acoustic signals exchanged by individuals, is the most satisfactory one. It is unnecessary to be able to ‘understand the language’ in order to test the hypothesis and, in addition, sounds may form only part of a language that may also include visual or other signals. A valid experimental design would be to present several individuals with a problem to which only one knows the solution. If one of the others solves the problem without prior learning, it would be legitimate to conclude that experience problem-solver had communicated with others in its group. How to do this is quite another matter of course.

The evidence that an elementary form of language exists in certain animals grows ever clearer. As we have seen in this chapter, new experimental techniques have shown that vocal communication in animals can be more complex and more similar to a language than was thought possible even a few years ago. The case of the Diana and Campbell’s monkeys mentioned above even provides evidence of the use of syntax by another primate species. We have also noted that there must have been a stage in human evolution when only a protolanguage existed. Therefore the possibility that something similar existing in other animal species ought not be rejected without putting the idea to the test.

I am convinced that this hypothesis is worth testing experimentally and I have performed an initial experiment using the methodology described above, with the magpie as the study species. The test was unsuccessful, but I shall describe the experiment in case it stimulates someone else to improve on my approach. The starting hypothesis was that if magpies can communicate with each other, and if one magpie can benefit from providing another with information of some benefit, such as where to find more appetising food, the experienced bird should tell others about the location of the resource.

The experiment was carried out in cage that was two metres wide, one metre deep and one and a half metres tall, divided into two chambers by an opaque board, so that it was impossible to see from one chamber into the other. The two chambers were joined by a small corridor with separate entrance and exit doors. The entrance was opened and when the desired magpie entered the corridor it was closed and the exit was opened. This gave the magpie access to the other chamber in which there were mealworms, a favourite food. For each trial three magpies were put together into the other half of the cage, in which less favoured food (dog food) and water were available. One of the three magpies was an individual that had been trained to extract mealworms from a matchbox, something that magpies learn easily if the box is left partly open at first. From time to time, the magpies were allowed to enter the other half of the cage, but only one at a time. Here there were a few mealworms that the magpie soon ate. After a week, once the magpies were familiar with the arrangements, the mealworms in the test half of the cage were provided within closed matchboxes. The previously trained individual extracted them without any difficulty. The prediction was that it might later ‘inform’ one or both of the other magpies where the worms were, and that by doing so it might gain social status (earlier observations had established the social hierarchy of the three magpies; which was the most dominant and which the least). If it did this, then one of the other magpies, which was unfamiliar with the matchbox routine, would also prove capable of opening the matchboxes. The controls were groups of three magpies none of which had been trained to remove mealworms from matchboxes and so should not be able to do so during a similar period.

Three trials were performed with three different groups of magpies and none proved successful. In truth, I was not surprised despite having been very keen on the idea when I first thought of it. I gradually realised that I was demanding something very difficult of my subjects because I was asking the birds to pass on information about a totally novel element, the matchbox, which does not occur in the magpies' natural environment. To convey such information would require not an embryonic language but one as complex as our own.

For an experiment such as this to stand a higher chance of success the ideal would be to base it on predation. The selective pressures for the evolution of a minimal language to complement the well-known alarm calls are much stronger, as was shown in the case of the Siberian jays. I am convinced that, before long, someone will demonstrate the existence of a protolanguage in an animal species.

Chapter 11. The animal mind

11.1. Introduction

In this final chapter we shall examine the abilities and limitations of the minds of non-human animals in comparison with our own minds. This comparison has preoccupied humankind uninterruptedly ever since the days of the ancient philosophers of Antiquity. The proposed mental differences and similarities between man and the other animals are highly diverse and very often contradictory. It has been suggested at least once, by the 'mentalists', led by the psychologist George Romanes, that the animal mind is the equal of the human one although arrested at an earlier stage of development. However, during the history of science and philosophy it has most often been maintained that human mental capacities are far superior to those shown by other animals. It has always been the case that the differences are emphasised whereas the similarities have largely been overlooked. Thus, as recently as the mid 20th century, the possibility that humans might have instincts was denied as was the possibility that other animals might have certain mental capacities, however slight.

The magnitude of the differences between the human mind and that of other animals is of course evident. The human brain is three times larger than would correspond to a primate species of our size. It has played a fundamental role in the great evolutionary success of our species because it has allowed us to invent and develop the technologies needed to survive and to colonise the entire planet. Thanks to our brains we have discovered and constantly improved the great diversity of tools that are indispensable to our survival, as well as the ingenious hunting techniques that served us so well during our hunter-gatherer days. Clothing, navigation and the domestication of animals and plants are among our brain achievements, and these have allowed us to establish ourselves in the most remote and inhospitable corners of the Earth.

Nevertheless, despite all these differences, there are also numerous and significant similarities. For example, our brain is very similar in its basic structure to that of all other mammals, although relatively large and with a more highly developed cerebral cortex. The fundamental architecture of the brain shares its ancestry with that of all other mammals. Moreover, the human brain and that of our closest relative, the chimpanzee (*Pan troglodytes*), have evolved apart for only between five and seven million years. It is thus surely logical to believe that some human mental capabilities must also be represented in other animals, even if only in an incipient form. Since the 1960s, when Jane Goodall began to publish her observations of wild chimpanzees, the evidence that the mind of non-human animals is considerably more complex than previously thought has become progressively more refined. We nowadays accept that some of the 'superior capabilities' of the human mind may also be encountered among other animals (Griffin 1992).

Throughout history we human beings have always promoted the self-congratulatory notion that we are a species apart, quite distinct from all the rest. Many characteristics that have been presumed to be unique to humans, and thus not shared with any other animal, have been suggested. The chief ones are given in Box 11.1 and many are associated with our mental capacity. We shall consider these in this chapter.

PROPOSED 'UNIQUE' HUMAN ATTRIBUTE	AUTHOR	COMMENTS
Man is a political animal	Aristotle	Coalitions and alliances are common in chimpanzees and other social primates
The capacity for reason	Descartes	See text
Making conscious decisions	Marx	See text
Having sexual relations purely for pleasure	St Augustine	Chimpanzees and bonobos (*Pan paniscus)* also have these (see Chapter 5)
Producing and storing garbage	Jean Dorst	Many social insect species also do this
Making and using tools		See Box 11.2
The invention of war		Chimpanzees also fight and kill individuals of other groups
Language		See Chapter 10
The theory of mind or 'the Machiavellian mind'		See text

The capacity for future planning	

See text |

Art	

Bowerbirds display artistic tendencies in their bowers.

Several animals have become famous for the quality of their paintings, which have featured in highly successful exhibitions |

Conscience and free will	

See text |

Ethics and the sense of fairness	

See text |

The moral sense Religion	Charles Darwin	There are no convincing demonstrations of its existence in other animals (see text)

Nothing similar seems to exist in other animals (see text) |

The rebellion against the reproductive instinct that all other living things follow to leave the maximum possible number of successful descendants	This book	Human intelligence has allowed our species to make use of contraception and deliberate abortion

Box 11.1. The principal attributes proposed as unique to humans throughout history. The source is given where known. The comments column clarifies what is currently known.

11.2. Cognition

This complex term spans all those mechanisms by which all animals, humans included, acquire, process, store and act upon the information that reaches them from the environment (Shettleworth 1998). Those mechanisms thus encompass the ones whose existence in non-human animals is accepted; such as stimulus perception, learning, memory and decision-making. They also include others that traditionally have been thought to be exclusive to the human species; such as reasoning, logical deduction, the capacity for solving novel problems, the capacity for future planning and many others associated with social relationships. The final three categories are considered in the following sections.

We shall not go into detail regarding those capabilities that all animals are thought to share. Instead we shall simply make some general observations and comparisons with the extent of those capacities in humans. First, however, we shall consider a widely-held idea that is unsupported by the scientific evidence, the belief that animals with relatively large brains have the most highly developed cognitive capacities. As it is, the human brain is not the largest, either in absolute or in relative terms. In absolute terms the brains of such animals as whales and elephants are far larger, which is unsurprising given their enormous body sizes. However, in relative terms we are also far outstripped by some small mammals. For example, the mouse brain is twice as large as the human one, relative to body size. We now know that, contrary to what was thought some decades ago, a larger brain does not necessarily mean a greater cognitive capacity. In fact, some cognitive abilities in vertebrates are very similar in different groups independently of brain size (Salas *et al.* 2003). It should also be borne in mind that some very simple, microscopic organisms, such as protozoans and bacteria, are capable of detecting certain stimuli, such as those coming from food and from toxic substances, which enables them to react appropriately. In other words, despite not having anything resembling a brain they can perform some of the functions associated with one.

Further examples of the lack of a relationship between relative brain size and cognitive capacities are provided by honeybees (*Apis mellifera*) and fruit flies (*Drosophila melanogaster*). The tiny brains of the honeybees show some cognitive abilities comparable to those of mammals (Giurfa 2003). Likewise, fruit flies have been shown to possess a mechanism for spatial memory very similar to that of primates, one that allows them to resume some purpose on which they had previously decided, after having been ‘distracted’ (Neuser et al. 2008).

Contrary to what many people believe, when it comes to learning, the scientific discoveries of the past few decades have revealed that the human capacity for learning is not as superior to that of other animals as used to be thought. In general we humans are very good at learning things that are linked to our reproductive success. For example, we find it hard to distinguish between different polygons with complex shapes, but we can discriminate the smallest differences between human faces. Much the same applies to other animals, they are adapted to learn that which they need and will make use of in their daily lives. Some learn some highly specific abilities that have not been important in human evolution and they far outstrip us on these. For example, rats are better than humans at learning to avoid poisons, and birds that store as many as 10,000 seeds in order to eat them in winter, are far better at finding them again than we would be. In other words, learning capacity differs greatly among species according to their actual requirements. Some species are adapted to learn some things and other species to learn others and what they learn well is what has tended to increase their fitness during the course of their evolution. Thus, for example, pigeons quite soon learn to peck at an illuminated switch in order to obtain food. However, although they learn to fly away from an electric shock at first exposure, they cannot be taught to peck a switch to turn off the current (Macphail *et al.* 1995). This makes sense according to our earlier argument; the correct response to a threat is to fly away, while the way to get food is to peck for it.

As we have said, it is now generally thought that animals share some of the cognitive capabilities that were previously considered exclusive to humans (Griffin 1992). We shall not go into detail on such matters as reasoning and the taking of conscious decisions because these, in the absence of unambiguous proof, lend themselves greatly to speculation. However, it would not be surprising if irrefutable proof of their existence in other animals is obtained some day, because such capacities as logical reasoning and deductive logic have important innate components in human beings (Mealey 2002). In contrast, some activities that humans perform very well, but that computers cannot readily manage, such as crossing a field littered with obstacles or throwing a stone at a target, have been shown to involve nearly automatic processing. Such very common activities as riding a bicycle or driving a car, or practising most sports, are carried out automatically, without any conscious involvement whatsoever.

In the following sections we shall examine two cognitive abilities considered to be peculiar to man: the capacities for solving novel problems and for future planning.

11.2.1. The capacity for solving new problems

One of the most impressive cognitive abilities that was thought to be exclusive to humans is the capability to solve a new problem other than by trial and error. The earliest demonstrations that chimpanzees at least shared this ability were obtained by Wolfgang Kohler in the 1920s, in a classic series of experiments in which the apes had to solve various problems in order to get food. The best known of these is the one in which some bananas were hung from the ceiling so that the only way of getting them was to stack up some boxes that were available and then to climb up the stack. At least some individuals solved this problem and other similar ones.

Here is another example that demonstrates that such a capacity is within the reach of other species. Bernd Heinrich, of Vermont University, USA, presented ravens (*Corvus corax*) with a problem linked to obtaining food (Heinrich 1996). Pieces of meat were hung from a branch at the end of a cord. The ravens first tried to get at the meat from below, but the test was set up so that this could not be done. Three ravens succeeded at their first attempt in solving the problem in the only way possible: perching on the branch and lifting the cord by pulling upwards, in the manner in which water is drawn from a well. The cord had to be lifted in several stages in order to reach the meat so the ravens pulled with one foot and held on to the retrieved cord with the other. The ravens showed that they understood the problem because when a stone was attached to the cord they did not pull it up, but they did so immediately when meat was on the cord even if a different type of cord was used.

