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Human Life Course

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For Lorna

Foreword

OUR ATTEMPT to understand social behavior is an ancient and abiding concern. From the earliest philosophers to the most recent discussions of human sociality, this concern with the nature of society and social evolution predominates. Lacking a satisfying and comprehensive theory, the human social sciences have vacillated between disparate, often contradictory, social theories. Especially troublesome have been attempts to reconcile the pervasive and opposing forces of cooperation and competition, which, because of the lack of a coherent framework, have remained unintegrated and misunderstood features of social life. The revolution in evolutionary theory, over the last two decades, has thus excited many researchers who feel that natural selection is the key which has been missing from every discipline's study of social behavior. This book offers a cogent and lucid treatment of the subject, one that both documents the fundamental processes involved and advances the field to a new level of integration.

While Darwin's original insights continue to inform the subject, the synthesis we now call sociobiology only began to take modern form in the late 1960s through the writings of such theorists as W. D. Hamilton, G. C. Williams, and John Maynard Smith. The exciting rejuvenation of behavioral biology that subsequently occurred in the 1970s is difficult to convey to those too young to have been participants. Armed with a powerful new theoretical framework and notebooks full of hypotheses to be tested, a new generation of ethologists and naturalists turned to field studies. Established journals were soon dominated by the emerging ideas and data of sociobiology, and several new journals appeared that were entirely devoted to the subject. It is therefore not surprising that the great majority of some 750 references in this text are from articles published since 1975. But it is a testament to the vitality of the field, and to the insight of the author, that he is

also able to reach back across seven decades to reinterpret data and, for example, pose an intriguingly plausible explanation concerning the nature of deer antlers.

Inevitably such an exuberant outpouring of theory and data has spawned a multitude of subfields. Trivers has judiciously sifted the literature to discuss just those issues and examples that are most useful in promoting an understanding of the present state of the discipline. A particular virtue of the book is the author's single-minded dedication to applying the principles of natural selection to social phenomena. In fact, the book brings together the most data ever gathered on this subject in one place. Another noteworthy accomplishment is that Trivers has enormously broadened the range of data and theory applicable to social evolution. This is apparent throughout the volume, but one of his more remarkable achievements is that, for the first time, the plant world is repeatedly brought into a book largely concerned with social behavior in the animal kingdom. Only a few years ago it would have been considered ludicrous to treat the social behavior of plants and humans in the same volume, and yet Trivers has shown that, with powerful theory, there are good reasons to consider them in the same encompassing framework.

Trivers has done more than introduce the reader to the field of sociobiology; he has advanced theory. His treatment of critical topics, such as kinship, is done in new depth; he leads the reader across an astonishing range of behavioral phenomena, stretching from the intracellular level to the social organization of primates. The breadth of his conception invites one to find new patterns and unity in social evolution. The extension of such principles to human behavior has inevitably been controversial; far from shying away from human applications, Trivers has consciously sought vivid ways to illustrate their operation in human daily life. His discussion of these issues is distinguished from many others by its discernment and responsibility.

One final way in which this book is distinctive is its use of visual materials. Trivers has taken extraordinary pains in his selection of illustrations and tables, and they contribute significantly to the intellectual impact of the book. Indeed, readers can get a flavor of modern ethology from reading the picture captions alone.

Trivers is a pivotal figure in the development of modern evolutionary biology, and brings to his survey of the field a uniquely authoritative voice. He leads the reader through the imposing accumulation of theory and evidence with clarity and precision. His insights and synthetic treatment provide the most outstanding and illuminating introduction to the field that now exists.

Irven DeVore
Professor of Anthropology and Biology
Harvard University

Preface

EVERYBODY HAS a social life. All living creatures reproduce and reproduction is a social event, since at its bare minimum it involves the genetic and material construction of one individual by another. In turn, differences between individuals in the number of their surviving offspring (natural selection) is the driving force behind organic evolution. Life is intrinsically social and it evolves through a process of natural selection which is itself social. For these reasons social evolution refers not only to the evolution of social relationships between individuals but also to deeper themes of biological organization stretching from gene to community.

Having emphasized the generality of social evolution, I hasten to say that we retain a special interest in our own species, which is social in a complex series of overlapping ways. We are, thus, inevitably more interested in some species than in others and in some problems rather than in others. Consider, for example, male parental investment. We are one of a small minority of species wherein the male commonly invests some parental care in his offspring. We, thus, find ourselves interested in details of bird behavior—details that would otherwise escape our notice—because birds also have high male parental investment, along with a host of associated traits. While emphasizing the general themes of social evolution I have chosen throughout the book topics important to our own evolution, from kinship and parent-offspring conflict to deceit and self-deception.

Audience

This book is written for two audiences. It is written for the general reader who wishes an introduction to the subject of social evolution,

and it is written for the undergraduate taking an introductory course in sociobiology, animal behavior, evolutionary biology, anthropology, or related disciplines. This book is meant to be self-contained, in the sense that it presupposes no background in biology, and Chapter 5 reviews useful background information on genetics and its relation to behavior and learning.

Organization

There are five introductory chapters. These serve to introduce the reader to Darwin's theory of evolution through natural selection (Chapters 1 and 2), relate natural selection to social traits (Chapter 3), consider the road not taken (Chapter 4), and review genetics and its relation to behavior and learning (Chapter 5). In organizing the material this way, I have purposely taken the reader as quickly as possible to the core of our subject (Chapter 3) and postponed alternate systems of logic and the subject of genetics.

Chapters 6–16 are the heart of the book. They describe an interconnected body of theory and evidence on the principles underlying social evolution. We begin with the central concept of kinship (Chapter 6) and its application to parent-offspring relations (Chapter 7) and reproductive altruism (Chapter 8).

Chapters 9–14 cover sexual selection, the sex ratio, and sex. Finally we close with material which is relevant to social interactions in general: cooperation (Chapter 15) and deceit and self-deception (Chapter 16).

Approach

A wealth of work has appeared in the past ten years on all the major topics of social evolution, including kinship, sex, sex ratio, cooperation, mate choice, and so on. So my first aim in writing this book has been to provide an up-to-date summary of our understanding of social evolution, including especially recent work, both theoretical and empirical.

I have tried throughout the book to emphasize evolutionary logic and to leave out material that would only serve to detract from the general themes of social evolution. These I have conceived to follow from the importance of reproduction itself. Thus I have concentrated on variation in the production of surviving offspring (natural selection), on the genetics of reproduction (kinship), on the parent-offspring relationship, on non-reproduction, on parental investment and on sex, including sexual selection and the sex ratio.

Some of the most exciting and useful material in biology is visual. To give the reader a taste of the rich visual material on social evolution I have made a special effort to collect together photographs, supplemented with excellent drawings by Carla Simmons. Rather than assemble photographs as so many isolated portraits, only loosely related to the text, I have tried to find visual material that is directly connected to the points under discussion and I have linked together series of photographs or drawings on common subjects in order to give a deeper impression.

Quantitative information is illustrated by graphs and tables. Once again I have preferred to link together graphs and tables on common themes, so as to give a deeper treatment. In choosing graphs and tables I have been drawn to those that describe the action of natural selection, or variables closely associated with it.

To make the book easier to read I have removed all references from the text, retaining them only in figure and table captions. At the same time, to give the reader easy access to the rest of the bibliography, I have prepared bibliographic notes—beginning at the end of the text—which are keyed to the page number of text to which they refer. If one is reading page 85 in the text and wishes to see the accompanying references, flip to the bibliographic notes and look for the notes that go with page 85. This arrangement has also permitted me to add references on related topics. In this I have had both the advanced student and teacher in mind as well as undergraduates wishing to write term papers on any topic in the book. Please note that where reference to a subject is given in a figure caption or table and no additional references are offered, I have not bothered to repeat the reference in the bibliographic notes.

For years I have taught the material in this book, accompanying it with weekly problem sets on the major topics of social theory (natural selection, group selection, kinship, sexual selection, the primary sex ratio and so on). These problem sets, along with exam questions, are available from the publisher upon request.

This book seeks to provide an in-depth introduction to the subject of social evolution, a subject which gives us a foundation for a scientific understanding of human behavior.

Robert Trivers
Professor of Biology
University of California, Santa Cruz

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Robert Trivers

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Chapter 1

A Scientific Theory of Organic Creation

TWENTY YEARS AGO as an undergraduate in college I was interested in problems of human behavior, especially social behavior. I wanted to know why we do what we do and toward what purpose our lives are organized. I longed for a scientific understanding of human behavior, that is, an understanding based on first principles and, wherever possible, grounded in pre-existing knowledge.

I dabbled in several disciplines, but found myself disappointed in each. History, political science, economics, and psychology all expressed interesting views on human behavior, but none of these views seemed to have a secure foundation in pre-existing knowledge. For example, Western economics usually assumes that individuals are out to maximize personal gain, but where is the scientific justification for this assumption? And what exactly is "personal gain"? Much of psychology at the time assumed that human behavior is built entirely from learning experiences and that a theory of learning is the actual basis for any theory of human behavior. But psychology could give no coherent account of how these learning abilities are organized in us and toward what end we are learning what we are learning.

Then, within months of graduating from college, my life was turned around. I was asked to write children's books on animal behavior, and for the first time I became exposed to facts about the social lives of other animals. I shall never forget the shock and pleasure of learning that the social lives of other creatures are subtle and complex, both similar to ourselves and different. In particular, I was very much struck by pictures of adult male baboons *Papio cynocephalus* disciplining juveniles. Dominant adult males like to watch juveniles play and often keep a close watch on their activities (Figure 1-1). Should one of the youngsters be injured or cry out, one of the adult males may stride over, grab the offending juvenile, and administer a bite to the neck; the

Figure 1-1

Adult interest in juveniles. An adult male baboon watches an infant and a juvenile at play. Should he intervene, he will do so in response to the individual showing distress. (Photo: Irven DeVore, Anthro-Photo)

juvenile howls as if mortally wounded, and the male strides off (Figure 1-2). Partly as a result of the punishment juveniles receive from dominant males, juveniles often show fear in the presence of these males (Figure 1-3).

These pictures of the disciplinary episodes among baboons had a profound effect on me for two reasons, I think. First, baboon discipline seemed at least superficially similar to something I had experienced in my own life, namely, parental discipline. This immediately suggested that there was something common to the two kinds of discipline and that one should search for a deeper explanation of discipline that would apply to both species. Baboon discipline was also striking because it was conducted entirely in silence: the adult baboon made no sound while disciplining the youngster. By contrast, human parental discipline is almost always accompanied by a barrage of words meant to represent to the offspring the reason for the discipline. On the one hand, the moral structure of the universe is described; on the other hand, the offspring's behavior. There is a need to align the two, hence the discipline. But if baboons conduct their discipline without words, it suggests that the verbiage in human discipline may just be so many words. It may be a rationalization on the parent's part, or it may be at the least the way in which the parent represents to itself and oth-

Figure 1-2

Adult discipline in the ba boon. (a) A dominant m baboon in Kenya disci plines a juvenile by grab bing and biting it; anothe baboon looks on. The bi does not break the juve nile's skin; it may be pain ful but is not injurious. (b) The male strides off while the juvenile howls in anguish. Although dor nant males are the most likely males to be the fathers of the youngsters, whether this male is the f ther is not known. (Photo Irven DeVore, Anthro-Photo)

Figure 1-3

Respect for authority. Th fear and respect that juve niles show a dominant male is captured here. Juv niles are often disciplined for manhandling or mis treating younger juveniles (Photo: Irven DeVore, Anthro-Photo)

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Figure 1-4

A gull breeding colony. These gulls are breeding in Maine. In the foreground (left to right) are a gull in its territory, a couple in theirs, another gull in its territory, and another couple. Usually at least one bird remains in the territory. (Photo: William Drury)

provide an explanation for the phenomenon of parental discipline. Later we shall see that there are fundamental reasons for conflict between parents and offspring, and that parents may at times be favored by natural selection to discipline their youngsters even when this is not in the best interests of the young (see Chapter 7). Verbiage, it may be noted, is virtually defined by its biological inexpensiveness. The difference in cost between true and false statements must be trivial, at least as measured by energy expended in speaking (compare "yes" and "no"), so verbal reality is likely to be a poor guide to social behavior.

If we ask ourselves what kind of explanation might underlie the social behavior of a variety of creatures (where would such an explanation come from?) then it seems clear after a little reflection that any explanation must be based on a theory of how these creatures were created. Where do baboons and other creatures come from? How were we all created? How does the process by which we were created shed light on our behavior now? This is the problem we will take up in this first chapter. We will begin with a description of purposive organization in an animal. We will then consider the system of logic that Darwin replaced and describe his notion of evolution through natural selection. We shall see that in Darwin's system, living creatures have been constructed over immense stretches of time by a process going on around us all the time: the differential survival and reproduction of individuals. This is natural selection and according to our best under-

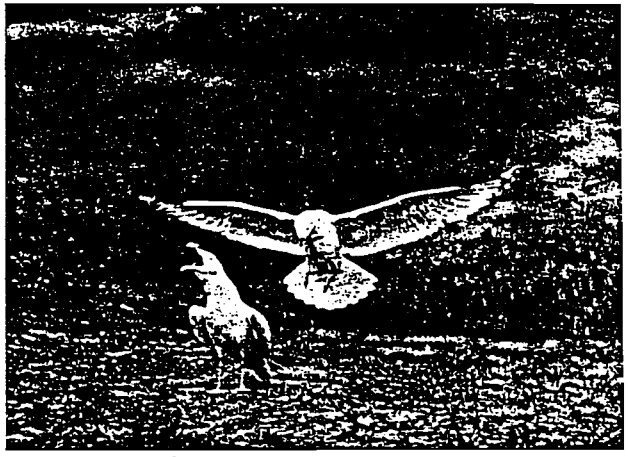

Figure 1-5

A pair of gulls returns home. As is common in this situation, the bird that has landed gives a "long call." This is a form of territorial assertion: it draws attention to the returning birds and to their territory. It says, in effect, "We're home!" (Photo: Niko Tinbergen)

Organisms Are Designed to Do Something: The Breeding Biology of Herring Gulls

The greatest problem in biology has always been to explain the special characteristics of living creatures. If we compare even the humbliest creature, say, a virus, with an inanimate object, such as a rock, the living creature appears organized to *do* something; it acts as if it is trying to achieve some purpose. Let us consider an example: the breeding biology of herring gulls. (Throughout this book we will use the herring gulls—and their close relatives, the other gulls and terns—to illustrate the principles we describe. We choose them partly because they have been unusually well studied, especially by Niko Tinbergen and his students.)

When we watch the intricate breeding pattern of a species such as the herring gull, we see a wonderful series of coincidences by which the gulls are organized so as to reproduce successfully in a particular setting. For example, the view of a gull breeding colony in Figure 1-4 shows that nests are more or less evenly spaced. Experimental work suggests that this pattern may reduce the chance that each nest and its eggs will be discovered by a predator. Boundaries of territories are maintained by aggressive interaction between neighboring pairs (Figures 1-5 to 1-7). The activities of a pair are synchronized so that a male feeds his mate while she is developing the eggs and the couple

Figure 1-6

The upright threat posture of a herring gull at high intensity. Notice how the wings are held slightly apart from the body, in preparation for a possible strike on the opponent. The neck is held rigid and forward, while the beak is pointed down, all of which prepare the bird for delivering a sharp peck. These intentional movements, which prepare for action, also give away useful information to others. (Photo: Niko Tinbergen)

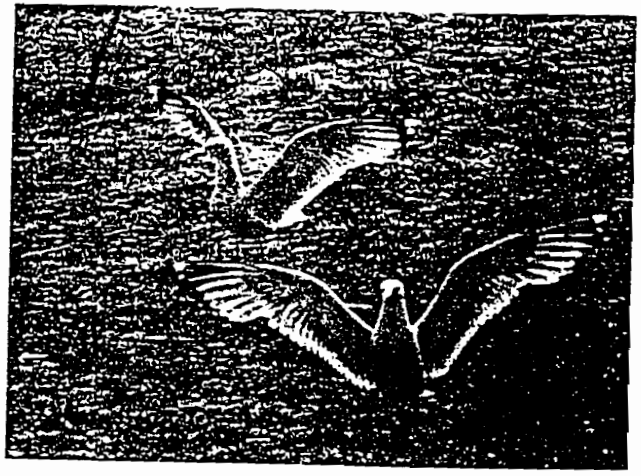

Figure 1-7

After a charge. The male in front has just been driven off by the other male and is still facing away. Such disputes help establish the boundary between territories. Each bird tends to be dominant in its own territory, presumably because extra space is less valuable to each gull than is protecting its home space. (Photo: Niko Tinbergen)

Both birds regularly alternate sitting on the eggs so that the eggs are rarely left uncovered and each parent has time to feed. A brood patch develops on the underbelly of each gull, and this is placed directly onto the eggs when they are being brooded. The brood patch is devoid of feathers and highly vascularized so that it transfers large quantities of heat to the developing eggs. When an adult settles onto eggs to incubate, there are an up-and-down motion, a rotating motion, and a foot-shuffling motion, all of which help bring the eggs into close contact with the brood patch.

Three eggs are commonly laid, a number from which the gulls are usually capable of raising the most surviving young. (Those laying only two eggs are typically young, inexperienced, or in poor condition.) Gull eggs are speckled and grey in color, matching their background (Figure 1-10). Although they are laid two days apart, the eggs are not brooded until the last one is laid; thus all the young tend to hatch at about the same time. More exact hatching synchrony probably results from the chicks' "peeping" to each other while still in their

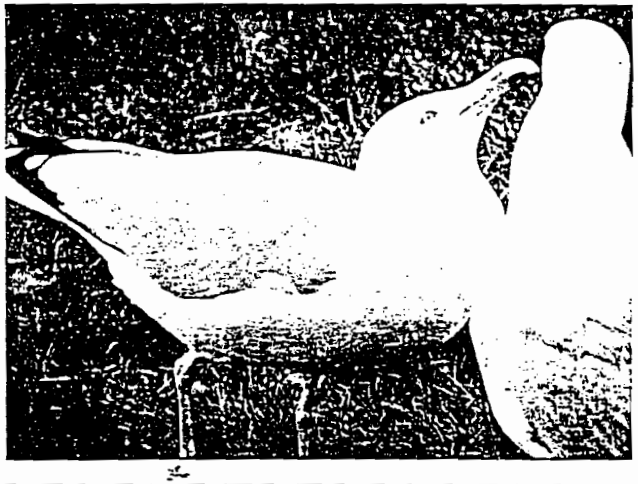

Figure 1-8

Courtship feeding in the herring gull. The female (on the left) is begging for food from the male, whose neck swelling indicates he is about to regurgitate food. The behavior of the female is similar to that of a chick begging food from its parent and is, likewise, accompanied by a begging call. It is noteworthy that this begging call is also used by both sexes to invite copulation. An intimate association between food and sex is found in many species, including insects (see p. 252) and humans ("You can't make love on an empty belly"). (Photo: Niko Tinbergen)

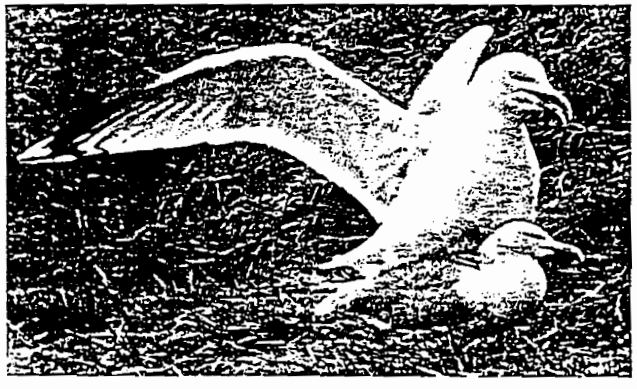

Figure 1-9

A couple copulates. The male (on top) presses his cloaca to the female's and transfers sperm. The copulation lasts only a few seconds. (Photo: Niko Tinbergen)

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eggs. Parents also make sounds during this time that they will later make to their chicks—warning calls and calls that solicit approach—and a chick deprived of hearing these calls while still in the egg later takes longer to react appropriately. At hatching, parents remove the eggshells, whose inner white surfaces attract the attention of predators.

Gull chicks are born with a pattern of spots on their heads unique to each one (Figure 1-11), and these are thought to make it easier for the parents to recognize their own chicks. In any case, within three days, parents recognize their own young and repel or eat intruding chicks. Once mobile, the chicks learn the boundaries of their parents' territory within a few days and stay within them. The chicks are not left alone by their parents until the chicks are about three weeks old, the age at which they can resist attempts by other gulls to eat them. Since the color of the chicks matches the background in which they live, they are often difficult to spot, even at close distances. Both parents feed the young and each has a red spot on its lower beak at which the chick has an inborn tendency to peck; this in turn induces the parent to regurgitate food, and so on (Figures 1-12 and 1-13).

The behavior, physiology, and morphology of gulls is highly organized in a series of coincidences that tend to promote reproduction. How did this remarkable pattern come about, and what exactly is it that these birds are trying to achieve? Put another way: how is it that we living creatures display a purpose and what exactly is the purpose we display?

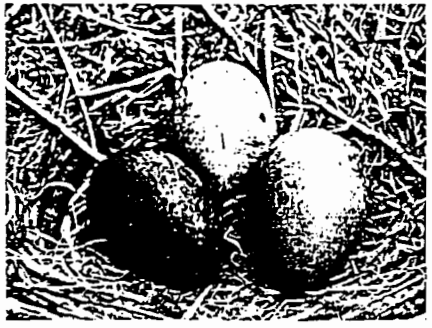

Figure 1-10

A typical gull's nest. The eggs are greyish brown and speckled to blend in with the background. The depression and nesting material give the eggs a protected place where intensive warming by the parents can take place. (Photo: Niko Tinbergen)

Figure 1-11

Individual head markings. Two newly hatched gull chicks show the spots on the head that are thought to aid in parental recognition since they are so distinctive and vary from chick to chick. (Photo: William Drury)

Darwin's Revolution

In 1859 Charles Darwin established two things. First, he showed beyond a reasonable doubt that evolution had taken place here on earth. And second, he discovered the causal agent behind evolutionary change, something he called *natural selection*. For this reason, natural selection is the key concept in all of biology. It explains how we got the traits we have. To appreciate the importance of Darwin's revolution, let us glance at the system of logic he replaced.

To the problem of how creatures happen to display purposive behavior, Western biologists before 1859 usually answered as follows: God created all species of living creatures fully formed, and these species have not changed since creation. Because species have not changed since they were created, it seemed easy to deduce directly the intention of God by studying living creatures themselves. Thus by studying diverse living creatures and their relationships in nature we are studying the mind of God. For those who believed in God, this was biology's finest hour, for it was then an integral part of natural theology. The

Figure 1-12

Stimulating a parent to feed. The gull chick pecks at the red spot on its parent's beak, stimulating feeding (next photo). Experiments show that chicks have an innate tendency to peck at red spots at the end of long beak-like objects. (Photo: William Drury)

Figure 1-13

Feeding offspring. A parent regurgitates a fish to its young. The offspring will tear it apart and consume it. (Photo: William Drury)

entire living world functioned as a giant unchanging machine. Individuals were parts of species that were parts of a larger whole, everything designed to work together in an unchanging way. Some species were expressly created for the use of others, for example domesticated species.

Into this picture there entered some embarrassing evidence. People began to dig up and recognize a great variety of fossils, that is, the remains of creatures clearly organized like ourselves but which no longer existed. How was one to explain fossils? The great majority of biologists responded to the discovery of fossils by embracing the theory of catastrophism, or earlier separate existences of the universe. Instead of imagining that species evolved one from the other, and that fossils were the remains of creatures that had once existed but had died out while evolution swept by them, biologists instead imagined that God had created the world a number of separate times, each time destroying the previous creation. According to this view, evolution on earth did not take place, only the mind of God evolved. As God's mind became more mature and more subtle, God swept aside earlier creations and replaced them with newer, more mature versions. Weak as the theory of catastrophism sounds, it was positively sophisticated when compared with modern-day creationism, which tries to explain the fossil record by reference to a single giant flood that swept nearly all of "lower creation" to its grave, magically depositing the carcasses in the highly ordered pattern we observe in the fossil record. Darwin's work was resisted by some scientists, not because it disproved the existence of God, but because it disproved the particular view of God to which they had become attached: a God who insisted that any creation remains unchanged until it is subject to complete revision.

By "evolution" Darwin meant both modification over time and descent from common ancestors; that is, creatures have changed in shape and behavior over vast periods of time, and, in addition, all lineages traced backwards eventually converge. If we go back about 20 million years, we ourselves are connected to all other apes. Likewise, about 150 million years ago our lineage converges with those of all other mammals. And finally, if we go back a half billion years, all vertebrates are seen to have sprung from a single common ancestor.

In this book we will emphasize Darwin's concept of natural selection, but it is worth nothing that Darwin himself amassed a variety of subtle arguments in favor of evolution. For example, he used findings from zoogeography—that is, the geographic distribution of species—to show that if God created the world unchanged in a single moment, he did so very illogically. Thus, Darwin pointed out, oceanic islands often have freshwater ponds and lakes similar to those found on the mainland, yet containing no frogs or salamanders. Such creatures can clearly survive in these ponds, as accidental introductions by humans have shown several times, so the question naturally arises: Why did

God not place frogs and salamanders in these freshwater ponds and lakes, which he also created?

In an evolutionary view, there is at once an explanation. Oceanic islands are the tops of mountains that were once completely covered by water. (Some, for example, rose above the water about 30 million years ago.) If this is true, then living creatures must have reached the islands from the mainland. The only way frogs can cross from the mainland is by rafting, that is, by clinging to a branch or a tree that has fallen into the ocean and been swept out from the mainland. But frogs breathe through their skin, and their skin needs to stay moist, so they are vulnerable to desiccation and to salt water. They cannot survive even several days in the hot sun, much less the weeks and months required to raft to an oceanic island. By contrast, reptiles can withstand drying out for considerable periods of time. A single pregnant female who happened to raft to an oceanic island could have colonized the island. Thus we might expect to find on oceanic islands those forms that easily colonize across great distances of seawater, and this is precisely what we do find. In addition to lizards we find such small mammals as rats, who are capable of rafting, and bats, who are capable of flying. But we do not find large mammals, which have a much more difficult time rafting great distances. Nor do we find wet-skinned creatures like frogs and salamanders.

To back up this interpretation, Darwin performed a number of experiments. In one, he kept large vats of seawater in his basement and placed in the seawater seeds of plants found on oceanic islands. He removed the seeds at various intervals (such as 110 days) and planted them to see if they would germinate. This evidence was compared with his calculations of how long it would take the prevailing currents to carry a seed from the nearest mainland to the islands. He showed repeatedly that many of the experimental seeds were capable of germinating even after prolonged immersion in seawater, permitting colonization of even the most distant oceanic islands. In the creationist view of zoogeography, God acted capriciously and illogically, failing to place creatures in habitats where they were well suited to survive. By the evolutionary view, the distribution of creatures today follows a logical pattern, since life must come from life, sometimes across the ocean. Creatures on oceanic islands are often similar to creatures on the nearby mainland, but typically they are of different species, sometimes quite different. In other words, these species have evolved since the time they reached the island. Thus, a study of zoogeography alone suggests that creatures have evolved here on earth, and there exists no other good explanation for the distribution of creatures today.

We will say nothing more about the evidence in favor of evolution, but will take it for granted. The evidence is now vast and interconnected and the interested—or skeptical—reader can find it summarized in the books referred to in the bibliographic notes for this chapter.

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Natural Selection

In Darwin's view, evolution resulted from two factors: heritable variation and differential reproductive success. By *heritable variation*, Darwin meant that in each living species there is variability, some of which is inherited by the offspring. By *differential reproductive success*, Darwin meant that in each species some individuals leave many surviving offspring, some leave few, and some leave none at all. If these two components are coupled, we are likely to see changes in the heritable constitution of a species. If individuals with some heritable variations—what we would now call *genetic variations*—happen to leave more surviving offspring than individuals with other genetic variations, then these genetic variations have become more numerous. If the same bias is repeated generation after generation, we can expect to see considerable change in the genetic constitution of a species.

What determines differences in reproductive success, that is, differences in the number of offspring individuals produce? For Darwin, the most important factor was high, non-random, *pre-reproductive mortality*; that is, of the creatures who are conceived, most die before reaching reproductive age, and this mortality is non-random, striking some individuals more frequently than others.

Darwin realized that high pre-reproductive mortality was a logical necessity. It followed from a single fact regarding nature, namely, that over long periods of time, the amount of living material on the earth does not increase, or increases very slowly. This means that for a typical species, numbers must remain relatively constant from generation to generation. There might be huge fluctuations in numbers in many species, but taken over long periods of time, it is logically necessary that numbers increase only very slowly, if at all. Otherwise the total biomass of living creatures would increase year after year. Once we assume that numbers remain relatively constant, then it is easy to calculate how many individuals in each generation die before reproduction. For example, in the largest species of Pacific salmon, most individuals reproduce at age five and then die. The adult female produces about 6,000 eggs, and it takes only one male to fertilize the eggs. If numbers stay constant over long periods of time, then we know that for every two breeding salmon adults, roughly two will be alive five years later. In other words, 5,998 out of 6,000 eggs laid will have perished.

Herring gulls produce three eggs a season, and it has been calculated that those who survive to reproductive age can produce about ten clutches of eggs (a total of 30) in a lifetime. Since two adult herring gulls are replaced a generation later by two on an average, then 28 of the 30 eggs (or offspring) must perish before reproducing. Studies in nature show that most of this mortality occurs while the birds are still very young. In some populations about 25% of the eggs laid fail to

hatch. Of the chicks that hatch out, another 40% die before fledging, most of them in the first week. Twenty percent of the remainder die by the age of three months (end of September) and another 20% before the end of winter.

On the east coast of the United States and in England, herring gulls were an endangered species 80 years ago, while nowadays they are considered a pest. Beginning in about 1900, for reasons that are not well understood but may be coincident with increasing amounts of the human garbage that the gulls have come to exploit, herring gull numbers have doubled every generation. We know that this increase in population cannot continue indefinitely, but it is interesting to note that even while it has been going on, there has been very high pre-reproductive mortality. Since the gulls double in number every generation, we know that two adult gulls have been replaced a generation later by four. This means that of the 30 eggs typically laid, 26 perish prior to reproductive age.

Human beings probably have, along with elephants, the slowest natural rate of increase of any living creature, and we know that until the discovery of agriculture about 10,000 years ago, human numbers increased very slowly. If a woman who survives through adulthood has about six children, then we know—for numbers to have stayed constant—that four of these six must have perished. We know from studies of contemporary hunter-gatherer cultures that about 20% of the children born perish in the first year of life.

Since the total amount of living material stays roughly constant from generation to generation, high pre-reproductive mortality is a logical necessity, otherwise the numbers of all creatures would increase very rapidly. Darwin saw clearly that the tremendous reproductive potential of all creatures must result in intense competition to survive, a competition, he imagined, that would result in non-random differential mortality. Those creatures who happen to be born with characteristics that make it easier to survive will endure while others will fall by the wayside. Thus, natural selection could be a very powerful process in nature, quickly molding a species to fit the environment in which its members find themselves.

What is the evidence for *non-random* mortality? In the next chapter we shall review a variety of studies showing non-random mortality, but for now let us consider a description of an actual death in nature.

Gustav Rudebeck studied the behavior of sparrow hawks *Accipiter nisus* for many years and kept an account of some of the kills he saw these birds perform.

October 17, 1937

A female sparrow hawk was flying quite low over a sandy stubble field. Suddenly it wheeled around rapidly, alighted, and almost disappeared, although

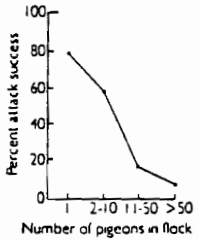

Figure 1-14

Predatory success as a function of size of prey group. The percent of attacks by a goshawk *Accipiter gentilis* that resulted in capture of a wood pigeon *Columba palumbis* is plotted as a function of the size of the wood pigeon groups. The hawk was released at a distance of about 60 meters from the pigeons. Note that the predator's success rate steadily declines with increasing prey group size, apparently as a result of greater vigilance by the prey (see next figure). (*From* Kenward 1978)

the ground was flat and the vegetation very low. Two starlings (*Sturnus vulgaris*) flew up where the hawk alighted. After some minutes, the hawk arose again with a starling in its claws, but settled in a bush surrounded by tall grass. . . . This was a surprise attack from a short distance. The sparrow hawk was flying low but did not otherwise take cover. It apparently discovered the starlings rather late, but before any one of the three birds noticed the danger. The flock of starlings, consisting of only three individuals, was remarkably small. The sparrow hawk appeared probably at a moment when the three starlings happened to be in such a position that they did not observe the danger. Such a coincidence must be practically out of the question for large flocks of starlings.

Rudebeck suggests that group size may be a deterrent to mortality from predators. Any individuals with a genetic tendency to live around other individuals may suffer lower predation and thereby leave more surviving offspring. We have reason to believe that this explanation applies very widely in nature, and it has been suggested that the primary selective force causing creatures to gather in groups is predation pressure. To give but one example: when a goshawk is released at a standard distance from flocks of wood pigeons, its predatory success rate falls steadily as pigeon flock size increases, apparently because the hawk is detected more quickly (Figures 1-14 and 1-15). From each individual pigeon's standpoint the gain in survival is striking: from a one in five chance of surviving when alone to a 99.8% chance when in a group of 50.

Mortality selection is not the only kind of selection. We can live a full life and still never reproduce. More exactly, individuals differ as adults in their capacity to reproduce. For females this usually means differences in fecundity, differences that can be very large: female cod fish differ more than five-fold in their capacity to produce eggs, even when all are the same age (Figure 1-16). Adults can also have their reproductive success limited by access to members of the opposite sex, as the biographies of many male animals show. For example, studies of bullfrogs *Rana catesbeiana* always turn up a sizable proportion of males who appear to achieve no reproductive success. The cause? Female choice. Bullfrog males take to the ponds during the breeding season and spend the evenings croaking in order to attract females, who are, in turn, uninterested in the males until they have a full set of eggs. Stephen Emlen has described the behavior of females who are ready to breed.

When ripe, however, females immigrated into the pond via the small inlet stream, left the cover of the shoreline, and approached the male choruses. These approaches evidently were guided at least in part by the sound of the males' calling, since females could be attracted to a tape recorder by playbacks of chorusing. However, direct observations revealed that females were *not*

strongly attracted to males calling from isolated territories; in all observed instances (N = 16) females passed by such males and continued on to the large choruses.

Once a chorus was reached, a female adopted an extremely "low" posture and moved from territory to territory without eliciting any noticeable response from the resident males. After many hours of remaining "low" in first one territory and then another, the female appeared to select a mate, swimming up to him and seemingly making physical contact. Only then would the male respond by immediately seizing her in amplexis.

These observations suggest that an important factor affecting male bullfrog reproductive success is female choice, and that females prefer to swim to large choruses of males because they can then more easily sample the available males in order to make their choice. Thus a male may have characteristics that permit him to survive into adulthood and, indeed, into ripe old age, yet if he lacks characteristics that attract females—or that give success in male-male competition—then from the viewpoint of selection, he may as well have died when young. So important did Darwin consider intrasexual competition and intersexual choice, that he called it by a separate name: ***sexual selection.***

In summary then, natural selection refers to differential reproductive success in nature, where reproductive success is the number of surviving offspring produced. This differential reproductive success consists of differences in survival rates and differences in reproductive capacity, including differences in fecundity and (in sexual species) differences in the ability to best members of one's own sex in competition for access to the members of the other sex.