11.2.2. The capacity for future planning

The ability to plan for future needs implies the existence of highly complex cognitive abilities such as have always been thought to be unique to humans. At one time, it was thought that pigeons and rats can solve some future-related problems, but they can only do so over very short periods. However, some recent impressive discoveries show that some animals are capable of performing actions that will help them at some point well into the future. For example, both bonobos and orang-utans (*Pongo pygmaeus*) have been shown to be capable of selecting, transporting and guarding tools that they would need later on (up to 14 hours later in fact; Mulcahy & Call 2006). Nevertheless, the most noteworthy discoveries in this area involve not our closest relatives but a bird, the western scrub jay (*Aphelocoma californica*), a member of the crow family that hides seeds on which to feed afterwards during periods of scarcity. Remarkable studies by Joanna Dally and her co-workers at Cambridge University, UK, have shown that these jays do not hide and rediscover seeds at random, as used to be thought. Instead they are capable of remembering what type of food they have hidden and where and when they hid it. In addition, an individual bears in mind whether or not it was seen by another bird when concealing food (Dally *et al.* 2006).

One of the investigations by Dally *et al.* went even further. California jays have been shown to be able to store food according to quite exact forecasts of future needs, something that no earlier investigations had revealed. The investigators performed an experiment in which each jay was kept in a cage with three compartments where they were trained for six days during which food availability was manipulated, so that it was scarce during the mornings in one of the side compartments. The birds were then tested and it was found that they stored food for their future needs in order to resolve two different situations. They preferred to store food in the place where they had learned that they might experience hunger the following morning. They also stored each of the two food types available to them in the place where they expected that food would otherwise be unavailable (Raby *et al.* 2007).

11.3. Making and using tools

Tool use is considered to mean making use of an external object as if it were an extension of an animal's body. Some of the best known examples of tool use under natural conditions are described in Box 11.2. Observations made in captivity are excluded.

The chimpanzee is undoubtedly the species that makes the most extensive use of tools. By the 1970s Jane Goodall had described thirty different types of tool use that, in addition, differed significantly between chimpanzee populations. Nevertheless, the most surprising and striking known example of tool use involves the New Caledonian crow, a species that uses twigs to obtain food from its natural environment. Alex Weir and his co-workers at Oxford University, UK, have carried out some remarkable experiments using captive birds. Food was supplied to the crows in a small basket with handles that was placed within a tube out of reach of the birds' beaks. Instead of twigs the birds were supplied with wires that were curved at one end to a greater or lesser extent to form hooks. The birds inserted the hooked end of a wire into the tube and used it to hook the handles and lift out the food basket. The most fascinating event occurred, however, on an occasion in which individuals had to choose between a hooked wire and a straight one. One of the crows selected the curved wire but another, a female, chose the straight wire and bent it into a hook that allowed it to get the food. In other words, this female proved capable of manufacturing its tool and it did so quickly and without hesitation. Subsequent experiments showed that this was not a chance event since the bird proved capable of manufacturing an appropriate tool on nine out of ten trials (Weir *et al.* 2002).

SPECIES	TOOL USED	COMMENTS
Song thrush		

(*Turdus philomelos)* | Smashes snail shells open against a stone in order to eat the contents | See next |

Lammergeier (*Gypaetus barbatus*)	Lifts large bones up into the air and drops them from a considerable height on to rocks, so that they smash open, exposing the marrow	Neither this case nor the previous one are examples of tool using, strictly speaking, according to the definition in the text
Egyptian vulture (*Neophron percnopterus*)	Smashes open the eggs of ostriches (*Struthio camelus*) by lifting a stone with its beak and dropping it forcefully on the shell	This is an example of tool use since the stone may be considered an extension of the bird's body
Woodpecker finch (*Cactospiza pallida*)	Holds a cactus spine in its beak and uses it to extract insects from holes and crevices in trees	The finch sometimes manipulates the cactus spine so that it suits the intended purpose better
New Caledonian crow (*Corvus moneduloides*)	Uses twigs and leaves to obtain food	Capable of manipulating both twigs and leaves, changing their shapes to serve various purposes
Sea otter (*Enhidra lutris*)	Floats belly-up with a large stone on its chest. The shelled molluscs on which it feeds are held in the fore-paws and smashed open against this stone	

Indian elephant (*Elephas maximus*) African elephant (*Loxodonta africana*)	Tear off branches that are then held in the trunk and used to drive flies away and to scratch themselves

Orangutan (*Pongo pygmaeus*)	Both sexes use tools to stimulate themselves sexually (sexual toys) Put leaves in the mouth to amplify calls	Schaik *et al.* (2003) decribe various types of tool use
Chimpanzee	Use twigs to probe into termitaries to 'fish' for termites	

Break open nuts by using a large stone as an anvil on which the nuts are placed and then broken open with a stick or another stone | Whiten *et al.* (1999) describe and discuss numerous instances of tool use |

Box 11.2. Some examples of tool use in different animal species under natural conditions. |

11.4. Culture

What constitutes culture varies considerably according to the discipline that defines it. Some anthropologists insist that genuine culture involves transfer of information between individuals by means of language, something that would limit the existence of 'true' culture to the human species. Nevertheless, a more logical definition from a biological viewpoint considers culture to be the transmission of behaviour to the following generation by means of observation or social learning, so that it becomes a particular characteristic of that population. Thus defined, cultural transmission gives rise to an evolutionary change that occurs through social learning instead of being genetically based. There thus coexist two interrelated inheritance systems that may give rise to two parallel evolutionary processes, one of them genetic and the other cultural.

Box 11.3 gives some of the most important examples of culture that have been noted among animals. Those involving primates are particularly common but clear examples of culture also exist among other species.

SPECIES	CULTURE	COMMENTS
Passerine songbirds	Different song dialects exist in different populations	Well documented among quite a few species (e.g. the song sparrow, *Melospiza melodia*)
Blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*)	Opening milk bottles	One of the best-documented instances of cultural transmission
Orca (*Orcinus orca*)	Hunting techniques vary	Some populations have hunting techniques peculiar to themselves
Bottlenosed dolphin (*Tursiops truncatus*), humpback whale (*Megaptera novaeangliae*) and orca	Different dialects exist in their acoustic signals	Dialects differ significantly between populations
Japanese macaque (*Macaca fuscata*)	Potato washing	

Wheat cleaning

Activity involving stones: piling them up, rubbing them together, rolling and dropping them, hugging them etc | Known to have been discovered by a young female, known as Imo

Also discovered by Imo

Not apparently having a particular function and interpreted as a form of play |

Capuchin monkey (*Cebus capucinus*)	Social behaviour (relationships between individuals) differs between populations	Gestures, postures and forms of contact between individuals vary
Orangutan (*Pongo pygmaeus*)	Some males and females use tools to stimulate themselves sexually	In addition, Schaik *et al.* (2003) describe 23 cultural variants that differ significantly between populations
Chimpanzee	39 culturally transmitted behaviours have been described	Whiten *et al.* (1999). See text

Box 11.3. Some examples of animal culture. | One of the best-documented cases of cultural transmission involves the behaviour developed by blue and great tits in the early 1920s, when they learnt to open the milk bottles that the milkmen deliver to English doorsteps in the early mornings. They did this by pecking through the aluminium foil caps, in order to get at the cream below. This behaviour originated in one part of the London suburbs but in just 25 years the trait had spread throughout England, Wales and part of Scotland as well as across to Ireland.

Another interesting example involves orcas or killer whales. Various populations of this carnivorous cetacean have developed at times very complex hunting strategies that are particular to each pod. For example, a pod in the Strait of Gibraltar specialises in capturing bluefin tuna (*Thunnus thynnus*) by employing two spectacular techniques. One consists of robbing fishermen of fish that they have hooked. The other involves corralling the fish against the tunny nets, or almadrabas, which comprise walls of netting extending from the shore for up to 2.5 km out to sea.

Perhaps the most fascinating example of animal culture is that of the Japanese macaques that wash potatoes and wheat. Japanese ethologists discovered this behaviour when it began and observed the learning process that followed. They began to study the macaques in 1950, initially by watching the behaviour of different individuals in a particular group. In 1952 the investigators began to leave potatoes in the open on a beach, near the forest edge, in order to make observation easier. A year later some of the macaques were taking the potatoes to the shore and washing them before eating them. This behaviour was an important discovery for the macaques because they were able to remove soil from the potatoes, and thus no doubt improved their taste. This practice was invented by a young female known as Imo. The first others to learn it were also individuals of her own age. Within five years 80% of all group members younger than eight years old washed their potatoes. However, curiously only 18% of the overeights proved capable of learning to do so.

Probably the most important account of animal culture is that by Andrew Whiten, of St. Andrews University, UK, and his collaborators. This is a comparative study with contributions by investigators from the seven zones in which chimpanzees had been studied for over ten years (Whiten et al. 1999). They analysed 65 forms of behaviour and concluded that 39 of these were culturally transmitted, because they were normal in some areas but absent from others that lacked the necessary ecological conditions for those behaviours to emerge. Because of this review, there has been general acceptance that culture exists in animals other than humans. The study presented clear results that are very hard to criticise, at least on scientific grounds.

Human culture, naturally, is very much more complex and far-reaching. Nevertheless, we can say that our cultural traditions are not entirely random in origin nor are they the outcome of the whims and fashions of local groups. Many studies have shown that in most cases, when customs that have arisen in different places are compared, they are found to be potential adaptations to the local circumstances. For example, inter-cultural use of spices in cooking has been related to the need for food preservation (Billing & Sherman 1998). The inhabitants of warmer regions, where such foods as meat and fish perish quickly, have a traditional cuisine centred on the abundant use of spices that, as is well known, have significant antimicrobial properties. Such spices are much less used in colder regions.

Another widespread tradition may well also be adaptive. When it comes to choosing a mate some cultures have a tradition in which a bride price is paid, i.e. the parents of the groom pay the bride's parents in order to agree on the marriage. In some other cultures it is the parents of the bride who have to pay a dowry to the groom or his parents. A comparative study reveals that the bride price is paid in those societies that permit polygyny, which means that women are scarce and much in demand for marriage (Gaulin & Boster 1990). In contrast, payment of a dowry is widespread in communities where monogamy is imposed. The amount of the dowry depends on the bride's beauty and other qualities (her reproductive value; see Chapter 4), but above all on the status and wealth of the groom's family. In other words, payment of a dowry is made in order to marry a daughter into a family of the highest possible status, so some authorities regard dowry payment as a form of competition between women, assisted by their parents, to acquire the men with the most resources (see Chapter 4), while also improving the social standing of the bride's family.

These and many other examples reveal that many human traditions are at least partly explicable as being cultural adaptations that are the outcome of an 'evolutionary' process that does not involve a genetic change, but simply a change in socially transmitted conventions.

11.5. Consciousness and self-awareness

Consciousness in humans is considered the mental state in which we normally find ourselves, except when in deep sleep. The condition is readily identified in relation to human beings, in that if we are conscious we are capable of making conscious decisions. The problem is to know whether or not other animals are also capable of this state. Before addressing this question we should bear in mind that two main types of consciousness may be thought to exist: basic consciousness and higher level consciousness. Basic consciousness allows an individual to make decisions based on the current situation and its acquired experience, without necessarily needing to understand the concepts of past and future or having to be self-aware. This type of consciousness exists in birds, mammals and some other animal groups. There are many species whose members decide what to do not only by bearing in mind where they are and where they want to go to, but also considering their previous experiences, for example, those relating to difficulties posed by terrain or the presence of predators.

Higher level consciousness implies higher cognitive levels including detailed long-term memory, more complex social communication, an ability to distinguish between past, present and future and especially self-awareness. For these reasons it has traditionally been regarded as exclusive to our species. Self-awareness is one of the most fascinating mental attributes of the human species. Not only do we have a mind, we are also aware that we have one and can act accordingly. We are aware of the concept of 'me' and can distinguish it perfectly well from that of 'them', which relates to our fellow human beings.

Are non-human animals self-aware? It has been assumed, since the pioneering work of Gordon Gallup, a psychologist at New York State University, USA, that the fact that an individual can recognise its reflection in a mirror as itself and not as a congener - by using it to explore unfamiliar parts of its own body - is an indicator of self-awareness. Gallup did his first experiments with chimpanzees and he discovered that, at first, they behaved as if faced by a same-sex congener. Thereafter they began to perform test movements while looking in the mirror. After a while, which could be anything from a few minutes to several days, they began to use the mirror to explore some otherwise hidden parts of their own bodies (Gallup 1970). In other words, they showed behaviour similar to that of two-year-old children faced with a mirror. He also thought up an intriguing experiment in which sedated chimpanzees were painted with a mark above the right eyebrow and another on top of the left ear. When the chimpanzees woke up he noted their behaviour during thirty minutes in the absence of the mirror and then for another thirty minutes when the mirror was present. During this second period they touched the marked areas much more often than during the first stage. After touching the marks they also looked at and sniffed their fingers (Gallup 1970). The experiment showed that the chimpanzees genuinely used the mirror to explore their own bodies and that they were aware of what they were doing.

Recognition experiments involving mirrors have been carried out on a great number of animal species since Gallup's early studies. Most of these other species either behave as if they are confronted by a congener (as in some fish and birds) or otherwise they just ignore the reflection after a short time (as do cats and dogs). We could therefore conclude that these lack self-awareness. But what about our other fellow primates? According to a review by de Veer & Van den Bos (1999), chimpanzees, bonobos and orangutans all used the mirror to explore their own bodies. Among other anthropoid apes, gorillas failed to do so (with the exception of two human-raised individuals) and neither did gibbons. The mirror experiment has also been tried with many other primate species but only one of them, the cottontop tamarin (*Saguinus oedipus*), used it for self-exploration. These findings appear to show that only some of our closest relatives possess self-awareness. Nevertheless, it has recently been shown that at least two non-primate mammals, the bottlenose dolphin and the Indian elephant, also recognise themselves in mirrors (Plotnik *et al.* 2006).

These findings indicate that self-awareness only exists in mammals with large brains and with quite complex social systems. However, an extraordinary and unexpected discovery was made recently. Helmut Prior, of Goethe University, Germany, and his co-workers have found that a corvid, the magpie (*Pica pica*), is also capable of recognising itself in a mirror (Prior *et al.* 2008). Their discovery is of great significance because it implies that a high level of cognitive capacity, as is needed to recognise oneself in a mirror, has evolved independently in birds and mammals, two vertebrate groups whose evolutionary histories diverged many millions of years ago.

11.6. Awareness of shared consciousness

A step beyond self-awareness is being conscious of the minds of others and acting accordingly. This capability goes under a diversity of names, chiefly ‘Machiavellian intelligence’ and the ‘theory of mind’. Both refer to the idea that at least some primates are conscious both of their own mental processes and those of others, allowing them to predict the motivation and behaviour of other individuals in order to exploit or respond effectively to these companions.

A good test that an animal is conscious of the thinking of others is to show the existence of premeditated deception. To claim this requires great caution, however, because it is very hard to decide whether a deception is the result of a previously conceived plan. Three types of deception may be distinguished in animals: that which results from a premeditated plan that demands high cognitive capacity; that which only requires associative learning; and that which is simply the result of an innate evolutionary strategy. We shall consider these briefly in reverse order, that is from the least complex to the form that is most demanding of cognitive ability.

Most deceptions have a significant innate component. Even we humans often act first and only notice that we have been deceptive afterwards. Throughout this book we have seen a great variety of examples of deceptive behaviour, all of which are responses favoured by natural selection. Examples include extra-pair copulations (Chapter 5) and the behaviour of the males of some polygynous bird species that succeed in being taken for bachelors by singing to attract a second female far away from the nest where their first female is incubating (Chapter 6). An example that makes it obvious that a deception, however perfect, need not be premeditated is the case of the bee orchids (Chapter 9) that imitate a female hymenopteran to attract males who, while trying to copulate the flower, pollinate the orchid without the plant having to repay them with nectar or pollen in exchange.

Other types of deception, although always having an innate basis, may be determined by associative learning, without any need for complex cognitive abilities. The barn swallow (*Hirundo rustica*) behaviour that we studied in detail in Chapter 10 provides an example. A male swallow that sees that its female is being courted by another male gives an alarm call that interrupts the courtship. The alarm call is deceptive because it is given in the absence of an approaching predator. This behaviour is probably not based on a conscious decision, but is simply activated when the deceiver is confronted by the threat that another male will copulate with the alarm caller’s female.

It may be that, in addition to any innate impulse, the calling individuals have learnt that the alarm call interrupts courtship. Associative learning of this type, in which a specific behaviour results in a benefit, surely explains nearly all the instances of 'conscious deception' that owners attribute to their dogs and cats. Nobody can know for sure what passes through an animal's mind but 'Occam's razor' applies here. This is a basic scientific principle that postulates that the simplest explanation is generally the valid one. In this case, if an animal's behaviour can be explained by associative learning, it would be wrong to accept that it is actually due to high cognitive capacity.

An investigation by Emilie Genty and her coworkers at the D.E.P.E. centre in Strasbourg, France, has produced the results that come closest to demonstrating premeditated deception in a non-human animal species, although the investigators offered a simpler explanation. Four brown lemurs (*Eulemur fulvus*) were trained over a long period to indicate to their trainer under which of two bowls a raisin had been hidden. The trainer put the raisin under one of the bowls in view of the lemur. When the animal indicated where the raisin was the trainer would show herself to be cooperative and would give it to the lemur. The experiments proper began once this procedure had been mastered. These involved an additional experimenter who instead behaved competitively, by eating the raisin when the lemur showed where it was. One of the four lemurs now changed its behaviour; it pointed out where the raisin was to the cooperative experimenter, but often pointed to the empty basin in the presence of the competitive experimenter (Genty *et al.* 2008). The investigators considered that the behaviour of the lemur that deceived the competitive experimenter was not necessarily due to conscious deception. They suggested a simpler explanation that the long training process allowed it to learn (via a complex process of associative learning) to inhibit or reduce its learnt response when it was confronted with the competitive experimenter.

Conscious and premeditated deception demands much higher cognitive abilities than simply learning to deceive. In fact, in humans, whereas children learn to lie almost as soon as they can speak, at around the age of two-and-a half years, premeditated deception is very rare before the age of four (Newton *et al.* 2000).

Unambiguous instances of premeditated deception in non-human animals are very rare. After reviewing all available data, Byrne (1995) concluded that they can only be accepted to occur in three species: the chimpanzee, the orang-utan and the gorilla, being particularly evident in the chimpanzee. A subsequent review of the abundant experimental and observational data on chimpanzees concluded that they are more than sufficient to confirm this capability. The ability of chimpanzees to respond appropriately in very different situations, especially when confronted with novel problems, suggests that they learn from experience and make use of it to solve future challenges, employing deception when required *(*Call 2001). This account gives a fascinating example. A young chimpanzee wanted to approach its mother to suckle but she was engaged in mutual grooming with a male and rejected the infant because it was already quite grown up. The youngster began to shriek and make gestures to bluff that it had been attacked by a nearby adolescent, all the while running towards its mother. She responded by taking the infant in her arms and allowing it to suckle. This is an anecdote but, because no attack had occurred, all the indications were that the youngster bluffed in order to get what it wanted.

11.7. Emotions

Emotion is a central topic in psychology and has been the subject of a great number of books and articles. However, its role in non-human animals has received little attention. Psychologists tend to recognise two types of emotions, primary and secondary. The first group includes fear and other innate emotions (see Box 11.4). Even babies experience primary emotions from their earliest days. Many primary emotions are also exhibited by other animals, most clearly in our closest relatives, the anthropoid apes. This is unsurprising given the evident adaptive advantages of particular emotions. For example, it is highly advantageous to an individual's survival that fear should provoke flight, either to its mother if it is an infant or to a more secure place if it is an adult.

In humans, secondary emotions develop from the primary ones as a child grows and experiences new social situations. A stimulus provokes a bodily response (emotion) that, once detected, affects the mind (the sensation of emotion). Social emotions drive a child to repeat those behaviours that lead to positive emotions and to avoid those that provoke negative ones.

PRIMARY EMOTIONS SECONDARY (OR SOCIAL) EMOTIONS

Fear	Guilt
Anger	Shame
Joy	Loyalty
Sorrow	Revenge
Surprise	Compassion
Disgust	Remorse
Curiosity	Gratitude

Box 11.4. The chief primary and secondary emotions.

Emotions play a key role in making 'conscious' decisions because they favour that, from the start of the reasoning process, only those reasonable options that give rise to positive emotions, whereas those leading to negative emotions are rejected (Barrett *et al.* 2002). This mechanism allows decisions to be taken far more quickly than would be possible if all possible costs and benefits had to be evaluated every time. Making decisions would then be impossible because the mind cannot perform these largely unconscious processes without the input of the emotions (Barret *et al.* 2002).

The indispensable influence of emotions on decision making was made clear by Antonio Damasio, a renowned Portuguese neurobiologist (cited by Ridley 1997), who analysed the brains of twelve patients who had accidentally lost a small part of their prefrontal lobes. None suffered any memory loss and their intelligence was unimpaired by the accident. However, they had lost their emotions and this rendered them incapable of taking decisions.

Do other primates also display secondary emotions? They do, in my opinion. Bearing in mind that the emotions, as with other mental abilities, resulted from an evolutionary process that began long before the emergence of the human species, primates at least should possess something similar. Nevertheless, as we have noted, this topic has been little studied in other animals and so it remains open to speculation.

11.8. The sense of justice

Emotions can be regarded as mental mechanisms that favour the maintenance of a diversity of social obligations. The sense of fairness is very closely associated with certain secondary emotions such as guilt, loyalty, revenge and gratitude, which have been the subject of some outstanding work with non-human subjects. One of the most notable is Marc Hauser's work with rhesus macaques (*Macaca mulatta*), to which we referred in Chapter 10. Here individuals that discovered food, and were caught eating it without having informed their companions, were the targets of more aggression from other group members than those who signalled when they found food. Such aggression constituted the punishment of the selfish individuals (Hauser 1992).

Chimpanzees also engage in collective punishment of antisocial individuals. In his suggestively entitled book 'Chimpanzee politics', Frans de Waal notes that males often form mutual-help coalitions, thanks to which they gain access to a diversity of resources, not just food but also females. He also provides evidence that coalition members attack those that shy off or refuse to help during an inter-group conflict (de Waal 1993).

One of the best indications of the existence of a sense of fairness in animals was furnished by Sarah Brosnan and Frans de Waal, of Emory University, USA, in their work on the black-capped capuchin monkey (*Cebus apella*). They performed a series of experiments with ten individuals, five males and five females, tested in pairs. The tests made use of two small, adjacent cages that allowed the monkeys to see and hear each other and the experimenter. The experiment involved providing the monkeys with a granite token that they could exchange for a piece of cucumber or for their much-preferred food, a grape. The experimenter stood before one of the cages with the left palm extended in a begging gesture and the right hand in the pocket of his laboratory coat. If the individual handed over its token the experimenter gave it its food reward, in full view of the other monkey. The process was then repeated with the second monkey. The experiment involved four types of tests, the two experimental ones in which the monkeys received the same or different foods and two control ones, one a control for effort in which food was given without any token in exchange, and one a control for food type (Brosnan & de Waal 2003).

The results proved fascinating. The monkeys refused to hand over the token when they saw that their companion got a better reward for the same effort. This was even more the case when the companion got the better reward without any effort at all, i.e. without first handing over the token. It seems therefore that capuchin monkeys, as with humans, are capable of evaluating their rewards by comparing them with those received by other individuals. They got no reward if they did not hand over token but, notwithstanding, they rejected an otherwise acceptable reward when they saw that a companion was getting a better reward for the same effort (Brosnan & de Waal 2003).