Natural Selection and Herring Gull Breeding Traits

We are now in a position to return to our original questions. How is it that herring gulls are organized to do something, and what exactly are they organized to do? Our answer: Gulls have been subject to natural selection for millennia and, indeed, for eons, and this selection has continually woven together those traits that gave their possessors high reproductive success in the environments in which they found themselves. The result of this selection is individual gulls alive today who are organized to maximize the number of their surviving offspring.

When we see gulls defending territories within which to breed, we must assume that gulls who do not defend territories—or defend ones too small or unnecessarily large—leave few or no surviving offspring. If so, then in competition with gulls such as we see today, their traits would have been eliminated from the population long ago. The "coincidence" of gulls developing traits—such as coloration of eggs and

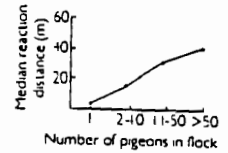

Figure 1-15

Reaction distance as a function of group size. The distance in meters at which wood pigeons took flight in response to an attacking goshawk is plotted as a function of the size of the pigeon flocks being attacked. Rudebeck's hypothesis is confirmed: larger group size means an earlier response to predators. (*From* Kenward 1978)

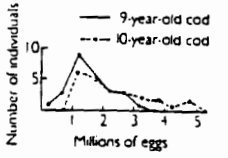

Figure 1-16

Variation in fecundity. Number of females containing a given number of eggs is plotted for a population of 9- and 10-year-old Atlantic cod *Gadus callarias*. Notice the large variation in fecundity in each age class, due largely to differences in size: the most fecund females have more than five times the reproductive success of the least fecund. (*From* May 1967)

Figure 1-17

Camouflage. Notice how well this gull chick blends in with its background, even when viewed from a short distance. This camouflage tends to protect the chick from visually hunting predators such as birds of prey, and presumably resulted from natural selection. (Photo: William Drury)

young—that match the environment in which the gulls nowadays live is explained by natural selection acting in similar contexts in the past. Since the background against which gulls breed often has a particular appearance, selection via visually hunting predators will result in the evolution of gull eggs and chicks that match this background; those that were not thus camouflaged were preyed upon in greater numbers (Figure 1-17).

Natural selection has also produced wonderful coincidences of social organization: males and females cooperating to raise young, or parent and offspring with matched traits that facilitate parental care. These social characteristics evolve because other gulls are part of each individual gull's environment and, like all other parts of the environment, may have selective effects. Parents will be selected for who recognize their own chicks (failure to do so might lower reproductive success by wasting parental care on unrelated young or even by parents eating their own chicks). Since the offspring benefit thereby, they will be selected to make themselves more easily recognized. Thus, spots on the heads of chicks will co-evolve with parental ability to recognize them. A similar argument applies to the offspring's recognition of the parent.

This view of herring gull life as a result of natural selection need not rest alone on plausibility and faith in our evolutionary logic. Because mortality among young birds is high prior to their flying and because mortality can often be measured fairly precisely, we can check

to see whether variation in gull traits is associated with variation in reproductive success. We can further check to see whether traits shared by many individuals are those that usually give high reproductive success. In the next chapter we shall see that for gulls there is now a variety of such measures, most of which show powerful selection acting on breeding traits, usually in favor of common characteristics. I hope we shall also see, throughout the book, that the hypothesis of organization to maximize individual reproductive success uniquely explains a whole world of facts concerning the way living creatures act.

Summary

All living creatures are organized to do something. The study of evolution shows us how this came about and what exactly it is that we are organized to do. Prior to Darwin, most biologists believed in a series of unchanging living worlds, all but the most recent creations having been obliterated, leaving only fossils as evidence of their existence. Darwin showed that evolution had taken place, all living creatures today being descendants of but one (or a very few) original species. Evolution, in turn, has taken place because of natural selection.

Natural selection is the differential reproduction in nature of individuals. Some individuals leave many surviving offspring and the genetic traits of those who do become more numerous in succeeding generations. Thus, individuals alive today are expected to be organized to maximize the eventual number of their surviving offspring.

A major component of natural selection is high pre-reproductive mortality. In all species (with the exception of recent human history), more individuals die in each generation than survive to reproductive age. In addition, selection also acts on reproductive output in adulthood. Some of this reproductive output is determined by access to members of the opposite sex, and this is called sexual selection.

Chapter 2

Natural Selection

If Darwin gave us a scientifically valid theory of organic creation (as I believe he did) then it is of value to us to understand the details of this theory. The central concept is that of *natural selection*, because it is natural selection—working on genetic variation—that produces evolutionary change. In that sense, natural selection constructs us, piecing together our various genetic parts through time. In Chapter 5 we will consider exactly what we mean when we say "genetic trait," but for now let us concentrate on the other half of our equation: the differential reproduction of individuals in nature.

After Darwin wrote *The Origin of Species*, many objections were raised to the concept of natural selection. It was claimed that selection was too weak a force to bring about substantial evolutionary change. It was said that life on earth had existed for too short a time for natural selection—acting alone—to produce the wonderful array of complex creatures we see today. And so on. Time has not been kind to these objections. Natural selection has repeatedly been shown to act as a powerful force in nature, capable of producing measurable change even in a single generation. Life, in turn, is now known to have existed on this planet for almost four *billion* years. Alternative schemes for evolutionary change have repeatedly been devised and found wanting; more importantly, we have yet to discover a fact of nature that requires a new theory of evolutionary change. Quite the contrary, we have unearthed a series of facts regarding the social lives of animals which are uniquely explained by our theory (see, for example, Chapters 6 and 11).

In this chapter we will concentrate on the concept of natural selection, primarily by reviewing various examples. We begin by considering the concept itself and emphasize that natural selection is a creative process. We then review its relationship to evolutionary change. We

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show that selection pressures in nature are often strong and that immense periods of time have been available for selection to act. We show that even differences in apparently trivial traits may be associated with variation in reproductive success, and that no trait is adaptive in all environments. We briefly review the way in which function can be studied. And, finally, we give an overview of the way in which selection acts on one well-studied species.

The Individual That Leaves the Most Surviving Offspring

A shorthand way of describing natural selection is to say that it favors the individual that leaves the most surviving offspring, or favors the traits that permit an individual to leave the most surviving offspring. Let us examine this statement, word by word.

First, natural selection refers to *individuals*, it does not refer to groups or species, and this distinction is vital. It is individuals that are purposively organized, and they are organized to leave surviving offspring. In the pre-Darwinian view, it was common to imagine that some species were created expressly to benefit others: authors sometimes imagined that salmon swam upstream so as to leap into the arms of waiting mammals and birds. This notion is denied in the Darwinian view: the fish do not give themselves up gladly. They attempt to escape their predators, and precisely because of this, predators have to struggle to catch their prey and can only catch some individuals, not all.

The same distinction between groups and individuals applies to interactions within a species. In the old view, individuals could easily be designed to sacrifice for the benefit of the species. They may choose not to reproduce, when they easily could, in order to benefit the species as a whole. In the new view, it is difficult to see how sacrifice of reproductive output could survive in the face of genetic variation and natural selection. Any individual genetically inclined *not* to sacrifice would leave more surviving offspring and the genetic tendency would spread, whether the long-term consequences were good or bad. The alternative view, that life is organized so as to benefit the species or group, has been so widespread and important that we devote an entire chapter to it (Chapter 4).

Second, natural selection favors individuals that *maximize* the number of their surviving offspring. Sometimes, pushing to reproduce too many will result in producing less, but we never expect a pair of herring gulls to say to themselves, so to speak, "Well, we've bred successfully for three or four years, and we've produced 10 surviving offspring; why don't we just retire and live out our days without the quacking of chicks and this constant regurgitating of food?" No, organisms are expected to be maximizing machines. Organisms are expected to attempt to increase their reproductive success over anything they have already achieved.

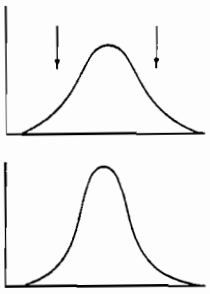
Third, individuals are selected to maximize the *number* of surviving offspring they produce. This is an important feature of Darwin's theory of creation; at the heart of the theory lies a number. This—more than anything—makes the theory scientific: we can actually measure the creative process and we can devise simple equations in which these measurements appear. In this book we will emphasize measurements of differential survival and reproduction, since these show us directly how natural selection is acting.

Finally, Darwin's theory emphasizes the production of *surviving offspring*. Life is organized around the production of children. This means that we expect behavior to be organized in a clear hierarchy in which activities are biologically meaningful only insofar as they eventually contribute to the production of surviving offspring. Instead of a disorganized list of items that we may care to invest ourselves in, such as children, leisure time, sexual enjoyment, food, friendship, and so on, Darwin's theory says that all of these activities are expected to be organized eventually toward the production of surviving offspring.

Natural Selection as a Creative Process

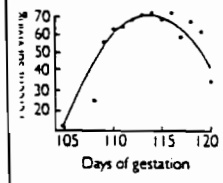
Because the processes of death and destruction constitute the selection pressures in nature, it has often been claimed that natural selection is not a creative process but a force that merely weeds out the misfits, leaving the fit the same as before. A famous analogy helps us see why this view is erroneous. Imagine that we are trying to create the word "cat" by removing three letters at a time from a bin containing a hundred copies of each letter in the alphabet. The probability of removing all three at once is $6 \times (1/26)^3$, or about one chance in 3,000. Now imagine that after removing three letters from the bin, we discard them before choosing another three letters. In 867 attempts we will have emptied our bin, so most of the time we will fail to form the word "cat" before our supply of letters runs out. This example is analogous to viewing natural selection as a random, destructive process.

Now, instead, imagine that whenever we remove a "c," an "a," or a "t" from the bin we return it again while discarding any other letter. As time proceeds, the bin becomes richer in the three letters we seek. Our chances of forming "cat" improve until we are guaranteed of doing so long before the supply is exhausted. Imagine, further, that whenever we happen to draw two of the right letters, we are permitted to staple them together before returning them to the bin. Now, our chances of drawing the three letters are even greater. This example is



igure 2-1

tabilizing selection. 1) The number of individuals possessing kidneys of given size is plotted for n imaginary population. rrows denote individuals iffering greatest mortality. 1) The same population ne generation later. There is been no change in the erage kidney size and the gree of variability has deeased slightly.



gure 2-2

rvival of piglets as a nction of length of gestan. Percent survival of glets to six weeks of age shown as a function of ngth of gestation, meared in days. Selection is bilizing, since both exmes are associated with wer survival. (*From* Cox 65).

analogous to viewing natural selection as a directed, creative process. A very improbable event, the construction of a particular living creature, or a particular adaptation, is made more probable because the various elements tend independently to increase in frequency within the population. Beneficial traits are, thus, knitted together through time.

Through natural selection, species automatically become more fitted to their circumstances. Predators, for example, remove those creatures that are slower, or less alert, or less sociable, and so on, so that over time the prey species improves in its ability to evade predators. At the same time, natural selection acts back on the predators, favoring those that are swifter, more alert, and sometimes more sociable. Thus species cut against each other, and like knives, each is sharpened in turn. Through this process, there is certainly progress toward more complex and subtle adaptations, or in the words of Darwin:

> There is grandeur in this view of life with its several powers having originally been breathed into a few forms or into one, and whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning, endless forms, most beautiful and most wonderful, have been and are being, evolved.

Natural Selection and Evolutionary Change

Natural selection is a simple concept: it refers to differences in reproductive success (abbreviated RS) among individuals in nature. Genetic traits associated with high reproductive success will tend to predominate in future generations. Our attention is focused on variability within a population. We wish to see how variability in the traits of individuals is associated with variability in RS. This represents an important break with pre-Darwinian biology. In the old system, each species was imagined to have been created according to some ideal type. Variation was just so much noise superimposed on the ideal type. After Darwin, the variation itself was seen as real and important, while the notion of an ideal type was recognized as a useless abstraction.

When thinking about the evolution of a trait it is useful to picture variability in the trait and consider how selection affects this variability. Picture the frequency of people with various-sized kidneys. If selection acts against individuals with extreme-sized kidneys, selection is said to be stabilizing, since it keeps the average value of the trait constant (Figure 2-1). This is the most common form of selection, namely, pressure against the extremes. Sometimes stabilizing selection can last

for eons. Opossums, for example, have hardly changed in external morphology in 150 million years. This constant state must have been maintained by stabilizing selection, because without some kind of selection, variability in the opossum would have steadily increased.

For another example of stabilizing selection, consider length of gestation in pigs. Among pigs, unlike most mammals, increasing litter size is not associated with shorter gestation time, so the effect of selection on gestation time can be seen directly from its effect on subsequent survival of the piglets. This effect is substantial (Figure 2-2). Optimal gestation time is about 114 days. Larger and smaller values are associated with lowered survival. A gestation time only two days longer or shorter (that is, a 2% change in gestation length) is associated with a five percent decrease in survivorship. With successive increments the effect on survivorship is more severe. Surprising as it sounds, even smaller differences in time spent inside the mother by members of the same litter have even greater effects on survival. This is because first-born pigs grab the best teats on which to suck and suck these teats throughout nursing. Piglets are very aggressive in the first two hours after birth and act as if they know that the teats highest on the mother's belly are the richest in milk (Figures 2-3 and 2-4). The piglets who are born in the second half of the litter suffer about twice the chance of dying before three weeks of age that the first-born suffer (Table 2-1).

Table 2-1 The Relationship of Birth Order to Birth Weight and Mortality*

Birth Order	Average Birth Weight (kg)	Mortality by 21 Days of Age (%)	Survivors' Average Birth Weight Minus Non-Survivors' Average Birth Weight (kg)
1	1.21	9.1%	.29
2	1.21	9.3	.23
3	1.24	6.8	−.03
4	1.21	15.9	.28
5	1.25	19.0	.16
6	1.11	20.9	.11
7	1.20	20.9	.17
8	1.21	17.1	.08
9	1.20	17.6	.40
10	1.11	30.0	.17
11	1.19	28.6	.09
12	1.19	17.6	.03

Source: Hartsock and Graves 1976.

* Five piglets dying from congenital disorders were excluded.

Figure 2-3

Aggressiveness as a function of teat order. The percentage of all fights over teats at a given position is plotted as a function of teat position. Number 1 is the most anterior teat (closest to the mother's head). Notice that piglets fight more often over access to anterior teats, a nice example of aggressiveness adjusted to the value of the prize (see next figure). (*From* Hartsock, Graves, and Baumgardt 1977)

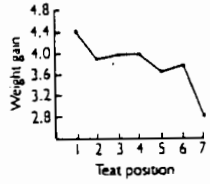


Figure 2-4

Weight gain in pigs as a function of teat order. The weight gain, in kilograms, from birth to three weeks of age is plotted as a function of teat position (see previous figure). In addition to anterior teats being superior in milk, part of the association may be due to the fact that larger piglets grab these teats first. (*From* Hartsock, Graves, and Baumgardt 1977)

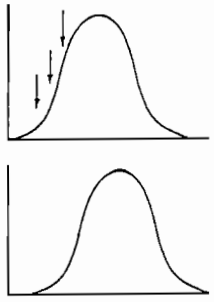


Figure 2-5

Directional selection. (a) The number of individuals possessing kidneys of a given size (in millimeters) is plotted for an imaginary population. Same as Figure 2-1(a) except mortality (arrows) now works against one extreme only. (b) The population one generation later: the average kidney size has increased due to selection against those with small kidneys.

If selection acts against one extreme of a sample but not the other it is said to be directional because its effect is to move the average value of the trait toward the extreme that has higher reproductive success (see Figure 2-5). Notice that after several generations of selection, the mean value of the trait may have moved outside its original distribution. An example of directional selection is the steady increase in brain size in the human lineage over the past three million years. We must assume that in generation after generation there was a tendency for selection to operate against individuals with relatively smaller brains. Incidentally, brain size apparently has not increased over the past 100,000 years so we assume that the earlier directional selection has given way to stabilizing selection. Studies of the fossil evidence from many animal groups suggest that new lineages often evolve quickly in various directions and then remain stable for long periods.

Selection can also act against the middle, favoring the extremes. In such a case it is said to be disruptive, since its effect is to split the original distribution into two distributions (Figure 2-6). Wherever two forms have evolved from one, disruptive selection has been at work. The two sexes were created, and are maintained, by disruptive selection in which intermediate forms are at a decided disadvantage. (Compare Figures 2-7a and 2-7b.) Many other dimorphisms are maintained in a similar way. In a bird called the ruff, males come in two forms (Figure 2-7(a)). The dark-colored form defends a territory aggressively and courts females. The light-colored form is non-aggressive and does not defend a territory, but instead approaches a dark-colored male, seeking to be permitted to court females from within the dark-colored bird's territory while remaining subordinate to him. This dimorphism must have evolved by selection acting against intermediate forms and favoring the two distinct forms.

The Intensity of Selection

The intensity of selection is a function of the variability in reproductive success. Where variability is high, selection is strong. What evidence we have shows that selection in nature is often surprisingly strong. A variety of studies in plants and animals show selective values of at least 5% and many show values of 50% or higher. Experiments yield similar results. For example, the distance between nests in herring gulls is strongly influenced by egg predators such as crows. When crows are attracted to eggs laid in a pattern, those that are closer together suffer higher mortality. In one trial, when eggs were only 0.5 meters apart, 24 of 27 were found by a crow, while of 27 eggs placed 8

meters apart, only 5 were found. This is a five-fold increase in mortality due to spacing!

In the herring gull (or in closely related species) selection has been shown to act on the size of eggs laid, on the number of eggs laid, on the date eggs are laid, on the order in which eggs are laid, on nest density, on the location of colonies relative to predators and sources of food, on the amount of food fed by a male to a female during courtship, on the tendency of adults to remove egg shells from the vicinity of their nests, and also on the tendency of mates to remain paired in succeeding years. We note that the increase in reproductive success associated with these traits is often 5% or more. *Notice in addition that gulls can cause strong selective effects on each other.* Courtship feeding, breeding density, and rates of cannibalism all affect reproductive success and all are caused by the gulls themselves. Let us consider one of these in a little detail: the cannibalism of young chicks by adults other than their parents.

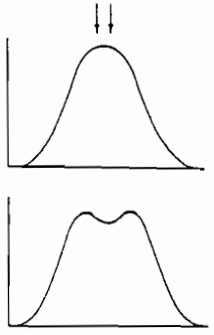


Figure 2-6

Disruptive selection. (a) The number of individuals possessing kidneys of a given size (in millimeters) is plotted for an imaginary population. Same as Figure 2-1(a) except that mortality acts against the middle, favoring both extremes. (b) One generation later, the population has begun to separate into two distinct groups, those with large kidneys and those with small kidneys.

Gulls are notorious killers during the breeding season and will peck to death or worry to death chicks that wander into their territories (Figure 2-8). In addition, in some colonies a few individuals specialize in preying on chicks as a source of food. As Jasper Parsons showed, mortality from this source can be considerable: at least 23% of over 1400 herring gull chicks marked at hatching were cannibalized before they fledged, yet only one in 500 adults was acting as a cannibal (Table 2-2).

Cannibals are individuals that leave their own nests in search of live chicks from other nests. These chicks are taken from their own nest sites and swallowed in flight or carried back to the cannibal's nest site, where they are eaten (Figure 2-9). Cannibals depend on chicks for their food and take a relatively constant number throughout the breeding season. Since most gulls breed during the middle of the season, the smallest percentage of chicks is eaten at that time (Table 2-3). The effect is substantial: fewer than 8% of chicks hatched at midseason perish to cannibals, but more than 20% of early and late hatchlings are cannibalized. Incidentally, predation is believed to often favor clumped patterns of breeding because individuals breeding alone are, for various reasons, ar greater risk. For example, Parsons found that cannibalized nests had fewer close neighbors: cannibalized nests had an average of 2.07 other nests within 3 meters, while a random sample of nests had 2.74 nests within that range ($P < 0.002$). This safety in numbers probably occurs because a cannibal is more easily attacked by several gulls simultaneously when they are breeding close together.

Cannibalism is also selective in other ways. Young chicks are especially at risk since they are easily swallowed: the average time of death was 7 days after hatching. Cannibals also take a higher proportion of

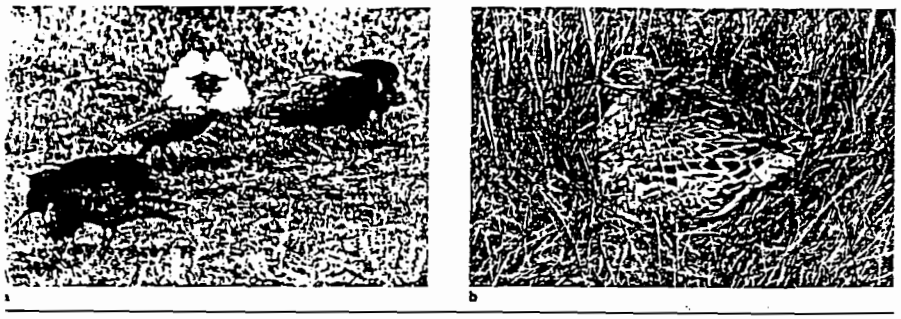


Figure 2-7

Dimorphisms maintained by disruptive selection. (a) *Male dimorphism.* Male ruffs *Philomachus pugnax* come in two forms: a white non-aggressive satellite form and a black territorial form. The two black males are pointing at the ground with their beaks, a typical response to arrival of a satellite. (Photo: C. S. Doncaster) (b) *Sexual dimorphism.* In contrast to the male ruff, the female (or reeve) is camouflaged. She alone sits on the eggs and cares for the young. (For the evolution of sexual dimorphism, see Chapter 9.) (Photo: J. B. Bottomley and S. Bottomley)

Figure 2-8

Territorial aggression. A well-grown herring gull chick that has wandered into a neighboring territory is attacked. The adult pecks the chick around the head and neck. Smaller chicks are often killed in such circumstances. (Photo: Jasper Parsons)

Table 2-2 Fate of 1,415 Young Herring Gulls Ringed at Hatching on the Isle of May in 1968

	Number of chicks	Percent of total
Known to have fledged	609	43.0%
Eaten by cannibals	329	23.3
Dead, with head scars	47	3.3
Dead, no visible injury	256	18.1
Not accounted for	174	12.3

Source: Parsons 1971.

chicks hatched from the third—and last—egg laid, presumably because these chicks are smaller and weaker (Figure 2-10). As these examples show, mortality does not strike randomly but acts more harshly against some classes of individuals than others. The gulls themselves have strong selective effects on each other.

Although cannibals as a group were no less successful at breeding than were the other gulls, one gull showed that he had a hard time

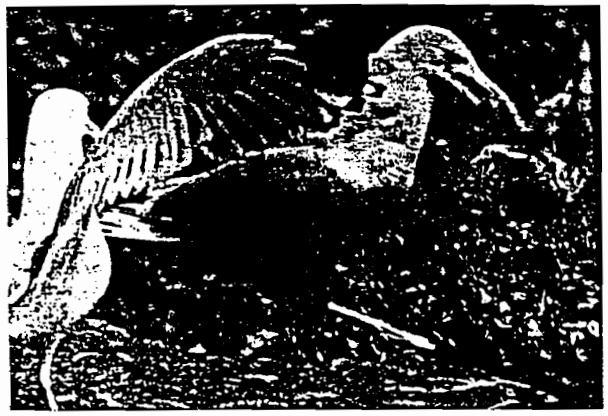


Figure 2-9

A cannibal in action. An adult herring gull grabs a young chick while the parent challenges ineffectually. The chick will be carried to the intruder's territory and swallowed. (Photo: Jasper Parsons)

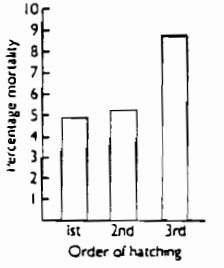
Table 2-3 Seasonal Variation in the Numbers of Chicks Eaten by Four Cannibal Herring Gulls at the Isle of May in 1968*

	Date of Hatching						
	Before 5 June	*5–9 June*	*10–14 June*	*15–19 June*	*20–24 June*	*25–29 June*	*After 29 June*
Number of chicks ringed	99	201	289	443	260	84	22
Number of chicks eaten	22	22	21	34	29	23	7
% eaten	22.2	11.0	7.3	7.7	11.2	27.4	31.8

Source: Parsons 1971.

*The significance of the seasonal variation is $P < 0.001$.

separating the feeding and care of his own offspring from the killing and consumption of others. He ate 40 chicks while he was incubating his own three eggs. When they hatched, he continued to catch chicks and bring them back to his nest but *he failed to kill them*, so that within a week he had eleven chicks at his nest, all of which he fed! Two, including one of his own, died during a rain storm, and the cannibal subsequently ate eight of the nine remaining, including both of his own, so he succeeded in fledging only one chick, someone else's. This observation shows how a trait can cut back on itself, interfering with its own spread.



igure 2-10

ercentage mortality from annibalism as a function f hatching order. The difference in mortality between first and third chicks s significant ($P < 0.05$). *From* Parsons 1971)

The Time Available for Evolution

The strength of a selection pressure and the time needed for it to produce change are inversely related. The weaker the selection pressure, the greater is the time required to effect a given amount of change, but relatively modest differences in reproductive success translate into rapid evolution. Consider, for example, two females. Female A produces six surviving offspring, as do her descendants, while Female B and her descendants only produce five each. This is a difference in RS of almost 17%. When repeated generation after generation such a difference in reproductive success can bring about striking changes in relative frequencies. In 25 generations, B's frequency will drop to one percent of its original value. If A and B are initially equally frequent, after 25 generations only one in a hundred individuals will be type B. If A and B differ much less in reproductive success, the same change will require many more generations. Thus, a one percent difference in

Table 2-4 Time and Number of Generations Available for Selection to Act on Various Traits (Approximate)

Trait	Time	Number of Generations
Mental apparatus associated with human language	Uncertain, perhaps 2 million years	50,000
Mental apparatus associated with human technology	5 million years	250,000
Adaptation to living in social groups of the complexity of baboons and macaques	30 million years	3 million
Adaptation to living in small, face-to-face groups of kin, friends, dominants, etc.	At least 50 million years	10 million
Vertebrate physiology, sensory equipment, mental life	½ billion years	200 million
Chemical machinery of the cell, including machinery for reproducing genes and decoding genes	3 billion years	billions

reproductive success requires about 265 generations to effect a change in relative frequency of two orders of magnitude. In humans this means it takes about 10,000 years for a trait with a 1% selective disadvantage to go from 99% of the population to less than one percent.

Yet 10,000 years is but the blink of an eye in evolutionary time. When we consider various human traits we see that enormous numbers of generations must have been available for selection to operate, the more so the more broadly the trait is shared with other living creatures (Table 2-4). Thus, our cellular machinery has evolved during literally billions of generations; our multicellular body, during hundreds of millions of generations; and our social life dominated by relatives and friends, for at least 3 million generations; and so on.

The more uniquely human a trait is, the less time must have been available for selection to act. The best evidence suggests that we are at least 5 million years separated from a common ancestor with the chimpanzees. The traits that differentiate us from chimpanzees have passed through at least 200,000 generations of selection. Most of the rapid increase in brain size took less than 100,000 generations. The development of religion and art has probably experienced about 10,000 generations of selection. Insofar as variation in religion and art affected individual reproductive success, there has been ample time even for weak effects to produce biological evolution in these traits. By con-

trast, the last 10,000 years have seen enormous changes in human life. Yet this time is too short for any but the strongest pressures to have produced much change. Of course, human warfare stands out as one such pressure. So does selection associated with disease organisms, which were probably spread more easily as urban populations flourished and people undertook long-distance migrations.

Even Trivial Traits Can Be Associated with Reproductive Success

Since selection pressures in nature are often strong, since even weak selection pressures produce substantial change in relatively few generations, and since there is so vast a stretch of time during which natural selection has operated (always as determined by the local environment), we expect that organisms will show numerous elaborate and subtle contrivances to advance life in the circumstances they face. Since we are largely ignorant of the effect living traits have on reproductive success, we must not mistake this ignorance for the face of nature. It is better to begin with the assumption that even apparently trivial traits can affect reproductive success, especially when these traits are widely shared by individuals of a species. Anything less than this bias will tempt us to abandon prematurely the search for an understanding of how living traits function.

Consider one apparently trivial trait, the exact shape of the human head, in particular, the degree to which it is round. The human head as viewed from above can be characterized as relatively round or relatively long. Dividing the width of the skull by its length gives us a "cephalic index," a crude measure of its roundness. For the current human population the index is about 0.83, meaning that the average head is longer than it is wide by about 20%.

One might suppose that minor variation in so minor a trait has no appreciable effect on survival, but this is not so, at least not for Polish army recruits in the late 1920's. A part of the massive Military Anthropological Study of Poland (which covered 120,000 individuals, on each of whom 70 measures were taken) survived the Warsaw Uprising in 1944 to give us a large (N = 6229), homogeneous sample of men: most of the recruits were 21–25 years of age, all came from nine counties in the northeastern corner of pre-war Poland (now USSR), and all were farmers. The region was poor, women had high fertility, and mortality in the first year of life hovered around 20%. Besides his cephalic index, we know for each recruit the number of his surviving siblings and the total number of siblings ever born.

As Figure 2-11 shows, the shape of a recruit's head is associated with the number of his surviving siblings. Round-headed soldiers have more surviving siblings than do long-headed ones, but stabilizing selection must also be acting, since at the extremes individuals do less well than near the mean. (This, incidentally, is a common feature of directional selection: it often has a stabilizing component.) Why the association between shape of head and number of surviving siblings? We know it does not result from differential fertility. In fact, long-headed people gave birth to slightly more children, but a higher proportion of these children died (32%, compared to 28% for round-headed people). Unfortunately, nothing is known about the reason that shape of head affects survival, but it is worth noting that there appears to be a long-standing trend toward round-headedness in humans: we are more round-headed than apes and monkeys, and skulls dug up about 700 years ago in Polynesia, India, and Poland give average cephalic indices of only about 0.73.

In principle, then, it seems like a bad idea to assume that *any* trait is neutral or lacks association with reproductive success. Of course, there are exceptions to this rule. For example, "as useless as teats on a boar" expresses our inability to see any function for nipples on male mammals. These are apparently maintained in males because of strong selection on females.

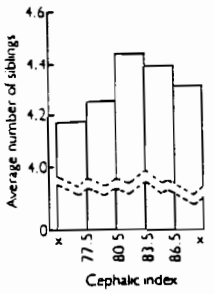


Figure 2-11

Number of siblings as a function of shape of head. The number of surviving siblings is given as a function of the cephalic index (head-width/head-length) for Polish army recruits in the 1920s. Note that selection appears to be both stabilizing and directional (in favor of higher indices). (*From* Bielicki and Welon 1964)

No Trait Is Adaptive in All Environments

The environment determines the action of natural selection. Indeed, details of the environment determine exactly how selection operates. We have seen already that the presence of sparrow hawks can select for sociality in starlings. Keep the environment otherwise constant but remove this sort of mortality and we may see a tendency for starling flocks to become smaller. Thus, traits are only adaptive with reference to a particular environment and few, if any, traits are adaptive in all contexts.

Consider an example: brain size. Humans stand at the end of a long line of positive selection for this trait, but such selection is far from universal. Birds and mammals have experienced 150 million years of positive selection for brain size, more strongly in some groups, such as monkeys and whales, than in others; but in fish, amphibians, and reptiles, there has been no change in brain size (relative to body size) during the past 300 million years. Indeed, in some specialized circumstances, brains and associated nervous systems have disappeared entirely. Tapeworms, which live in the human gut, lack a brain but are descended from free-living forms such as planaria, which have brains and are capable of simple learning.

Since traits are only defined as useful by reference to a given environment, the concept of natural selection provides no objective support

for terms like "higher" and "lower." Darwin made notes to himself to stop referring to higher and lower animals, but this usage had been built into the taxonomy constructed by Linnaeus a century before, and it has persisted to this day. Schemes for elevating some creatures above others typically do so on the basis of similarity to ourselves, but this is obviously an egocentric approach. Groups of species can be compared according to the number of species within a group, but this leads to the conclusion that some environments favor many species while others do not. There are, for example, 300,000 species of beetles, nearly one-fourth of all animals. J. B. S. Haldane, a famous evolutionist, was once asked by a group of clerics what a lifetime's study of evolution suggested to him about the nature of the Creator, and he responded, "An inordinate fondness for beetles."

The chief effect of using terms like "higher" and "lower" is to underestimate the powers of other creatures; "lower" animals, for example, are often assumed to be too dumb to act in their own self-interest. Unfortunately this assumption—often unconscious—merely blinds us to the true nature of these creatures. I think a better bias is the one William Drury taught me when I was his student: "Never assume the animal you are studying is as dumb as the one studying it."

The Study of Function

Since traits are adaptive with reference to particular environments, the study of function naturally seeks correlations between the environment and the action of natural selection. Consider an example. Between 1942 and 1944, 198 young men died in basic training from heat stroke in the U.S. Army. The Army analyzed the reasons for the deaths. When temperature versus humidity was plotted for the times of these deaths, it was discovered that mortality occurred whenever temperature or humidity was high, both of which variables make it difficult to keep one's body cool. Were the soldiers a representative sample of all soldiers? No. Those who died were typically overweight for their body size (see Figure 2-12). This is not surprising since fat interferes with the body's ability to dissipate heat.

More generally, larger people suffer heat and humidity more intensely than do smaller people, since larger people have smaller surface areas relative to their weight. Thus, we are not surprised to discover that throughout the world there is a clear correlation between mean annual temperature and human body weight, heavier people being more common at lower temperatures. Human body *shape* is also correlated with temperature because different body shapes produce relatively more or less surface area. Thus, in climates where people

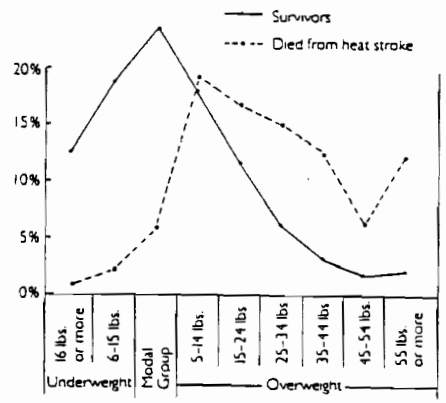


Figure 2-12

Relationship of death from heat stroke to weight for a given size in humans. Plotted is the percentage of 100,000 surviving men and the percentage of 124 who died from heat stroke as a function of the degree to which these men were overweight or underweight. There is a very strong tendency for those who died to be overweight. (*From* Schickele 1947)

need to dissipate a lot of heat, they have long, slender fingers and long limbs relative to trunk size. An Eskimo, by contrast, is short and has a large trunk and short extremities. The deaths from heat stroke in the Army just described were also related to geographic origin. Those raised in warmer climates were less likely to suffer mortality, but whether this was due to acclimatization or a genetic difference in the populations is not known.

Note that we have combined two kinds of information. On the one hand we have correlated mortality data with both environmental and personal variables. On the other hand, we have correlated environmental variation with variation in the distribution of a trait within a species. It is much easier to gather the second kind of information than the first, so most of our understanding of function comes from a study of how biological traits co-vary with the environment and with other traits. The following example illustrates the general methodology.

Most mammals give live birth; most reptiles lay eggs. Why this difference? Among reptiles, a tendency for females to retain eggs within their bodies has evolved repeatedly. The mammalian system of reproduction ultimately resulted from a tendency of certain reptile females to retain their eggs for several days before laying them. What is the functional significance of this trait? We have no data linking reproductive success with variation in egg retention, so we must discover the correlates of a tendency toward live-bearing. It has been estimated that live-bearing has evolved more than 30 times among reptiles. A study of these species compared to 1000 species of egg-layers shows that live-bearing habits are associated with two variables—cold climate

Table 2-5 The Relationship Between Habitat or Presence of Maternal Care and Frequency of Live-bearing or Egg Retention in Lizards and Snakes

Habitat	Percent of All Lizard and Snake Species	Percent Live-bearers in Genera with Both Egg-laying and Live-bearing Species	Percent Species with Egg Retention
Cold climate	44%	74%	72%
Wet soil	12	11	13
Arboreal	10	8	8
Maternal Care (at level of genus)	11	24*	33

Source: Shine and Bull 1979.

Note: Both cold climate and maternal care are associated with trends toward live-bearing, while wet soil and arboreal habitats are not.

* In egg-laying forms.

and a tendency for females to care for their young after eggs are laid (Table 2-5).

Studies of the effect of temperature on egg development suggest that a female benefits by retaining eggs within her because this permits faster development: females choose warm portions of their habitat, thus boosting their temperature, while eggs, once laid, are no longer mobile. Egg retention also protects against lethal temperatures and females that brood eggs gain a further benefit from egg retention: it shortens their brooding time, partly offsetting the cost of carrying the eggs. We therefore expect brooding species to be more likely to retain eggs than non-brooding species. Thus, comparative evidence suggests that two factors may have operated in early mammalian evolution: if early mammals lived in colder climates (or were active at night) and if they already showed parental care, internal development would have been favored.

Natural Selection Acting on Red Deer

To get an overview of the way in which natural selection acts on a single species, let us choose a particularly well-studied species, the red deer *Cervus elaphus* and concentrate on the factors controlling variation in lifetime reproductive success.

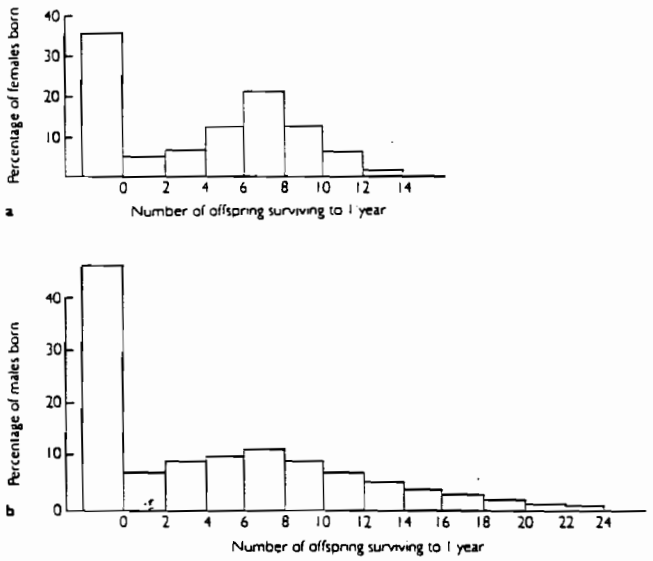


Figure 2-13

Lifetime variation in reproductive success for females and males in red deer. The percentage of (a) females born or (b) males born who achieved a given lifetime RS (measured as surviving offspring to a year of age) is plotted for red deer. Notice that variation is substantial for each sex but greater in males. These data are especially valuable because they give us a clear overview of the operation of natural selection on a single species. (*From* Clutton-Brock, Guinness, and Albon 1982)

In Figure 2-13 we see that there is substantial lifetime variation in RS for both males and females, but this is greater for males. For all females born, about 35% produce no surviving offspring, while some raise 13 young to one year of age. For all males born, more than 40% produce no surviving offspring, while some father as many as 24. Thus, the maximum RS of a male is twice that of a female, and selection is more intense on males.

What controls variation in reproductive success? Although social factors have effects in both sexes, these are much more pronounced in males. For females each offspring is costly to rear, as may easily be seen by noting the superior condition or survival of adult females without offspring compared to those with dependent young (Figure 2-14). Maternal condition appears to be the key factor controlling survival of a female's offspring. Mothers in better condition give birth earlier to heavier offspring, and, in general, both these factors have a positive effect on survival of offspring (Figure 2-15). In addition, in mother–offspring pairs shot throughout the year, the size and condition of the offspring is positively correlated with the condition of its mother. Dominant females outreproduce subordinates (Table 2-6), presumably because dominance gives them greater access to areas with better forage.

Figure 2-14

Difference in mortality rate between red deer mothers who are nursing and those who are not. The annual mortality rate of nursing mothers minus that of non-nursing mothers is plotted as a function of maternal age. Non-nursing mothers either failed to give birth or lost the calf early in the season. (*From* Clutton-Brock 1984)

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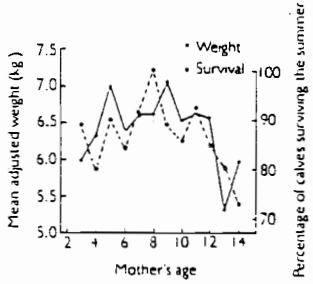
gure 2-15

eight at birth and sur-val through the summer a function of mater-l age in red deer. Birth ight, in kilograms, (ad-ted for sex of calf and ar of birth) and survival e of calves until October plotted as a function of other's age in red deer. ote the close, positive re-ionship between birth ight and survival. (*From* utton-Brock, Guinness, d Albon 1982)



Although females prefer to travel in the company of female kin, the size of such groups is, curiously enough, negatively associated with the survival of their sons—but not their daughters (Figure 2-16).

Social factors have a critical influence on male RS. In the fall mating season, males fight with each other to control mating access to groups of females (Figures 2-17 and 2-18). During this time, the frequency of fighting and the number of injuries sustained is positively associated with the frequency with which females are conceiving. Just like the piglets in Figure 2-3, red deer males appear to adjust their aggressiveness to the value of the prize being fought over. Males virtually stop eating and undergo a precipitous decline in condition (Figure 2-19). Because some males are large, in excellent condition, and good fighters they are able to obtain exclusive mating access to groups of females during the time when these females are conceiving (Figure

Table 2-6 Measures of Breeding Performance in Female Red Deer According to Dominance Rank *

Breeding Performance Measure	Dominance Rank	
	Subordinate	*Dominant*
Median age of first breeding (years)	3.9	3.48
Median weight of calves at birth (lbs)	6.4	6.8
Percent calf mortality in first year	45	28
Mean lifespan (years)	9	11
Median number of calves reared to one year of age	2.3	6.0

Source: Clutton-Brock et al. 1984.

* Females were divided into two equal groups based on rank. All differences are significant except percent calf mortality, which is nearly significant ($P < 0.10$).

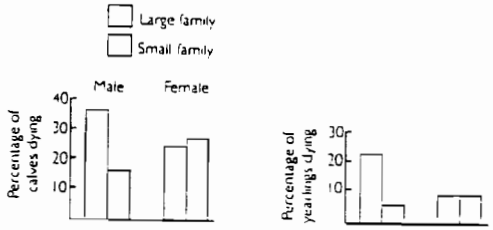


Figure 2-16

Social effects on reproductive success in red deer. The percentage of individuals dying in their first year of life (calves) and in their second (yearlings) is plotted separately for males and females, depending on whether their mothers were part of large family groups or small ones (large groups were those above the median size for their area). Note that large size of kin group has no effect on daughter's survival, but significantly reduces that of sons. Thus, social effects may be strongly sex-specific. The selection pressure shown may favor mothers who give birth to relatively more daughters when they are in large groups. (*From* Clutton-Brock, Guinness, and Albon 1982)

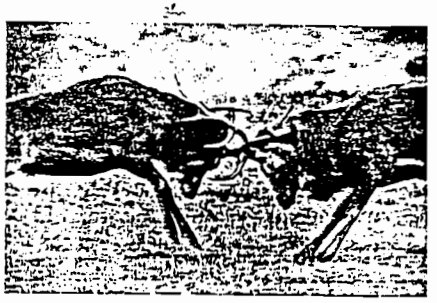


Figure 2-17

Red deer males fighting. The male on the left leaps up and forward in an attempt to dislodge his opponent. Such struggles have a strong influence on male RS since they will help determine access to breeding females (see next figure). (Photo: Timothy Clutton-Brock)

Figure 2-18

A male with his harem. A six-year-old red deer male with a group of breeding adult females. He is roaring, a form of aggressive display intended to intimidate rivals (and possibly attract females). As long as the females stay with him and no other male drives him off, he will enjoy nearly exclusive mating with the females. The number of days in which he holds such groups at the key time and the size of the groups have a strong influence on his lifetime RS (see Figure 2-20). (Photo: Fiona Guinness)

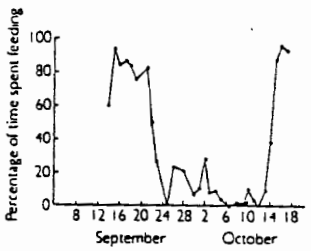


Figure 2-19

A cost of reproduction in male red deer. The percentage of time a nine-year-old male spent feeding during the 1974 rut. Note that for three weeks at the height of the rut he hardly feeds at all, yet this is a time of nearly continual intense activity: fighting other males, roaring, herding females, mating, and so on. Only those males able to feed well the rest of the year and in early life and to minimize the drain of parasites will be able to develop the body size, antler size, and energy reserves that give success in male–male competition. 1974 was a very good year for this male, in terms of number of females held, and presumably mated, at the critical time (see next figure). (*From* Clutton-Brock, Guinness, and Albon 1982)

2-20). This causes a large part of the variation in male RS. Females probably accentuate these effects by gathering in larger groups during the rut and by moving away from less preferred males. Early gains in development have later effects on male RS, since the size of a male's antlers at 16 months predicts mating success five years later. Even though competition to hold large harems is intense, those able to hold them live longer than those holding smaller harems, presumably because the same kinds of traits that aid a male in holding females also aid in survival (see Figure 14-12).

These data show that there is strong selection acting on red deer in nature, that selection is more intense on males than on females (that is, there is greater variation in male RS) and that RS in females is controlled by ability to invest in offspring, while male RS is controlled by ability to inseminate females. We shall see in Chapter 9 that this is a very general—but by no means universal—rule in animals.

Summary

Natural selection refers to differences in reproductive success among individuals in nature. Natural selection is a creative process, since it binds together traits in novel and unlikely combinations. Studies of natural selection show that selection pressures in nature are often surprisingly strong. The time required for a trait to evolve is a function of the strength of the selection pressure, and there has been abundant time for most traits to show significant selection. For this reason it is a bad idea to assume that any trait is without selective value. The environment determines the action of natural selection, and no trait is adaptive in all environments. The study of function proceeds largely through the search for correlations between the distribution of environmental factors and the distribution of biological traits. An overview of natural selection acting on one species (red deer) shows that variation in reproductive success is greater in males than in females, apparently because RS in males is more tightly tied to social interactions.

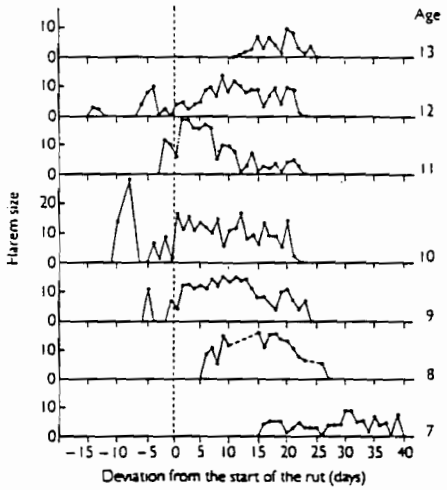


Figure 2-20

A successful male's reproductive life. The number of adult females held each year by one particular male (the same male as in the previous figure) is plotted as a function of deviation from the start of the rut (defined as the time when, throughout the population, females first tend to settle down in one male's area on successive days). Note that in his peak years, this male held as many as ten females for two weeks or more at the time when many were probably conceiving. Note also the day-to-day variation in harem size—females joining and leaving, both in groups and individually. Thus, in spite of intense male–male competition to exclude others, there is enormous scope for female choice (see Chapter 14). (*From* Clutton-Brock, Guinness, and Albon 1982)

Chapter 3

Elementary Social Theory

We are now in a position to apply our theory of creation to social traits, that is, to consider how natural selection affects social traits. These are traits that affect at least one individual other than the possessor of the trait, so the simplest social theory begins with two individuals. We imagine that one individual, the actor, initiates some action that affects a second individual, the recipient. We measure the effects in units of reproductive success; that is, we measure whether the behavior increases the reproductive success of the actor (benefit) or decreases it (cost) and we measure the same thing for the recipient. Neglecting zero effects, we have at once four kinds of social acts: the actor confers a benefit but suffers a cost (altruistic), the actor gains while inflicting a cost (selfish), both parties gain (cooperative), and both parties suffer (spiteful) (see Figure 3-1).

In this chapter we will illustrate the four kinds of social acts and consider the way in which selection acts on each. We will concentrate on altruistic behavior because it is both common and apparently opposed by the action of selection. Three explanations will be reviewed: kinship, return effects, and parasitism. A consideration of the subordinate role in paper wasps serves to illustrate the important concept of inclusive fitness. We close by observing that our social theory applies to creatures very broadly, including plants and parasites.

Altruistic Traits

An altruistic act is one that confers a benefit on someone at a cost to the other. Since cost is measured by a decrease in reproductive success, we know that altruistic acts are opposed by natural selection's working on the actor. They result in the production of *fewer* surviving off-

Actor	Recipient	
⊗	○	
B	C	Selfish
C	B	Altruistic
B_1	B_2	Cooperative
C_1	C_2	Spiteful

igure 3-1

he four categories of so-ial traits. The actor causes n effect on the recipient nd on self. (*B* is benefit, : is cost, both measured ı units of surviving off-ɔring.)

spring. Yet altruistic traits are widespread in nature. Examples include honey bee and ant workers foregoing personal reproduction to help the queen reproduce, birds helping a pair raise their young, lionesses nursing cubs that are not their own, ground squirrels warning each other of the approach of enemies, and chimpanzees attempting to raise orphans.

Let us consider an example in more detail. In 1977, Shigeyuki Aoki discovered a previously unknown phenomenon in aphids: in *Colophina clematis* the first larval stage hatching from an egg comes in two forms, one of which never molts but remains in the first stage, where it acts as a soldier protecting the lives of the other form (Figure 3-2). The normal form molts through several stages to reach the adult form, but since the soldier form does not molt, it never reproduces. The aphid soldier is a reproductive altruist, sacrificing its

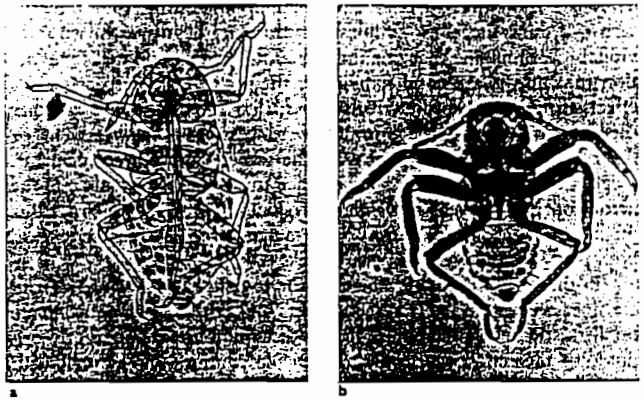


Figure 3-2

An aphid soldier and her identical twin. Two first-stage larvae of the Japanese aphid *Colophina clematis*. On the left (a) is the normal or primary-type larva, which has thin, uniform legs and long mouth parts (seen running down the center of its body) for sucking the sap of plants. The secondary form (b) acts as a soldier, defending her siblings by attacking predators (such as caterpillars), grabbing tight hold with her enlarged forelegs and midlegs and biting with her shortened mouth parts, usually killing the predator. Only primary-type larvae molt to the next stage and eventually reproduce. Both forms are produced asexually by the same mother; genetically they are like identical twins. (Photo: Shigeyuki Aoki)

entire potential reproduction for the sake of others, yet it has evolved several new features associated with its role: enlarged forelimbs and midlimbs, a tougher outside, and a shorter mouthpiece. Aoki soon discovered other species with similar forms (Figure 3-3).

We also now know that soldier forms have evolved independently in the aphids at least three times. In one species the soldier form itself has split into a larger and a smaller form (Figure 3-4). The soldiers are very effective at attacking and killing predators much larger than themselves; in some species, biting soldiers are produced in great numbers capable of driving off humans. In *Astegopteryx styracicola*, for instance, the aphids live inside partly hollow plant structures (galls), only one of which, the size of an orange may contain 100,000 aphids, of which 55% may be soldiers. These are second-stage larvae, which do not molt again but patrol inside and outside the gall; if the gall is

Figure 3-3

Aphid soldiers on the attack. Soldiers of the Taiwanese aphid *Pseudoregma alexanderi* (magnified 20 times) lie embedded on a predatory syrphid fly larva they have killed. They remain clamped to their victim even though both have been preserved in alcohol. Each soldier has two sharp horns on its head, although none is visible here because all have been buried in the victim. In this species, soldiers come in two forms, a large one and a smaller one (see next figure). (Photo: Masahisa Miyazaki)

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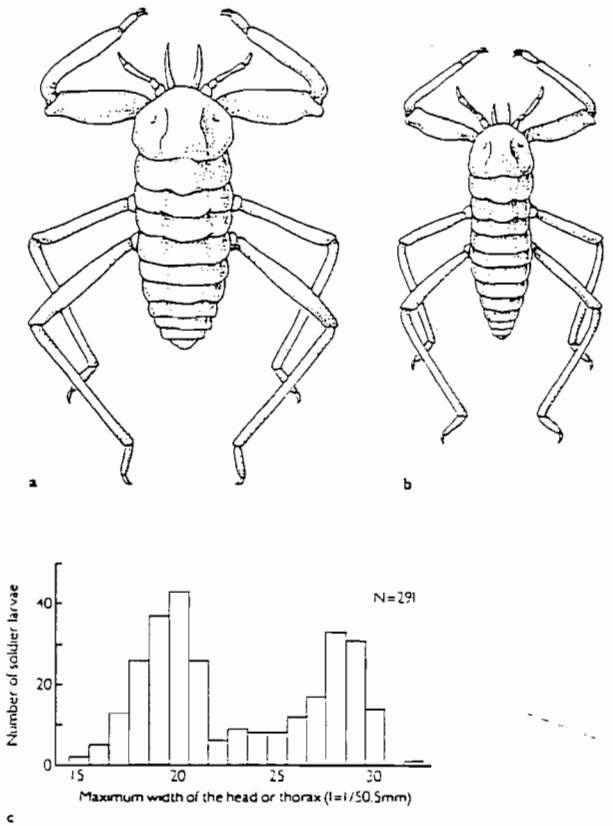

Figure 3-4

Two soldier forms in one aphid species. In *Pseudoregma alexanderi* the soldiers come in two forms: (a) a large form and (b) a small form. Whether they are specialized to attack different prey is not known. Notice the greatly enlarged forelegs and the heavily sclerotized body (dark coloration). (c) The number of soldier larvae having a head (or thorax) maximum width of a given value. Notice that most individuals fall into one or the other category. (Aphid soldiers drawn from a photo by Shigeyuki Aoki; bar graph from Aoki and Miyazaki 1978)

shaken, the larvae readily fall on—and bite—whatever is doing the shaking.

Our first problem, then, is to explain how natural selection might favor the spread of altruistic traits. There are three main ways: through kinship, through reciprocity, and through parasitism. The first two explanations show that apparent sacrifice by the actor may be genetically self-serving, while the third shows that selection on the recipient may induce altruism even when this is costly to the actor.

Kinship

The best way to understand the importance of kinship is to take a gene's eye view of social interactions. Under what conditions will a gene enjoy a net benefit after an interaction between two individuals? Consider an altruistic interaction in which an actor, at a cost of *C*, confers on a recipient a benefit of *B*. Imagine, for simplicity, that there is a single gene in an altruist directing the altruistic action. The gene suffers a cost in reduced copies in offspring of magnitude *C*. If the recipient is unrelated to the altruist, then the altruistic gene only suffers a cost, and decreases in frequency, but if the recipient is related to the actor, then there is some probability that the recipient also has a copy of the altruistic gene, by direct descent from a common ancestor. We call this probability the *degree of relatedness*, and symbolize it by *r*. For only a fraction of the time, equal to *r*, is the altruistic gene found in the recipient and enjoying there a benefit (Figure 3-5). The altruistic gene enjoys a *net* benefit when the benefit to the recipient times the degree of relatedness to the recipient is greater than the cost suffered by the altruist, or when

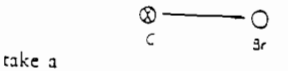

Figure 3-5

Kin-directed altruism. The actor is related to recipient by *r*. For every altruistic interaction, the actor's genes receive a cost; they also receive a benefit for a proportion of the time, equal to *r*.

$$Br > C$$

To solve particular cases, we need to be able to calculate degrees of relatedness. This is easy to do in a species such as our own, in which each individual gets roughly half its genes from each parent (who are typically unrelated to each other) and passes on half its genes to each offspring. Thus, *r* between offspring and parent is ½ and between parent and offspring is ½. With these two *r*'s we can generate the other *r*'s by tracing out the genealogical connections.

Consider your half-sibling, related through your mother but not through your father (Figure 3-6a). The probability is one-half that a gene in yourself will be found in your mother and, if she has the gene, one-half that she passed it to your sibling. Since ½ × ½ = ¼, *r* between you and your half-sibling is ¼. For natural selection to favor altruism toward your half-sibling, benefit must be greater than four times cost.

What is your degree of relatedness to your full-sibling? Since the two of you are related through both parents, it is necessary to consider both genealogical connections and add the values together (Figure 3-6b). As we have seen, the probability is ¼ that your sibling has any of your genes via your mother. Similarly, the probability is ¼ that your sib has any of your genes via your father. Since ¼ + ¼ = ½, *r* between full-siblings is ½. For altruism to a sibling to be favored, benefit need only be greater than two times cost.

Finally, consider your degree of relatedness to your cousin—for example, your mother's sister's child (Figure 3-6c). Assuming your

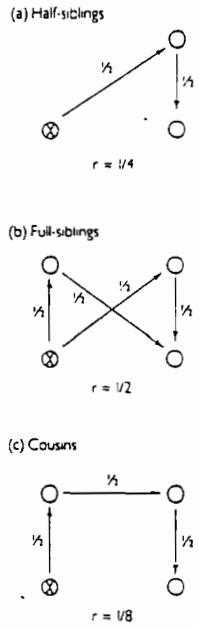

Figure 3-6

Common degrees of relatedness in our own species: (a) half-siblings (related through one parent), (b) full-siblings (related through both parents), (c) cousins. Notice that we always begin with the actor and trace genealogical connections to the recipient.

mother and her sister are full-siblings, we reason as follows: if you have a gene, the probability is ½ that your mother had it; if your mother had it, the probability is ½ that her sister had it, and if her sister had it, the probability is ½ that she passed it on to her child. Since ½ × ½ × ½ = ⅛, r between first cousins is ⅛.

The general rule for calculating a degree of relatedness is obvious. As we trace a genealogical connection from one individual to another, we *multiply* the r's that connect the various individuals. If two individuals are related through more than one genealogical connection, we *add* the values together that are obtained for each genealogical connection. Note that it is not necessarily true that one individual's degree of relatedness to another is the same as the other way around (for exceptions, see pp. 129 and 178). Thus, we want to be careful always to specify the *direction* of relatedness (A's relatedness to B) and, in calculating this r, to begin with A and end with B.

J. B. S. Haldane, the famous population geneticist, presented the essential features of kinship theory in 1955 in a popular essay on population genetics. To make matters dramatic, Haldane considered a gene that led an individual to try, at the risk of drowning, to save a drowning individual. He argued that you would have to save a cousin more than eight times as often as you drown yourself in the attempt in order for this gene to be positively favored. He then did a very curious thing: having stated the general principle, he at once severely restricted its scope. He said that the two times he himself had jumped into the river to save a drowning individual, he had acted at once without considering the possible degrees of relatedness. Thus he imagined that creatures in general would tend not to discriminate between possible recipients according to the relevant degrees of relatedness, but would instead have to react according to the *average* degree of relatedness they enjoyed to others in the area. If we travel in groups of 50 or more, as humans certainly do, then the average degree of relatedness must usually be fairly low ($r << 1/10$), so Haldane's restriction rendered kinship relevant only in special circumstances.

It is possible that a trace of egotism kept Haldane from seeing the importance of the general argument he was advancing, so quickly did he push forward his own two cases of altruism, but it seems more likely that he feared the political consequences of arguing, as we would, that selection will rapidly favor the ability to *discriminate* between intended recipients on the basis of degree of relatedness (so that average r is only relevant under special circumstances). If this latter possibility is the reason, then it was certainly not the last time someone blinded himself for fear of the consequences of an idea. If Copernicus dethroned us from the center of the universe and Darwin from the center of organic creation, then work on the evolution of altruism has dethroned us once again, making altruism more general than we had appreciated and more deeply self-serving. This has been a painful realization for some, generating minor spasms of resistance to this way of thinking.

In any case, it fell to William Hamilton, a lowly British graduate student in the late 1950's and early 1960's, to appreciate the importance of this reasoning. Curiously enough his attempt to make the theory more complete and to show its broad application was barely appreciated at the time. Indeed, he was told in 1963 that his work was not up to the standards of the University of London and he could not receive his Ph.D. for it. In order to gain employment, he rushed into print in 1964 a paper entitled "The genetical evolution of social behavior." This turned out to be the most important advance in evolutionary theory since the work of Charles Darwin and Gregor Mendel. We will devote Chapters 6–8 to Hamilton's kinship theory and its applications.

For now it is worth noting that each of the examples of altruism mentioned above is usually mediated in nature by kinship. Typically, ant and bee workers help their mothers to raise fertile sisters and brothers (pp. 169–179), and birds help one or both parents (pp. 184–192), lionesses nurse cubs of sisters or cousins, ground squirrels warn sisters, daughters, aunts and other relatives (pp. 110–114), and uncles and aunts adopt chimpanzee orphans. Regarding aphids, it is worth noting that they reproduce in two different ways: sexually, generating degrees of relatedness like those in our own species, and asexually, resulting in offspring genetically identical to the mother and to each other. It is during the asexual stage that soldiers are produced, and at that time benefit needs merely to be greater than cost for altruism to flourish.

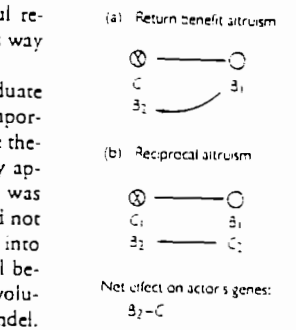

Figure 3-7

Return benefit altruism. (a) The initial act by the actor somehow leads to a return benefit for the actor (B_2). Where this is larger than the initial cost (C), selection will favor the initial altruism. (b) One special category occurs when the return benefit comes because the recipient chooses to act altruistically in return (reciprocal altruism).

Return Effects and Reciprocity

A second way in which selection may favor an altruistic act occurs when the act induces a return benefit to the actor larger than the initial cost (Figure 3-7). In effect, the altruism becomes a form of cooperation. Consider, for example, certain interactions that take place in the ocean between so-called host fish and their cleaners. Along coral reefs in the tropics it is common to find species of small fish specialized as cleaners of other fish. They remove ectoparasites from the skin, gills, and mouths of various species of host fish. They are strikingly colored and advertise their profession with a special dance. Their hosts, in turn, often adopt a trance-like posture while being cleaned.

This interaction is symbiotic: the host loses an ectoparasite, the cleaner gains a mouthful of food. But hosts also sometimes act altruistically toward their cleaners, warning them of danger. Since host and

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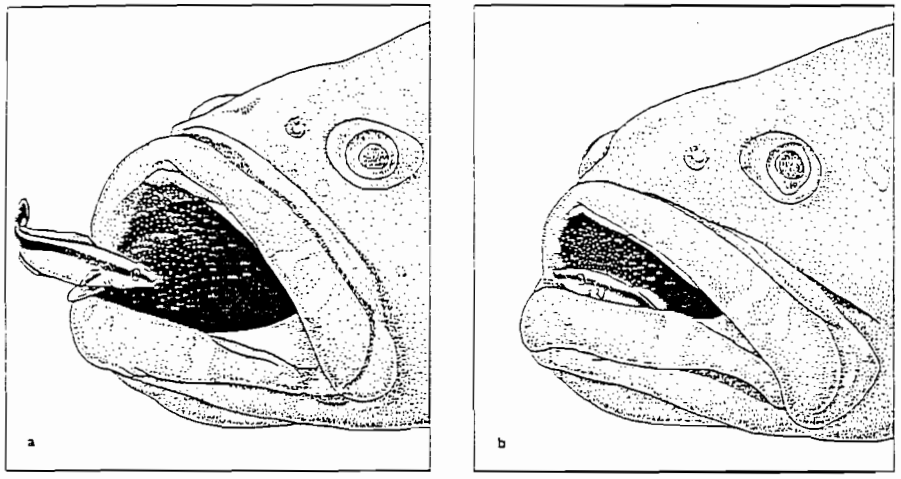


Figure 3-8

Return-benefit altruism: warning a cleaner to depart. (a) The cleaner fish *Labroides dimidiatus* is shown entering the mouth of a host fish to clean it. Should the host need to depart, it may signal the cleaner (b) by partly closing its mouth, upon which signal the cleaner exits. The host may benefit by being cleaned again in the future by the same cleaner.

cleaner are members of different species, kinship cannot be the explanation. Instead, there is good evidence that hosts often return to the same cleaner to be cleaned and, insofar as the host gains from dealing with a particular cleaner (for example, easy to locate), the host may be selected to watch out for its welfare. When a grouper fish has a cleaner in its mouth and is attacked by a predator, it does not swallow the cleaner and flee; it warns the cleaner to exit, the cleaner exits, and then the grouper flees (Figure 3-8). Note the significance of repeated interactions between the pair for this kind of altruism to evolve.

An important kind of return effect occurs when an individual chooses to act altruistically toward another who has already acted altruistically in the past. In effect, two individuals trade altruistic acts. This can be called reciprocity or *reciprocal altruism*. For example, a baboon will sometimes help another baboon in a fight (Figure 3-9). The individual who is helped is more likely in the future to aid the individual who first helped. Thus, baboons appear to trade aid in fights. The key problem is how to discriminate against cheaters, individuals who receive the benefits of altruism without reciprocating. Where individuals frequently interact, the cheater may be spotted and future altruism toward that individual curtailed. If so, the cheater may suffer in lost future altruistic benefits more than it saves in foregoing altruistic acts of its own. We shall see in Chapter 15 that some interactions between birds, between monkeys, between dolphins and whales, and between humans can be explained as cases of reciprocal altruism.

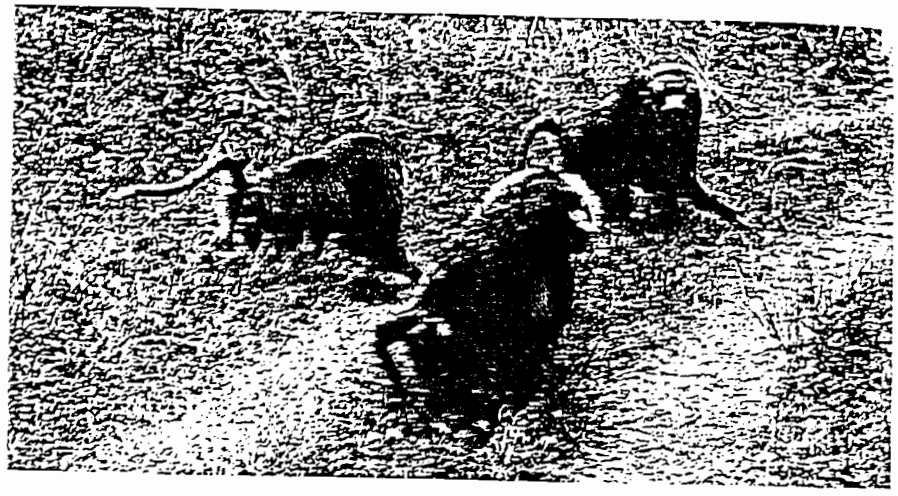


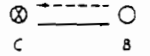
Figure 3-9

Cooperative behavior in baboons. Two adult male baboons chase a third, who gives an eyelid threat in return. Such fights are often over sexual access to females near their time of ovulation. The cooperating males are almost certainly not closely related. Evidence of reciprocal benefit in such alliances is reviewed on pp. 372–373. (Photo: Irven DeVore, Anthro-Photo)

Note one difference between kinship and reciprocity as factors promoting altruism. In the case of return effects, we must remain alive to receive the return effect. There is always some chance that we will not survive to enjoy the return benefit, and this chance of mortality will lead us always to devalue future effects when compared to present effects. Of course there are other factors which may affect the chance of future interactions, such as uncertainty regarding the cheating tendencies of one's partner, and these must also act to devalue possible future effects.

Social Parasitism

A third way in which altruism may be selected is through parasitism. The recipient *induces* altruism that would normally be directed elsewhere or not displayed at all (Figure 3-10). Perhaps the best-known examples are the brood parasites of birds, species whose members are wholly specialized to lay their eggs in the nests of other birds so the hatchlings will be reared to independence by them. Since this is disadvantageous to the host, selection has favored counteradaptations on each side. The host was selected to toss out any odd-looking egg. This has led to the evolution of remarkable egg mimicry by the brood parasites. The host was in turn selected to count its eggs and abandon the nest if it contained too many eggs. This led to the behavior of throwing



Net effect on actor's genes: C

Figure 3-10

Parasitized altruism. The recipient *induces* an altruistic act by the actor. The actor is uncompensated, suffering a cost C, and is selected to avoid the altruism. Larger benefit (*B*) to the recipient may lead to more rapid evolution of skilled inducers, which will tend to occur when the parasites are less numerous than their targets, since the cost per target per generation will be low but benefit to parasite per generation high.

out one host egg for each parasite egg laid. The competition continues at hatching. The parasite has been selected to hatch first and to eject the other eggs from the nest so as to monopolize subsequent parental care. When the host eggs hatch first, the hosts may crush the parasite to death against the side of the nest. The inner beaks and throats of the parasites have, like the eggs, evolved striking resemblances to the same parts of the hosts. These are the parts of the chick the parent sees just before feeding. At the very end of the relationship, the parasite may be fed even when it is several times the size of its parents and markedly different in appearance.