Although this experiment does not reveal anything on what motivated the responses of the capuchin monkeys, it seems quite likely that secondary emotions played an important role, just as they would in humans. The sense of fairness is universal among human cultures and is thought to be one of the pillars of the evolution of cooperation in our species. Given that there are many other cooperative species, it should not surprise us if the sense of fairness also exists in some of these animals. The black-capped capuchin study suggests that the rejection of unequal treatment may have evolved well before the emergence of the human (Brosnan & de Waal 2003).

In another interesting study, a group of chimpanzees were allowed to participate in an 'ultimatum game', an experimental technique often used with humans. It involves two participants; person A is given money that he or she needs to share with person B. A must make B an offer and, if B accepts, the money is shared between them accordingly. If B rejects the offer, both get nothing. A selfish economic model predicts that A will offer as little as possible and that B will accept whatever is offered because something, however little, is better than nothing. The prediction is not fulfilled with humans, where A tends to offer 40-50% of the money and B tends to reject any offer below 20%, a result that reflects the human sense of fair play.

Keith Jensen at his co-workers at the Max Plank Institute of Evolutionary Anthropology, Leipzig, Germany, carried out a series of similar tests on chimpanzees. Two individuals were placed in facing cages such that they could see each other and the experimental apparatus. One chimpanzee, equivalent to person A, could use a cord to pull a tray with one of two possible offers halfway within the reach of the other chimpanzee. The other, equivalent to person B, had the option to use another cord to bring the tray close enough for both of them to obtain the food rewards. Alternatively, it could refuse to do so, in which case neither chimpanzees got any food. One of the two offers was always 8/2, that is, eight raisins for the individual that made the offers and two for the one who has to decide whether to accept or not. This offer was confronted to a second one that could be 5/5, 2/8, 8/2 and 10/0. The results revealed that chimpanzee B accepted any offer other than 10/0. In other words chimpanzee behaviour fulfils the predictions of the selfish model, contrary to what happens with humans. It would thus seem that chimpanzees do not have a sense of fairness. This conclusion is also supported by the finding that in a similar game with humans, when person B rejected an unfair offer he or she tended to be cross, whereas chimpanzees did not seem irritated by 10/0 offers (Jensen *et al.* 2007).

11.9. Morality and religion

The moral sense, which is the capacity for distinguishing right from wrong, and the capacity for believing in a superior, infinitely powerful entity, are considered to be two of the most sublime and universal of human characteristics. These attributes are present in all human cultures (see Box 11.5 for definitions and comments). It is true that there are complex, nuanced circumstances in which it may be hard to decide between right and wrong, and different people may well disagree in particular cases. However, in more straightforward situations, most people usually have a clear and similar idea of what is right and what is wrong, even if they belong to different cultures (Broom 2003). This coincidence of opinions suggests the possibility that our moral sense may be determined, as least in part (see Chapter 1), by our genes; in other words, that it is one more outcome of natural selection. Many books and publications offer a large diversity of arguments in support of just such a possibility.

There is a clear connection between this section and the previous one, because the moral sense demands an innate capacity for fairness. Nevertheless, the fact that an animal may have a sense of fairness, as we saw in the capuchin monkey example, does not necessarily means that it also has a moral sense. To be moral it must be associated with goodness instead of evil, and these abstract concepts are generally considered to apply exclusively to humans.

Does anything resembling the moral sense exist in animals? Consider the following example. In most birds, if the female loses her mate at the start of the breeding season, she will strive to find another male as soon as possible and will pair with him. Nevertheless, there are some strictly monogamous species, such as the jackdaw (*Corvus monedula*), where, if such an event happens, the female does not seek a replacement, but instead becomes listless and relatively inactive, as if sad or depressed, and this condition may endure for years (Lorenz 1982). As we have noted on several occasions, the crow family, to which the jackdaw belongs, is distinguished by having large brains and outstanding cognitive capacities. Does this then mean that jackdaws have a moral sense? Not necessarily, but it is possible that they have certain primary emotions, something resembling sorrow or disgust, that may reduce their instinctive drive to find a new mate.

- The **moral sense** involves deciding whether something is right or wrong, correct or incorrect, and acting accordingly.
  - o It is universal among human beings.
  - o Nearly everyone agrees that, from a moral viewpoint, altruism is good and selfishness is bad.

o The moral sense is present in everybody irrespective of religion or of whether they are atheists.

• **Ethics** is the discipline concerned with the study of matters associated with morality.

• A **religion** is a system of beliefs and rules that are considered to emanate directly or indirectly from some intangible power, whom individuals venerate and follow throughout their lives (Broom 2003).

o All human societies have or have had some type of religious belief and all are convinced that their religion is the true one.

o The qualities attributed to the divinities are simply exaggerations of human characteristics, such as absolute power, immortality and supreme wisdom.

o Being a believer makes people more confident.

o Religious belief increases solidarity within a society but it also increases antagonism between groups with different religions.

o Religion promotes the emergence and stability of societies.

o Belief in a moral god favours the development of social inequalities, both political and economical.

Box 11.5. Definitions and some widely accepted characteristics of morality and religion. After Ridley (1997), Broom (2003), Meyerstein et al. (2006) and Norenzayan & Shariff (2008).

Group members have been seen to help sick individuals in a number of social species, as reported for whales, rhesus and Japanese macaques and elephants (see review by Broom 2003). This does not necessarily imply a moral sense, however. It may be explicable in terms of simpler systems such as kin selection and reciprocity (see Chapter 8).

Although some have suggested that the moral codes of other species need not be the same as human morality, and others have maintained that ‘many aspects of human morality have their equivalents in the societies of other animals’ (Broom 2003), there does not seem to be any scientific evidence that any non-human animal possesses a moral sense. Nevertheless, because it is improbable that the human moral sense evolved without a predecessor, we may predict that there should be indications of morality in non-human animals, at least in primates. Accordingly, Frans de Waal has gathered numerous examples of ‘possible moral behaviour’, in chimpanzees especially (de Waal 1997).

Religion, on the other hand, is based on a belief in the existence of one or more superior beings that are responsible for all that exists and everything that happens (see definition in Box 11.5). Religion is a form of cultural expression that, as with language, is particular to the community that gave rise to it. Again like language, it requires an essential indoctrination, preferably during childhood, for an adult later to be a defender and practitioner of that religion.

Religions are generally based on moral codes that are the basis of their emergence and development. This, together with their universality, indicates that religions may be yet another product of natural selection. Human beings may be genetically predisposed to believe in totipotent, superior beings who will prescribe guidelines on how to conduct their lives. Religious belief is probably adaptive because a group that is convinced that it can count on the support of a powerful god will battle with greater conviction and determination and its members will tend to conquer their neighbours. They would then deprive them of their lands and other resources, enabling their population to increase, perhaps going on to conquer other territories in the future. Viewed in this way, religious belief could act as a very effective mechanism in favour of a group's evolutionary success (see Chapter 8).

Considerable interest has recently awakened in the scientific study of the role of religion as a facilitator of social cohesion in human beings. For some time, the social sciences have proposed that religions act to favour cooperation between the members of a community. This has been seen as the chief adaptive benefit of religion, particularly for members of large groups. The idea is supported by the well documented fact that religious societies tend to be more stable and longer lasting than areligious groups. Richard Sosis, of Connecticut University, and Eric Bressler, of McMaster University, both in the USA, have performed a comparative analysis of 83 19th century societies, both religious and lay, with a view to establishing why the religious ones tended to last longer than those based on purely social motives. Their chief aim was to put the 'costly signals hypothesis' to the test. This suggests that the rites, taboos and other obligations that religions impose are themselves responsible for the stability of religious associations. They examined over twenty types of religious obligations that different societies impose on their members and their statistical analysis found that, in accordance with the hypothesis, the number of costly demands imposed explained the endurance of religious societies, but not of lay ones (Sosis & Bressler 2003). These and others of their findings support the idea that the religious groups that impose the costliest obligations tend to have the most committed members, which thus gives the association its greater stability.

To conclude, although it is certainly the case that such human mental faculties as the moral and religious senses have not been demonstrated in other species, there is more than sufficient reason to credit Darwin when he asserted, approaching 150 years ago, that there is continuity between human mental capabilities and those of other animals (Darwin 1871). The only scientifically acceptable position nowadays is to accept the continuum between the minds of our closest relatives and that of the human species.

References

Abele, L. G. y Gilchrist, S. (1977): Homosexual rape and sexual selection in acanthocephalan worms. *Science* 197: 81-83.

Alam, N. (1995): Birth spacing and infant and early childhood mortality in a high fertility area of Bangladesh: age-dependent and interactive effects. *J. Biosoc. Sci.* 27: 393-404.

Alatalo, R. V.; Carlson, A.; Lundberg, A. y Ulfstrand, S. (1981): The conflict between male polygamy and female monogamy: the case of the pied flycatcher, *Ficedula hypoleuca. Am. Nat.* 117: 738-753.

Alberts, S. C.; Buchan, J. C. y Altmann, J. (2006): Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim. Behav.* 72: 1177-1196.

Albuquerque, A. C. S. R.; Sousa, M. B. C.; Santos, H. M. y Ziegler, T. E. (2001): Behavioral and hormonal analysis of social relationships between oldest females in awild monogamous group of common marmosets (*Callithrix jacchus*). *Int. J. Primatol.* 22: 631-645.

Alcock, J. (1993): *Animal Behaviour: An Evolutionary Approach.* Sinauer Associates, Sunderland.

Alcock, J. (2001): *TheTriumph of Sociobiology.* Oxford University Press, New York.

Allen, R. (1997): Agriculture and the origins of the state in ancient Egypt. *Expl. Econ. Hist.* 34: 135-154.

Alvarez, F. y Arias de Reyna, L. (1974): Reproduction de la Urraca, *Pica pica* en Donana. *Donana Acta Vert.* 1: 43-65.

Alvarez, F. y Flores, M. (1997): *Cymothoa exigua* (Isopoda: Cymothoidae) parasitando al pargo *Lutjanus peru* (Pisces: Lutjanidae) en Manzanillo, Colima, Mexico. *Rev. Biol. Trop.* 44-45: 391-394.

Amos, B.; Twiss, S.; Pomeroy, P. y Anderson, S. (1995): Evidence for mate fidelity in the gray seal. *Science* 268: 1897-1899.

Andres, J. A. y Cordero Rivera, A. (2000): Copulation duration and fertilization success in a damselfly: an example of cryptic female choice? *Anim. Behav.* 59: 695-703.

Apicella, C. L. y Marlowe, F. W. (2004): Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evol. Hum. Behav.* 25: 371378.

Arimura, G.; Ozawa, R.; Shimoda, T.; Nishioka, T.; Boland, W. y Takabayashi, J. (2000): Herbivory induced volatiles elicit defence genes in lima bean leaves. *Nature* 406, 512-515.

Arnold, S. J. (1976): Sexual behaviour, sexual interference and sexual defence in the salamanders *Ambystoma maculatum*, *A. tigrinum* and *Plethodon jordani. Z. Tierpsychol.* 42: 247-300.

Arnqvist, G. (1998): Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393: 784-788.

Arnqvist, G. y Rowe, L. (2002): Antagonistic coevolution between the sexes in a group of insects. *Nature* 415: 787-789.

Arroyo, B. E.; de Cornulier, Th. y Bretagnolle, V. (2002): Parental investment and parent-offspring conflicts during the postfledging period in Montagu's harriers. *Anim. Behav.* 63: 235-244.

Aviles, L. (1997): Causes and consequences of cooperation and permanent-sociality in spiders. En J. Choe y B. Crespi (eds.). *The Evolution of Social Behavior in Insects and Arachnids*, pp. 476-498. Cambridge University Press, Cambridge.

Axelrod, R. (1984): *The Evolution of Cooperation.* Basic Books, New York.

Ayasse, M.; Schiestl, F.P.; Paulus, H.F.; Lofstedt, C.; Hansson, B.; Ibarra, F. y Francke, W. (2000): Evolution of reproductive strategies in the sexually deceptive orchid *Ophrys sphegodes*: how does flower-specific variation of odor signals influence reproductive success? *Evolution* 54: 1995-2006.

Backwell, P. R.Y. y Passmore, N. I. (1996): Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes. Behav. Ecol. Sociobiol.* 38 : 407-416.

Baglione, V.; Canestrari, D.; Marcos, J.M. y Ekman, J. (2003): Kin selection in cooperative alliances of carrion crows. *Science* 300: 1947-1949.