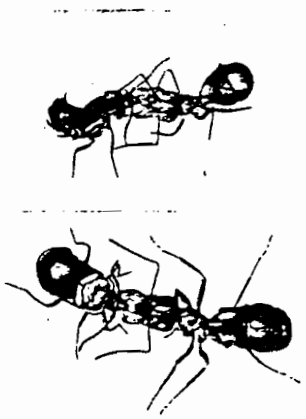


Figure 3-11

Induced altruism. The beetle *Atemeles pubicollis*, on the left, begs food from the ant *Formica polyctena*. At top it can be seen tapping the ant's inner mouth parts with its forelegs. At bottom it is being fed. The beetle is unusual among ant parasites because it lives in *Formica* nests in the summer as larvae and young adults, but lives in *Myrmica* nests in the winter (see next two figures). (Photos: Bert Hölldobler)

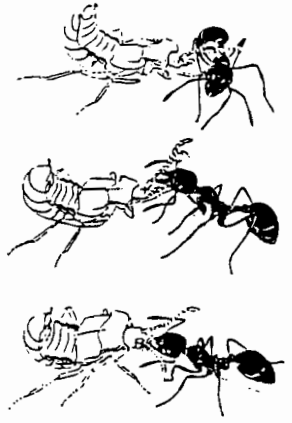


Figure 3-12

Social parasitism. The beetle *Atemeles pubicollis*, on the left, begs food from the ant *Myrmica laevinodis*. At top, the beetle gets the attention of the ant by tapping her on her side with its antennae. In the center, the ant turns and the beetle taps her mouth parts with its front legs. At bottom the ant responds by regurgitating food—just as she would when given similar signals by a nest mate. The most vulnerable ant is the one that has just fed and is searching for a nest mate with whom to share the food. (*From* Hölldobler 1970)

Similar parasitisms have evolved repeatedly in connection with the social insects (social bees and wasps, ants, and termites). For example, bumblebee nests are vulnerable to a closely related parasite, *Psithyrus*. In some species, the parasitic female approaches the nest cautiously, avoiding workers, and seeks to reach the underside of the comb, where males often rest. She will then spend a day or two rubbing herself against the nest and the males. Only when she has acquired the smell of the nest will she approach the real queen, whom she quickly stings to death. She then lays eggs of her own, which are cared for by the newly orphaned workers as if they were siblings. For the case of beetles parasitizing species of ants see Figures 3-11 to 3-14.

Although parasitized altruism is really a form of selfish behavior, the actor being the recipient of the altruism, we should note that all systems of altruism are vulnerable to parasitisms in which individuals

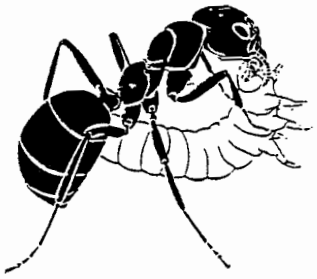


Figure 3-13

A beetle larva is fed by an ant. Larvae of the *Atemeles* beetle shown in the previous figure beg for food from worker ants much as do ant larvae, but the beetle larvae beg more vigorously; in mixed groups they are fed in preference to the ant larvae! They also feed on the ant larvae and on each other. (*From* Hölldobler 1967)

Figure 3-14

Ambivalent behavior while being parasitized. This highwayman beetle *Amphotis marginata* has just begged food from an ant *Lasius fuliginosus*. The ant has discovered the parasitism and rears back preparatory to attack, but the beetle will retract its legs and wait for the ant to depart. The highwaymen locate foraging trails of ants by scent and then ambush food-laden workers returning to the nest, begging food by tapping ants on their mouth parts the way nest mates would. (Photo: Bert Hölldobler)

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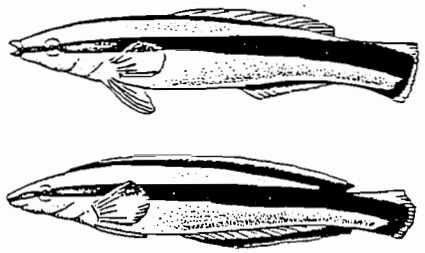

Figure 3-15

Cleaner and mimic. Above is *Labroides dimidiatus*, a cleaner; below is *Aspidontus taeniatus*, a species that mimics the cleaner in appearance and behavior in order to attack host fish. (*From* Wickler 1968)

pretend a degree of relatedness they do not possess or a degree of reciprocity they will not express. Even the cleaner–host relationship in the ocean has been invaded by a parasite. One species advertises itself like a common cleaner but instead of cleaning, darts in and seizes a piece of the startled host's flesh (Figure 3-15). These considerations are by no means irrelevant to our own lives. Since there will be selection to misrepresent our actions to others—for example, pretending to be altruistic only to be selfish—it is useful to pay attention to the real effects of our actions as well as to the way in which they are represented. Real effects, of course, are measured in terms of survival and reproduction. While in our own species such effects are often indirect and hard to measure, it will still be useful to conceptualize benefits and costs as ultimately affecting survival and reproduction. When Harvard University paid me a salary for lecturing on reproductive success, which was inadequate to sustain any of my own, I felt myself to be the victim of more than an amusing irony; when the dean told me that low pay was a mark of academic excellence, I thought I was being offered ego-gratification instead of real benefits.

Selfish Traits

A selfish act is one from which the actor gains a benefit while it inflicts a cost on the recipient. Natural selection operating on the actor favors selfish acts, but the potential recipient is selected to avoid receiving the costs. We can speak of a co-evolutionary struggle between the tendency to perform selfish acts and the tendency to avoid being harmed by the selfish acts of others. Note that the relative size of benefit to cost is the relative strength of the selection pressures operating on the two parties. Thus, there is a natural tendency for defenses to be especially well developed towards highly selfish acts. This means that one should

always search for counter-strategies when considering selfish acts, the more so, the greater the cost inflicted. For example, male Langur monkeys *Presbytes entellus* often kill infants under the age of six months when they first take over a group of adult females. This behavior inflicts a large cost on the reproductive success of the bereft mothers, and consequently has favored numerous counterstrategies on the part of the females (see pp. 71–77).

The same two factors that favor the spread of altruism, kinship and reciprocity, affect selection as it acts on selfishness. A genetic correlation between actor and recipient means that copies of the genes leading to selfishness located in the recipient will suffer some of the costs of their activities. Thus our rule for the positive selection of altruism through kinship is matched by a similar rule for the negative selection of selfish traits. Natural selection opposes the spread of selfish traits whenever the cost inflicted on the recipient times the actor's degree of relatedness to the recipient is greater than the benefit to the actor; that is, whenever

$$Cr > B$$

Likewise, selfish acts can generate return effects that render their net effect on the actor negative. An important subset is reciprocal selfishness, or (as we shall see later) the withholding of altruistic benefits from selfish individuals.

Being a Subordinate Paper Wasp: The Concept of Inclusive Fitness

Before going on to the other kinds of social traits, let us pause and consider the way in which selfish and altruistic traits may interact in a particular case. We choose the paper wasp *Polistes fuscatus* and concentrate on a decision many females must make: whether to work as a subordinate on someone else's nest or found a nest of her own.

In Michigan, adult female paper wasps, which are inseminated in the fall, overwinter alone but often gather together in small groups in the spring to found nests: in one study about half the wasps joined others in founding nests while the other half nested alone. In the early stages of social nesting the females struggle for dominance (Figure 3-16). This struggle soon produces a linear dominance hierarchy in which each female is dominant to all those beneath her in the hierarchy. One effect of dominance is to reduce the size of the subordinate wasp's ovaries. In Figure 3-17 we see for a related species the ovaries of females from one nest, arranged in order of dominance: the lower an individual is in the hierarchy, the smaller are her ovaries. Experiments show that a subordinate's ovaries will grow if we permit her to rise in

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Figure 3-16

Dominance interaction in a paper wasp. The dominant female *Polistes fuscatus* on the left has elevated her body and is biting the leg of the subordinate female who holds herself in a characteristic posture: head, body and antennae low. (Photo: Mary Jane West Eberhard)

dominance, and conversely, if we permit a dominant wasp to be dominated by another, her ovaries will shrink.

Correlated with dominance and ovary size is egg production, as we see for one wasp nest described in Table 3-1: not only did the dominant female lay most of the eggs but she ate four out of the five laid by the second-most dominant, while only two of hers were eaten (Figure 3-18). Dominance is thus a selfish trait that increases the egg production of the most dominant female while lowering that of subordinates. The subordinates, in turn, do the bulk of the work. In Table

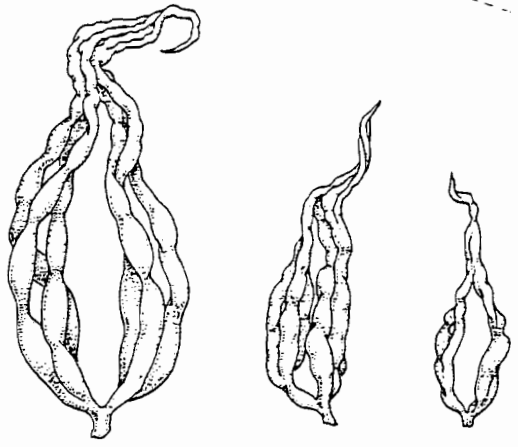

Figure 3-17

The association between dominance and ovary size in paper wasps Polistes gallicus. The ovaries of females from one nest are shown in decreasing order of dominance, left to right. *From* Pardi 1948)

Table 3-1 The Number of Eggs Laid, the Number of Eggs of Others Eaten and the Number of Loads of Food or Paper Brought to the Nest Per Hour in *Polistes Fuscatus* as a Function of Dominance

Dominance Rank of Female	Number of Eggs Laid	Number of Eggs of Others Eaten	Foraging Rate (loads/hour)
1	9	4	.08
2	5	2	.50
3	0	0	1.41
4	0	0	1.56
5	0	0	1.80
6	0	0	1.22
7	0	0	1.50

Source: West Eberhard 1969.

3-1 each subordinate typically brings about a load and a half of food or paper to the nest, while the most dominant female rarely leaves the nest. As a result, subordinates are less likely to survive into the summer and rarely rise to dominant status.

Why does a subordinate wasp bother to help? Why doesn't she leave and found a nest of her own? A careful study by Katherine Noonan sharpens this question for us. In her study, a female nesting alone produced, on average, 18.25 reproductive offspring, while a dominant female produced about 26.7 offspring and a subordinate only 5.2. Comparing reproductive successes, a subordinate makes a considerable sacrifice, compared to nesting alone, and should be selected to desert. But her sacrifice increases the reproductive success of the most dominant female, and if the subordinate is related to her, then we ought to include this effect in our calculation of the subordinate's genetic success.

We now know for several *Polistes* species that adult females arising from the same nest are mostly sisters and preferentially congregate in the spring. For *Polistes fuscatus*, Noonan estimated that at least 75% of the times a female associates with another, she is associating with her sister, while she associates with non-sisters at least 7% of the time. As expected, the wasps discriminate on the basis of kinship: in experiments sisters were accepted on nests for 15 minutes 67% of the time while non-sisters were accepted only 9% of the time. In nature, individual female wasps with few surviving sisters rarely join others, while females with many sisters often do, suggesting that when sisters are not available, a female chooses to reproduce alone. As we shall see later (pp. 177–179), wasps, along with ants, bees and a few others, are unusual among animals in that males arise from unfertilized eggs and

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Figure 3-18

Egg laying and egg guarding. (a) A female *Polistes fuscatus* lays an egg in a cell while holding nest pulp in her mouth. She had just aggressively solicited the pulp from nest mates. Usually she applies the pulp to the nest just before egg laying. (Photo: Mary Jane West Eberhard) (b) Having laid an egg in a cell a female *P. fuscatus* inspects the cell. This inspection may last for 20 minutes and is accompanied by heightened aggressiveness to nest mates. It probably serves to protect the newly laid egg from consumption by a nest mate. Most eggs that are consumed are eaten within 15 minutes of being laid. (Photo: Mary Jane West Eberhard)

carry only one set of genes. All their sperm cells are identical, causing full sisters to be unusually closely related ($r = \frac{3}{4}$). This means that for every increase in reproductive success that a subordinate worker gives to her sister, she places ¾ as many genes into the population as if she had produced the additional young herself.

Using Noonan's figures, a subordinate is usually related to a dominant by $r = \frac{1}{4}$ and she has increased the RS of this female by 14.3 offspring. Thus, in addition to producing 5.2 offspring of her own, the subordinate female wasp also added the genetic equivalent of 10.7 more, for a total output of 15.9 (measured in units of her own offspring), which is just short of the 18.25 that females nesting alone achieve. This is exactly what we would expect, since females nesting alone—like dominant females—tend to be larger than subordinates and are therefore expected to do better. But we expect the two strategies to give similar genetic outputs; otherwise, a selection pressure would exist for females to shift toward the more profitable strategy.

Note that we have computed something new. To an individual's reproductive success we have added her effects on the reproductive success of her relatives, after devaluing the effects by her degree of relatedness to these relatives. Hamilton called this quantity an individ-

ual's *inclusive fitness*, since it includes not only her own reproductive success (that is, fitness) but also the effects on the reproductive success of relatives. More precisely, we can speak of a gene's effect on an individual's inclusive fitness: the amount by which the gene increases or decreases the reproductive success of the individual, plus the amount by which it increases or decreases the reproductive success of relatives, each amount devalued by the appropriate degree of relatedness. Just as Darwin's concept gave us a single number by which to measure natural selection, so Hamilton's wider concept also gives us a single number. We see from our example that natural selection does not favor the traits of the individual who maximizes her reproductive success but rather the traits of the one who maximizes her inclusive fitness.

Cooperative Traits

Cooperation finds a peaceful home in evolutionary theory, since selection acting on both parties favors the cooperative exchange. But cooperative actions often consist of two individuals subject to a series of costs and benefits over a period of time, so that we are naturally curious as to the extent to which they experience the costs and the benefits equally. For example, the sexual division of labor in lion hunts rather favors the male, since going upwind of herds of wildebeest and frightening them to move downwind is less tiring and less dangerous than waiting downwind and killing a wildebeest out of the thundering herd. Yet when they rejoin the females, males tend to take the "lion's share," so that the costs of the hunt are borne preferentially by the females, while the benefits appear to be preferentially enjoyed by the males. This could be viewed as a selfish interaction within the larger cooperative exchange.

Spiteful Traits

The final category of social interaction appears to have the least to say for itself. Spiteful interactions inflict costs on both parties and should be opposed by selection's acting on both. Repaying with harm someone who has harmed you is a spiteful act, since it costs you something to inflict the harm (compared to doing nothing).

Some people have been tempted to imagine that when $C_2 >> C_1$, spiteful behavior may improve the *relative* fitness of the actor. For example, two people are standing near a 4,000-meter drop, and with a shove costing very little energy, one sends the other over the cliff. Does the actor's relative standing in the species rise sufficiently to offset the cost? The factor of kinship is relevant to this discussion because if the

two individuals are related, the action will be inflicting a double cost on the genes of the spiteful individual. The average degree of relatedness to any member of the species ($\bar{r}$) is usually very low, less than $1/1000$, so that you would have to travel very large distances in life to meet people to whom you are less related than you are to the average in the species. Spiteful behavior could only affect positively the spiteful individual's reproductive success if the cost inflicted is exceedingly high and directed preferentially toward those to whom one is very distantly related.

A good example of spiteful behavior comes from mountain sheep *Ovis canadensis*. In the winter, mountain sheep often feed at the top of a hill. Lower down on the hill the forage is better, but the risk of predation is sufficiently greater so that the sheep prefer to forage high on the hill. It sometimes happens that an adult male is injured in the winter; such an individual may choose to feed lower on the hill because he needs extra energy to recover from his injury and is willing to risk the greater chance of predation in order to recover.

When a male leaves the feeding group to feed lower down on the hill, he is sometimes followed by another male lower in the dominance hierarchy. This male does not feed but instead spends his time harassing the injured male. This is spiteful behavior. The subordinate male risks increased predation and expends energy in order to harm another individual. What is the function of this spite?

In the following spring, when the breeding season begins, the male's position in the dominance hierarchy will determine his access to females. By attacking an injured male in the winter, the subordinate male increases the chances that the more dominant individual will succumb to his injuries. Thus the subordinate may rise in the dominance hierarchy and during the breeding season receive a payoff in increased access to females and, hence, increased reproductive success. The spiteful behavior thus appears to be selected for because it is associated with a return benefit. Indeed, one could lump together the initial cost and later benefit, and if the benefit outweighs the cost, term the entire behavior selfish. It seems preferable, however, to classify behavior according to its immediate effect on animals, since the later return is by no means certain, and we are often not in a position to view the return. So, we can classify the behavior as spiteful, and argue that it is ultimately selfish when it is associated with the right kind of return benefit to the actor. For another example, see Figures 3-19 and 3-20.

Some people have imagined that selection may favor garnering more resources than necessary for personal reproductive success, in order the better to limit the reproduction of others. But experimental tests of the hypothesis do not provide support. For example, neither territory size nor rate of territorial defense increases in tree swallows when excess nest boxes (useless for the actor but useful for others) are

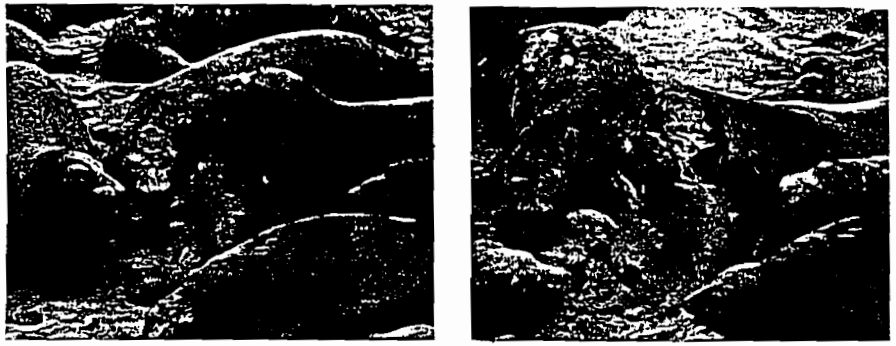

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Figure 3-19

Gang murder in the elephant seal. (a) Four adult females gang up and kill a pup less than one week old, repeatedly biting it on the head and rump but especially on the head. One female who hovered nearby but did not take part may have been the mother. The episode lasted about five minutes. The pup was alive two hours later but in very bad shape; it died the following day. (b) From LeBoeuf's field notes: "One female, marked FYS, was more vicious and persistent than the others and she spearheaded the attack. She bit, shook and flung the pup in the air at least six times, always biting it on the head. . . . Whenever the attack started to subside, FYS would renew it with a savage bite. At one point she even bit another female on the nose and shook her." It is not known whether these females gain a return benefit (via reduced competition with their offspring), which if true would mean that this apparently spiteful behavior is actually selfish. Notice other dead pups in the picture. (Photos: Burney LeBoeuf)

Figure 3-20

An orphan is attacked again. An elephant seal pup, about three weeks old and hopelessly separated from its mother, is bitten by an adult female, who stretches over her own pup to do so. Mothers are vulnerable to stolen nursings, especially when asleep, and in elephant seals there is enormous maternal investment in each pup, mostly by way of milk. (Photo: Burney LeBoeuf)

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provided. Of course, if there is a return benefit, such spite may be favored. Thus, in several macaque monkey species, adult females go out of the way to harass infant and juvenile daughters of others. This harassment apparently results in lowered female survival, compared to male, and begins when females are still in the womb! Mothers bearing female fetuses are attacked more often than mothers bearing male fetuses, and in laboratory settings they require medical attention more often; mothers requiring such attention are more likely to abort. Only females remain within the monkey troop as adults where they attempt to reproduce and to support the reproduction of female relatives. Since group size is limited by resources, attacking the daughters of others may increase the space available for one's own offspring. For female attacks on females about to copulate, see Figure 3-21.

Social Theory Applies to Plants

When I first became interested in the social lives of other species, I imagined that I was interested only in social *behavior*, meaning animals, particularly those that lived in groups. As time wore on, I came to see that social reality is much deeper than behavior. It can embrace changes in morphology, as we have seen in soldier aphids and in the enlarged or reduced ovaries of paper wasps. Thus, our social theory should also apply to plants. A tree, for example, sucks nutrients and water from the soil while striving for sunlight above ground, all of which tends to make life more difficult for its neighbors. Were a plant closely related to its neighbors, it might be selected to remove less resources from the soil and invest less energy in growth: this should leave more resources, including sunlight, for its neighbors. If their gain were greater than the donor's loss, and the corresponding degrees of relatedness high enough, selection would favor this "act" of altruism, namely, reduced investment in exploiting the environment. Note that this could evolve without the plant's measuring degrees of relatedness. It could be selected to respond instead to its usual r to neighbors, but if there is typically variation in relatedness to neighbors, plants will also be selected for that discriminate: roots may be able to recognize neighboring roots, or leaves may be able to recognize subtle differences in the chemicals emitted by neighboring leaves.

Whether any of these interactions, in fact, occurs is not yet known, but they are made more likely by the recent, remarkable discovery that plants—like animals—in effect "warn" each other of impending dangers to which the plant can take countermeasures. Unlike warning calls in animals, the activity takes place not in seconds but over a period of days, and the danger is not instant destruction by a predator but slow destruction by plant-eating insects. Also, we do not yet know

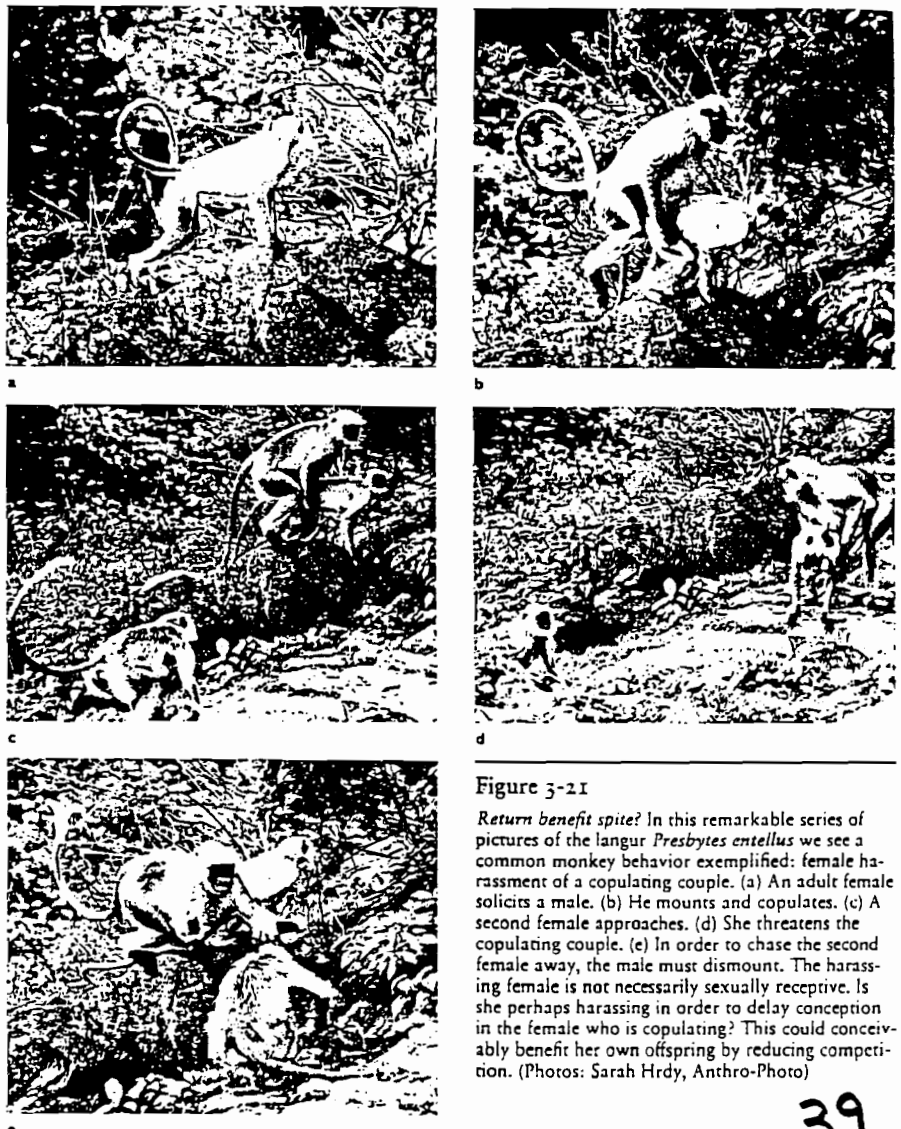

Figure 3-21

Return benefit spite? In this remarkable series of pictures of the langur *Presbytes entellus* we see a common monkey behavior exemplified: female harassment of a copulating couple. (a) An adult female solicits a male. (b) He mounts and copulates. (c) A second female approaches. (d) She threatens the copulating couple. (e) In order to chase the second female away, the male must dismount. The harassing female is not necessarily sexually receptive. Is she perhaps harassing in order to delay conception in the female who is copulating? This could conceivably benefit her own offspring by reducing competition. (Photos: Sarah Hrdy, Anthro-Photo)

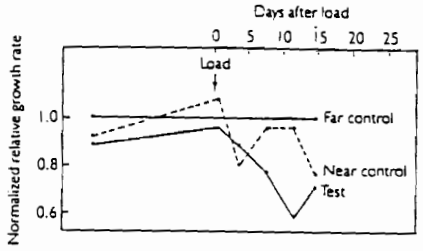

Figure 3-22

The relationship between quality of leaves and distance of the tree from an infected tree. Plotted are the relative growth rates of caterpillars raised on leaves taken from two trees, compared to growth rates on the distant control trees. Test trees are those loaded with caterpillars on day 0. Near trees are those located 3.3 meters away. Distant control trees are 1.6 kilometers away. By day 11.5 the drop in growth rate of the caterpillars on leaves of the test trees is significant, by 14.5 days the decline for near trees becomes significant. (*From* Rhoades 1983)

whether an injured plant elaborates a signal to that effect or whether other plants merely respond to the injury itself.

We have known for many years that a plant whose leaves are being eaten by insects may take countermeasures such as reducing the nutrients available in its leaves or increasing the percentage of toxins, which reduces the survival of insects grown on the leaves. We now know that in several species *neighbors* of the infested tree also take countermeasures. For example, among Sitka willow trees *Salix sitchensis*, neighbor trees 3.3 meters away from a tree infested with caterpillars take countermeasures which adversely affect the survival of the caterpillars, and almost as quickly as does the tree itself (14.5 days instead of 11.5: Figure 3-22). Since there are no connections between the roots of these trees and since neighbors as far as 60 meters from the attacked tree may take countermeasures, the warning is apparently communicated by the release and detection of airborne chemicals. Although it seems likely that this has involved selection on both the sender to elaborate a clear signal and on the recipient to detect it, this is not known. If neighboring trees are often related, as seems likely, then selection may favor those trees that warn their neighbors. As we shall see later, many of our theories developed for animals also apply to plants. Plants, for example, express mate choice (see Chapter 14) and may vary the sex ratio among offspring much as do animals (p. 287).

Applications to Parasites

We can illustrate the application of our social theory to parasites by considering parasites that alter the behavior of their host to their own advantage by making it more likely that the host will be eaten by a

particular class of predators; this is advantageous to the parasite because its next host is one of these predators. The helminth worm *Ligula intestinalis* infects the gut of various fishes, where it somehow causes these fish to make themselves more vulnerable to fish-eating birds, which are the next host of the worm. Infected fish swim more slowly, more often alone, closer to the surface of the water, and in warmer, shallower water near the shore. The effect on bird predation rate may be substantial: in one species of fish 30% of those eaten by cormorants *Phalacrocorax carbo* were infected by this worm, while only 6% of the fish's overall population was similarly infected.

There is one case of parasitic manipulation in which the individual causing the effect is not the same one gaining the benefit. The parasite is the liver fluke *Dicrocoelium dendriticum*, and it infects ants prior to infecting ungulates such as sheep. An ant picks up the flukes in its food and most of them migrate into the ant's body cavity, where they encyst and await their next host. But one fluke (or occasionally two or three) migrates close to a major nerve controlling the ant's mouth parts. Here the fluke encysts and alters the ant's behavior: instead of returning to its nest in the evening, the ant climbs a blade of grass, bites down, and hangs on until morning. Since sheep feed on grass mostly in the evening and early morning, this must greatly increase the chance that the ant will be eaten by sheep. But the fluke controlling the ant dies with the ant; only the worms encysted in the ant's body cavity are capable of infecting sheep. Since the flukes that infect ants reproduce asexually, all those within an ant *may* be identically related, although this is not known. Ants may sometimes or often ingest flukes from several sources, thereby reducing degrees of relatedness. Our ignorance here only serves to underscore the point we are making. Critical facts are sometimes missing because it is only recently that we have begun to conceptualize the problem of the altruistic plant or parasite in such a way as to require these facts.

One form of cooperation between parasites that may be fairly general is a reduction in immediate exploitation of the host, the better to drain it over the long haul. It is possible, for example, that an individual infected by more than one strain of malarial parasite suffers a more severe attack than someone infected by a single strain, whose members, being asexually reproduced, are genetically identical and may more easily be selected for restraint in exploiting their host. This is consistent with some recent evidence showing that intensity of infection, as measured by number of parasites per red blood cell in a lizard, correlates with an increasing tendency to produce a 1:1 sex ratio of malarial parasites. This is consistent because, as we shall see in Chapter 11, 1:1 sex ratios are associated with outbreeding and reduced r's, while the female-biased sex ratios found in mild infections are, in

other creatures, associated with close inbreeding and high degrees of relatedness.

Whatever the facts, we can see from these examples that life is intrinsically social. All creatures must consume something of value in order to live and must consume more in order to grow and reproduce. This consumption is often at the expense of other members of the same species, so that even staying alive may, in effect, be a selfish act. Reproduction, in turn, is intrinsically social—genes and energy are invested in the production of others—and in many species this also requires the cooperation of two individuals (male and female).

Summary

Neglecting zero effects, there are only four categories of social traits: altruistic, selfish, cooperative, and spiteful. These are defined by reference to their effects on actor and recipient. An altruistic trait is one that benefits the recipient at a cost to the actor. While superficially opposed by natural selection, such traits are common in nature, as illustrated by soldier aphids, a special form that does not reproduce but acts to defend its siblings from predators. Altruistic traits may have evolved by three different routes: kinship effects, return effects, or parasitism.

Kinship may favor altruism whenever there is some chance that any gene found in the actor has a copy located in the recipient via direct descent from a common ancestor. This chance is called degree of relatedness (r). Natural selection favors altruism whenever $Br > C$, where B is benefit and C is cost. Degrees of relatedness may easily be calculated by multiplying together r's that connect two individuals genealogically. When individuals are related through more than one individual, r's for the different genealogical connections are summed.

Selection may also favor altruism when it induces a return benefit sufficient to offset the initial cost. An important category is reciprocal effects, in which individuals trade altruistic acts. This kind of altruism will evolve only if altruists are able to interact often enough to discriminate against individuals who do not reciprocate by withholding altruistic benefits from them. Selection may also favor the inducement of altruism, a form of social parasitism.

Selfish traits benefit the actor at a cost to the recipient. When these are related, selection opposes selfish acts whenever $Cr > B$. Selection may also oppose selfish acts because of their return effects. In paper wasps, females dominate others on their nest; this is a selfish act. Subordinate females often choose to remain on the nest, where they primarily help the dominant female reproduce. Although subordinates achieve much lower reproductive success than solitary females, when

we add to this their effect on the reproductive success of their sisters, they achieve almost the same genetic representation as solitary females. Natural selection favors not the individual that maximizes her reproductive success but the individual that maximizes her inclusive fitness, where this includes personal reproductive success plus effects on relatives, devalued by the appropriate degrees of relatedness.

Cooperative traits benefit both actor and recipient but may often have selfish components. Purely spiteful behavior is favored only under highly specialized and unlikely conditions, but apparently spiteful behavior can be favored when it, in fact, induces a return benefit.

Social theory applies to all species. Staying alive and reproducing are often selfish acts and their expression in any species may be limited by r's to neighbors or by return effects. Reproduction is a social event and, in addition, often requires the cooperation of two individuals. Social effects in plants and parasites are illustrated by the fact that trees sometimes, in effect, warn each other of impending attack, while some parasites are known to sacrifice their lives for others.

Chapter 4

The Group Selection Fallacy

After 1859 there were three main ways in which people tried to blunt the force of Darwin's argument for evolution and natural selection. The first was to raise doubts about whether evolution had occurred, incidentally distracting attention from the more important concept, natural selection, the force directing evolution. The second was to acknowledge natural selection but to minimize its significance by making it appear to be very weak in its effect. In a long-lived species such as humans, death and reproduction are fairly rare events, so it is easy to imagine that in day-to-day life, most of what we do has very little effect on our survival or reproduction. But as we have already seen in Chapter 2, even apparently trivial traits such as birth order in piglets may be subject to strong selection.

The third approach was to replace the idea that natural selection acts on the individual with the notion that natural selection acts for the benefit of the group or the species. This fallacy has been so widespread and so powerful in its repercussions that it deserves special treatment. Indeed, I remember well the grip it had on my own mind—and the confusion it generated—while I was still an undergraduate. So many disciplines conceptualized the human condition in terms of individual versus society. Sociology and anthropology seemed to claim that the larger unit was the key to understanding the smaller one. Societies, groups, species—all evolved mechanisms by which individuals are merely unconscious tools in their larger designs. In the extreme position, the larger groups were imagined to have the cohesiveness and interconnectedness usually associated with individual organisms. We call this the "group selection fallacy" or "species benefit fallacy," which claims that selection has operated at a higher level than the individual, that is, at the level of the group or species, favoring traits that allow

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these larger units to survive. In this chapter we review some examples of species-benefit reasoning in biology, and describe their flaws.

Species-Advantage Reasoning Within Biology

Darwin was very clear on the idea that natural selection favors traits that benefit the individual possessing them but that are not necessarily beneficial for larger groups, such as the species itself. Indeed, on several occasions he explicitly rejected species-advantage reasoning. For example, Darwin gathered evidence showing that in many species the two sexes are produced in a roughly 50:50 ratio, yet he could not see how natural selection might affect the sex ratio. He concluded:

> I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous for the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.

That is, when Darwin could not solve the problem in terms of natural selection, he held his peace and did not invent a higher-level explanation. Fisher solved the problem in 1930 (see Chapter 11).

Darwin regarded his work as a clear break with past biology, which believed in an instantaneous creation of an unchanging world whose various parts functioned together like so many parts of a clock. In this view it was easy to imagine that individuals could be created to subserve the interest of the species or, indeed, the interest of other species. Darwin's concept required that life be created over long periods of time by a natural process based on *individual* differences in reproductive success.

We might imagine that Darwin's successors clearly grasped his concept and began to apply it systematically to all biological phenomena, but quite the opposite seems to have happened. After a brief period, biologists returned en masse to the species-advantage view, only to cite Darwin as their support! For example, since it was then clear that numerous species had become extinct, it was easy to imagine that natural selection refers not to differential individual success but to differential success of species; that is, natural selection favors traits that permit species to survive. It certainly seems true that extinction is a selective process; that is, species that become extinct are not a random set of species available at the time. But this selection does not explain the traits of the species that do survive. To explain the traits of the species that do survive, we must understand how natural selection acts *within* each species.

Thus, for over 100 years after Darwin, most biologists believed that natural selection favors traits that are good for the species. In retrospect, there seem to be at least three reasons for this curious development. First, the existence of altruistic traits in nature seemed to require the concept of species advantage. As we have already seen, this is an illusion. Most examples of altruism can easily be explained by some benefit to kin or return benefit to the altruist, but these explanations were not well developed until the 1960's and '70's.

The second reason for species-advantage reasoning is that biologists have mostly studied non-social traits and for these traits it matters little whether we imagine they evolve for the benefit of the species or for the benefit of those possessing the traits. For example, the human kneecap locks in place when we are standing upright, thereby saving us energy. Chimpanzees and gorillas lack such a locking device. The device evolved because it benefitted those possessing it, not because it helped the species itself survive, but the latter notion leads to no misunderstanding of how the kneecap operates, since we assume the kneecap benefits the species by benefitting those possessing it. By contrast, social traits immediately pose a problem, because a benefit may be conferred on one individual at a cost to another. Considering the benefit of the species, we may imagine that social traits will evolve as long as the net effect on everyone is positive. But—in the absence of kinship or return effects—selection on the actor favors selfish traits no matter how large the cost that is inflicted and never favors altruistic acts no matter how great the benefit conferred.

Finally, the early application of Darwinian thinking to human social problems frightened people back to thinking on the level of the species. Shortly after Darwin's work, "Social Darwinists" argued in favor of 19th-century capitalism in the following sort of way: The poor are less fit than the rich because they have already lost out in competition for resources (that is, because they are poor). Therefore, the rich should do nothing to ameliorate the condition of the poor since this would interfere with natural selection and, therefore, with nature's plan. Indeed, we can improve on nature's plan by actively selecting against the interests of the poor. Thus, for the good of the species, the poor should suffer their poverty, augmented by a biological prejudice against them!

But, in fact, fitness refers to reproductive success, or the production of surviving offspring. It can only be demonstrated after the fact. In principle, we cannot look at two people and say which is more fit until both are dead and their surviving offspring have been counted. If the poor leave more surviving offspring than do the rich, as is sometimes true, then they are, by evolutionary definition, more fit, and the whole argument can be stood on its head. In reaction to this kind of thinking, I believe, people returned to species-advantage reasoning, partly because it was incapable of saying much about social interactions *within* species, especially social conflict.

Male–Male Aggression and Differential Female Mortality: Good for the Species?

To get the flavor of species-benefit reasoning we must really study some examples. One comes to us from the Nobel-Prize-winning biologist, Konrad Lorenz, and argues that natural selection favors aggressiveness between males because it is good for the species:

> Darwin had already raised the question of the survival value of fighting, and he has given us an enlightening answer. It is always favorable to the future of the species if the stronger of two rivals takes possession either of the territory or the desired female.

Darwin had indeed argued that natural selection favors fighting, since it is often possible for one individual through force or threat of force to seize a valuable item, whether food, territory, or a contested female, but he did not speculate on whether this was good for the species as a whole. Since males have evolved a musculature and weapons to support fighting, which females of the same species have not, it seems safe to imagine that fighting and associated traits are beneficial to the males possessing them, but not to anyone else. Whether it is advantageous for the species to have the stronger of two males take possession of a desired female may depend upon female choice. Does the female, in fact, prefer the stronger of two males? And if so, why? That is, how does the female's mating with the stronger of two males improve the quality or quantity of her own offspring (see Chapter 14)?

A second example concerns mortality rates in certain female mammals. In most mammals the sexes are produced in a nearly 50:50 ratio. But since males suffer higher mortality, the adult sex ratio usually contains more females than males. This pattern appears to be reversed in several species of the small mammal genus *Reithrodontomys*. Females appear to survive less well than do males, so that the adult sex ratio is biased toward males. Why might this be so? One student of the subject has argued as follows:

> It is usual to assume that fewer males than females are necessary because a few males can inseminate many females, and therefore it is *bio-energetically more efficient* for males to be expendable, while females are at a premium because they bear the young. However, for a small, secretive mammal there may be a *selective advantage* in having many reproductively active males moving about to assure insemination of any female that comes into estrus rather than assume that one male may contact several females. . . . [E]xcess males are *advantageous* in assuring insemination through more frequent contact of male and female. [Italics mine.]

Note that the author explains higher mortality rates in one sex by reference to the entire species. Thus it is bio-energetically more efficient for males to be expendable because they invest very little in raising the young. Likewise, the author uses the concept of selective advantage at the species level. After all, it cannot be advantageous for females to die at a more rapid rate in order to make sure that surviving females will have many active sexual partners. The only way to explain the lower survival rate of one sex is to show that individuals of that sex possess traits that give them some advantage in reproduction, at the cost of lowered survival during the rest of their life. In other words, the cost–benefit analysis must be made at the level of the individuals themselves, not at the level of the entire species (see Chapter 12). Notice how easily the species-benefit theory given above can be changed so as to explain any pattern of mortality.

Infanticide in Langur Monkeys

One example of species-benefit reasoning has been studied in some detail and serves to illustrate some important differences between explanations based on natural selection and those based on group selection. The example is infanticide in langur monkeys *Presbytes entellus*—the deliberate murder of infants by adult males. Reported since the 19th century, langur infanticide is common in several localities although it is not universal (Figure 4-1). Similar behavior has been reported in lions, gorillas, some other species of monkeys and many others.

Langur monkeys travel in groups of about 10–20 adult females and their young, to which is attached a single, dominant adult male. The other males travel in large, all-male groups, dominant members of which occasionally try to displace the adult male attached to a group of adult females. When such displacement is successful, the new male often starts to kill dependent offspring. In particular, he tries to kill infants up to about six months of age or older, but begins by concentrating on the youngest. In addition, he often kills infants that are born during the first months following his takeover, but not thereafter.

In a graphic account Sarah Hrdy has described male behavior in the wake of a takeover:

> In the early afternoon of August 12, 1972, the Hillside troop feeds quietly in the trees lining the drive of the Phiroze school. There is an undercurrent of tension, however. Very deliberately, females in the troop avoid Mug. If Mug climbs into a tree where a female is feeding, she immediately moves to another tree. If Mug follows, the female returns to the tree where she was before. At 4:00 p.m., the male, who is grunting softly, climbs to the top of a nearby roof. From his high vantage point, Mug strikes a sentinel's pose and stares off into the distance. Then, abruptly, the stocky gray form descends from his rooftop perch, charges directly at Itch, and grabs at the infant clinging to her belly. Itch whirls to face Mug, plants her front paws as she lunges at him, grimaces, and bares her teeth. Within seconds of this assault, old Sol, the one-armed female

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Figure 4-1

Summary of cases of probable infanticide involving two troops of langurs. Under the name of each troop is the male or males associated with the troop. Shifty pursued a double-usurper strategy for several years, that is, he attempted to drive all other males from two troops at the same time. Notice that the repeated disappearance of infants is associated with male take-overs. (*From* Hrdy 1977)

Hillside troop		Bazaar troop
Mug, resident male supplanted by Shifty	1971 June August	3 adult males
6 missing infants (2 killings witnessed	take-over	
Mug alternates with Shifty	double-usurper strategy	Shifty
3 missing infants (1 killing witnessed) and many unsuccessful assaults by Mug	1972 June-August	*3 missing infants*
Mug and 5 new males (including Righty) alternate with Shifty	1973 February-March double-usurper strategy	Shifty
1 missing infant and several unsuccessful assaults		
Mug holding his own against Shifty	1974 January take-over	Shifty
Righty	1975 April take-over	Mug
not known if infants missing		*not known if infants missing*
no male or Righty	May serious attempt at merger	Righty
		2 missing infants (1 killing witnessed) and many unsuccessful assaults
Slash-neck	October	Righty
2 missing infants		

Pawless, and a third, unidentified female join in the counterattack. The three defenders interpose themselves between Mug and Itch, lunge at the male, and chase him up a tree. In the wake of this assault, a trembling Itch is left alone to hold her infant Scratch, who is spattered with flecks of blood.

Mug had recently begun associating with the Hillside troop and on August 12 he repeatedly charged Itch and her infant and on each occasion other females intervened. Attacks on this and other infants continued throughout August and into September. Although it is sometimes claimed that infants are injured in attacks on adult females, the following description by Hrdy suggests the reverse is more likely.

Figure 4-2

Two females fight to save an infant. In this famous photo, two langur females, Pawless and Sol, intervene daringly to rescue Scratch, Itch's infant, from Mug, a male who has spent more than a month trying to kill the infant. The infant is severely wounded (see next photo). Pawless lacks one arm. She and Sol are older, low-ranking females, without infants, who repeatedly intervene on behalf of Scratch and other infants. One year later Itch was the only female to come to the aid of Pawless when her infant was attacked by another set of male invaders. (Photo: Sarah Hrdy, Anthro-Photo)

Maternal negligence was almost surely at issue in the second attack on Scratch that I witnessed on September 5, when Itch let Scratch fall out of a jacaranda tree. Mug was sitting alertly on a wall 50 feet away. When the infant fell, he raced to it, reaching it just split seconds before Sol and Pawless, who had been sitting on the wall on either side of him. The mother was the last of these four individuals to reach her infant. Only by a fierce assault were the females able to wrest the infant from his attacker. After Itch had retrieved her infant, Sol persisted in chasing and slapping at Mug.

On September 9 an attack thwarted by two adult females left Scratch severely injured (Figures 4-2 and 4-3).

Figure 4-3

Victim of an infanticidal attack. Itch sits with her badly injured offspring, Scratch, the morning after the attack shown in the previous photo. Mug's toothmarks are visible on the infant's head and the infant has also suffered a deep wound to its lower abdomen and upper thigh. Scratch subsequently disappeared. (Photo: Sarah Hrdy, Anthro-Photo)

This langur infanticidal behavior has traditionally been explained as a social pathology with no adaptive meaning or as a device for regulating population numbers. In the latter explanation, infanticide is practiced for the good of the species: it tends to ensure that population numbers will be in tune with available resources. This hypothesis predicts an association between the density of monkeys and the frequency of infanticide. In fact, infanticide does occur more frequently in densely populated areas, but apparently because take-overs are then more frequent. No other feature of the behavior can be explained as a device to regulate population size. Why does the population only need regulation when a new male takes over? Some males may be associated with a group of females for as long as five years. Why do males kill only young infants, which are vulnerable to mortality anyway and make a small contribution to future numbers? The best way to regulate a population would be to kill juvenile and sub-adult females. We would also like to know why it is the male who regulates the population. It would be easier if females ceased to breed when numbers were becoming large. Finally, why do females resist the killing impulses of the males?

The facts just cited easily fit an interpretation based on individual advantage. The male did not father the offspring he kills. If he is distantly related to the male he displaces and to the adult females—as seems typically to be the case—then he is only distantly related to the offspring that he kills. So the cost to the male is small, while he enjoys an almost immediate benefit in reproductive success. By killing a suckling infant, the male brings its mother more quickly into reproductive readiness. This is because females who are nursing infants are not ovulating and thus are not ready to produce their next offspring. By killing off their infants, the male saves himself the amount of female effort that would have been expended on unrelated offspring. Females who lose infants come into estrus within weeks, sometimes within days (see Figure 4-4).

When langur infants are about eight months old, they are weaned and no longer inhibit maternal reproduction. They are no threat to the male's reproductive success and he ignores them. The male's preference for killing the very young is also explicable, since these are the ones that will require the greatest investment before their mothers are freed to breed again. Finally, since the gestation period is about seven months in langurs, if a male kills infants born during the six months succeeding his takeover, he will not kill any of his own but will continue to kill those fathered by the previous male.

Figure 4-4

An infanticidal male copulates. Shortly after his takeover of the Hillside troop in 1971 Shifty copulated with females whose infants had disappeared. Here, one estrous female waits to the left while Shifty copulates in the mist with her troopmate. Both of these females lost infants shortly after Shifty's take-over. (Photo: Sarah Hrdy, Anthro-Photo)

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We expect the langur mothers to resist the male's behavior. Their own reproductive success is directly harmed by the murder of their infants, so we expect natural selection to favor countermeasures. Several of these have now been described. First, females may join the old male in fighting a takeover by a new male. Second, after the takeover, older females, typically related to the mother, may join her in resisting the assault; they are sometimes successful (see Figure 4-2). Third, females with older (but still dependent) young may leave the group with the old male or travel alone on the border of the group until the infant is past the age of vulnerability (see Figures 4-5 and 4-6). They presumably trade a greater risk of predation for a lowered risk of infanticide.

Finally, females may employ deceit so as to fool the new male into accepting their infant. One female came into estrus when the old male was still in the group. He copulated with her many times and a month later she failed to have her period and was judged to be pregnant. Another month later she again failed to have her period and showed changes in coloration that confirmed she was pregnant. At this time, the old male was ousted from the group and a new male took over. Within days this female came into estrus (or pseudoestrus, since she presumably was not ovulating). She copulated numerous times with

Figure 4-5

Female counter-strategy to male infanticide. After the attack on her infant, Pawless and her daughter travelled much of the time apart from the rest of their Hillside troop. Except for one occasion, they returned only when the former male, Shifty, was present and the invading males absent. Pawless later rejoined the troop. (Photo: Sarah Hrdy, Anthro-Photo)

the new male. Five months later she gave birth to an infant who was almost certainly conceived seven months earlier. The new male tolerated the infant as if it was his own.

Because many adult females are associated with a single adult male, there is tremendous pressure from all-male bands to displace the breeding male. This pressure appears to be especially intense where the monkeys are found at high numbers. Such a system, in which only a few males breed who are themselves at constant risk of being displaced by other males anxious to breed, puts a premium on breeding as fast as possible. This is presumably why infanticide is so well developed in langurs. For scenes of infanticide in another monkey, a ground squirrel, and a wasp see Figures 4-7, 4-8, and 4-9.

Consequences of Species-Advantage Reasoning

Species-advanrage reasoning has some important consequences. First, it tends to elevare one individual's self-interest to that of the species, thereby tending to justify that individual's behavior. In our example, the adult male's self-interest has been elevated to that of the species: it

Figure 4-6

Another female counter-strategy. Two adult females with offspring temporarily join the males ousted from their troop: the large male in the foreground on the left, grinding his teeth just prior to an encounter with other males, and his eight sons. (Photo: Sarah Hrdy, Anthro-Photo)

Figure 4-7

A different kind of infanticide. In the Belding's ground squirrel *Spermophilus beldingi*, infanticide occurs but is not caused by breeding males. Perpetrators are either yearling males, as in this case, or newly immigrated adult females, who may thereby open up some space for their offspring. Yearling males typically cannibalize their victim, as in this case, consuming the head and thoracic area first. This is perhaps the benefit they gain. The victim shown is the youngest victim recorded; it still has webbed feet and is about five days old. (Photo: Paul Sherman)

Figure 4-8

Victim of foul play. Species: red colobus *Colobus badius*. *Age*: about five weeks. *Sex*: male. *Cause of death*: repeated bites to the head and body. *Alleged assailant*: "Whitey," sub-adult male, rapidly rising in rank, precocious in development, subsequently attacks or murders all other infants under six months of age, with the exception of his half-sibling. *Evolutionary reason*: Whitey acts to bring mothers of the murdered infants into sexual receptivity. His own mother migrated into the group when he was *in utero*. Thus, he is only distantly related to the infants he attacks. (Photo: Lysa Leland)

is given a new name. What he is concerned with is population regulation, something that is beneficial to all. By contrast, the viewpoint of natural selection should make us suspicious of the notion that one individual's self-interest is the same as that of the species. Instead, we expect individuals to act in their own self-interest. In a verbal species such as our own, we also expect individuals to represent these actions as being in everyone's self-interest.

Secondly, group-selection reasoning distracts our attention from conflict within social groups and from maneuvers that have evolved to mediate such conflict. Hence, unconsciously such reasoning tends to render other individuals powerless. "The male has the power and the power is good for the species." Such reasoning prevents us from predicting female counterstrategies and from seeing the limits to male power. By contrast, an approach based on natural selection demands these counterstrategies. We expect to find them, and we analyze any social interaction from the standpoint of each of the individuals affected by it.

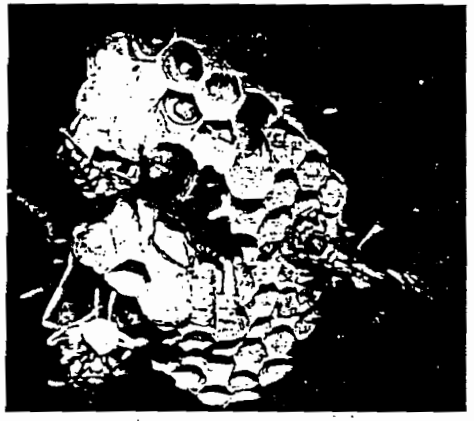

Figure 4-9

Yet another kind of infanticide. While the nest is being consumed by a predatory beetle, one female wasp *Polistes versicolor* has seized a larva and begun to eat it (lower left). The larva is probably her niece or nephew but may be her offspring. Since the larva will almost certainly die anyway, its consumption by a close relative may actually increase its inclusive fitness. Whether this has rendered the experience pleasurable to the larva is another matter. Note the three eggs in the top cells, capped pupal cells to their left, and the larva in the cell immediately below the middle egg. (Photo: John Pickering)

The concept of natural selection also has implications for the ease with which nature can be studied. Little as we know about the causes of individual mortality, we know much less about the disappearance of species or large groups within species. Differences in individual reproductive success often show up within a single generation; costs and benefits may be registered over much shorter periods of time. But extinction of groups or species occurs over many generations. Thus, species-advantage thinking permits us to argue too easily on any side of a question. Arguing from natural selection promises to eliminate some alternatives as logically unsound, and others as contrary to the facts.

The Group Selection Theory of V. C. Wynne-Edwards

Species advantage reasoning might have continued right into the 1980's were it not for V. C. Wynne-Edwards. In 1962, he published a massive,

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beautifully written book in which he reviewed hundreds of species and presented the first coherent view of social behavior based on group selection. If his theory was true, almost all of animal behavior could be viewed as the product of group selection. If it was false, then by extension, many other examples of species-advantage and group-selection arguments would be seen as false.

Wynne-Edwards argued that there is a process of group selection going on within each species that is analogous to species selection in that it eliminates some groups within the species while leaving others to survive. Which groups does group selection favor? Wynne-Edwards argued that the primary problem that organisms face is eating themselves out of house and home. Since creatures are capable of reproducing very rapidly, they are capable in times of plenty of increasing so greatly in numbers that they may then be incapable of surviving in times of shortage. The only way to overcome this problem, Wynne-Edwards argued, is to evolve mechanisms within the group that tend to prevent individuals from reproducing in times of plenty in order later not to oversaturate the food supply.

My own contact with Wynne-Edwards' thinking was brief but vivid. In preparing a children's book on caribou, I had come across an exciting new explanation for the function of caribou antlers: antlers are devices by which the caribou species regulates its own numbers within safe limits. Caribou males use their antlers during the rutting season to fight with other males. Antler contact is sexually arousing to these males and, prior to the rut, solitary males will often thrash their antlers in bushes, sometimes achieving an erection. If bushes are scarce, males may not get aroused prior to the rut and may perform poorly during the rut, thus lowering the group's reproductivity. When environmental conditions are unfavorable, bushes are few in number, male caribou will fail to be aroused, and population reproduction will be limited. Antlers function as devices through which the species limits its own numbers in order to decrease its chances of extinction.

I thought this idea was splendid—it provided a larger meaning for the caribou's antlers and his associated reproductive behavior. I was so excited I tried out the idea on my teacher, a biologist overseeing my writing, and I will never forget his reaction. He sat there, the way a priest might if his favorite altar boy had come and relayed heresy to him. He wanted to be friendly, but there was a deeply pained expression on his face. He turned sideways and said to himself, "Sounds like Wynne-Edwards to me."

He began to point out flaws in the argument. Imagine, he said, that there is genetic variability in the tendency of caribou males to be sexually aroused by thrashing in bushes. Imagine that some males do not require the thrashing in order to become aroused. These males will outbreed those that do. Their numbers will begin to increase in the

population. At first this will have only a small effect on total population size. Generations must go by before the spread of this "reproductively selfish" type is so far advanced that population numbers may be dangerously high, yet by this time many of these individuals will have dispersed to new areas and populations formerly lacking this selfish type. Once again they will increase in numbers. Given natural selection and dispersal, there is no way the species can retain the tendency to shut off reproduction when bushes are scarce. In addition, he said, there is no evidence that reproduction by female caribou is ever limited by male sexual arousal. There is, in fact, intense male–male competition to fertilize females, and most males are excluded from breeding by the activities of other males, not by failure to become aroused. Thrashing in bushes, he said, is a way of cleaning antlers and practicing their use, and antlers evolved because they are useful weapons for increasing the number of females one can guard from other males.

His arguments left me in a state of confusion. If he was right, then whole worlds of sociology, anthropology, and political science came crashing to the ground. He seemed to be saying that individual reproductive advantage is such a powerful force in nature that benefit to group or species can be neglected as a possible explanation; that group selection is illogical because it requires individuals and their descendants to stay put for long periods of time, even in the face of impending group extinction, which would strongly select for dispersal.

To help me through this crisis, my teacher had me read the work of Wynne-Edwards and his chief opponent, David Lack. I read them for three straight days, one after the other. At first, Wynne-Edwards reconvinced me every time I reread him. But as I continued, his grasp on my thinking began to weaken. Finally, Wynne-Edwards let go completely and slipped off into the surrounding gloom. The evidence was clear: natural selection refers to differences in *individual* reproductive success. When ascribing a function to a trait it only makes sense to see how the trait increases the reproductive success of those bearing the trait, not the reproductive success of the group or the species.

The Evidence Against Wynne-Edwards' Theory

David Lack and other biologists organized several kinds of arguments and evidence against Wynne-Edwards' theory. To give a clearer picture of the possibility of evolution for population regulation, let us review them briefly here. Four points seem especially important.

(1) *There are no natural phenomena that require Wynne-Edwards' explanation.* That is, there are no behaviors that cannot more easily be explained in terms of natural selection. This is important because the

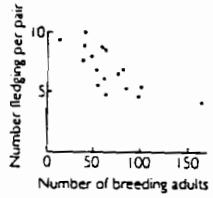

Figure 4-10

The relationship between reproductive success and density. Number of chicks fledged per pair is plotted as a function of number of breeding pairs of great tits in Oxford, England. Notice that as density increases, breeding success declines. (*From* Lack 1966)

existence of unexplained phenomena would necessitate a new or revised theory.

Consider one example. Wynne-Edwards argued that a dominance hierarchy is group selected because in times of food shortage a dominance hierarchy may force individuals at the bottom of the hierarchy to starve to death or die quickly from causes related to lack of food, thus permitting individuals at the top to survive in good condition. A more equitable arrangement might see all the individuals in substandard shape, none of which has a good chance of surviving continued food shortage. This is, in fact, a consequence of a dominance hierarchy, but not necessarily its evolved function.

Dominance hierarchies are maintained in many social species throughout the year, whether food is scarce or abundant. Indeed, stronger hierarchies exist with regard to access to members of the opposite sex than with regard to food. These hierarchies function to give the dominant individual, without fighting, resources it would probably be able to seize if it did fight for them, while the subordinate loses what it would be likely to lose anyway, but saves energy and the risk of injury. The strategy of being subordinate is to accept the lesser of two evils—dispersion or subordinance—in the face of another individual's dominance. Where individuals survive very poorly outside a social group, dispersion may be the more costly alternative.

(2) *There is a natural regulation of animal numbers that operates to prevent the kind of massive extinctions Wynne-Edwards imagined.* This is because of density-dependent factors that operate on mortality and reproduction. That is, when density is low, mortality is likewise low and reproductive rate high, while at high numbers it is more difficult to stay alive and to reproduce, so mortality is high and reproductivity low. Thus, population numbers naturally tend to increase when low and to decrease when high.

Consider, for example, the breeding biology of the great tit *Parus major*. When density of breeding pairs is high, each pair is able to raise only a few offspring (Figure 4-10). So there is a direct relationship between the amount of resources presently available and current reproductivity. Since creatures are attempting to maximize the number of their surviving offspring, they will produce many young when resources are widely available, but will adjust their reproduction downward as resources become more scarce. What we do not expect to find is individuals reproducing at well below the rate they could successfully, all in anticipation of distant, future, population-wide side effects. Thus, in many ways the most important kind of evidence against Wynne-Edwards concerns the actual reproductivity of animals in nature. Could animals easily do better? Wynne-Edwards argues yes; Lack says no.

(3) *Actual data on breeding success suggest that animals are reproducing as rapidly as circumstances permit and without concern over the possibility that the species will survive some future resource limitation.* Since Wynne-Edwards predicts that creatures with a very low rate of increase are capable of reproducing much more rapidly, it is natural to test his theory on birds that have small clutches. For example, the laysan albatross *Diomedea immutabilis* lays only one egg a year. Could it raise more young if it laid more eggs? To find out, a chick was added to each of 18 nests a few days after hatching. This created 18 nests with two chicks. These nests were compared to 18 nests with only one chick. After three and a half months, only 5 chicks survived from the 36 in the experimental nests, while 12 of the 18 chicks from the one-chick nests survived. Parents were unable to find enough food to feed two chicks, and most of these starved to death. Similar manipulations with other birds produced similar results. Thus, so far as we can measure, the typical clutch size in nature appears to be that which maximizes the number surviving to independence (see Table 4-1).

(4) *Group selection is a weak force and depends on very low migration rates.* Wynne-Edwards' group-selection theory is really a return-effect argument in which the effect takes a very long time to

Table 4-1 Relationship Between Brood Size and Number of Chicks Fledged in the Swift *Apus apus*

Year	Brood Size*	Percent Lost	Number Fledged per Brood
1958	1	28.6%	0.71
	2	4.7	1.95
	3	8.3	2.75
	4	50.0	2.00
1959	1	0	1.00
	2	0	2.00
	3	0	3.00
	4	31.2	2.75
1960	1	0	1.00
	2	5.6	1.89
	3	22.2	2.33
	4	70.0	1.20
1961	1	0	1.00
	2	2.8	1.95
	3	22.2	2.33
	4	65.0	1.40

Source: Perring 1964.

* Broods of 4 were created artificially by adding a newly hatched chick to broods of 3. Broods of 4 occur naturally less than 1% of the time.

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return and during which time individuals are free to migrate away from the effect they are producing. If numbers are beginning to reach a level at which extinction would be likely, individuals will be selected to move to less densely settled areas. Thus, at the heart of Wynne-Edwards' theory there is a logical flaw involving animal movements. Wynne-Edwards' theory requires that individuals be restricted to groups, forced to suffer the consequences of each other's over-reproduction, and free only occasionally to colonize areas vacated by extinction of the over-reproductive.

Perhaps because people of my generation first learned what natural selection really meant by reading Wynne-Edwards, we retain a soft spot in our hearts for him. As much as anyone else he "fathered" a whole new line of work in animal behavior. By inadvertently revealing the folly of the alternative, he brought about a renewed appreciation of natural selection: natural selection seems to insist that traits prove themselves at a very local level if they are to become part of life. Typically they must sustain the life of the individual bearing them or increase its reproductivity. Failing this, they must aid closely related individuals, and the less related the recipient, the larger must be the benefit/cost ratio. In addition, some traits do not benefit the organism or its relatives immediately but by somehow inducing a return benefit later. The less certain the return now, the greater must be its later benefit. Evolution is, thus, conservative, tending to build up life-sustaining systems via their local effects, and insisting that the more locally a trait is harmful the more beneficial must be its larger effect if it is to become part of life.

In our desire to see some unity and harmony in life we sometimes wish that natural selection did not act on individuals. How nice it would be, we think, if evolution favored traits that were good for the species, the biosphere, or the universe. Perhaps wisdom lies in trying to see virtues in the way in which life actually evolves. By favoring traits that are locally useful, life is provided a secure foundation for improvement. Attributes negative to themselves are rapidly eliminated, and natural selection gradually weaves together a whole series of individually beneficial traits. Kinship and reciprocity, in turn, provide bases on which selection can mold larger cooperative units.

Summary

Darwin's theory of natural selection refers to differences in individual reproductive success, yet for 100 years after Darwin most biologists imagined that selection favors traits that are good for the group or the species. Examples of such reasoning include the notion that males fight in order to elevate to breeding status genes that are good for the species and the notion that females suffer higher mortality in some species in order to increase the number of available mates for those who do survive.

Infanticide in langurs and some other animals has been interpreted as a group-selected device that regulates population size, but this interpretation fails to explain why males kill only dependent young, and kill only during the months immediately following a group takeover. It also fails to explain female counterstrategies. All these facts, however, are readily explained by the argument that infanticide of unrelated young by males increases the number of young they father and is thus favored by natural selection, while selection of females favors avoiding the murder of their young. Species-benefit reasoning distracts our attention from social conflict and too easily rationalizes the behavior of one actor as being beneficial to all.

The species-advantage tradition in biology came to an end when Wynne-Edwards' massive group-selection theory was shown to be in error. In particular it was shown that birds are reproducing in nature as fast as resources permit, and population numbers are regulated by external checks that act in a density-dependent manner, favoring survival and reproduction when numbers are relatively low. The concept of group selection relies on unrealistic return effects to counteract the spread of traits favored by natural selection. Traits that lower individual reproductive success tend automatically to be eliminated from the population so that later, possible indirect benefits to the species itself are irrelevant to the traits' fate within the species. All traits must begin as rare in a species and can increase in frequency only if they increase the survival and reproductivity of those bearing the traits.

Chapter 5

Genetics, Behavior, and Learning

We can no longer postpone the subject of genetics. Since we know that evolutionary change results from natural selection acting on genetic variability, it will be useful for us to have a concrete image of the gene and some understanding of how genes affect development. To better understand kinship we also need to pay attention to the way in which genes propagate themselves. And because behavior and learning are often assumed to lack genetic components, we need to review a few findings that suggest otherwise.

We begin with a description of the biparental system of inheritance found in humans and many other species. We then describe how genes reproduce themselves and control the ongoing chemical machinery of the cell. We give an example of a simple genetic trait and we review the way in which genes are passed from one individual to another. Regarding behavior, we review studies that show that behavioral traits, like any others, are genetically variable and can evolve. Finally, we close by citing evidence that even the most general kinds of learning abilities in animals have been shaped by the action of natural selection.

The Diploid Genetic System of Human Beings

Humans have what is known as a *diploid* sexual genetic system; that is, the system is bi-parental, with each person having two sets of genes, one from each parent. Two processes are involved: one is the production of sex cells, each of which has only one set of genes, and the second is the union of one sex cell from each parent to form a new individual. Let us begin our account with the union of sex cells.

Figure 5-1

A full set (23 pairs) of human chromosomes. Since this individual is XY, he is male. The banding reveals chromosome structure. The vast majority of human genes are located on these 23 pairs of chromosomes, but a few are also found in organelles. (Photo: Beverly S. Emanuel)

Imagine a human sperm cell about to penetrate an egg cell. Each cell contains a nucleus and each nucleus contains one set of 23 chromosomes. A *chromosome* can be thought of as a chemical thread along which is arrayed a series of genes, like beads along string. Along a typical human chromosome there may be 20,000 genes or more. For most of the life of the cell, the chromosomes are dispersed throughout the nucleus, and are not visible.

Surrounding the nucleus is cytoplasm, which is the chemical material in which occur most of the cell's chemical reactions. Although the nucleus is surrounded by a membrane, the membrane is permeable in both directions. Within the cytoplasm are organelles. These provide special functions such as energy (mitochondria) or photosynthesis (chloroplasts). Every cell organelle has some genetic material that helps direct the activities of the organelle. Thus, two kinds of genetic material are united when sperm and egg unite: nuclear and extranuclear. Because there are at least 1000 nuclear genes for each organelle gene, we expect the nucleus to control the development of most traits.

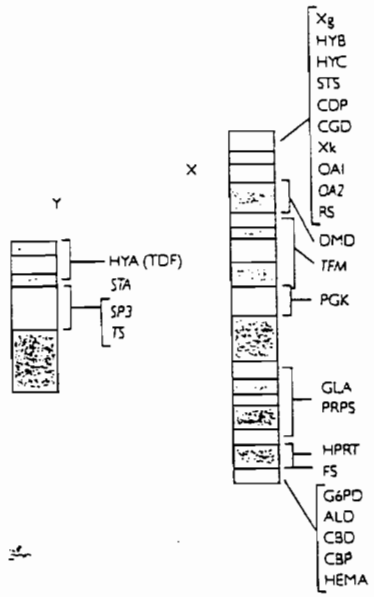

Figure 5-2

Gene maps for the X and Y chromosomes in humans. Depicted are some of the 115 loci found on the X chromosome and their relative locations. Note how comparatively few traits are found on the Y chromosome. This may be because it has been largely shut down by the action of the other chromosomes (see p. 136). *HEMA* refers to the locus controlling hemophilia, *CBD* and *CBP* to the loci controlling color blindness. (Redrawn from map by V. A. McKusick)

When egg and sperm nuclei fuse, 23 pairs of chromosomes are brought together. At certain stages of their life chromosomes condense and can be photographed. These pictures have allowed us to portray the chromosomes in order of decreasing size (Figure 5-1). In every pair of chromosomes, except for the sex chromosomes in the male, each member of a pair is matched to the other, having the same length and the same structure, ultimately ensuring the same structure of genes along its length. Any arbitrary location on a chromosome is called a *locus* (plural: *loci*). There are two genes at each locus, one on each of the paired chromosomes. For a map of genetic loci on the human sex chromosomes (X and Y) see Figure 5-2. We can list all of an individual's genes; we call such a list the individual's *genotype*. The resulting structure, physiology, and behavior we call the individual's *phenotype*.

As we travel down the length of two paired chromosomes, we can compare the genes at each locus. We can ask if they are the same, in which case the individual is said to be *homozygous* at that locus, or different, in which case the individual is *heterozygous*. To the extent that the genes tend to be identical at most loci, the two sets of genes are redundant. At one time it was believed that most of the diploid genotype was redundant. This had the corollary that natural selection

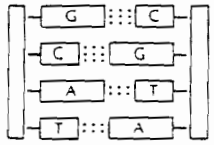

Figure 5-3

The basic structure of DNA. Two backbones run parallel to each other. At regular intervals on each backbone are stuck bases (A, T, C, and G), which form chemical bonds with the complementary base pair stuck on the other backbone. A and T are complementary; so are C and G. The genetic code within an individual refers to the precise sequence of base pairs in its DNA.

was infrequent, locus by locus, and that most of the genetic variation that did occur was deleterious. Once the proper techniques were developed, it was discovered that many loci within each individual are heterozygous. It has been estimated, for example, that within the typical human, 10% of all loci are heterozygous. Consistent with this discovery we believe that natural selection may be active at many of the loci, and that much of the variation may be maintained by frequency-dependent selection that favors genes when they are rare and opposes them when they are common.

We can also compare genes at the same locus in a variety of individuals. For example, we can sample a population to see the degree to which loci are heterozygous in the population. Among humans, about 30% of all loci show some variability within any population of 50–200 individuals.

How Do Genes Replicate Themselves, and How Do They Control Development?

Chromosomes were discovered and photographed in the 19th century; by the early 20th century, chromosomes were known to be the places along which genes were located. But until the 1950's, two problems baffled biologists: how exactly do genes reproduce themselves, and how do they control development? These questions were answered with the discovery of the chemical structure of *deoxyribonucleic acid* (*DNA*), which is the principal material of chromosomes. Far from being a string with a bunch of beads on it, a single strand of DNA is more like railroad tracks held together by a series of ties (Figure 5-3). Each tie consists of two parts, each of which is attached to a track. The parts of the tie come in four different lengths. Thus, DNA consists of two long parallel strands of backbone material connected by what are called base pairs—pairs of chemical bases of complementary length. Each base pair is connected to a backbone, and the two sets of base pairs are joined together by chemical bonds. The backbones are twisted so as to form two parallel helices; hence the nickname for DNA: the double helix.