Baglione, V.; Canestrari, D.; Marcos, J. M.; Griesser, M. y Ekman, J. (2002): History, environment and social behaviour: experimentally induced cooperative breeding in the carrion crow. *Proc. R. Soc. Lond.* B 269: 1247-1251.

Baldi, R.; Campagna, C.; Pedraza, S. y Le Boeuf, B. J. (1996): Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Anim. Behav.* 51: 717-724.

Balmford, A.; Rosser, A. M. y Albon, S. D. (1992): Correlates of female choice in resource-defending antelope. *Behav. Ecol. Sociobiol.* 31: 107-114.

Barrett, L.; Dunbar, R. y Lycett, J. (2002): *Human Evolutionary Psychology.* Palgrave, New York.

Bartels, A. y Zeki, S. (2004): The neural correlates of maternal and romantic love. *Neuroimage* 21: 11551166.

Bateson, M.; Nettle, D. y Roberts, G. (2006): Cues of being watched enhance cooperation in a real-world setting. *Biol. Lett.* 2: 412-414.

Bensch, S. y Hasselquist, D. (1994): Higher rate of nest loss among primary than secondary females: infanticide in the great reed warblers? *Behav. Ecol. Sociobiol.* 35: 309-317.

Betzig, L. L. (1986): *Despotism and Differential Reproduction: A Darwinian View of History.* Aldine, New York.

Billing, J. y Sherman, P. W. (1998): Antimicrobial function of spices: Why some like it hot. *Q. Rev. Biol.* 73: 3-49.

Birkhead, T. R. (2007): *Promiscuidad.* Laetoli, Pamplona.

Bonckaert, W.; Vuerinckx, K.; Billen, J.; Hammond, R. L.; Keller, L. y Wenseleers, T. (2008): Worker policing in the German wasp *Vespula germanica. Behav. Ecol.* 19: 272-278.

Bourke A. F. G. (1994): Worker matricide in social bees and wasps. *J. Theor. Biol.* 167: 283-292.

Bowles, S. (2006): Group competition, reproductive levelling, and the evolution of human altruism. *Science* 314: 1569-1572.

Brantley, R. K. y Bass, A. H. (1994): Alternative male spawning tactics and acoustic signals in the plain fin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). *Ethology* 96: 213-232.

Briskie, J. V.; Montgomerie, R.; Poldmaa, T. y Boag, P. T. (1998): Paternity and paternal care in the polygynandrous Smith's langspur. *Behav. Ecol. Sociobiol.* 43: 181-190.

Brizendine, L. (2006): *The Female Brain.* Morgan Road, New York.

Broom, D. M. (2003): *The Evolution of Morality and Religion.* Cambridge University Press, Cambridge.

Brosnan, S. y de Waal, F. B. M. (2003): Monkeys reject unequal pay. *Nature* 425: 297-299.

Brown, W. M.; Cronk, L.; Grochow, K.; Jacobson, A.; Liu, C. K.; Popovic, Z. y Trivers, R. (2005): Dance reveals symmetry especially in young men. *Nature* 438: 1148-1150.

Brumm, H. y Slater, P. J. B. (2006): Animals can vary signal amplitude with receiver distance: Evidence from zebra finch song. *Anim. Behav.* 72: 699-705.

Bshary, R. y Grutter, A. S. (2006): Image scoring and cooperation in a cleaner fish mutualism. *Nature* 441: 975-978.

Buchan, J. C.; Alberts, S.C.; Silk, J.B. y Altmann, J. (2003): True paternal care in a multi-male primate society. *Nature* 425: 179-181.

Buss, D. M. (2007): *La evolution del deseo.* Alianza Editorial, Madrid.

Buss, D. M.; Shackelford, T. K.; Kirkpatrick, L. A.; Choe, J.; Hasegawa, M.; Hasegawa, T. y Bennett, K. (1999): Jealousy and beliefs about infidelity: Tests of competing hypotheses in the United States, Korea and Japan. *Person. Rel.* 6: 125-150.

Buss, D. M.; y 50 colaboradores (1990): International preferences in selecting mates: A study of 37 societies. *J. Cross-Cult. Psychol.* 21: 5-47.

Byrne, P. G. y Keogh, J. S. (2009): Extreme sequential polyandry insures against nest failure in a frog. *Proc. R. Soc. B* 276:115-120.

Byrne, R. (1995): *The Thinking Ape: Evolutionary Origins of Intelligence.* Oxford University Press, Oxford.

Cade, W. H. (1979): The evolution of alternative male reproductive strategies in field crickets. En M. Blum y N. A. Blum (eds.). *Sexual selection and reproductive competition in insects,* pp. 343-379, Academic Press, London.

Call, J. (2001): Chimpanzee social cognition. *Trends Cog. Sci.* 5: 388-393.

Carranza, J.; Garda-Munoz, A. J. y Vargas, J. de D. (1995): Experimental shifting from harem defence to territoriality in rutting red deer. *Anim. Behav.* 49: 551-554.

Carre, D.; Rouviere, C. y Sardet, C. (1991): In vitro fertilisation in ctenophores: Sperm entry, mitosis, and the establishment of bilateral symmetry in *Beroe ovata. Dev. Biol.* 147: 381-391.

Carreiras, M.; Lopez, J.; Rivero, F. y Corina D. (2005): Neural processing of a whistled language. *Nature* 433: 31-32.

Carter, C. S. y Getz, L. L. (1993): Monogamy and the prairie vole. *Sci. Am.* 268: 100-106.

Cartwright, J. (2000): *Evolution and Human Behaviour*. Macmillan Press, London.

Chagnon, N. A. (1988): Life histories, blood revenge, and warfare in a tribal population. *Science* 239: 985992.

Chomsky, N. (1957): *Syntactic Structures*. Mouton, The Hague.

Chuang-Dobbs, H. C.; Webster, M. S. y Holmes, R. T. (2001): The effectiveness of mate guarding by male black-throated blue warblers. *Behav. Ecol.* 12: 541546.

Clark, R. D. y Hatfield, E. (1989): Gender differences in receptivity to sexual offers. *J. Psicol. Hum. Sex.* 2: 39-55.

Clutton-Brock, T. (2007): Sexual selection in males and females. *Science* 318: 1882-1885.

Clutton-Brock, T. H. y Parker, G. A. (1995): Punishment in animal societies. *Nature* 373: 209216.

Connor, R. C.; Heithaus, M. R. y Barre, L. M. (1999): Superalliance of bottlenose dolphins. *Nature* 397: 571-572.

Conradt, L. y Roper, T. J. (2005): Consensus decision making in animals. *Trends Ecol. Evol.* 20: 449-456.

Cooper, M. A.; Aureli, F. y Singh, M. (2007): Sex differences in reconciliation and post-conflict anxiety in bonnet macaques. *Ethology* 113: 26-38.

Cornwallis, C. K. y Birkhead, T. R. (2006): Social status and availability of females determine patterns of sperm allocation in the fowl. *Evolution* 60: 14861493.

Cote, I. M.; Vinyoles, D.; Reynolds, J. D.; Doadrio, I. y Perdices, A. (1999): Potential impacts of gravel extraction on Spanish populations of river blennies *Salaria fluviatilis* (Pisces, Blennidae). *Biol. Conserv.* 87: 359-367.

Coutinho, E. M. (2002): Gossypol: a contraceptive for men. *Contraception* 65: 259-263.

Crespi, B. J. (2001): The evolution of social behavior in microorganisms. *Trends Ecol. Evol.* 16: 178-183.

Dally, J. M.; Emery, N. J. y Clayton, N. S. (2006): Food-caching western scrub-jays keep track of who was watching when. *Science* 312: 1662-1665.

Daly, M. y Wilson, M. I. (1988): *Homicide.* Aldine de Gruyter, Hawthorne, Nueva York.

Darwin, C. (1859): *On the Origin of Species by Means of Natural Selection or the preservation of Favored Races in the Struggle for Life.* John Murray, London.

Darwin, C. (1871): *The Descent of Man, and Selection in Relation to Sex.* John Murray, London.

Davies, N. B. (1983): Poliandry, cloaca-pecking and sperm competition in dunnocks. *Nature* 302: 334336.

Davies, N. B. (1992): *Dunnock Behaviour and Social Evolution.* Oxford University Press, Oxford.

Davies, N. B. (2000): *Cuckoos, Cowbirds and Other Cheats.* T & A. D. Poyser, London.

de la Torre, S. y Snowdon, C. T. (2002): Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea. Anim. Behav.* 63: 847-856.

de Moraes, C. M.; Lewis, W. J.; Pare, P. W.; Alborn, H. T. y Tumlinson, J. H. (1998): Herbivore-infested plants selectively attract parasitoids. *Nature*: 393: 570-573.

de Quervain, D. J.-F.; Fischbacher, U.; Treyer, V.; Schellhammer, M.; Schnyder, U.; Buck, A. y Fehr, E. (2004): The neural basis of altruistic punishment. *Science* 305: 1254-1258.

de Veer, M. W. y Van den Bos, R. (1999): A critical review of methodology and interpretation of mirrorself-recognition research in nonhuman primates. *Anim. Behav.* 58: 459-468.

de Waal, F. (1997): *Bonobo: The Forgotten Ape.* University of California Press, Berkeley.

de Waal, F. B. M. (1993): *La poh'tica de los chimpances: el poder y el sexo entre los simios.* Alianza Editorial, Madrid.

de Waal, F. B. M. (1997): *Bien natural: los ongenes del bien y del mal en los humanos y otros animales.* Herder S.A. Editorial. Barcelona.

Diamond, J. (1992): *TheThird Chimpanzee.* HarperCollins Publishers, New York.

Dijkstra, M. B.; Nash, D. R. y Boomsma, J. J. (2005): Self-restraint and sterility in workers of *Acromyrmex* and *Atta* leafcutter ants. *Insect. Soc.* 52: 67-76.

Dixson, A. F. (1987): Observations on the evolution of the genitalia and copulatory behaviour in male primates. *J. Zool., Lond.* 213: 423-443.

Dockery, M. y Reiss, M. (1999): *Behaviour.* Cambridge University Press, Cambridge.

Domb, L. G. y Pagel, M. (2001): Sexual swellings advertise female quality in wild baboons. *Nature* 410: 204-206.

Dominey, W. (1980): Female mimicry in male bluegill sunfish - a genetic polymorphism? *Nature.* 284: 546548.

Eberhard, W. G. (1996): *Female Control: Sexual Selection by Cryptic Female Choice.* Princeton University Press, Princeton.

Efferson, C.; Lalive, R. y Fehr, E. (2008): The coevolution of cultural groups and ingroup favoritism. *Science* 321: 1844-1849.

Ekman, J.; Bylin, A. y Tegelstrom, H. (2000): Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behav. Ecol.* 11: 416-420.

Evans, S. y Poole, T. B. (1983): Pair-bond formation and breeding success in the common marmoset *Callithrix jacchus jacchus. Int. J. Primatol.* 4: 83-97.

Fehr, E.; Bernhard, H. y Rockenbach, B. (2008): Egalitarianism in young children. *Nature* 454: 10791083.

Ferh, E. y Gachter, S. (2002): Altruistic punishment in humans. *Nature* 415:137-140.

Fischhoff, I. R.; Sundaresan, S. R.; Cordingley, J.; Larkin, H. M.; Sellier, M.-J. y Rubenstein, D. I. (2007): Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii. Anim. Behav.* 73: 825-831.

Fisher, S. E.; Vargha-Khadem, F.; Watkins, K. E.; Monaco, A. P. y Pembrey, M. E. (1998): Localisation of a gene implicated in a severe speech and language disorder *Nat. Genet.* 18: 168-170.

Francis, C. M.; Anthony, E. L. P.; Brunton, J. A. y Kunz, T. H. (1994): Lactation in male fruit bats. *Nature* 367: 691-692.

Frisch, K. V. (1976): *La vida de las abejas.* Editorial Labor, S. A., Barcelona.

Fujisawa, K. K.; Kutsukake, N. y Hasegawa T. (2006): Peacemaking and consolation in japanese preschoolers witnessing peer aggression. *J. Comp. Psychol.* 120: 48-57.