The chemical structure of DNA is ideally suited to DNA's reproducing itself, for if each of the chemical bonds holding the two strands together were broken, then we would end up with two backbones, each containing a set of bases sticking out from it (see Figure 5-4). Owing to their chemical structure, the bases tend naturally to attract their complementary pairs from the surrounding chemical soup. Once this has happened, enzymes within the nucleus construct a second backbone. Thus, in principle, the reproduction of DNA is simple: enzymes separate the DNA into two parts and each separated half of

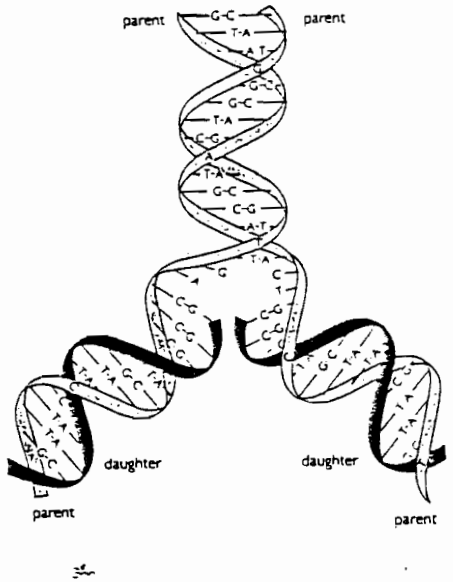

Figure 5-4

The replication of DNA. The two parental strands of DNA are shown bound to each other by the chemical bonds between the bases sticking out from their backbones. At a certain point these strands are separated—the chemical bonds between the complementary bases having been broken—and each naked backbone with bases sticking out attracts the complementary bases from the surrounding chemical soup and new backbones are added. The result: the reproduction of one double helix into two. A, T, G and C denote the four different types of bases.

the molecule acts as a template on which the complementary half is assembled.

An enormous amount of genetic reproduction goes on in the development of each individual organism. Bear in mind that we humans begin as a single cell and end up with more than 100 billion cells. Each time two new cells are produced from a single cell, the entire genetic constitution of the nucleus must be duplicated, and the two halves separated cleanly into two daughter cells. This is achieved by an elaborate and remarkable mechanism that almost invariably replicates (or reproduces) all the genes faithfully and inserts a full set of genes into each new cell. Occasionally a tiny section of DNA *mutates*, or undergoes a spontaneous change in structure. Most mutations appear to result from mistakes in the replication of DNA. In this way, one particular base pair may be replaced by another pair or simply deleted or added to the genotype (see Figure 5-5). Within a section of DNA large enough to code for a single protein, this kind of mutation probably happens once in 100,000 replications. These rare events are the basis for all evolutionary change.

The ability of DNA to act as a template, which permits the duplication of genes, also provides the basis for genetic control of cellular processes. Genes exert their effects on the cell in the following manner.

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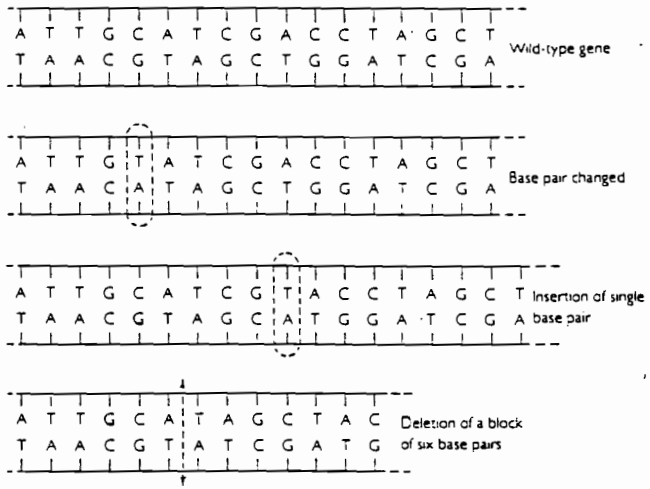

Figure 5-5

Three classes of mutation. At top is the common, or "wild-type," gene. Below it are three kinds of mutations: base pair changed, base pair added (or deleted), set of pairs deleted (or added). A, T, G, and C refer to the four kinds of bases.

A certain enzyme separates a small section of the DNA helix. Each separated section then attracts its opposite base pair and another enzyme constructs a backbone along this small section of bases. This new backbone is made of ribonucleic acid (RNA), a material only slightly different from DNA. The genetic material then comes back together, that is, the helix strands are again parallel and connected, but a unit of messenger RNA has been produced that migrates out of the nucleus and connects with other RNA segments at connecting places called "ribosomes." These segments then act as templates for sections of RNA that connect to amino acids, the building blocks of proteins. Thus, proteins are built up by having a linear array of messenger RNA molecules attract the linear array of amino acids that make up the proteins. Proteins, in turn, run the cellular chemical machinery. Enzymes are proteins and enzymes control the rate of chemical reactions. The reactions determine what substances enter and leave the cell, how the cell is constructed, how it grows and divides, and so on. This great biochemical discovery is summarized as follows:

DNA → RNA → protein.

Every cell in the body has a full set of genes, yet cells are remarkably different. There are nerve cells, muscle cells, cells that secrete hormones, cells that devour invading organisms, and so on. This cellular differentiation is brought about by the selective turning on of different genes in different cells. Part of the genetic machinery consists of the

genes that regulate the process by which other genes are turned on and off. The process by which a single set of genes in one cell controls development into an exceedingly complicated multicellular creature such as the human being is still not a well understood process. But cells are known to differentiate very early in the embryo's development as a result of differences in intracellular environment, and successive differentiation into tissues creates new environments that tend to naturally turn on appropriate genes, leading to further differentiation.

Since DNA → RNA → protein, each gene may be thought of as a portion of DNA that creates a single protein. In this sense a single gene determines a single trait (protein). But since a protein can have many different effects on other parts of the body, each gene typically affects many traits. Likewise, each trait typically requires the action of many different genes. Sometimes a single gene has a major effect on the appearance of the individual bearing it. For example, the gene for blue eyes, when carried in two copies, produces blue eyes instead of brown eyes. But there are always other genes which have at least a minor effect on the same trait. These genes are sometimes called modifier genes, since their effect is to modify a trait. Thus, some individuals have slightly bluer eyes, some have blue-green eyes, some have blue eyes with a little speckling, and so on. These minor variations are caused by differences in the other genes these individuals carry. The importance of modifier genes is that they permit much subtler traits to evolve than if genes had only major effects and one set of genes never modified another.

A Simple Genetic Trait in the Giant Water Bug

Let us consider a simple example of a genetic trait. Normal individuals of the giant water bug *Abedus herberti* are uniformly mottled brown on their backs, but occasionally an individual appears in nature with a bright yellow stripe running down its back (Figure 5-6). When such abnormal individuals are brought into the laboratory and mated with each other and with normal individuals, the yellow stripe is found to be inherited by the offspring and inherited with particular frequencies, suggesting that the trait is controlled by a single dominant gene. Let us symbolize this gene by S and the normal gene by s. S is said to be dominant over s when individuals who are heterozygous (that is, with an Ss gene pair) have the striped trait rather than the normal trait or some intermediate version. When two heterozygous water bugs mate with each other, four kinds of offspring are expected, in equal numbers: SS, sS, Ss, and ss. Since the first three kinds all bear a stripe, offspring of the mating will have the stripe three times as often as they lack it. When an Ss individual mates with a normal ss, offspring will come in

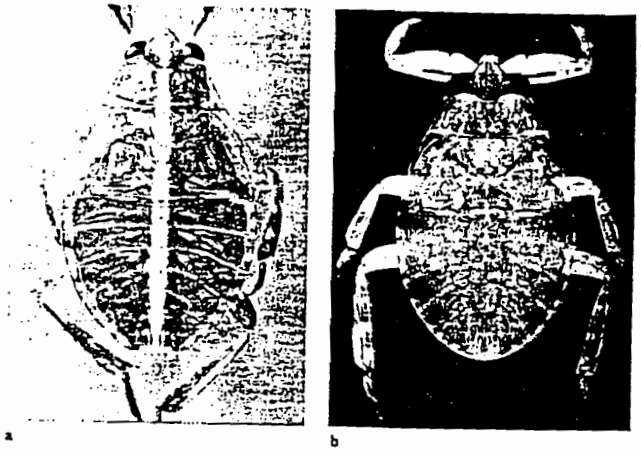

Figure 5-6

Simple genetic trait in the giant water bug. On the left is a larva with a bright yellow stripe running down the center of its back. *On the right* is a normally colored larva, for comparison. Controlled breeding demonstrates that the yellow stripe is under the control of a single dominant gene. (Photos: Robert Smith)

two equally frequent forms, Ss and ss. These are precisely the ratios Robert Smith obtained when he performed these matings. Were the trait controlled by genes at more than one locus, other ratios would result from these various matings. The study of such trait ratios has permitted biologists to identify a series of genetic traits and to map their locations, relative to each other, on chromosomes. (For an example of such a map in our own species, see Figure 5-2).

The isolation of simple, easily identified genetic traits such as the yellow stripe in giant water bugs is useful to students of social behavior because the traits permit kinship to be measured. For example, if we wish to know whether the first or the second of two males that mate with a female fertilizes the greater number of her eggs, we can use striped and normal males in competition with each other and count the number of striped offspring produced (see pp. 266–267).

The Transmission of Genes: Meiosis and Recombination

As cells reproduce themselves, they undergo a process called mitosis, in which each of the chromosomes in the nucleus is duplicated and the two full sets of chromosomes separate from each other and migrate to a separate daughter cell (see Figure 5-7 left). There is one exception to this rule in our own species: when sex cells are being formed, only half

of the chromosomes go into each sex cell, and one and only one chromosome from each pair enters the sex cell. The process by which the chromosome pairs are separated and placed in the sex cells is called *meiosis* (Figure 5-7 right). Each pair of chromosomes segregates independently, so successive sex cells produced by the same individual differ greatly in their chromosomal makeup. Since there is a 50/50 chance that any given chromosome will be found in a sex cell, and since there are 23 pairs of chromosomes, there are 2^{23} possible combinations of chromosomes that can be found among the sex cells.

The variability of sex cells is further increased by *crossing over*: when two chromosomes are duplicated prior to meiosis, the pairs attach to each other somewhere along their lengths and exchange parts (Figure 5-8). Crossing over has the effect of further increasing the number of possible combinations of genes among offspring. You might think that the effect of crossing over is about the same as having twice as many chromosomes, each half as large. But crossing over can occur anywhere along the length of a chromosome, so almost all combinations of genes will eventually be separated from each other during meiosis. Thus, new combinations can be formed between almost *any* two genes and passed on to offspring.

In summary: Sexual reproduction involves meiosis and recombination. Crossing over further increases recombination, suggesting that the primary function of sex is to generate genetic novelty among the offspring. The production of genetic novelty naturally tends to break up gene combinations that selection in the past had brought together, although this price is presumably repaid by permitting a better evolutionary response to the new conditions facing the next generation. The exact way in which selection favors the production of genetically variable offspring is considered in Chapter 13.

Genetics and Behavior

Regarding inheritance of behavioral traits, it is important to recognize that our nervous system has an enormous effect on our behavior and that every nerve cell has a full set of genes, many of which are turned on in order to regulate the chemistry of the cell. The chemistry of the nerve cell, in turn, affects the transmission of messages across the cell and from one cell to another. Thus, genes can affect the transmission of neural impulses and can, in principle, have minute and specific effects on behavior. We are still largely ignorant of how most of these effects come about, but evidence from breeding experiments in animals leaves no doubt that many behavioral traits have a genetic basis.

Let us consider a typical example of a breeding program affecting a behavioral trait. In the field cricket *Gryllus integer*, males adopt one

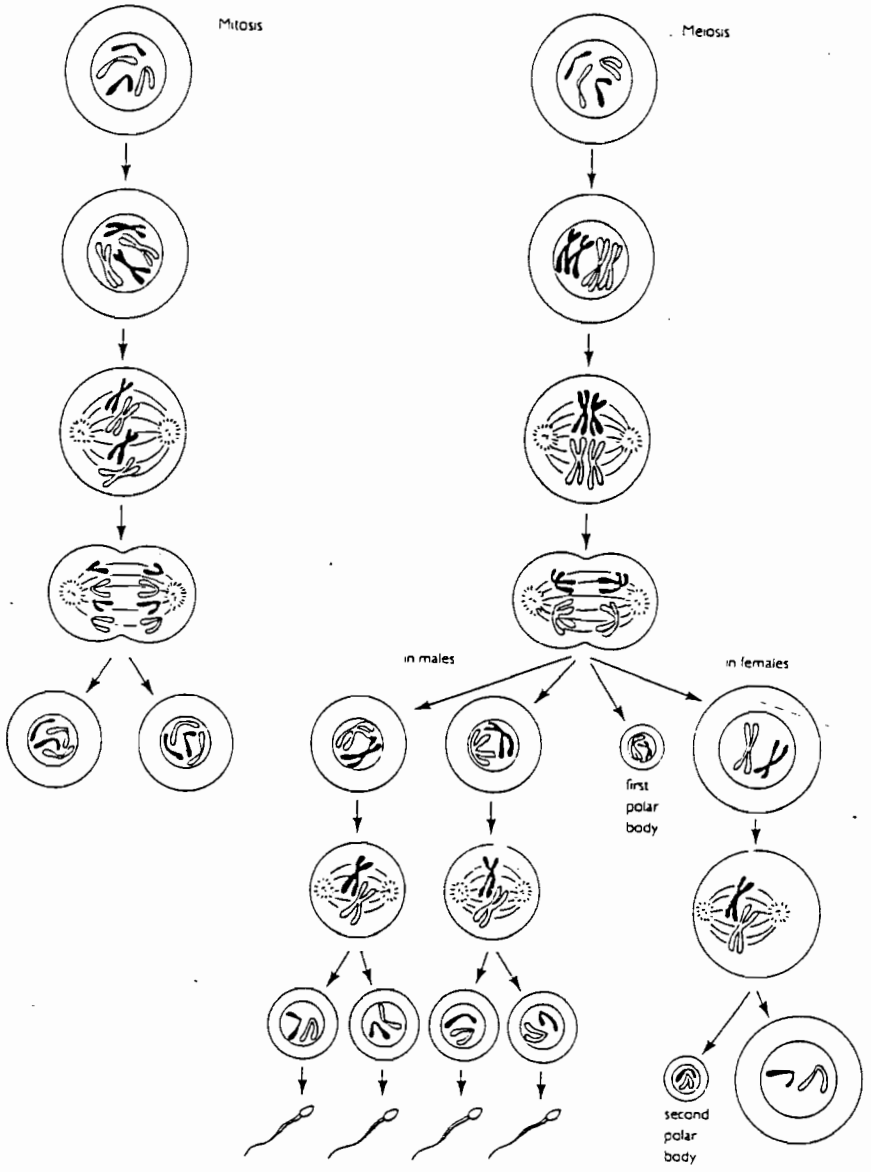

Figure 5-7

Mitosis and meiosis. On the left the process of mitosis is summarized; *on the right*, meiosis, which differs in its later stages in males and females. In the first stage, two pairs of chromosomes are shown. These then reproduce themselves and pair. In the next stage, the paired and doubled chromosomes become attached to the spindle apparatus (which is shown radiating out from two points in the cell). The spindle apparatus then pulls one of the doubled chromosomes from each set (two per pair) to the opposite sides of the cell. The cell now splits into two. One parent cell with a full set of chromosomes has given rise to two with full sets of chromosomes. In meiosis in females, the cell's cytoplasm is split very unevenly and the smaller daughter cell degenerates (first polar body). Meiosis continues with one more cell division, one member of each pair of chromosomes being pulled to opposite sides of the cell. Again in females one of the daughter cells degenerates (second polar body). Each final product of meiosis has only one set of chromosomes (here shown as one each from the original two pairs). In females some chromosomes some of the time are able to avoid migration into polar bodies; this favors their spread (pp. 138–139).

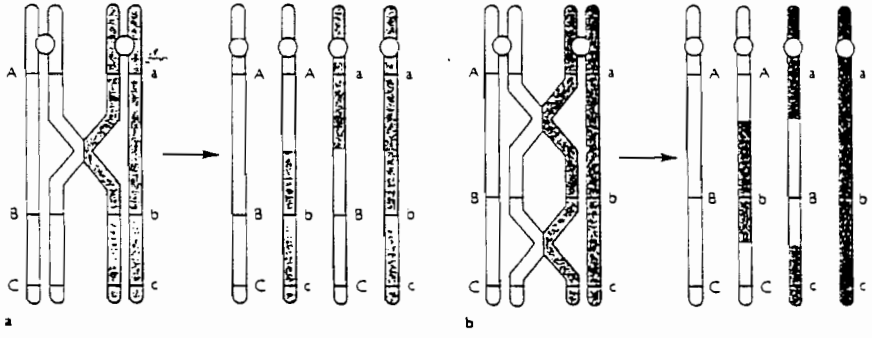

Figure 5-8

Crossing over. (a) Matched pairs of chromosomes exchange parts during meiosis (only one member of each pair exchanges parts). (b) Exchange may occur at more than one location. Crossing over increases enormously the degree of genetic variability generated by meiosis. Rates and locations of crossing over are thought to be under the control of selection. For factors favoring production of increased genetic variability among offspring, see Chapter 13.

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of two strategies for mating with females. They either call frequently to attract females or they call infrequently or not at all and intercept females attracted to calling males. It is possible that the strategy adopted by the male depends entirely on circumstances—for example, males in isolation call more frequently than those in groups—but the existence of two strategies implies past selection on genetic variation, and it would be surprising if this variation had been entirely exhausted. William Cade initiated a breeding program that has settled the matter. The average calling time of each male cricket over a series of evenings was measured. In the first generation several males at the low end of calling frequency and several at the high end were mated with females chosen at random. Within one generation the high and low lines differed significantly in average calling time and this difference increased with succeeding generations selected in the same directions (Figure 5-9). In short, the trait of calling time has a true genetic component such that intense, artificial selection produces substantial change in the trait in only four generations. Incidentally, one disadvantage of calling is that it attracts a parasitic fly whose larvae consume the male crickets within seven days, while otherwise they might survive for weeks. Non-calling males are much less vulnerable to the parasite. The frequency of fly parasitism varies year by year, which is interesting because we now believe that fluctuating selection, especially from parasites, may favor the maintenance of large amounts of genetic variability (see pp. 322–324).

A variety of other techniques have also been used to demonstrate the genetic components of behavior. For instance, studies of the offspring of controlled matings like those used with the giant water bug have isolated a series of genes in mice and fruit flies that have behavioral effects. The creation of inbred lines of mice (and dogs) differing genetically from each other reveal behavioral differences even when the environment is held constant. Crosses between closely related bird species that differ in their behavior produce offspring with a mixture of behaviors, suggesting a mixture of genes acting at several loci. The examples go on. Taken together they suggest that behavioral traits are no different from other traits in having genetic components.

Nor is this conclusion different for human beings. The study of the genetics of human behavior has largely concentrated on seeing to what degree the behavior of genetic relatives is more alike than the behavior of otherwise similar people. Of course, genetic relatives are more likely to share similar environments than are two randomly chosen people, so special attention has been directed to the study of twins. Twins come in two genetic kinds, but are otherwise similar. Identical twins result from the duplication of a fertilized cell, so every gene found in one twin is also found in the other. Fraternal twins come from two different egg cells, each of which has been fertilized by a different sperm cell, so they are genetically equivalent to full siblings (same father). The two kinds of twins are not environmentally identical; for example, fraternal twinning rates vary as a function of mother's age and ethnic group while identical twinning rates do not. Nevertheless, twins' environments are largely similar, and a comparison between the two categories is instructive. When identical twins are compared with fraternal twins on a variety of psychological traits, including IQ, identical twins are found to be especially similar, while fraternal twins often differ as much as do singleton siblings (Table 5-1 and Figure 5-10).

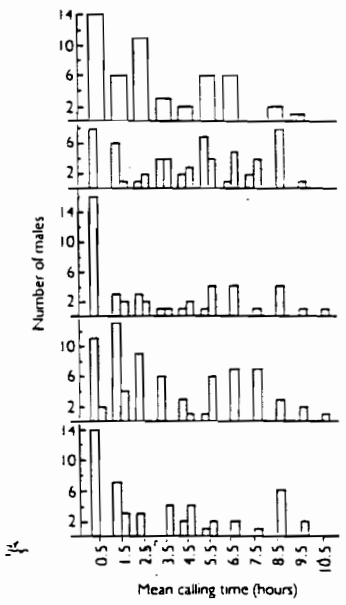

Figure 5-9

Artificial selection for singing and silent behavior in field crickets. Each graph shows the number of males that sang for a given number of hours per night. The top distribution is before selection. The next graph is after one generation of selection, and so on. Black bars represent offspring of males selected because of reduced calling time; white bars, offspring of males that called for prolonged periods. The black and white distributions are significantly different in every generation. (*From* Cade 1981)

Although these findings are valuable, the study of identical twins often reveals striking similarities in very specific characteristics even when the twins are separated at birth and reared apart (Figure 5-11). Thomas Bouchard has studied such pairs of identical twins intensively. Consider one such pair. Oskar and Jack, who are 47 years old, were separated shortly after birth (Figure 5-12, p. 102). Their mother took Oskar to Germany, where he was raised as a Catholic and a Nazi by his grandmother, while Jack was raised in the Caribbean as a Jew by his father and spent part of his youth in Israel. As might be expected, the men now lead very different lives. Oskar is an industrial supervisor in Germany, married, and a skier, while Jack runs a clothing store in

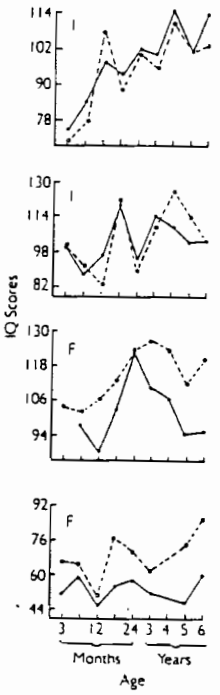

Figure 5-10

IQ scores for identical and fraternal twins. Each graph shows IQ scores as a function of age for a pair of twins. The top two are for identical twins (I), the bottom two for fraternal twins (F). Note the closer correspondence between the identical twins. (*From* Wilson 1978)

Table 5-1 The Average Correlation Between Identical Twins or Fraternal Twins in Various Personality Measures (as Well as Height and Weight)

Trait	Number of Studies	Average Correlation Between Twins*	
		Fraternal	*Identical*
Extraversion	30	.25	.52
Neuroticism	23	.22	.51
Masculinity-Femininity	7	.17	.43
Conformity	5	.20	.41
Flexibility	7	.27	.46
Impulsiveness	6	.29	.48
Height		.50	.93
Weight		.43	.83

Source: Bouchard 1984.

* A score of 1.0 shows perfect correlation; 0 is uncorrelated.

San Diego, is separated from his wife, and enjoys sailing. The following is taken from a recent article describing Bouchard's work.

Their families had never corresponded, yet similarities were evident when they first met at the airport. Both sported mustaches, and two-pocket shirts with epaulets. Each had his wire-rimmed glasses with him. They share abundant idiosyncrasies. The twins like spicy foods and sweet liquors, are absent-minded, fall asleep in front of the television, think it is funny to sneeze in a crowd of strangers, flush the toilet before using it, store rubberbands on their wrists, read magazines from back to front, and dip buttered toast in their coffee.

Another pair of identical twins, Irene and Jeanette, age 35, were separated after birth and brought up in England and Scotland. They turn out to have the same phobias.

Both are claustrophobic and balk when invited into a cubicle for their electroencephalograms. They independently agree to enter the cubicle if the door were left open. Both are timid about ocean bathing; they resolve the problem by backing in slowly. Neither likes escalators. Both are compulsive counters of everything they see, such as the wheels of trucks; both count themselves to sleep.

Some of these similarities are surely coincidental, but it may be doubted whether all are. Identical twins as a genetic category are very unusual because every single gene (except very rare mutations) is identically shared. Thus, even traits with multiple genetic effects (probably the majority of all traits) have an identical genetic basis in identical twins. By contrast, at each variable locus of a full sibling, there is only a half chance of genetic identity by virtue of relatedness. Thus, traits affected by many loci will be similar between such siblings but rarely *identical*.

Many human traits—the language we speak, the religion we practice, the table manners we display—have a very large environmental

Figure 5-11

Postures of identical and fraternal twins reared apart. The top row shows three sets of identical twins; each individual was separated from its twin shortly after birth and raised separately. Below, for comparison, a set of fraternal twins, similarly reared apart. For their photo, the twins were simply asked to stand with their backs to the wall, yet the identical twins unconsciously assumed similar postures (notice the placement of the hands). (Photos: Thomas Bouchard)

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Figure 5-12

Identical twins reared apart. Oskar Stohr, the twin on the left, and Jack Yufe were separated shortly after birth and raised apart, and were not until recently reunited. Striking behavioral similarities in such twins give evidence of genetic components of behavior. (Photo: Robert Burroughs)

component. We speak Chinese because we are raised in a Chinese-speaking family, not because we have Chinese-speaking genes. But strong environmental effects do not mean that genetic effects are completely absent. Perhaps generations of speaking a language with certain sounds has made learning easier where these sounds are concerned. Or there may be genetic variation in the ease with which any language is acquired. And so on. Judging from the enormous variety of animal behavior that has evolved, there has been enormous genetic variation in the past in behavioral traits.

Innate Components of Learning Abilities

According to classical learning theory, animals have a very general ability to learn; yet the more we have studied learning abilities, the more impressed we have become with their specificity. Far from having a single general ability to learn, animals have a variety of more or less specific learning abilities, each tailored by natural selection to a particular task.

Consider the way in which male birds learn to sing, a subject that has been unusually well studied. We now know that learning plays a part in the development of almost all bird song. In order to develop his species-typical song, a male bird must hear other birds singing. He usually has the innate ability to recognize his own species' song and memorizes it in preference to others. In some species the sensitive period for such learning is over long before the male actually begins to sing, so the bird does not learn to sing through simple imitation (itself a sophisticated form of learning). Rather, once the bird starts to sing, he listens to what he sings and tries to match it to the song he has earlier memorized.

When we compare different species we find that even closely related bird species often differ in the details of their song learning. In some species the period of memorization ends before the birds sing, in others it ends in their first season of singing, and in some species males continue to memorize new songs throughout their life. The accuracy of the mimicry also varies—from species in which copying is very exact to ones in which only elements are copied and each individual bird supplies many novel elements. Species also differ in the degree to which individuals copy the song of another species: some do not, some copy only elements, and some copy the song of another species only when they can interact with the individuals producing the song. Still other species perform remarkable feats of copying. For instance, young marsh warblers *Acrocephalus palustris* in their first year of life move south in the autumn from Europe to East Africa, learning the sounds around them as they go, which do not include the calls of adults of their own species. Upon return in the spring each male mimics, on average, the sounds of 76 other species; these are produced in rapid succession, jumbled together in different patterns, almost like a continually varying account of the male's fall and winter travels!

What these and other studies suggest is that learning abilities, like other behavioral traits, have evolved very precise forms in different species. No simple general process can account for vocal learning in any one bird species, much less its variability across several species. We are only now beginning to wonder why selection favors different forms of vocal learning in different birds. One clue comes from considering the intended listener. In some species, male song is primarily a form of territorial assertion, meant to repel other males. In such species, males may be under pressure to develop a species-typical song early in the breeding season, which will select for early, more or less exact copying, sometimes supplemented by later mimicry of territorial

neighbors. In other species, song is primarily directed at females and this may select for more variable male repertoires, based partly on mimicry of other species.

The role of the female in molding male song has recently received dramatic confirmation in the cowbird *Molothrus ater*. Adult females prefer the song of their own subspecies, and a male housed during vocal learning with a female tends to develop her preferred song—even when the male is of another subspecies and only hears his own subspecies' song! Males also develop more original songs when housed with cowbird females (instead of members of other species); this presumably reflects female preference. Male cowbirds appear to have evolved to notice the effect of bird song on adult females of their own species and to mimic or retain those elements that females prefer. Once again we see that natural selection has fashioned a very specific form of learning to fit a particular situation.

Natural Selection and Food-related Learning in Rats

Perhaps the most general learning ability is the ability, through trial and error, to modify behavior in response to reward and punishment; yet this general ability still shows biases that may be interpreted in terms of selection. In classical learning theory any stimulus can come to evoke any response, but the response must be reinforced (rewarded or punished) within seconds for learning to occur. These two assumptions provided an attractive image of trial-and-error learning: the animal is completely open-minded and it uses closeness in time as its indicator of causality. We now know that neither assumption is true.

Consider a rat tasting food that differs in flavor (sugared or unsugared) or in size of item (large or small). John Garcia and his coworkers showed that when electrical shock is paired with the size of the food item eaten, the rat quickly learns to avoid the size being punished but does not learn to associate the flavor of the food with electrical shock, even though the rat is shocked immediately after beginning to eat the wrong-flavored food. By contrast, when food is paired with x-ray treatment—which induces illness an hour later—the rat quickly learns to avoid the flavored food but does not learn to associate size of food item eaten with suffering the illness. The experiments showed that both cues were capable of being learned and both forms of punishment were capable of teaching, but learning occurred only for certain combinations of stimulus and punishment (Table 5-2): flavor could easily be associated with sickness, but size of pellet could not; size of pellet could be associated with electrical shock, but flavor

Table 5-2 Design of Garcia's Rat Learning Experiment*

Group	Cue	Reinforcer
1	Size of pellet	X-ray (illness)
2	*Flavor of pellet*	*X-ray (illness)*
3	*Size of pellet*	*Shock (pain)*
4	Flavor of pellet	Shock (pain)

Source: Garcia et al. 1968.

* Combinations that produced learning are italicized.

of pellet could not. For the results of parallel experiments using water, see Figure 5-13.

Garcia's findings can be interpreted in terms of natural selection. In nature, an animal can often get sick from eating tainted food, so selection favors an animal predisposed to assume that physical sickness is more likely to result from food it has eaten than from other causes. The taste of food, in turn, provides the most useful information about the food's tendency to cause sickness, while the size of food items does not. By contrast, physical punishment (in Garcia's case, electric shock) may often be associated with cues such as size of items in nature, while rarely being associated with the taste of items. The underlying assumption is that natural selection favors efficient means of learning. If an animal were completely open-minded, that is, considered all possible stimuli as being equally likely to produce a given reinforcement, it would be slow to make some connections, and it would probably be unable to make others. If an animal has appropriate biases, it learns some things very quickly, at a cost of being unable to learn unlikely combinations.

Another important implication of Garcia's findings is that animals are sometimes capable of setting up associations in spite of long delays between stimulus and punishment. Garcia waited as long as 12 hours after feeding the rats before inducing sickness with x-rays and still got conditioning to taste of food items. Indeed, rats can develop an aversion to flavored water when x-rayed an hour later, even if a dry meal has intervened; if two meals have intervened, however, rats tend to avoid the more novel of the two. We can see from these results why it would be a bad idea to design a living creature that responded to immediate reinforcement *only*. In life, some causal connections involve a long time delay, yet they are important for the animal to apprehend. Once we grant that an animal should, in some cases, be able to search further than a few seconds backwards in time for causal connections, then we see that if it were totally open-minded, it would have a very large array of possibilities to consider: everything that had happened

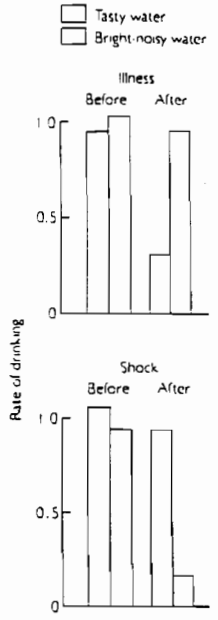

Figure 5-13

Biases in rat learning. The rate at which rats drank either tasty or bright-noisy water before and after each was paired with illness-inducing x-rays (above) or electric shock (below). Tasty water is either salty or saccharine, while bright-noisy water is water that turns on a bright light and a clicking sound whenever it is tasted. Notice that the rats fail to learn that drinking bright-noisy water may cause illness and tasty water may cause shock. (*From* Garcia and Koelling 1966)

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to it in the five or ten hours before becoming ill might be the cause of the illness. Given this large array of possibilities, the animal gains from being biased toward those possibilities that are most likely. In Garcia's case, the animal gains from the assumption that bad food or water causes sickness and a whole series of other activities do not.

Other Examples of Biased Learning

Strains of rats have long been known to display what might be called "innate hypotheses." For example, without any reward, some strains of rats tend naturally to turn left on a T-maze more than 50% of the time. Others turn left less than 50% of the time. Some strains of rats learn visual cues more quickly than spatial cues. Others learn spatial cues more quickly. These findings indicate the ease with which selection could affect changes in learning in rats. Although humans undoubtedly possess more sophisticated and complex modes of learning than do rats, such capabilities could only have evolved from past genetic variation and there is no reason to suspect that such variation has now disappeared in our line.

The type of response an animal makes may also affect the form of learning it shows. We have known for many years that dogs can be conditioned to a variety of sounds. We have recently learned that the type of response demanded of the dog will affect the kind of sound to which it most easily responds. For example, we can compare the quality of sound given versus the direction from which it comes. In one study, the quality of sound was varied by using either a buzzer or a metronome, while the direction of sound was varied by having the sound come from in front of the dog or from behind it. When the dog was taught to use its right paw or its left paw to press a bar, it could associate direction of sound with the use of one paw or the other. But it was unable to learn that the quality of sound was associated with which paw it uses so as to give reward under one combination and no effect under the other. By contrast, when it was taught merely to press a bar or not to press a bar, it quickly associated this task with different qualities of sound, but not so well with their direction of origin.

Similar results have been achieved with monkeys, and they can be interpreted in the following way. In nature, sounds coming from different directions may naturally prompt an animal to make different initial movements. The animal may wish to orient toward the sound, and hence to move right or left, depending on the direction from which the sound comes. The quality of sound is much less likely to be associated with a directional bias in the movement of the animal. On the other hand, animals must often learn to habituate to sounds not associated with any danger or special opportunities. Thus, they quickly learn that

quality of sound can be associated with responding (pressing bar) or not responding. Usually in nature, a particular sound has a benefit or cost no matter what direction the sound comes from. Since this is not invariably true, animals must be capable of learning not to respond to a particular sound from a particular direction, but they find this learning task a relatively difficult one.

The state of deprivation of an animal also affects the way in which it learns. Compare, for example, the behavior of thirsty versus hungry rats in a T-maze, where the reinforcement is, respectively, water or food. Thirsty animals rewarded with water learn more quickly when the water is always in the same position in the maze (either left-hand side or right-hand side) than do hungry rats responding to food in a constant position. But hungry rats learn more quickly than do thirsty rats when the reward changes position in the T-maze. This difference can be interpreted as follows. In nature, water is more likely to be found in the same place day after day. Standing bodies of water are usually not quickly depleted. By contrast, food usually occurs in smaller quantities, which can be quickly eaten by other animals. Thus, it makes sense to search in the same place for water, but to try alternate locations more often when looking for food.

Finally, regardless of the reinforcer, animals rarely show perfect learning. That is, no matter how long reinforcement has continued, animals rarely achieve 100% correct responses. After continuous reinforcement, animals usually achieve about 95% correct responses, which suggests that they have a built-in tendency to vary their behavior, even in the face of continuous reinforcement. This may be adaptive in nature, even if some rewards continue in a constant pattern, since other rewards may be nearby with even higher positive effects.

Much more could be said about animal learning, but I hope the examples chosen convey the idea that even this most plastic part of our makeup has evolved detailed features through the action of natural selection. For the remainder of the book we will have little more to say about the way in which genes control development of traits, or the effects of learning on behavior, but so far as we can see there is nothing mysterious in these phenomena, nor anything that runs counter to the logic we are developing.

Summary

Each human at conception receives 23 chromosomes from each parent. These chromosomes are the structures along which most of their genes are located. Genes, in turn, control development. Genes consist of stretches of DNA long enough to code for an individual protein. DNA consists of two support strands (backbones) connected by a se-

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Homosexuality in humans may be associated with benefits to kin, but the attitude of parents toward homosexuality in their offspring suggests that at least in our society this is not usually the case. In five species of gulls, lesbian couples are found at frequencies as high as 10% of breeding pairs. Although lesbian couples achieve lower reproductive success than heterosexual pairs, in some species they achieve measurable reproductive success, which may be preferable to not breeding at all.

Chapter 9

Parental Investment and Sexual Selection

In the mid-1960's I was studying free-living pigeons in Massachusetts. Pigeons are strongly monogamous and every night I watched three couples who regularly roosted outside my window. What soon became apparent was that the males seemed much more sexually insecure and aggressive than their mates. If a new couple arrived, the male was attacked more frequently by other males than the female was by other females. If a male arrived alone, he was attacked much more strongly than if he arrived with a mate. When settling near each other, males preferred to see their mates sitting on the outside, so that each male was between his mate and any other male. Prior to egg-laying, males were especially attentive to their mates, following them around closely and giving way in disputes over where to sit.

Why should male pigeons be more sexually insecure than females? Why should the sight of another male close to "his" female be harder for the male to bear than a similar sight for a female? Males act as if they are concerned their mates will mate with other males. Imagine that this occurs. A male risks having his offspring fathered by another male. If he works to raise unrelated young, he will suffer a large cost in reproductive success. By contrast, a female need have no such concern. No matter who her mate copulates with, a female's eggs are her own and any subsequent investment benefits her own genes. Of course, we do not expect the female to be indifferent to her mate's "extramarital" activities. They may divert time and energy and, more importantly, may lead to his desertion, but both sexes risk desertion: only the male risks being cuckolded.

Concern over cuckoldry suggests that monogamous males may be interested in sexual relationships outside the pair. This was easy enough to confirm. Each of the monogamous, sexually insecure males I observed courted females at a nearby park when his mate was at

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home on the eggs. Thus, males acted out a double standard, seeking for themselves what they acted to deny their mates.

The parallel to our own behavior is obvious. In most human cultures restrictions are placed on female sexuality that are not placed on males. In the past females were expected to be virgins at marriage, or even risked being put to death if found in adultery. Chastity belts were imposed during separations and kings' harems were guarded by eunuchs. Women's feet may be bound to limit mobility and women may have their clitorises removed to decrease sexual interest, and so on.

The underlying difference between the sexes is one of investment. In both pigeons and humans a sexual act that is inexpensive for a male triggers a large, costly investment by the female. Even when a male helps his mate raise young, copulations with other females may give a big increase in reproductive success, while copulations of his mate with other males will tend to have the reverse effect. If lack of male investment can have this effect in a species in which males commonly care for their young, then it should have an even greater effect where males make no parental contribution at all, for in such species a male will be able in theory to fertilize many, many females, so that competition between males for access to females should be intense. The general rule in animals is that female investment leads to female choosiness and male lack of investment leads to male–male competition. In this chapter we review the reason for this rule. We begin with the classic experiments of A. J. Bateman on *Drosophila*. We then review the distribution of sex differences in animals and test the theory of relative parental investment by reviewing sex-reversed species. We briefly review sperm competition. We review examples of male dimorphisms generated by sexual selection and we close by describing the way in which male–male competition may explain sexual dimorphism in species lacking male parental investment.

The Effect of Relative Parental Investment

Darwin was the first to appreciate that a special kind of selection he called *sexual selection* occurred at the time of breeding. Individuals who do not differ in ability to survive may differ greatly in their breeding success. This, in turn, depends on two factors: (1) competition within one sex for access to members of the opposite sex and (2) choice by individuals of one sex for particular members of the opposite sex. Darwin realized that in nature it was often the males who competed with each other for access to females and females who were discriminating in choice of sex partners. This, he appreciated, could result in more extreme selection in males, that is, in greater variation

in male reproductive success than female reproductive success. To this intense selection Darwin attributed such male characters as antlers, tusks and fangs, bright and extravagant plumage, courtship song and dance, wings when one sex is wingless, and so on; but Darwin could not figure out why it was so often male–male competition and female choice and not vice versa. This key advance was made by A. J. Bateman in 1948 when he published an account of experiments on the factors associated with reproductive success in the two sexes of the fruit fly *Drosophila melanogaster*.

Bateman used flies with different genetic markers so that offspring could be assigned to their parents based on the presence of these markers. In a typical experiment he introduced five virgin females to five virgin males (or three of each) in a bottle and allowed them to spend several days together, mating and laying eggs. When offspring emerged, he classified them according to the genes of their parents. By noting which markers appeared together he was able to estimate the number of effective inseminations in which each fly participated. From these observations, he discovered two important differences between the sexes:

(1) *Males show greater variation in reproductive success than do females.* In all of the experiments only 4% of the females produced no surviving offspring, while 21% of the males failed to leave any surviving offspring. This implies that some males were very successful. In fact, in every single experiment, *variance* in reproductive success (a measure of variation) was greater in males than in females.

(2) *Frequency of copulation had no effect on female reproductive success (beyond the first copulation), but the more copulations a male had, the higher was his reproductive success.* Most females mated only once or twice. When Bateman studied the relationship between the number of copulations and the number of surviving offspring, he discovered that, providing females mated at least one time, additional matings had no effect on their reproductive success (Figure 9-1). By contrast, with each new mating, a male typically elevated his reproductive success. Since most females mated only once, each new mating by a male typically gave him a new batch of eggs to fertilize.

Bateman explained his results by reference to the difference in cost between sperm cells and egg cells. Each egg is expensive, and this cost limits the number that can be made. Most of the variation in female reproductive success is a function of variation in female condition. Those females capable of producing many eggs are presumably those that have more food reserves stored in their bodies. By contrast, sperm are so inexpensive that each could, on this basis alone, fertilize the eggs of dozens of females; but if one male fertilizes dozens of females, then dozens of males will be left with no one to fertilize. Thus the inexpensiveness of male parental investment naturally induces strong competition between them for access to females. At the same time it leads

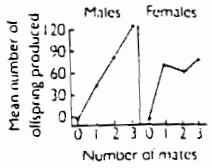


Figure 9-1

The fertility of males and females as a function of the number of their mates, in fruitflies. The reproductive success of a male and a female is plotted as a function of the number of mates in outbred *Drosophila melanogaster*. The data demonstrate a reason why males may attempt numerous copulations but not a reason for females. (*From* Bateman 1948)

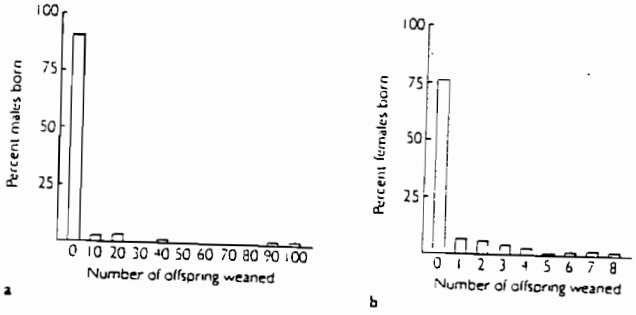


Figure 9-2

Variation in lifetime reproductive success of elephant seals. The percentage of males born or females born who produce a given number of offspring surviving to the age of weaning. Notice the enormous variability in male RS. (From LeBoeuf and Reiter *in press*)

males to be relatively undiscriminating in their choice of sex partners. To take an extreme, if they make a mistake and mate with a female of the wrong species, males will only lose a single batch of sperm. By contrast, a female may lose her entire set of eggs.

Bateman's interpretation should apply very widely in nature, for in most species of animals, parental care ends with the production of the fertilized egg. In these species, male parental investment is invariably very small compared to female PI, and we expect to find higher variation in male reproductive success than female. Likewise, we expect to see male–male competition for access to females, and female choice in favor of particular males. Finally, we expect to find males interested in copulating many times with a variety of females, while females may often be interested in copulating only a few times or once. Greater variation in male RS has now been confirmed for a variety of species in nature. As we have seen already (pp. 35–38), lifetime RS varies more widely in male red deer than in female and male RS is controlled by access to breeding females, while female RS is controlled by ability to invest in offspring. Similar evidence has been gathered for the elephant seal *Mirounga angustirostris* (see Figure 9-2).

It is important to emphasize that Bateman's argument only applies to species with negligible male parental investment. Whenever in a species a male typically invests the same amount per offspring as does the female, the sexes are expected to show equal variation in reproductive success, to be equally discriminating in choice of sexual partners, and to be equally limited in reproductive success by access to members of the opposite sex. For evidence on variation in reproductive success in a bird with high male parental investment see Figure 9-3.

The Major Sex Differences

The two sexes differ in a wide range of characters and these can be organized as follows. The sexes differ in: (1) relative parental investment, (2) degree of intrasexual competition for access to the opposite sex, (3) degree of choosiness in mating, and (4) life history parameters.

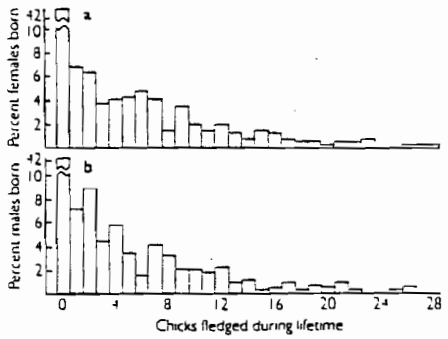


Figure 9-3

Variation in lifetime reproductive success of male and female kittiwake gulls. Shown are the percentage of female or male gulls *Rissa tridactyla* hatched who achieved a given lifetime reproductive success as measured by the number of chicks they fledged. Notice the similarity between sexes, but note also the enormous variability within each sex, suggesting the possible importance of mate choice in monogamous species (see Chapter 10). (From Clutton-Brock 1983)

(1) *Relative parental investment.* The single most important difference between the sexes is the difference in their investment in offspring. The general rule is this: females do all the investing, males do none of it. Parental investment can be defined as anything done for the offspring that increases its chance of survival while decreasing the parents' ability to produce additional offspring. As such, it includes the cost of producing the sex cell, but also includes any other time or effort expended on behalf of the offspring. Difference in investment is especially obvious in mammals. Females suffer the cost of pregnancy, the cost of nursing, and the additional responsibility of protecting the young and showing them a place in the world. The male's contribution to this entire enterprise is the sperm cell, weighing on the average one 10-trillionth of a gram.

One example serves to illustrate the difference for mammals. A female elephant seal weighing 650 kg gives birth to an offspring that weighs 50 kg. In the following five weeks the offspring may gain 100 kg, entirely from mother's milk (see Figures 9-4 to 9-6). Studies show that females lose 2 kg for every 1 kg the offspring gains. Thus females may lose as many as 200 kg. By contrast, the male who fathered the offspring weighed 2700 kg and contributed a few hours' production of sperm cells to ensure fertilization. Although mammals are dramatic

Figure 9-4

Mother and offspring. In this photo we see an adult elephant seal and her offspring. The mother herself does not feed while nursing. Age and dominance have a strong positive effect on a female's ability to rear pups to independence. (Photo: Burney LeBoeuf)

Figure 9-5

An orphan next to a nursing pup. The orphaned elephant seal pup on the left, about the same age (three weeks) as the other pup but considerably smaller through failure to nurse, is scarred over its back through attempts to nurse from females other than its mother (see also Figure 3-20). By contrast, the largest pup ever weighed (almost 300 kilograms) was a male who nursed from two mothers simultaneously. (Photo: Burney LeBoeuf)

Figure 9-6

Super-mother. A flock of elephant seal orphans (note scars) has discovered one of the few adult females willing to nurse each of them. Such a surrogate mother is usually a young adult, breeding for the first time, who has lost her own pup. Some of her investment may well benefit her in increasing her reproductive performance the following year. Since the orphans are dividing one mother between them, one is very large. (Photo: Burney LeBoeuf)

examples, in fact the same general sex difference is also found in creatures who lay eggs, which are invariably many orders of magnitude larger and more costly than the sperm cell with which they unite. Consider, for example, the eggs of birds, turtles, snakes, fish, and insects (see Figure 9-7).

There are exceptions to the general rule that relative parental investment (PI of male/PI of female) = 0. These exceptions are especially important because, as we have seen, relative parental investment controls the evolution of the other sex differences, so that the species that are exceptional in relative parental investment are also exceptional in other regards. Birds are the most prominent exception. In about 95% of the 8000 bird species, male parental investment is common. Other exceptions are the carnivorous mammals, some species of fish and frogs, and many species of insects. Species with male parental investment are reviewed in Chapter 10.

(2) *Degree of intrasexual competition.* The general rule regarding intrasexual competition is that males compete with each other for access to females, while females rarely compete with each other for access to males. Male competition, in turn, takes at least three forms: (a) aggressive interactions to limit the access of other males to a set of females, (b) competition to disperse and find sexually receptive females, and (c) competition in courtship to be chosen by females. Each

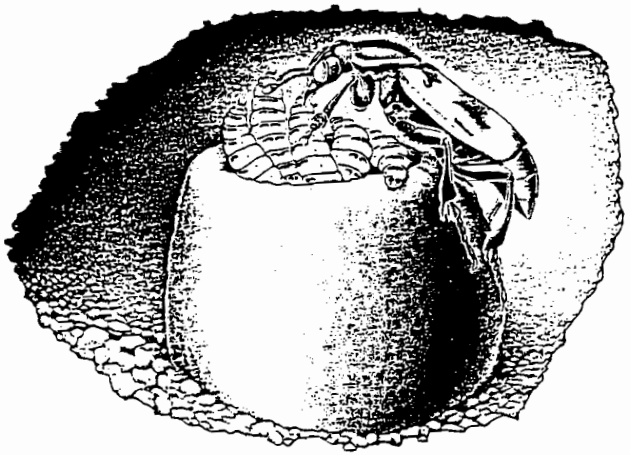


Figure 9-7

Maternal investment in a beetle. Like so many fledgling birds, the larvae of the burying beetle *Necrophorus vespillo* are fed by their mother, who is seen regurgitating food to one larva while another reaches to feed. The larvae rest in a depression excavated by their mother in a ball of rotting carcass provided by both parents. The larvae also feed from the ball. In some related species the male regurgitates food to the larvae but less so than the female. (Drawing by Sarah Landry, from Wilson, 1971).

Figure 9-8

Two elephant seal males fight. These two dominant elephant seal males are squaring off in a fight. Each will attempt to push its rival around and to wound the other on its heavily padded neck or more vulnerable flanks. These contests concern sexual access to the highly aggregated breeding females, seen here with their pups. By delaying the implantation of the early embryo in their uterus for several months, females are able to prolong development in their young so that the females can mate right after they have finished nursing their current offspring—instead of three months later. (Photo: Burney LeBoeuf)

of these differences in behavior has in turn generated a series of structures and physiological adaptations to support the behaviors.

Where there is a sex difference in aggressiveness, males are typically the more aggressive sex. This is especially pronounced at the time of breeding. Females rarely fight each other over access to males, yet males may fight for hours, wounding each other and on occasion killing (Figure 9-8). A series of structures has evolved to support this fighting. For example, males are usually the sex that is ornamented with weapons, such as the enlarged canine teeth of primates, antlers of deer, larger horn size in antelopes, tusks in pigs and elephants, horns on staghorn beetles, enlarged jaws (relative to body size) in lizards, and so on (see Figure 9-9). Naturally, males have the musculature to use these weapons, and this increases the cost of the weapons.

In most species of animals, males disperse more widely than do females. That is, if individuals of the two sexes are marked and recaptured sometime later, the male will have moved a greater distance. In plants it is the male sex cell that is mobile, while the female sex cell is stationary until pollination. Studies of movements in salamanders, snakes, turtles, lizards, and mammals show a consistent pattern of greater male dispersal. This is often especially pronounced during the mating season. In some species the sex difference appears at an early age. For example, male deer fawns at six months of age wander greater

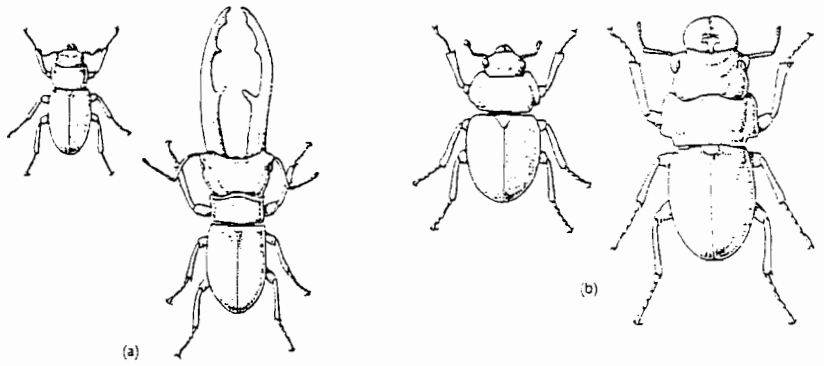


Figure 9-9

Sexual dimorphism in beetles. (a) Male and female of *Cyclommatus imperator*, the male having huge forceps-like mandibles, which in other species are used to lift another male off a surface such as the trunk of a tree. (b) Male and female of *Odontolabis lowei*, with the male showing well-developed pincher-like mandibles, probably useful for crushing. In both species the male's head is much enlarged in order to hold the muscles that move the mandibles. Notice also the enlarged body size. Such extreme examples of sexual dimorphism are usually found in the species with the greatest body size within a group (*From* Otte and Stayman 1979)

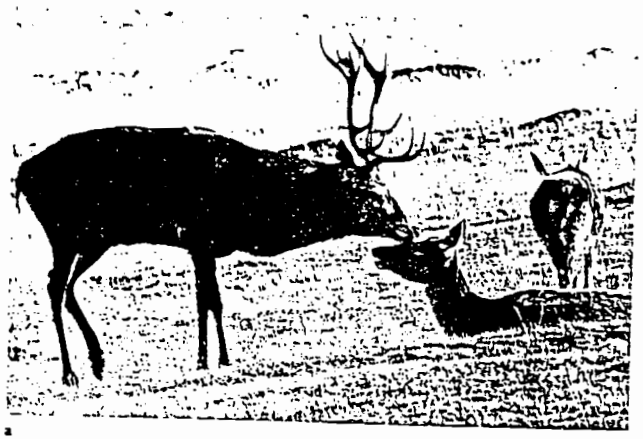
distances from their mother than do females. When one species of insect lacks wings, it is usually the female. As with the other rules, there are exceptions. Birds, which are exceptional in so many other ways, are the only large group of animals in which females regularly disperse greater distances than do males.

Males typically court females rather than vice versa. Males are often very active in courtship and display parts of themselves. They also are almost always the more conspicuous of the two sexes. Virtually all sounds that are produced during the breeding season are produced by males. Males are the more brightly colored of the two sexes, and in birds colorful parts of the plumage are often displayed to the female during courtship. For scenes of the rut in red deer, see Figure 9-10.

Underlying these differences may be a widespread tendency for the metabolic rates of males to be higher than the metabolic rates of females. For example, in the human species a boy's resting metabolic rate is about 5% higher than a girl's, and this sex difference persists

Figure 9-10

Male activities toward females during the rut in red deer. (a) Males frequently approach lying females and lick the back of their heads and necks, gradually working toward the front of their eyes, as shown here. This may be followed by an attempt to sniff and lick around the base of the tail. Bouts of sniffing and licking may last for several minutes and are usually terminated by the female moving away. (b) In addition to herding females attempting to leave his territory, a male often chases a female over short distances within the harem, his neck outstretched, sometimes with tongue extended. Such chases are terminated by the male and are often followed by a bout of roaring. (c) A male prepares to mount. The female has signaled her acceptance by spreading her hind legs, while the male licks her rump. (d) At the moment of ejaculation, the male may leap clear of the ground, as in this picture. Mating sequences between two individuals involve several mountings spread over an hour or more. (Photos: a, c Timothy Clutton-Brock; b, d Fiona Guiness)



a

b

c

d

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into adulthood (when corrections are made for differences in adult body weight).

(3) *Females are discriminating, males are not.* In most species females are highly discriminating in their choice of sex partners, while males are much less discriminating. A female is typically courted by many males and refuses access to all but one or a few. This choice is by no means random. Wherever female preference has been studied in nature, females have been shown to choose in very particular ways. Most females in a species choose in a similar way, so that the result of female choice is to give some males many copulations and many other males none (see Chapter 14).

By contrast, males court many females and will copulate with most or all if accepted. In addition, males will court inappropriate objects. For example, males have been observed courting other males, females of the wrong species, stuffed females, portions of stuffed females, and inanimate objects. Sometimes they are seen courting a combination of the above. In many frog species, courtship of males by other males is so common that males have evolved a special release call given to another male who has clasped him, which says, in effect, "Release me, I'm a male."

The fact that males will court stuffed females is useful for field biologists, since it means that stuffed females can be introduced to males in order to test their reactions under experimental conditions (see pp. 349–352). Biologists studying turkeys decided to see how much can be removed from a stuffed female and still produce a full male sexual response. It turns out that a head suspended 15 inches above the ground is capable of eliciting complete courtship behavior from some males. These males circle the head, display themselves, and behind the head jump into the air so as to land where the female's back would normally be. A wooden model of a female's head is less arousing than a stuffed head, but is still successful with some males. Indeed, some will even respond when the eyes, the eye sockets, and the beak have been removed.

It is not accurate to characterize the male as active during courtship and the female as passive. The process of choice is an active process. Often females move from male to male, eliciting courtship and responding in various ways to the courtship in order to make their choice. It was often claimed in the past that females of many species were unwilling to participate in sex and had to be courted by numerous males before being aroused to the point where they would indulge in sex. What appears to be true is that females are uninterested in sex with most of the available males and require courtship by many different males in order to make their choice. Thus males appear to be indiscriminately eager for sex, while females are choosy.

(4) *Sex differences in life history parameters.* In most species males suffer higher mortality than do females, and this is often true throughout their lives (see Chapter 12). Males may also mature at a different age than females.

Sex-role-reversed Species

To test Bateman's theory of parental investment and sexual selection, it would be ideal to find species in which males invest more in the production of offspring than do females. In such species we expect to find that female reproductive success varies more than that of males, we expect to see females limited in RS by their access to males, and we expect males to be more careful in choice of mating partner than are females. But relative parental investment is difficult to measure in nature, and it has proved easier to find examples of sex role reversal, which on inspection turn out to be associated with unusually high male parental investment. Since George Williams first drew our attention to sex-role-reversed fish and birds, a growing number of examples have come to light. These convergent examples give support to the view that relative parental investment is the underlying variable controlling the evolution of sex differences.

Insects. A couple of cases have now come to light of high male parental investment correlating with sex-role reversal. In the Mormon cricket, male investment in the form of a spermatophore may be considerable (Figures 9-11 and 9-12). In high-density areas—where food is relatively scarce—these large spermatophores are especially valuable yet difficult to produce. The result is female–female aggression for access to males, inflated female size (relative to male), and males that are discriminating. About half the copulations are terminated by the male before he transfers his spermatophore: females who are accepted are, on average, larger than those that are rejected and contain 60% more eggs. The result of sexual selection on females in high-density areas is an increase in the degree of variation in the number of their mates: some females, especially large ones, have their naturally high fertility augmented by many male spermatophores. In low-density areas—where the crickets are 1000 times less numerous—food is relatively abundant and many males are able to produce spermatophores. Even though male investment is relatively greater (as measured by percentage of body weight committed to each copulation), there is no female–female aggression, nor are males choosy!

Seahorses. In fish, the pipefish-seahorse family (Syngnathidae) has several species that appear to be sex-reversed. In each of these species a male invests in young by receiving the eggs of a female in his pouch

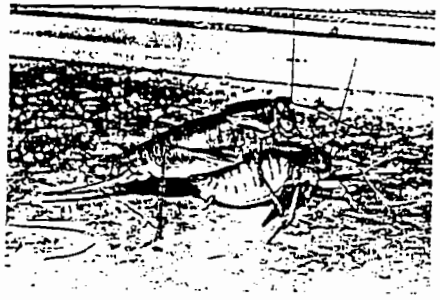

Figure 9-11

Sex-role-reversed cricket. The female Mormon cricket *Anabrus simplex* starts to mount the male prior to copulating. The male has already arched his abdomen in anticipation. The long structure at the female's rear is her ovipositor; through it she will lay her eggs. At copulation the male transfers a spermatophore, which may amount to 30% of his weight (see next photo). When he has a spermatophore ready, a male calls to attract a female. (Photo: Darryl Gwynne)

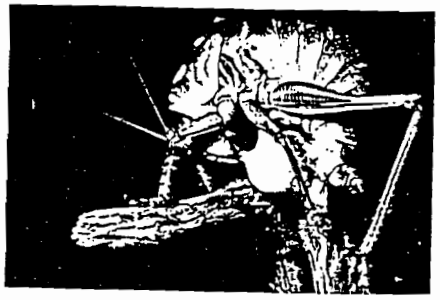

Figure 9-12

Consuming male parental investment. After mating, a female Mormon cricket turns and begins eating the large, protein-rich spermatophore that the male has just transferred along with his sperm. In a related species, heavier males are known to produce larger spermatophores, and females given a choice between two singing males that differ in weight prefer to mate with the heavier male. In the decorated cricket *Gryllodes supplicans* the spermatophore is consumed in two portions, the second of which contains the remaining sperm. The first portion is, on average, just large enough to ensure that all sperm are transferred before the second portion is eaten. (Photo: Darryl Gwynne)

and caring for the eggs in the pouch almost like a kangaroo. Several species have been studied in the laboratory. Courtship is mutual in these species but more active on the part of females. Females are more brightly colored than males and develop their coloration at the time of courtship. Coloration correlates with motivation to breed: the brightest females court with the greatest intensity. Males court by pumping water into their brood pouch so that it expands like a balloon; thus they appear to advertise their capacity to carry eggs. In turn, two field studies show that females typically contain more eggs than males carry within their brood pouches. In both sexes, larger size correlates with a greater number of eggs carried, but for the same size, females contain more eggs than do males. This is suggestive evidence that females may be limited in reproductive success by access to male brood pouches. Unfortunately, we lack information on how long males carry eggs compared to the time it takes females to produce a batch of eggs. In summary, in the Syngnathidae, male parental investment is unusually high and may be higher than female parental investment. In turn, females compete with each other for access to males, are more vigorous in courtship, and are more brightly colored.

The poison-arrow frog. In one frog, the Panamanian poison-arrow frog *Dendrobates auratus*, females are more vigorous in courtship than are males and have been seen chasing them. Females lay a clutch of eggs every 5–10 days, while males care for each clutch for 10–13 days until hatching and carry tadpoles to standing water. Males are also capable of caring for two clutches of eggs at the same time, and both sexes show aggression toward members of the same sex.

Sex-reversed birds. Sex-reversed birds are a mixed assemblage, including phalaropes, various shorebirds—such as the dotterel, various so-called primitive birds—such as the emu and tinanou, and the lily-trotting jacanas. These species are characterized by the following:

(1) Females invest nothing in the young after the eggs are laid. Males brood the eggs until chicks emerge and care for the chicks for several weeks.

(2) The young are precocious; that is, they are able to move about on their own shortly after hatching and are capable of feeding themselves.

(3) Some females are polyandrous; that is, they breed with more than one male per season, depositing a clutch of eggs with each male. Males always breed only once per season.

(4) Females usually outnumber males. This alone generates female–female competition to pair with males.

(5) Females are larger than males, more brightly colored, more aggressive, more active in courtship, and arrive first on the breeding grounds.

Female competition for males has been described as follows in the Wilson's Phalarope *Steganopus tricolor*:

> Immediately after arrival, courtship behavior increases gradually in intensity for a week or two, reaching a peak about mid-May. At this time it is common to see solitary males swimming nervously along the edges of grassy ponds pursued by several females. Often one female seems to be dominant or to have already formed a pair bond with a male. This female usually follows the male more closely and manages to stay between him and the other females. Occasionally, if another female approaches too closely, the dominant female attacks and drives her away. . . . The male usually watches attentively from several feet away or swims about aimlessly and nervously nearby.

Phalarope males are often happy to engage in an extra copulation; these, after all, cost a male very little, so that he is easily aroused to copulate with a female even if he is already encumbered with eggs or young. But at the time when eggs hatch, males drive away females and

do not permit them near their young. Females sometimes court a male at this time, so it at first seems curious that males should respond so aggressively to female courtship. Yet a female could destroy a male's young (much as does a langur male) in order to be able to deposit her own eggs with the male. Indeed, this appears to happen in another sex-reversed species, the jacana: a female take-over of another's territory was associated within a day with the disappearance of a male's clutch in the territory, suggesting female infanticide. The male repeatedly tried to distract the female's attention from his nest. Likewise, in the sex-reversed little button quail, females have been seen killing chicks in an enclosure in circumstances that suggest they might practice infanticide in nature. Incidentally, the sex-reversed button quail is the only bird known in which the female feeds the male during courtship, while the reverse is widespread.

The phalarope system and other examples of polyandry in arctic shorebirds are believed to have arisen through the habit of double-clutching. Where nest predation is high, females are selected to lay replacement clutches. At the same time, to reduce visibility, only one parent is selected to remain with the eggs. Since the young are precocious, only one parent is required after the chicks hatch. Thus, as females concentrated on laying replacement clutches, males became saddled with incubation and post-hatching care. This forced males into greater investment than females, in particular, requiring them to stay in the breeding habitat long after food resources were optimal, while females migrated to better feeding grounds. Greater investment led to greater mortality (see Chapter 12), which intensified female–female conflict for males. A second clutch could also be placed with a male who had no clutch, either through loss or failure to pair. This occasional polyandry further intensified female–female conflict.

Recently, Marion Petrie has conducted a remarkable study of the sex-reversed moorhen *Gallinula chloropus* that shows that large size in females is favored by female–female competition, while small size in males is maintained by the energy efficiency of high parental investment. Males perform 72% of the incubation, which is energy-expensive: they lose almost 10% of their body weight during the breeding season. Males in better condition at the beginning of the season spend more days incubating throughout the season and initiate more new clutches, while female condition has no effect on the number of clutches initiated. Instead, females fight with each other for access to males (more than vice versa) and court males (more than vice versa). Occasionally females are polyandrous but they seem primarily to compete for access to high quality males. Heavier females win fights more often and pair more often with males in good condition, as expected (Figure 9-13), but male condition is inversely correlated with male size, so that large females preferentially mate with small, fat

males! We see that large variation in male quality—rather than the number of mates a female may acquire—can induce female–female competition.

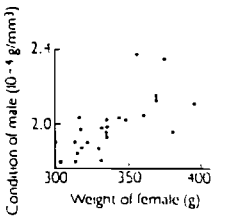

Figure 9-13

Relationship between male condition and female weight in mated pairs of moorhens. A male's condition (weight in grams × 10^{-4} divided by the cube of the length of part of his leg—tarsus plus metatarsus—in cubic millimeters) is plotted as a function of his mate's weight (in grams). Weights were either measured at the beginning of the breeding season or standardized to reflect values at that time. Note that heavier females are paired with males in better condition. (*From* Petrie 1983)

Sperm Competition

In one sense all male–male competition is just so much sperm competition (pollen in plants): sperm are so inexpensive that far more are produced than the eggs they fertilize, and in the absence of additional male investment in the young, males compete with each other in order to give their sperm differential reproductive success. Even when there is high male investment, there may be sperm conflict in the form of cuckoldry (see pp. 260–267). The differentiation into small, mobile male sex cells (sperm or pollen) presumably followed from the fact that more of them could be produced for the same cost without a commensurate decrease in fertilizing efficiency. Presumably, in sperm cells as well as in adult males, dispersal and mobility select against large size.

In insects, sperm competition is a major factor affecting male reproductive success. When two males copulate with the same female, the general rule is that the sperm of the second male takes precedence: last one in is first one out. Sometimes this competition is very aggressive. In the damselfly *Calopteryx maculata* the male's penis is designed both to deposit sperm and to remove any that has already been deposited (Figure 9-14). In other species the penis appears designed to enter the female's sperm storage organ and compress any existing

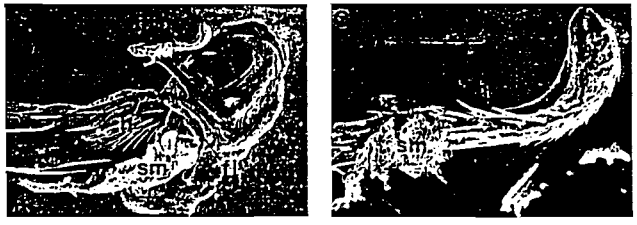

Figure 9-14

The penis of a damselfly: designed to remove sperm already deposited. (a) The penis of the male damselfly *Calopteryx maculata* showing the backward-projecting horn (hrn) and the hairs (h) that catch masses of sperm (sm). (b) A close-up of the horn. (Photos: Jonathan Waage)

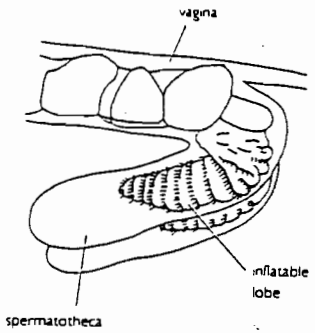

Figure 9-15

A penis for compressing rival sperm to a corner. The penis of the male dragonfly *Sympetrum rubicundilum* is shown inserted into the female's vagina. Note the two inflatable lobes extending into the female's sperm storage sac. They probably compress rival sperm to the far corner, from where they are unlikely to fertilize eggs. (*From* Waage *in press*)

sperm to a corner (Figure 9-15). In an acanthocephalan worm sperm competition takes the form of homosexual rape: after copulating, males use the same cement gland with which they usually seal off the female to seal off the genital region of male competitors!

Since the rule regarding insect sperm is last-in first-out, there is a premium to copulating just before oviposition. Often a male will choose to guard his mate for a period of time after sperm is transferred so as to increase the chance that oviposition will occur before remating. As expected, the frequency of this guarding is greater—and lasts for a longer period—when the adult sex ratio is more biased toward males. This makes sense since extra males will decrease the matings available elsewhere to each male, while increasing the chance that another male will mate with the female he is about to release.