Futuyma, D. J. (1998): *Evolutionary Biology.* Sinauer Associates, Inc., Sunderland, Massachusetts.

Gallup, G. G. Jr. (1970): Chimpanzees: self-recognition. *Science* 167: 86-87.

Gallup, G. G. Jr.; Burch, R. L.; Zappieri, M. L.; Parvez, R.; Stockwell, M. y Davis, J. A. (2003): The human penis as a semen displacement device. *Evol. Hum. Behav.* 24: 277-289.

Gangestad, S. W.; Thornhill, R. y Garver, C. E. (2002): Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: evidence for shifting conflict of interest. *Proc. R. Soc. Lond. B* 269: 975-982.

Gary, N. E. (1963): Observations of mating behaviour in the honeybee. *J. Apic. Res.* 2: 3-13.

Gatti, S.; Levrero, F.; Menard, N. y Gautier-Hion, A. (2004): Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoue, Republic of Congo. *Am. J. Primatol.* 63, 111-123.

Gaulin, S. J. C. y Boster, J. S. (1990): Dowry as female competition. *Am. Anthropol.* 92: 994-1005.

Genty, E.; Foltz, J. y Roeder, J.-J. (2008): Can brown lemurs (*Eulemur fulvus*) learn to deceive a human competitor? *Anim. Cogn.* 11: 255-266.

Gibson, M. A. y Mace, R. (2007): Polygyny, reproductive success and child health in rural Ethiopia: Why marry a married man? *J. Biosoc. Sci.* 39: 287-300.

Gilbert, L. E. (1976): Postmating female odor in *Heliconius* butterflies: a male contributed antiafrodisiac? *Science* 193: 419-420.

Gil-Burmann, C.; Pelaez, F. y Sanchez, S. (2002): Mate choice differences according to sex and age: an analysis of personal advertisements in Spanish newspapers. *Hum. Nat.* 13: 493-508.

Gillespie, T.W. y Hillyer, C.D. (2002): Blood donors and factors impacting the blood donation decisions. *Trans. Med. Rev.* 16: 115-130.

Giurfa, M. (2003): Cognitive neuroethology: disecting non-elemental learning in a honeybee brain. *Curr. Op. Neurobiol.* 13: 726-735.

Glazier, D. S. (2002): Parental care. En M. Pagel (ed.). *Encyclopedia of Evolution.* pp. 860-865. Oxford University Press, New York.

Glynn, S. A.; Busch, M. P.; Schreiber, G. B.; Murphy, E. L.; Wright, D. J.; Tu, Y. y Kleinman, S. H. (2003): Effect of a national disaster on blood supply and safety: the September 11 experience. *JAMA* 289:2246-2253.

Goldizen, A. W.; Mendelson, J.; Vlaardingen, M. van y Terborgh, J. (1999): Saddleback tamarin (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *Am. J. Primat.* 38: 57-83.

Goleman, D. (2006): *Social Intelligence: The New Science of Human Relationships.* Hutchinson, London

Gomez, M.; de Castro, E.; Guarin, E.; Sasakura, H.; Kuhara, A.; Mori, I.; Bartfai, T.; Bargmann, C. I. y Nef1, P. (2001): Ca^{2+} signalling via the neuronal calcium sensor-1 regulates associative learning and memory in *C. elegans. Neuron* 30: 241-248.

Goodall, J. (1986): *The Chimpanzees of Gombe: Patterns of Behavior.* Harvard University Press, Harvard.

Grant, P. R. y Grant, B. R. (2006): Evolution of character displacement in Darwin's finches. *Science* 313: 224-226.

Grant P. R. (1996): Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* 50: 2471-2487.

Green, D. J. y Krebs, E. A. (1995): Courtship feeding in Ospreys *Pandion haliaetus*: a criterion for mate assessment? *Ibis* 137: 35-43.

Greenlees, I. A. y McGrew, W. C. (1994): Sex and age differences in preferences and tactics of mate attraction: analysis of published advertisements. *Ethol. Sociobiol.* 15: 59-72.

Griesser, M. (2008): Referential calls signal predator behavior in a group-living bird species. *Curr. Biol.* 18: 69-73.

Griesser, M. y Ekman, J. (2005): Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus. Anim. Behav.* 69: 345-352.

Griffin, D. (1992): *Animal Minds.* University of Chicago Press, Chicago.

Griggio, M. y Pilastro, A. (2007): Sexual conflict over parental care in a species with female and male brood desertion. *Anim. Behav.* 74: 779-785.

Grim, T.; Kleven, O. y Mikulica, O. (2003): Nestling discrimination without recognition: A possible defence mechanism for hosts towards cuckoo parasitism? *Proc. R. Soc. Lond. B* 270: S73-S75.

Hamilton, W. D. (1964): The genetical evolution of social behaviour. *J. Theor. Biol.* 7: 1-51.

Hannonen, M. y Sundstrom, L. (2003): Worker nepotism among polygynous ants. *Nature* 421: 910.

Harcourt, A. H.; Harvey, P. H.; Larson, S. G. y Short, R. V. (1981): Testis weight, body weight and breeding system in primates. *Nature* 293: 55-57.

Harris, M. (2006): *Nuestra especie.* Alianza Editorial, Madrid.

Hashimoto, C. (1997): Context and development of sexual behavior of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *Int. J. Primatol.* 18: 1-21.

Hasselquist, D.; Bensch, S. y Von Schantz, T. (2002): Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* 381: 229-232.

Hauser, M. D. (1992): Costs of deception: cheaters are punished in rhesus monkeys (*Macaca mulatta*). *Proc. Natl. Acad. Sci. USA* 89: 12137-12139.

Heinrich, B. (1996): An experimental investigation of insight in common ravens, *Corvus corax. Auk* 112: 994-1003.

Heinsohn, R.; Ebert, D.; Legge, S. y Peakall, R. (2007): Genetic evidence for cooperative polyandry in reverse dichromatic *Eclectus* parrots. *Anim. Behav.* 74: 1047-1054.

Helle, S.; Lummaa, V. y Jokela, J. (2008): Marrying women 15 years younger maximized men's evolutionary fitness in historical Sami. *Biol. Lett.* 4: 75-77.

Hemelrijk, C. K. (1999): An individual-orientated model of the emergence of despotic and egalitarian societies. *Proc. R. Soc. Lond. B* 266: 361-369.

Hemelrijk, C. K. y Steinhauser, J. (2007): Cooperation, coalition, and alliances. En W. Henke; I. Tattersall y T. Hardt (eds.). *Handbook of Paleoanthropology*, pp. 1321-1346. Springer, Berlin.

Herrmann, B.; Christian, T. y Gachter, S. (2008): Antisocial punishment across societies. *Science* 319: 1362-1367.

Herrmann, E.; Call, J.; Hernandez-Lloreda, M. V.; Hare, B. y Tomasello, M. (2007): Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317: 1360-1366.

Hill, K. y Hurtado, A. M. (1996): *Ache Life History: The Ecology and Demography of a Foraging People.* Aldine the Gruyter, Nueva York.

Holmes, W. G. y Sherman, P. W. (1982): The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.* 22: 491-517.

Honza, M.; Voslajerova, K. y Moskat, C. (2007): Eviction behaviour of the common cuckoo *Cuculus canorus* chicks. *J. Avian Biol.* 38: 385-389.

Isack, H. A. y Reyer, H.-U. (1989): Honeyguides and honey gatherers: Interspecific communication in a symbiotic relationship. *Science* 243: 1343-1346.

Janik, V. M. y Slater, P. J. B. (1998): Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* 56: 829838.

Jasienska, G.; Ziomkiewicz, A.; Ellison, P. T.; Lipson, S. F. y Thune, I. (2004): Large breasts and narrow waists indicate high reproductive potential in woman. *Proc. R. Soc. Lond. B* 271: 1213-1217.

Jennions, M. D.; Moller, A. P. y Petrie, M. (2001): Sexually selected traits and adult survival: a metaanalysis of the phenotypic relationship. *Q. Rev. Biol.* 76: 3-36.

Jones, J. S. y Wynne-Edwards, K. E. (2000): Paternal hamsters mechanically assist the delivery, consume amniotic fluid and placenta, remove fetal membranes, and provide parental care during the birth process. *Horm. Behav.* 37: 116-125.

Juhas, M.; Eberl, L. y Tummler, B. (2005): Quorum sensing: the power of cooperation in the world of *Pseudomonas. Environ. Microbiol.* 7: 459-471.

Kahneman, D.; Krueger, A. B.; Schkade, D. A.; Schwarz, N. y Stone, A. A. (2004): A survey method for characterizing daily life experience: the day reconstruction method. *Science* 306: 1776-1780.

Karlsson, B. (1998): Nupcial gifts, resource budgets, and reproductive output in a polyandrous butterfly. *Ecology* 79: 2931-2940.

Keller, L. y Ross, K. G. (1998): Selfish genes: a green beard in the red fire ant. *Nature* 394: 573-575.

Kempenaers, B.; Verheyen, G. R. y Dhondt, A. A. (1997): Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics and offspring quality. *Behav. Ecol.* 8: 481-492.

Kempenaers, B.; Verheyen, G. R.; Van den Broeck, M. T. B.; Van Broeckhoven, C. y Dhondt, A. A. (1992): Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* 357: 494-496.

Komdeur, J. y Hatchwell, B. J. (1999): Kin recognition: function and mechanism in avian societies. *Trends Ecol. Evol.* 14: 237-241.

Krams, I.; Krama, T. y Igaune, C. (2006): Mobbing behaviour: reciprocity-based co-operation in breeding pied flycatchers *Ficedula hypoleuca. Ibis* 148: 50-54.

Krams, I.; Krama, T.; Igaune, C. y Mand, R. (2008): Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav. Ecol. Sociobiol.* 62: 599-605.

Krebs, J. R. y Davies, N. B. (1993): *An Introduction to Behavioural Ecology.* Blackwell Scientific Publications, Oxford.

Krekorian, C. (1976): Field observations in Guyana on the reproductive biology of the spraying characid, *Copeina arnoldi* Regan. *Am. Midland Nat.* 96: 8897.

Kutsukake, N. y Clutton-brock, T. (2008): Do meerkats engage in conflict management following aggression? Reconciliation, submission and avoidance. *Anim. Behav.* 75: 1441-1453.

Langmore, N. E.; Hunt, S. & Kilner, R. M. (2003): Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422: 157-160.

Lize, A.; Carval, D.; Cortesero, A. M.; Fournet, S. y Poinsot, D. (2006): Kin discrimination and altruism in the larvae of a solitary insect. *Proc. R. Soc. Lond. B* 273: 2381-2386.

Lorenz, K. (1982): *Hablaba con las bestias, los peces y los pajaros.* Labor S.A., Barcelona.

Low, B. S. (2000): *Why Sex Matters. A Darwinian Look at Human Behavior.* Princeton University Press. Princeton.

Lundberg, A. y Alatalo, R. V. (1992): *The Pied Flycatcher.* Poyser, London.

Mahsberg, D. (2001): Brood care and social behaviour. En P. H. Brownell y G. Polis (eds.). *Scorpions and research*, pp. 257-277. Oxford University Press, Oxford.

Marlowe, F. (1999): Male care and mating effort among hadza foragers. *Behav. Ecol. Sociobiol.* 46: 57-64.

Mateo, J. M. (2002): Kin-recognition abilities and nepotism as a function of sociality. *Proc. R. Soc. Lond. B* 269: 721-727.

McCracken, K. G. (2000): The 20 cm spiny penis of the Argentine lake duck (*Oxyura vittata*). *Auk* 117: 820825.

McDonald, D. B. y Potts, W. K. (1994): Cooperative display and relatedness among males in a lek-mating bird. *Science* 266: 1030-1032.

McNeill, W. (1976): *Plagues and Peoples.* Anchor books, New York.

Mcphail, E. M.; Good, M.; Honey, R. C. y Willis, A. (1995): Relational learning in pigeons: the role of perceptual processes in between-key recognition of complex stimuli. *Anim. Learn. Behav.* 23: 83-92.

Mealey, L. (2002): Evolutionary psychology. En M. Pagel (ed.), *Encyclopedia of Evolution*, pp. 541-546. Oxford University Press, New York.

Meyer, J. (2004): Bioacoustics of human whistled languages: an alternative approach to the cognitive processes of language. *An. Acad. Bras. Cienc.* 76: 405-412.

Meyerstein, F. W.; Brisson, L. y M0ller, A. P. *LifeTime: The Quest for a Definition of Life.* Georg Olms Verlag AG, Hildesheim.

Michiels, N. K. y Newman, L. J. (1998): Sex and violence in hermaphrodites. *Nature* 391: 647.

Miller, G. (2000): *The Mating Mind.* Anchor Books, New York.

Miller, G. (2007): Sexual selection for moral virtues. *Q. Rev. Biol.* 82: 97-125.

M0ller, A. (1990): Deceptive use of alarm calls by male swallows, *Hirundo rustica*: A new paternity guard. *Behav. Ecol.* 1: 1-6.

M0ller, A. P. (1987): Copulation behaviour in the goshawk *Accipiter gentilis. Anim. Behav.* 35: 755763.

M0ller, A. P. (1994): *Sexual Selection and the Barn Swallow.* Oxford University Press, Oxford.

M0ller, A. P. y de Lope, F. (1994): Differential costs of a secondary sexual character: An experimental test of the handicap principle. *Evolution* 48: 1676-1683.

M0ller, A. P. y Erritz0e, J. (1996): Parasite virulence and host immune defense: host immune response is related to nest reuse in birds. *Evolution* 50: 20662072.

M0ller, A. P.; Linden, M.; Soler, J. J.; Soler, M. y Moreno, J. (1995): Morphological adaptations to an extreme sexual display, stone-carrying in the black wheatear, *Oenanthe leucura. Behav. Ecol.* 6: 368375.

Mailer, A. P.; Soler, M. y Thornhill, R. (1995): Breast asymmetry, sexual selection, and human reproductive success. *Ethol. Sociobiol.* 16: 207-219.

Moreno, J. (2008): El mal llamado “darwinismo social” y la falacia naturalista: dos lacras a distinguir de la teoria de Darwin. *eVOLUCION* 3: 51-53.

Moreno, J. y Osorno, J. L. (2003): Avian egg colour and sexual selection: Does eggshell pigmentation reflect female condition and genetic quality? *Ecol. Lett.* 6: 803-806.

Moreno, J.; Soler, M.; M0ller, A. P. y Linden, M. (1994): The function of stone carrying in the black wheatear, *Oenanthe leucura. Anim Behav.* 47: 12971309.

Mosterm, J. (2006): *La naturaleza humana.* Espasa Calpe, Pozuelo de Alarcon (Madrid).

Mulcahy, N. J. y Call, J. (2006): Apes save tools for future use. *Science* 312: 1038-1040.

Mulder, R. A. (1997): Extra-group courtship displays and other reproductive tactics of superb fairy-wrens. *Aust. J. Zool.* 45: 131-143.

Mulder, R. A.; Dunn, P. O.; Cockburn, A.; Lazenby- Cohen, K. A. y Howell, M. J. (1994): Helpers liberate female fairy-wrens from constraints of extra-pair mate choice. *Proc. R. Soc. Lond.* B 255: 223-229.

Mulder, R. A. y Langmore, N. E. (1993): Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* 45: 830-833.

Nelson, J. (1995): Determinants of male spacing behavior in microtines: An experimental manipulation of female spatial distribution and density. *Behav. Ecol. Sociobiol.* 37: 217-223.

Nesse, R. M. y Williams, G. C. (2000): *^Por que enfermamos?*. Grijalbo, Barcelona.

Nettle, D. y Pollet, T. V. (2008): Natural selection on male wealth in humans. *Am. Nat.* 172: 658-666.

Neuser, K.; Triphan, T.; Mronz, M.; Poeck, B. y Strauss, R. (2008): Analysis of a spatial orientation memory in *Drosophila*. *Nature* 453: 1244-1247.

Newton, P.; Reddy, V. y Bull, R. (2000): Children's everyday deception and performance on false-belief tasks. *Br. J. Dev. Psychol.* 18: 297-317.

Norenzayan, A. y Shariff, A. F. (2008): The origin and evolution of religious prosociality. *Science* 322:5862.

Olsson, M.; Shine, R.; Madsen, T.; Gullberg, A. & Tegelstrom, H. (1996): Sperm selection by females. *Nature* 383: 585.

Ono, M.; Igarashi, T.; Ohno, E. y Sasaki, M. (1995): Unusual thermal defence by a honeybee against mass attack by hornets. *Nature* 277: 334-336.

Orians, G. H. (1969): On the evolution of mating systems in birds and mammals. *Am. Nat.* 103: 589603.

Panksepp, J. (1998): *Affective Neuroscience: The Foundations of Human and Animal Emotions.* Oxford University Press, Oxford.

Papachristoforou, A.; Rortais, A; Zafeiridou, G.; Theophilidis, G.; Garnery, L.; Thrasyvoulou, A. y Arnold, G. (2007): Smothered to death: hornets asphyxiated by honeybees. *Cur. Biol.* 17: R795- R796.

Parker, C.; Pusey, A. E. y Eberly, L. I. (2001): Egalitarianism in female African lions. *Science* 293: 690-693.

Pennings, S. C. (1991): Reproductive behavior of *Aplysia californica* Cooper: Diel patterns, sexual roles and mating aggregations. *J. Exp. Mar. Biol. Ecol.* 149: 249-266.

Petrie, M. (1994): Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* 371: 598-599.

Pietrzak, R.; Laird, J. D.; Stevens, D. A. y Thompson, N. S. (2002): Sex differences in human jealousy: a coordinated study of forced-choice, continuous rating-scale, and physiological responses on the same subjects. *Evol. Hum. Behav. 23:* 83-94.

Pilastro, A.; Biddau, L.; Marin, G. y Mingozzi, T. (2001): Female brood desertion increases with the number of available mates in the rock sparrow. *J. Avian Biol.* 32: 68-72.

Pinker, S. (1994): *The Language Instinct: How the Mind Creates Language.* Morrow, New York.

Pinker, S. (2003): *La tabla rasa.* Paidos, Barcelona.

Piper, W. H. (1997): Social dominance in birds: Early findings and new horizons. En V. Nolan, E. D. Ketterson y C. F. Thompson (eds.). *Current Ornithology. Vol. 14*, pp. 125-187. Plenum, New York.

Pizzari, T.; Cornwallis, C. K.; L0vlie, H.; Jakobsson, S. y Birkhead, T. R. (2003): Sophisticated sperm allocation in male fowl. *Nature* 426: 70-74.

Plotnik, J. M.; de Waal, F. B. M. y Reiss, D. (2006): Self-recognition in an Asian elephant. *Proc. Natl. Acad. Sci. USA* 103: 17053-17057.

Potts, W. K.; Manning, C. J. y Wakeland, E. K. (1991): Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature* 352: 619-621.

Pribil, S. y Searcy, W. A. (2001): Experimental confirmation of the polygyny threshold model for red-winged blackbirds. *Proc. R. Soc. Lond. B* 268: 1643-1646.

Prior, H.; Schwarz, A. y Gunturkun, O. (2008): Mirror- induced behavior in the magpie (*Pica pica*): evidence of self-recognition. *PLoS Biol.* 6(8): e202. doi:10.1371/journal.pbio.0060202.

Puurtinen, M. y Mappes, T. (2008): Between-group competition and human cooperation. *Proc. R. Soc. Lond. B* (in press).

Raby, C. R.; Alexis, D. M.; Dickinson, A. y Clayton, N. S. (2007): Planning for the future by wetern scrubjays. *Nature* 445: 919-921.

Radford, A. N. (2004): Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). *Ethology* 110: 11-20.

Ratnieks, F. L. W. y Wenseleers, T. (2007): Altruism in insect societies and beyond: voluntary or enforced? *Trends Ecol. Evol.* 23: 45-52.

Reeve, H. K. (1992): Queen activation of lazy workers in colonies of the eusocial naked mole-rat. *Nature* 358: 147-149.

Reeve, H. K.; Starks, P. T.; Peters, J. M. y Nonacs, P. (2000): Genetic support for the evolutionay theory of reproductive transactions in social wasps. *Proc. R. Soc. Lond. B* 276: 75-79.

Rhodes, G.; Simmons, L. W. y Peters, M. (2005): Attractiveness and sexual behavior: Does attractiveness enhance mating success?. *Evol. Hum. Behav.* 26: 186-201.

Ridley, M. (1997): *The Origins of Virtue.* Penguin, London.

Ridley, M. (2004): /,*Que nos hace humanos?* Taurus, Madrid.

Riemann, J. G.; Moen, D. J. y Thorson, B. J. (1967): Female monogamy and its control in houselfies. *J. Insect Physiol.* 13: 407-418.

Roces, F. y Holldobler, B. (1995): Vibrational communication between hitchhikers and foragers in leaf-cutting ants (*Atta cephalotes*). *Behav. Ecol. Sociobiol.* 37: 297-302.

Ruano, F. y Tinaut, A. (1999): Raid process, activity pattern and influence of abiotic conditions in the slave-making ant *Rossomyrmex minuchae* (Hymenoptera, Formicidae). *Ins. Soc.* 46: 341-347.

Rutte, C. y Taborsky, M. (2007): Generalized reciprocity in rats. *PloS Biol.* 5, e196, doi:10.1371/journal.pbio.0050196.

Sakata, H. (1994): How an ant decides to prey on or to attend aphids. *Res. Popul. Ecol.* 36: 45-51.

Salas, C.; Broglio, C. y Rodriguez, F. (2003): Evolution of forebrain and spatial cognition in vertebrates: conservation across diversity. *Brain Behav. Evol_*62: 72-82.

Savage-Rumbaugh, E. S. y Lewin, R. (1994): *Kanzi: at the Brink of the Human Mind.* John Wiley, New York.

Schmitt, D. P. y Buss D. M. (2001): Human mate poaching: Tactics and temptations for infiltrating existing relationships. *Pers. Soc. Psychol.* 80: 894917.

Schneider, J. M. (1995): Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). *Ins. Soc.* 42: 237-248.

Schwartz, M. (2008): *El sexo en la Biblia.* Belacqva, Barcelona.

Seed, A. M.; Clayton, N. S. y Emery, N. J. (2007): Postconflict third-party affiliation in Rooks, *Corvus frugilegus. Cur. Biol.* 17: 152-158.

Seeley, T. D. (2003): Consensus building during nestsite selection in honey bee swarms: the expiration of dissent. *Behav. Ecol. Sociobiol.* 53: 417-424.

Seeley, T. D. y Buhrman, S. C. (1999): Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* 45: 19-31.

Semmann, D.; Krambeck, H.-J. y Milinski, M. (2005): Reputation is a valuable within and outside one's own social group. *Behav. Ecol. Sociobiol.* 57: 611616.

Senar, J. C. y Camerino, M. (1998): Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proc. R. Soc. Lond. B* 265: 1515-1520.

Seyfarth, R. M.; Cheney, D. L. y Marler, P. (1980): Vervet monkey alarm calls: evidence of predator classification and semantic communication. *Science* 210: 801-803.

Shackelford, T. K. y Pound, N. (2006): *Sperm Competition in Humans: Classic and Contemporary Readings.* Springer, New York.

Shavit, Y.; Fischer, C. y Koresh, Y. (1994): Kin and nonkin under collective threat: Israeli networks during the gulf war. *Social Forces* 72: 1197-1215.

Shettleworth, S. J. (1998): *Cognition, Evolution and Behavior.* Oxford University Press, Oxford.

Shields, J. D. y Wood. F. E. I. (1993): Impact of parasites on the reproduction and fecundity of the blue sand crab *Portunus pelagicus* from Moreton Bay, Australia. *Mar. Ecol. Prog. Ser.* 92: 159-170.

Shultz, S. y Dunbar, R. I. M. (2007): The evolucion of the social brain: anthropoid primates contrast with other vertebrates. *Proc. R. Soc. Lond. B* 274: 24292436.