Duration of copulation itself may be lengthened in order to guard the sperm being deposited. In caged populations of the stink bug *Nezara virigidula* duration of copulation is more than doubled when there are two males for each female instead of vice versa (Figure 9-16). Note that copulation in this species may last for seven days! The record in insects for duration of copulation is 79 days and is held by a walking stick. In species of these insects, copulation is longer when the male is relatively smaller. This makes sense, because when the male is relatively small, he will mature at an early age; other things being equal, this should increase the adult sex ratio and, therefore, the degree of competition from other males.

This brief glimpse of sperm competition in a well-studied group with internal fertilization has not permitted us to review such well-developed phenomena as the production of mating plugs by males—physical barriers to further copulation, which may include part of the

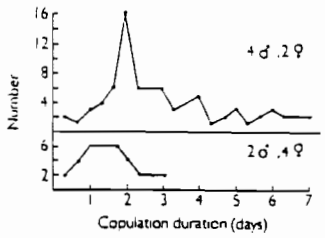

Figure 9-16

Relationship between adult sex ratio and length of copulation in an insect. The number of copulations is plotted as a function of their length, for a sex ratio of 4 males and 2 females (top) and 2 males and 4 females (bottom). Relatively more males result in longer copulations. (*From* McLain 1980)

male's body, as in honey bees *Apis mellifera* (which still does not prevent the female from copulating with as many as a dozen males!). Nor have we reviewed the evolution of traumatic insemination in bedbugs and others in which the male seems to short-circuit the normal means of sperm transport by piercing some portion of the female's body and injecting sperm directly. In some species, sperm is injected also into other males, where they migrate to join the sperm of the penetrated male! In this intense competition between sperm that are partly related and partly unrelated, selection has more often generated dimorphisms than between related eggs, though we must admit that we still know little regarding the way in which altruistic sperm confer their benefit (see pp. 121–124). Even the size of a male's testicles may partly reflect sperm competition: in monkeys and apes, testicles are larger (relative to body size) in species in which several males may mate with a single female during her fertile period, compared to species in which only one male typically copulates with a female (see Figure 9-17). Altogether, the world of sperm competition reinforces our impression that for most species male–male competition results from the low cost of individual sperm and the consequent competition between males to fertilize eggs with these sperm.

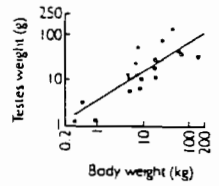

Figure 9-17

Weight of testes as a function of body size in monkeys and apes. The average weight of the testes (in grams) for males of various genera is plotted as a function of their body weight (in kilograms). Closed circles represent species with multi-male groups; open circles, monogamous species or single-male groups. Genera with multi-male troops have larger testes. (*From* Harcourt et al. 1981)

Alternative Mating Strategies and Male Dimorphisms

One of the curious facts of biology is that two very different forces have tended to produce dimorphism in nature. On the one hand, selection associated with reproductive altruism has generated complemen-

tary forms, such as soldier and reproductive aphids, worker and reproductive ants, altruistic and fertilizing sperm, and so on. On the other hand, male–male competition in species lacking male parental investment has also generated dimorphisms. We have already encountered the white and black morph of the ruff (p. 26); likewise, we have seen that there is a calling and non-calling strategy in crickets (p. 98). We now pause to review alternative mating strategies more fully because they serve to illustrate the way in which male RS depends on interactions with other males.

Male dimorphisms are believed to be generated by selection for alternate mating strategies. (For an example of a male dimorphism, see Figure 9-18). Alternative mating strategies occur because there is a strong interaction between the reproductive success of males such that each alternative does relatively well when it is infrequent. In many species males establish territories within which females will breed or around places from which adult females will emerge. When such territories are few in number, each new male establishing a territory can expect a gain in RS through greater exposure to breeding females; but when many such territories are held, most of the reproductive success available through this means is already being taken, and so an alternative strategy may do better. Instead of patrolling sites at which females will emerge, a male may do better to hover at nearby sites that females are likely to visit. Another alternative strategy is to remain within another male's territory, intercepting some of the RS associated with that place or male. In a chorus of calling crickets or frogs, a male frog may remain silent and mate with some of the females attracted to calling males. One advantage of the alternative strategy is that it may be less expensive to maintain. Non-calling crickets are parasitized less frequently by one fly than are calling males, and defense of a territory may be energy-expensive.

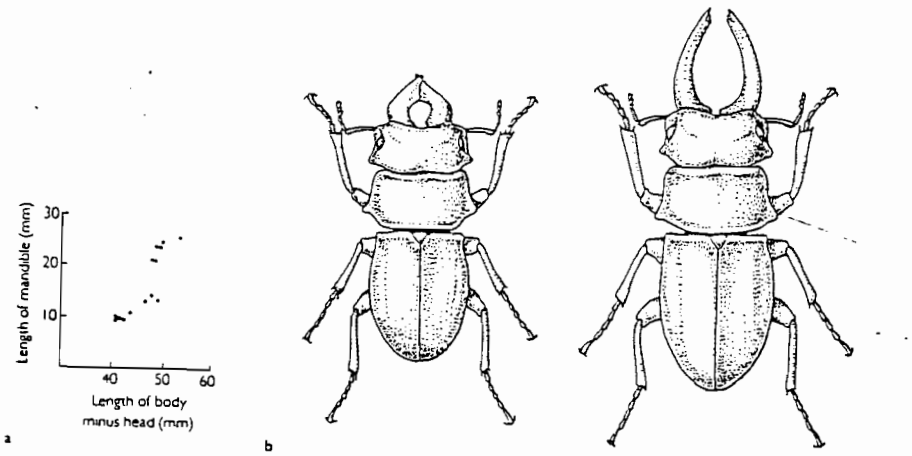

Figure 9-18

Male dimorphism in a beetle. (a) Mandible length (in millimeters) is plotted for males of the stag beetle *Odontolabis siva* as a function of length of body minus the head (in millimeters). Notice that the points form two clusters. (b) A small male and a large male are drawn, showing the change from a pincher-type mandible to a forceps-type. These are probably associated with different behavioral strategies. (*From* Otte and Stayman 1979)

We expect satellite males to be more often associated with high quality territory-holding males and to be more frequent where variation in territory quality is high. We also expect satellites to be more frequent where arrival of females is more synchronized, since each male will then have more difficulty monopolizing all the females. These predictions are supported in dragonflies. In one species, *Plathemis lydia*, males that defend the best sites for opposition are associated with up to four satellite males, while those on poorer areas have none. Female arrival is synchronized at the better sites but not at the poorer ones. With increasing number of female arrivals, copulation rates of territorial males fail to keep pace, presumably creating opportunities for satellites. Satellites are not found on ponds that appear to have little variation in quality of site.

The non-territorial strategy may involve deception. The male may need to remain inconspicuous or he may actually mimic a female, the better to gain access to his "mate's" reproductive success. Deceivers will do well when rare, as will territory holders. This kind of selection has actually generated complementary male morphs in a fish, one of which is considerably smaller than a territorial male and mimics a breeding adult female (see pp. 407–408).

The effect of size on alternative straregies is nicely illustrated by the digger bee *Centris pallida*. Males fight for control of sites from which females emerge from their pupae; the size of the male has an important effect on success in aggressive encounters. The very largest males achieve disproportionate reproductive success (Figure 9-19). Most smaller males do not take part in this competition but instead hover at nearby sites from which they have a good vantage point to dart after unmated flying females. In this species, offspring grow to maturity on provisions supplied by the mother. An advantage to the

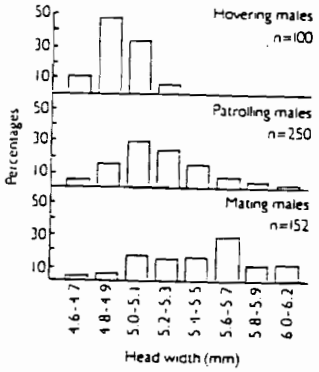

Figure 9-19

Size and its effect on alternate mating strategies and mating success in bees. The percentage of male bees *Centris pallida* of a given head width (in millimeters) that hovered, patrolled, or copulated. Sample sizes are indicated. (*From* Alcock 1979)

mother of smaller sons is that more of them can be produced for the same cost. In frogs the male adopting the alternate strategy is, on average, smaller than the territorial form (Table 9-1).

The most extreme male dimorphisms are found in fig wasps, in which a flightless form may coexist with a winged, dispersing form. The flightless form is often armed with huge mandibles—attached to an enlarged head—and will attack and kill other males. (For a parallel in bees, see Figure 9-20.) To understand this dimorphism we need to know a few facts about fig wasps. Each species of fig wasp lives in an obligate symbiosis with a species of fig tree: the fig provides the nutrients and home for the developing wasps and the latter pollinate the fig trees. Although males of these wasps are flightless and compete among themselves for matings within a fig, they are never heavily armed, nor are they seen to fight. The reason for this can be found in their breeding system: each female crawls into one fig and lays all her eggs there; although more than one female sometimes lays in a single fig, the offspring preferentially mate with their siblings. The result is high degrees of relatedness between the wasps, a fact that is confirmed by the strongly female-biased sex ratios produced by these wasps. (Such sex ratios are known to correlate in other species with mating between sibs: pp. 277–278.) High relatedness within each fig means that a male will value another male's reproductive success almost as much as his own and will place a similar value on his sister's RS. Both effects should inhibit lethal aggression: each male will not wish to see his sister unmated and may even value her occasional outbreeding (for the benefits it will bring her in genetic novelty and variability among her offspring).

A series of wasp species has parasitized the fig wasp–fig symbiosis, so that a single fig often houses several species simultaneously. In these

Table 9-1 Average Sizes of Males Adopting Alternative Strategies in Frogs

Species	Mean size of males (mm) *	
	Strategy 1	*Strategy 2*
Bufo bufo	Fight	Search
	65.8	61.9
Rana temporaria	Fight	Search
	67.9	62.9
B. calamita	Caller	Satellite
	69.6	63.4
Hyla cinerea	Caller	Satellite
	53.1	47.2
H. crucifer	Caller	Satellite
	45.1	43.0
H. regilla	Caller	Satellite
	44.2	43.9
H. versicolor	Caller	Satellite
	46.5	46.2
R. catesbeiana	Territorial	Satellite
	139.9	112.8

Source: Arak 1983.

* All differences are significant except that for *Hyla cinerea*.

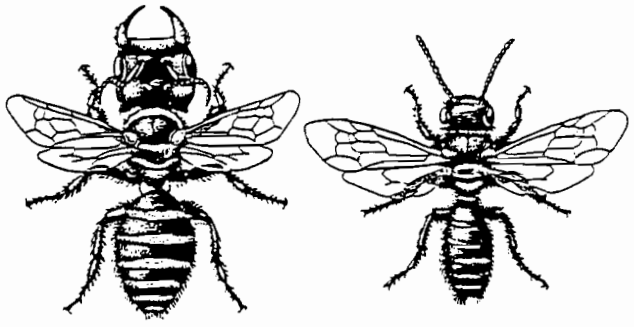

Figure 9-20

Male dimorphism in a bee. In this Australian species of *Lasioglossum*, males come in two forms: a large form, with huge head and mandibles, and incapable of flight, and a smaller, dispersing form. Presumably the armed form fights for access to females emerging from the communal nest from which he emerged. (*From* Houston 1970)

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species each female stays outside the fig and lays a few of her eggs in the fig by piercing it with a long ovipositor. Because several females commonly lay in each fig, the resulting males will often be competing with unrelated males for access to unrelated females. An enclosed space with large numbers of females waiting to be fertilized is conducive to a very severe form of male combat: a single male can monopolize many females not merely by chasing off other males (which is impossible) but by murdering them. In one species, in which all males are wingless and well armed, male mortality within each fig is high but uneven: large males are most likely to survive and medium-sized males may do the worst of all, suggesting selection for two morphs. The mixture of attack and caution that characterizes these males has been captured by William Hamilton as follows:

> A male's fighting movements could be summarized thus: touch, freeze, approach slowly, strike, and recoil. Their fighting looks at once vicious and cautious—cowardly would be the word except that, on reflection, this seems unfair in a situation that can only be likened in human terms to a darkened room full of jostling people among whom, or else lurking in cupboards and recesses which open on all sides, are a dozen or so maniacal homicides armed with knives. One bite is easily lethal. One large *Idarnes* male is capable of biting another in half, but usually a lethal bite is quite a small puncture in the body. Paralysis follows a small injury so regularly and quickly as to suggest use of venom. . . . If no serious injury results from the first or second reciprocal attempts to bite, one of the males, injured perhaps by loss of a tarsus or in some way sensing himself outmatched, retreats and tries to hide. Usually he finds an empty gall into which he plunges, turns, and comes to rest with mandibles agape at the gall's opening. From this position he can bite at the legs of the victor or another passing male with much less danger. Such an inactive male only ventures out again when long undisturbed and then very cautiously.

More surprising than the evolution of wingless males, which may or may not fight, is their coexistence in some species with winged males. These winged males avoid females within their fig but disperse to breed in other figs. As long as some figs—through chance—contain no males, there will always be opportunities for mating outside one's fig, and so the dispersing form should flourish when rare. Likewise—as long as females within one's fig can be mated as they first emerge—the wingless form will do well when uncommon. We thus expect the two forms to coexist in nature at some intermediate frequency. Since the winged form does not mate in its home fig and probably mates with very few females in figs containing at least one wingless male, the expected reproductive success of winged males should be in direct proportion to the proportion of females that develop in figs without any wingless males. By measuring this proportion in ten species of Brazilian fig wasps, William Hamilton showed that the fraction of males that are winged is about the same as the fraction of females that are not exposed to wingless males (Figure 9-21). This correspondence suggests that the alternative forms are giving about equal average payoffs, as required for long-term stability. Incidentally, this kind of explanation—in which the relative frequency of two forms of males is predicted by the relative frequency of the two kinds of females with whom they mate—will reappear when we come to explain the relative frequency with which the two sexes are produced (see Chapter 11). In the case of the fig wasps the underlying variable seems to be the number of young that habitually emerge within a fig. Where this number is low, males are winged; where it is high, males are wingless. Both forms occur at intermediate densities, winged forms being more common at lower densities (where more figs will contain females without wingless males).

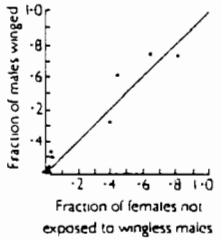

Figure 9-21

Fraction of males that are winged as a function of fraction of females that are not exposed to wingless males. Values are plotted for ten species of Brazilian fig wasps. Note the nearly 1 to 1 correspondence. (*From* Hamilton 1979)

Incidentally, competitive dimorphisms are by no means absent in females. In some species, female fig wasps can be divided into separate categories based on the length of their ovipositors, and different females within a single butterfly species may mimic in appearance members of several very different species. Circumstantial evidence suggests that the evolution of similar mimetic polymorphisms in males has often been countered by female choice for the ancestral form. More important than these polymorphisms is a dimorphism in female reproductive mode. In some species, sexual and asexual females coexist in the population; in others, females are sexual or asexual depending on conditions. But as we shall see, the payoffs from these two options are very different, so that their stable coexistence has generated something like a crisis for evolutionary theory (Chapter 13).

Sexual Dimorphism in Size and Male Fighting in Species Lacking Male Parental Investment

In species lacking male parental investment, there is tremendous variation in sexual dimorphism. Let us consider only closely related animals. In seals, sexual dimorphism in size ranges from species such as the northern elephant seal, in which adult males are at least three to seven times as heavy as adult females (depending on whether the latter are weighed just prior to giving birth or after weaning) to species such as Weddell's seal *Leptonychotes weddelli*, in which adult females are larger than males. Similar variation in male size and in armature is found in deer, although there is no underlying variation in relative parental investment. In both groups (seals and deer), male parental investment is negligible, consisting only of sperm cells. Similarly, in closely related groups of birds, such as the grouse family, sexual dimorphism in plumage may vary from negligible to considerable, while most of the species show little or no male parental investment. How

do we explain sexual dimorphism in species lacking male parental investment?

Two factors suggest themselves as important in explaining sexual dimorphism in species lacking male parental investment: first is the degree of variation in male RS and second is the particular set of conditions with which this variation is associated. Where variation in male RS is large, we expect male characters to be accentuated. Where this variation is associated with a particular trait, we expect this trait to be accentuated. Two critical factors affecting male reproductive success will be male–male competition and female choice. For male–male competition, we wish to know the distribution in space and time of breeding females; for female choice we wish to know to what degree females do choose and what they prefer (Chapter 14). In this section we will take one variable—sexual dimorphism in size—and see to what degree we can explain its distribution as a function of patterns of male–male competition. We shall assume for the moment that females are so many passive observers in this game and that their distribution in space and time is the key factor determining the form of male–male competition.

We know that in many—though not all—animal species, larger size gives an advantage in aggressive encounters. Thus, we expect to find an association between male–male aggression and enlarged male size. In snake species, males are usually the smaller sex, but in species in which males are known to fight with each other over access to females, the males are more likely to be larger. Where males fight over many females, instead of few, we expect larger male size to be associated with disproportionate gains in reproductive success: male size, relative to female, should be accentuated. Evidence from three different groups of mammals—seals, ungulates, and primates—has now been reviewed, and in all of these there is a strong, positive relationship between the number of females observed in male harems (that is, groups of breeding females defended exclusively by a male) and sexual dimorphism in body size (Figure 9-22).

The importance of female distribution in space at the time of breeding is suggested by the seals. Where females breed on land, they often form dense aggregations, probably for mutual protection, thus greatly accentuating male–male combat; males are especially large. When females breed on ice, they often do so alone or in small groups, and thus male combat will concern a dispersed resource and should be substantially reduced; size dimorphism may even be reversed. In addition, females tend to be more highly synchronized when breeding on ice, making male monopoly even more difficult.

There are other factors operating besides degree of harem polygyny. In the primates (monkeys, apes, and their relatives), degree of harem polygyny predicts some of the variation in size dimorphism, but

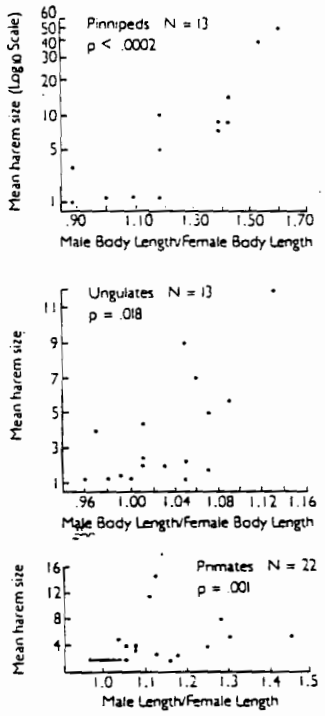

Figure 9-22

Harem size as a function of sexual dimorphism in body size in various groups of mammals. Top: pinnipeds (seals). Middle: ungulates (deer and antelope). Bottom: primates (monkeys and apes). Each point represents a species. For seals and primates harem size refers to the average number of breeding females per breeding male. For ungulates and the elephant seal the mean number of copulations per breeding male was used as the estimate of harem size. (*From* Alexander et al. 1981)

two other factors have strong effects: terrestrial species are more dimorphic than arboreal species and large ones are more dimorphic than small species. Neither of these effects is well understood. For example, male–male aggression may be more dangerous in trees than on the ground, or large size may make feeding in trees more difficult (reduced access to terminal buds). The association with body size has attracted a swarm of explanations, but none is very satisfactory.

Whatever the explanation for the association between body weight and sexual dimorphism, we know it is very general; for instance, smaller species of fig wasps and of stag beetles show reduced dimorphism. Notice in Figure 9-23 the enormous variation in sexual dimorphism in stag beetles, a result almost entirely of variation in the males. Presumably, sexual selection is acting with different intensity and in different directions in different species, but of the underlying causes we know little. Chief among our deficiencies is our ignorance of the factors controlling variation in *female* reproductive success.

Evidence from frogs suggests that the *time* distribution of breeding females may affect sexual dimorphism in size. This is because length of breeding season is associated with size dimorphism. Only frogs with a growing season of intermediate length show males larger than females—short seasons and especially long seasons are associated with larger females. This is explained by two opposing selection pressures: in explosive breeders too many females are simultaneously available for large males to mate disproportionately, while in species with long growing seasons the energetic costs of male–male competition are so severe that small size is preferable. Male frogs are known to feed less in the breeding season than females, to have smaller fat reserves, and, in one species, to lose as much as 30% of body weight during the breeding season. In *Physalaemus pustulosis*, calling males have significantly higher oxygen consumption than non-calling males. But note: this explanation fails to describe the way in which selection acts on *female* size and, we do not know how variation in female reproductive success is associated with variation in male characteristics.

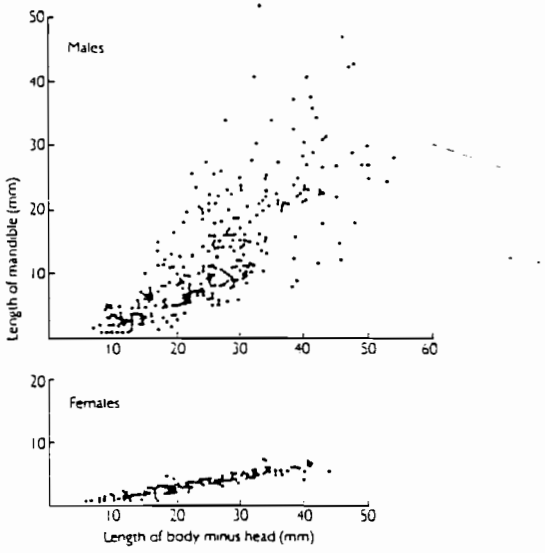

Figure 9-23

Sexual dimorphism in stag beetles. The length of an individual's mandible (in millimeters) is plotted as a function of length of body (in millimeters) minus the head for males and females of almost 400 species of stag beetles. Note that in males mandible length increases disproportionately with body size. Notice also the tremendous variability across males of different species, as compared to females. (*From* Otte and Stayman 1979)

A model for the way in which sexual selection acts differently on male and female size is provided by the Jamaican green lizard *Anolis garmani*. Adult male weight is 2.25 times as much as adult female weight, and the males achieve their greater size through faster growth rates (Figures 9-24 and 25). Large size increases survival in both sexes about equally, but in males size has a large positive effect on the number of copulations achieved per unit time, while in females it has a weak positive effect on the number of eggs laid per unit time (Figure 9-26). This effect on males apparently occurs because females distribute themselves in territories within trees and large males are able to

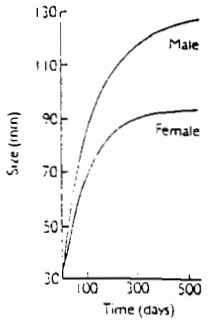

Figure 9-24

Sexual dimorphism in growth rate. Male *Anolis garmani* grow faster than females, at all sizes. Both sexes reach maturity at about the same age. (*From* Trivers 1976)

Figure 9-25

A conspicuous copulation in a dimorphic lizard. Male and female *Anolis garmani* copulate face down on the trunk of a tree, about a meter from the ground. The lizards are bright green—a color difficult to see in the foliage but easy to spot against the trunk. This male is probably about four times as heavy as the female with whom he is copulating. Copulations may last for 25 minutes. (Photo: Joseph Long)

defend a large territory (a tree or several trees) containing many adult females. There is no evidence that females prefer the larger of two males (interlopers that succeed in copulating are about the same size as territory holders), although females choose conspicuous perches on which to advertise sexual readiness and this presumably reflects a preference for the male able to copulate uninterrupted in public. In any case, sexual selection puts an enormous premium on high growth rates in males. These, in turn, show consistent differences: males who grow fast when small are likely to grow fast when large (Figure 9-27). In short, selection on males seems strongly to favor genes associated with rapid and efficient accrual of resources.

If aggressive male conflict is generating large male size in *Anolis garmani*, then we expect a reduction in the importance of male–male

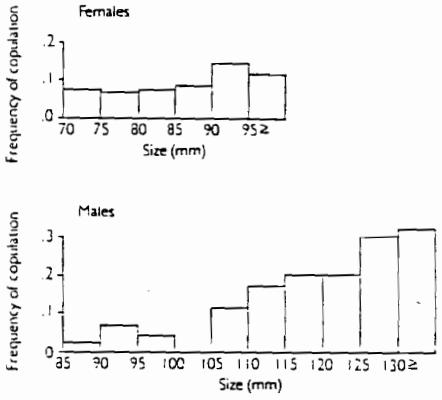

Figure 9-26

Effect of size on reproductive success of females and males, in a lizard. This graph shows the frequency with which females (top) or males (bottom) of *Anolis garmani* were seen to copulate as a function of body length (in millimeters) excluding the tail. Females are believed to copulate once per egg laid, so that frequency of copulation measures reproductive success in both sexes. The positive relationship between male size and reproductive success is significantly stronger than that relationship in females. Notice that intermediate-sized males (100–104 mm) copulate significantly less often than expected for their size, apparently because they are then being forced out of the territories of large males. Thus, we can see selection for a size-dependent change in male strategy. Small adult males may even accept an occasional homosexual copulation to remain in a large male's territory; two such copulations were observed. (*From* Trivers 1976)

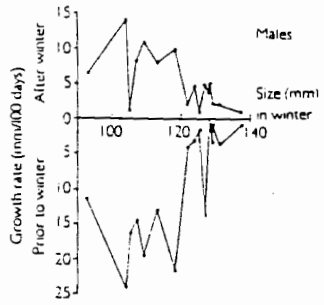

Figure 9-27

Growth rates are positively correlated throughout a male lizard's life. Shown are the growth rates (millimeters per 100 days) before and after winter of male *Anolis garmani* plotted as a function of size in winter (body length in millimeters minus tail). Note that the two lines look like mirror images: high growth rates prior to winter correlate with high growth rates afterwards. (*From* Trivers 1976)

combat to be associated with a reduction in size dimorphism. An instructive case is the closely related white-croaking lizard *Anolis valencienni*, among which adult males are only 1.8 times as heavy as adult females, probably because male reproductive success is less strongly influenced by size than in *garmani* (Figures 9-28 and 9-29). This may result from an underlying difference in the way in which females distribute themselves in the two species. In *garmani*, females are found in more or less non-overlapping feeding territories—maintained by aggression—while in *valencienni*, female home ranges overlap widely and females show no hostility toward each other. Two components of sexual selection change. Female choice probably becomes more important, and the ability of males to gain exclusive access to many breeding females is diminished. In fact, female *valencienni* often mate with dif-

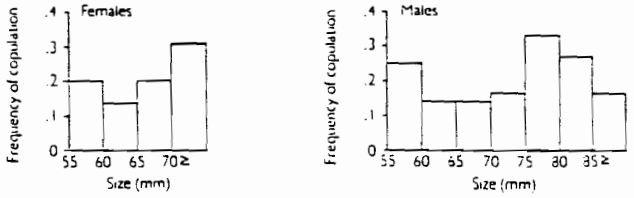

Figure 9-28

Frequency of copulation as a function of body size, in a lizard. The frequency with which adult males and adult females copulated is plotted as a function of body size in the lizard *Anolis valencienni*. Females may copulate several times per egg laid, so copulation frequency may not measure reproductive success in females. (*From* Hicks and Trivers 1983)

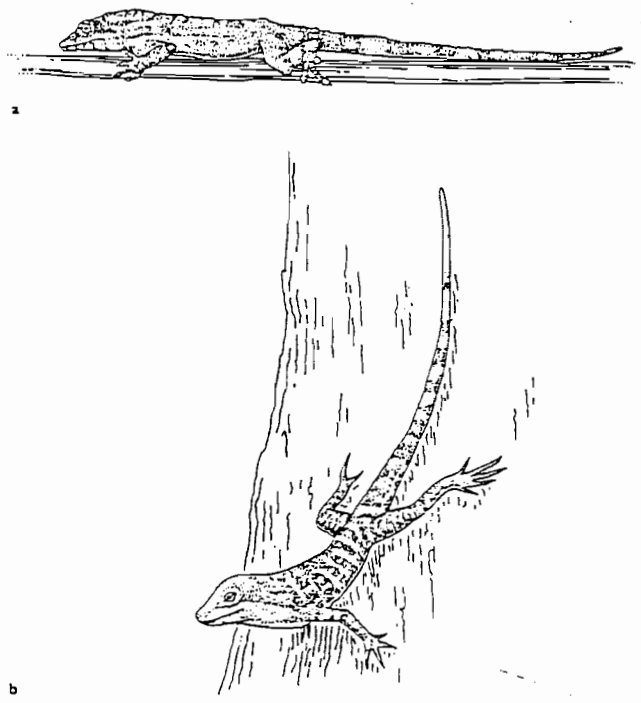

Figure 9-29

A percher and a searcher. (a) A large adult male *Anolis valencienni* is seen motionless, hugging the side of a stick. This species is unusually well camouflaged and less dimorphic in body size than either *lineatopus* or *garmani*. Members must be constantly on the move in search of cryptic, diurnally inactive insects and are, thus, more vulnerable to visually hunting predators and more strongly selected for camouflage. Perhaps the camouflage makes it harder for the lizards to spot each other, giving small males an advantage. (b) A large adult male of the Jamaican common lizard *Anolis lineatopus* perches high in his territory. From this place he will occasionally dash to catch active prey, mostly insects. He also displays at other territorial males and courts females within his territory. Unlike females, he defends a territory much larger than optimal for his feeding needs. Female home-range size is small in this species and sexual dimorphism in size relatively great (adult males weigh about 2.5 times what adult females do). (Drawn from author's photos)

ferent males on the same or successive days. Thus, lack of aggressiveness among females appears to have reduced the selection pressure for male combat.

Robin Andrews has discovered an entirely different factor underlying sexual dimorphism in body size in *Anolis* lizards. She concentrated on the difference between mainland species and island species. Individuals in mainland species (Central America) have little difficulty finding food: they feed infrequently and on large food items, and grow rapidly in nature at rates that are not increased in captivity by adding food. These species show little dimorphism in size (Figure 9-30). On islands (West Indies), *Anolis* species tend to be food limited: individuals in nature grow slowly, feed frequently on small food items, and grow faster in captivity when additional food is supplied. Yet sexual dimorphism in size is pronounced (Figure 9-31); that is, where food is difficult to find, males are especially large! This is a striking and unexpected discovery. We might think that male–male competition would tend to inflate male size in both settings, but be restrained more sharply when amount of food is limited. Instead, the reverse is found.

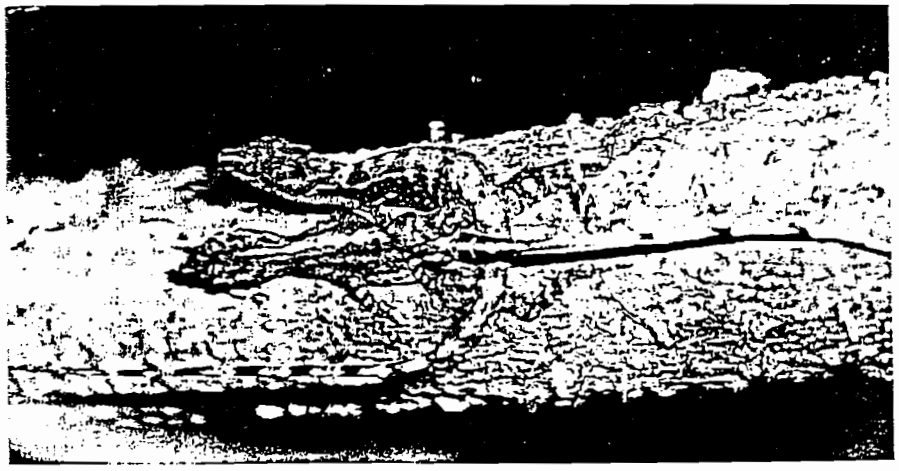

Figure 9-30

A relatively non-dimorphic mainland species. Male and female *Anolis limifrons* copulate on a branch in Panama. In this species females do not appear to be food-limited. (Photo: Robin Andrews)

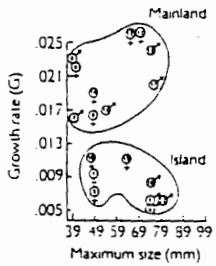

Figure 9-31

Growth rates of juvenile males and females in mainland and island species of Anolis *lizards.* Shown are the growth rate constants (G) which have been fitted to growth rate data for juvenile lizards. A higher G indicates a higher growth rate. These are plotted as a function of maximum body length (minus the tail) in millimeters. Each number refers to a particular species of *Anolis* lizard. Note that mainland species have higher juvenile growth rates but *less* sexual dimorphism in body size. (*From* Andrews 1976)

Andrews' discovery has an interesting feature when viewed from the female's standpoint. As we shall see in Chapter 13, it is useful to ask whether sexual selection elevates to breeding status genes in males that also benefit their daughters. For *Anolis* this appears to be the case. That is, where female RS is apparently strongly limited by ability to grow quickly, males grow especially fast and mate frequently at large sizes; thus their genes should give their daughters increased growth rates. Where female growth rate has a small effect on female RS, male size is not inflated. A similar argument can be applied to the difference between *A. garmani* and *A. valencienni*. Females are aggressive in the former and pacific in the latter. Other things being equal, we expect fast growth rates in female *garmani* to be more advantageous; and it is in this species that males attain especially large sizes, compared to females (see also pp. 353–358).

The correlation Andrews discovered is easily explained by reference to male–male competition. Food availability is closely associated with the density of lizards. On the mainland, lizard species are numerous, but individuals within each species are few in number: female home-range size is large and the ability of a male to sequester several females is correspondingly low. On islands the lizards are abundant, female home-range size is small, and one male may more easily monopolize several females. In turn, in territorial lizards sexual dimorphism in body size is inversely related to density (Figure 9-32). Note that this larger correlation for lizards in general retains the relationship between variation in female reproductive success and sexual dimorphism that was observed in *Anolis*. More densely crowded species will tend more often to be food limited, and aggressive interactions between females will be more frequent. Thus, where fast growth rate in females is especially favored, males attain especially large sizes.

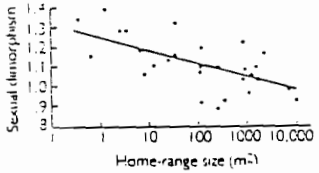

Figure 9-32

Sexual dimorphism as a function of female home range size in territorial species of lizards. Sexual dimorphism (adult male body length, minus tail, divided by adult female body length, minus tail) is plotted as a function of adult female home range size (in squared meters). A line has been fitted to the points. There is a highly significant negative correlation. (*From* Stamps 1983)

The pattern we have described in *Anolis* could have resulted from female choice—females when food limited or aggressive preferring large males, yet there is no evidence in *Anolis* that females prefer larger males, and in one dimorphic species females appear to be nearly indifferent to male size. It would be very interesting if male–male competition—without the intervention of female choice—tended to elevate to breeding status in males genes beneficial for females. Unfortunately we are usually unable to test for this possibility because while we may often know how male aggression (and thus size) relates to reproductive success, we know little or nothing about the factors controlling female RS.

Summary

The underlying variable controlling the action of sexual selection is the relative investment of the sexes in their offspring, where this is the relative amount of work or energy or risk they invest in raising offspring. The sex that invests less is expected to show greater variation in reproductive success, to compete within itself for access to members of the opposite sex, and to be subjected to more discriminating choice by the opposite sex than it itself expresses in mating. Evidence from *Drosophila* and red deer is consistent with this view.

In general, males invest little or nothing parentally in their offspring, but instead compete among themselves for access to females. This competition takes the form of aggressive combat to exclude others from breeding and searching for and courting females. Females

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