Silk, J. B.; Alberts, S. C. y Altmann, J. (2004): Patterns of coalition formation by adult female baboons in Ambroseli, Kenia. *Anim. Behav.* 67: 573-582.

Simmons, L. W.; Firman, R. C.; Rhodes, G. y Peters, M. (2004): Human sperm competition: testis size, sperm production and rates of extrapair copulations. *Anim. Behav.* 68: 297-302.

Simmons, R. E. (1988): Food and the deceptive acquisition of mates by polygynous male harriers. *Behav. Ecol. Sociobiol.* 23: 83 92.

Simon, J.-C.; Rispe, C. y Sunnucks, P. (2002): Ecology and evolution of sex in aphids. *Trends Ecol. Evol.* 17: 34-39.

Smith, E. A. (1998): Is Tibetan polyandry adaptive? Methodological and metatheoretical analyses. *Hum. Nat.* 9: 225-261.

Soler, J. J. y Soler, M. (2000): Brood parasite interactions between great spotted cuckoos and magpies: A model system for studying coevolutionary relationships. *Oecologia* 125: 309320.

Soler, J. J.; de Neve, L.; Martmez, J. G. y Soler, M. (2001): Nest size affects clutch size and the start of incubation in magpies: an experimental study. *Behav. Ecol.* 12: 301-307.

Soler, J. J.; Martmez, J. G.; Soler, M. y M0ller, A. P. (1999): Host sexual selection and cuckoo parasitism: An analysis of nest size in sympatric and allopatric magpie *Pica pica* populations parasitized by the great spotted cuckoo *Clamator glandarius. Proc. R. Soc. London, Ser. B* 266: 1765-1771.

Soler, J. J.; Mailer, A. P. y Soler; M., (1998): Nest building, sexual selection and parental investment. *Evol. Ecol.* 12: 427-441.

Soler, J. J.; Soler, M.; M0ller, A. P. y Martmez, J. G. (1994): Does the great spotted cuckoo choose magpie hosts according to their parenting ability?. *Behav. Ecol. Sociobiol.* 36: 201-206.

Soler, M. (2002): Coevolucion. En M. Soler (ed.). *Evolution: la base de la biologia*, pp. 221-224. Proyecto sur de ediciones, Granada.

Soler, M. (2002): *Evolution: la base de la biologia.* Proyecto Sur, Granada.

Soler, M. (2006): Grajilla - *Corvus monedula.* En L. M. Carrascal y A. Salvador (eds.). *Enciclopedia Virtual de los Vertebrados Espanoles.* Museo Nacional de Ciencias Naturales, Madrid.

http://www.vertebradosibericos.org/

Soler, M. y Soler, J. J. (1999): Innate versus learned recognition of conspecifics in great spotted cuckoos *Clamator glandarius. Anim. Cogn.* 2: 97-102.

Soler, M. y Soler, J.J. (1996): Effects of experimental food provisioning on reproduction in the jackdaw *Corvus monedula*, a semi-colonial species. *Ibis* 138: 377-383.

Soler, M.; Soler, J. J.; Martmez, J. G. y M0ller, A. P. (1995): Magpie host manipulation by great spotted cuckoos: Evidence for an avian mafia?. *Evolution* 49: 770-775.

Soler, M.; Soler, J. J.; M0ller, A. P.; Moreno, J. y Linden, M. (1996): The functional significance of sexual display: stone carrying in the black wheatear. *Anim. Behav.* 51: 247-254.

Sosis, R. y Bressler, E. R. (2003): Cooperation and commune longevity: a test of the costly signalling theory of religion. *Cross-Cult. Res.* 37: 211-239.

Spindler, E.-M.; Zahler, M. y Loos-Frank, B. (1986): Behavioural aspects of ants as second intermediate hosts of *Dicrocoelium dentriticum. Z. Paresitenkd.* 72: 689-692.

Sprecher, S. (2002): Sexual satisfaction in premarital relationships: associations with satisfaction, love, commitment, and stability. *J. Sex Res.* 39: 190-196.

Stahl, J.; Tolsma, P. H.; Loonen, M. J. J. E. y Drent, R. H. (2001): Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim. Behav.* 61: 257-264.

Stanback, M.; Richardson, D. S.; Boix-Hinzen, C. y Mendelsohn, J. (2002): Genetic monogamy in Monteiro's hornbill, *Tockus monteiri. Anim. Behav.* 63: 787-793.

Steinkraus, D. C. y Cross, E. A. (1993): Description and life history of *Acarophenax mahunkai*, n. sp. (Acari, Tarsonemina: Acarophenacidae), an egg parasite of the lesser mealworm (Coleoptera: Tenebrionidae). *Ann. Entomol. Soc. Am.* 86: 239-249.

Stroeymeyt, N.; Brunner, E. y Heinze, J. (2007): "Selfish worker policing" controls reproduction in a *Temnothorax* ant. *Behav. Ecol. Sociobiol.* 61: 14491457.

Stutt, A. D. y Siva-Jothy, M. T. (2001): Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius. Proc. Natl. Acad. Sci. USA* 98: 5683-5687.

Summers, K. (2005): The evolutionary ecology of despotism. *Evol. Hum. Behav.* 26: 106-135.

Tebbich, S.; Taborsky, M. y Winkler, H. (1996): Social manipulation causes cooperation in keas. *Anim. Behav.* 52: 1-10.

Tella, J. L. (2002): The evolutionary transition to coloniality promotes higher blood parasitism in birds. *J. Evol. Biol.* 15: 32-41.

Thompson, J. N. (2005): *The Geographic Mosaic of Coevolution.* Univ. Chicago Press, Chicago.

Thompson, J. N. y Cunningham, B. M. (2002): Geographic structure and dynamics of coevolutionary selection. *Nature* 417: 735-738.

Thorne, B. L. (1997): Evolution of eusociality in termites. *Annu. Rev. Ecol. Syst.* 28: 27-54.

Thornhill, R. (1976): Sexual selection and nuptial feeding behaviour in *Tittacus apicalis* (Insecta: Mecoptera). *Am. Nat.* 110: 529-548.

Thornhill, R. (1980): Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.* 28: 52-59.

Thornhill, R. y Alcock, J. (1983): *The Evolution of Insect Mating Systems.* Harvard University Press, Cambridge.

Thornhill, R. y Palmer, C. (2000): *A Natural History of Rape: Biological Bases of Sexual Coercion.* MIT Press, Cambridge.

Tinbergen, N. (1963): On aims and methods of Ethology. *Z. Tierpsychol.* 20: 410-433.

Tobena, A. (2006): *El cerebro erotico: rutas neurales del amor y el sexo.* L' Esfera dels llibres S.L., Barcelona.

Travisano, M. y Velicer, G. J. (2004): Strategies of microbial cheater control. *Trends Microbiol.* 12: 7278.

Treat, A. E. (1975): *Mites of Moths and Butterflies.* Cornell University Press, New York.

Trillmich, F. y Wolf, J. B. W. (2008): Parent- offspring and sibling conflict in Galapagos fur seals and sea lions. *Behav. Ecol. Sociobiol.* 62: 363-375.

Trivers, R. L. (1972): Parental investment and sexual selection. En B. Campbell (ed.). *Sexual Selection and the Descend of Man*, pp. 139-179. Aldine, Chicago.

Trivers, R. L. (1974): Parent-offspring conflict. *Am. Zool.* 14: 249-264.

Trivers, R. L. (1971): The evolution of reciprocal altruism. *Q. Rev. Biol.* 46: 35-57.

Troisi, A. y Carosi, M. (1998): Female orgasm rate increases with male dominance in Japanese machaques. *Anim. Behav.* 56: 1261-1266.

Turlings, T. C. J.; Loughrin, J. H.; McCall, P. J.; Roese, U. S. R.; Lewis, W. J. y Tumlinson, J. H. (1995): How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proc. Natl. Acad. Sci. USA* 92: 4169-4174.

Tyler, M. J. y Carter, D. B. (1981): Oral birth of the young of the gastric brooding frog *Rheobatrachus silus. Anim. Behav.* 29: 280-282.

van den Berghe, E. P. (1988): Piracy as an alternative reproductive tactic for males. *Nature* 334: 697-698.

van Schaik, C. P.; Ancrenaz, M.; Borgen, G.; Galdikas, B.; Knott, C. D.; Singleton, I.; Suzuki, A.; Utami, S. S. y Merrill, M. (2003): Orangutan cultures and the evolution of material culture. *Science* 299: 102-105.

Verner, J. (1964): The evolution of polygamy in the long-billed marsh wren. *Evolution* 18: 252-261.

Wahaj, S. A.; Van Horn, R. C.; Van Horn, T. L.; Dreyer, R.; Hilgris, R.; Schwarz, J. y Holekamp, K. E. (2004): Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. *Behav. Ecol. Sociobiol.* 56: 237-247.

Wallace, B.; Cesarini, D.; Lichtenstein, P. y Johannesson, M. (2007): Heritability of ultimatum game responder behaviour. *Proc. Natl Acad. Sci. USA* 104: 15631-15634.

Walls, S. C.; Mathis, A.; Jaeger, R. G. y Gergits, W. F. (1989): Male salamanders with high-quality diets have faeces attractive to females. *Anim. Behav.* 38: 546-548.

Walter, B. y Trillmich, F. (1994): Female aggression and male peace-keeping in a cichlid fish harem: conflict between and within the sexes in *Lamprologus ocellatus. Behav. Ecol. Sociobiol.* 34: 105-112.

Watts, D. P. (2004): Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* 25: 507521.

Wedekind, C.; Seebeck, T.; Bettens, F. y Paepke, A. J. (1995): MHC-dependent mate preferences in humans. *Proc. R. Soc. Lond. B* 260: 245-249.

Weir, A. A. S.; Chappell, J. y Kacelnik, A. (2002): Shaping of hooks in New Caledonian crows. *Science* 297: 981.

Wenseleers, T. y Ratnieks, F. L. W. (2006): Enforced altruism in insect societies. *Nature* 444: 50.

Weygoldt, P. (1980): Complex brood care and reproductive behavior in captive poison-arrow frogs, *Dendrobates pumilio. Behav. Ecol. Sociobiol.* 7: 329-332.

Whitehouse, M. E. A. y Lubin, Y. (2005): The functions of societies and the evolution of group living: spider societies as a test case. *Biol. Rev.* 80: 347-361.

Whiten, A.; Goodall, J.; McGrew, W. C.; Nishida, T.; Reynolds, V.; Sugiyama, Y.; Tutin, C. E. G.; Wrangham, R. W. y Boesch, C. (1999): Cultures in chimpanzees. *Nature* 399: 682-685.

Wikelski, M. y Baurle, S. (1996): Pre-copulatory ejaculation solves time constrains during copulation in marine iguanas. *Proc. R. Soc. Lond. B* 263: 439444.

Wiley, R. H. (1973): Territoriality and non-random mating in the sage grouse *Centrocercus urophasianus*. *Anim. Behav. Monogr.* 6: 87-169.

Wilson, E. O. (1975): *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge.

Wilson, K.; Thomas, M. B.; Blanford, S.; Doggett, M.; Simpson, S. J. y Moore S. L. (2002): Coping with crowds: Density-dependent disease resistance in desert locusts. *Proc. Natl Acad. Sci. USA* 99: 54715475.

Winslow, J. T.; Hastings, N.; Carter, C. S.; Harbaugh, C. R. e Insel, Th. R. (1993): A role for central vassopressin in pair bonding in monogamous prairie voles. *Nature* 365: 545-548.

Wyllie, I. (1981) *The Cuckoo*. London, Batsford.

Wynne-Edwards, K. E. (1995): Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Anim. Behav.* 50: 1571-1585.

Zuberbuhler, K. (2002): A syntactic rule in forest monkey communication. *Anim. Behav.* 63: 293-299.

Zuk, M. (2002): *Sexual Selections: What we Can and Can't Learn About Sex from Animals*. University of California Press, Berkeley.

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Manuel Soler
Adaptive Behaviour
Understanding the Human Animal
2012

ISBN: 978-84-695-2471-8
First published in 2009 in Spanish by Editorial Smtesis. Original title: *Adaptation del comportamiento: comprendiendo al animal humano.*