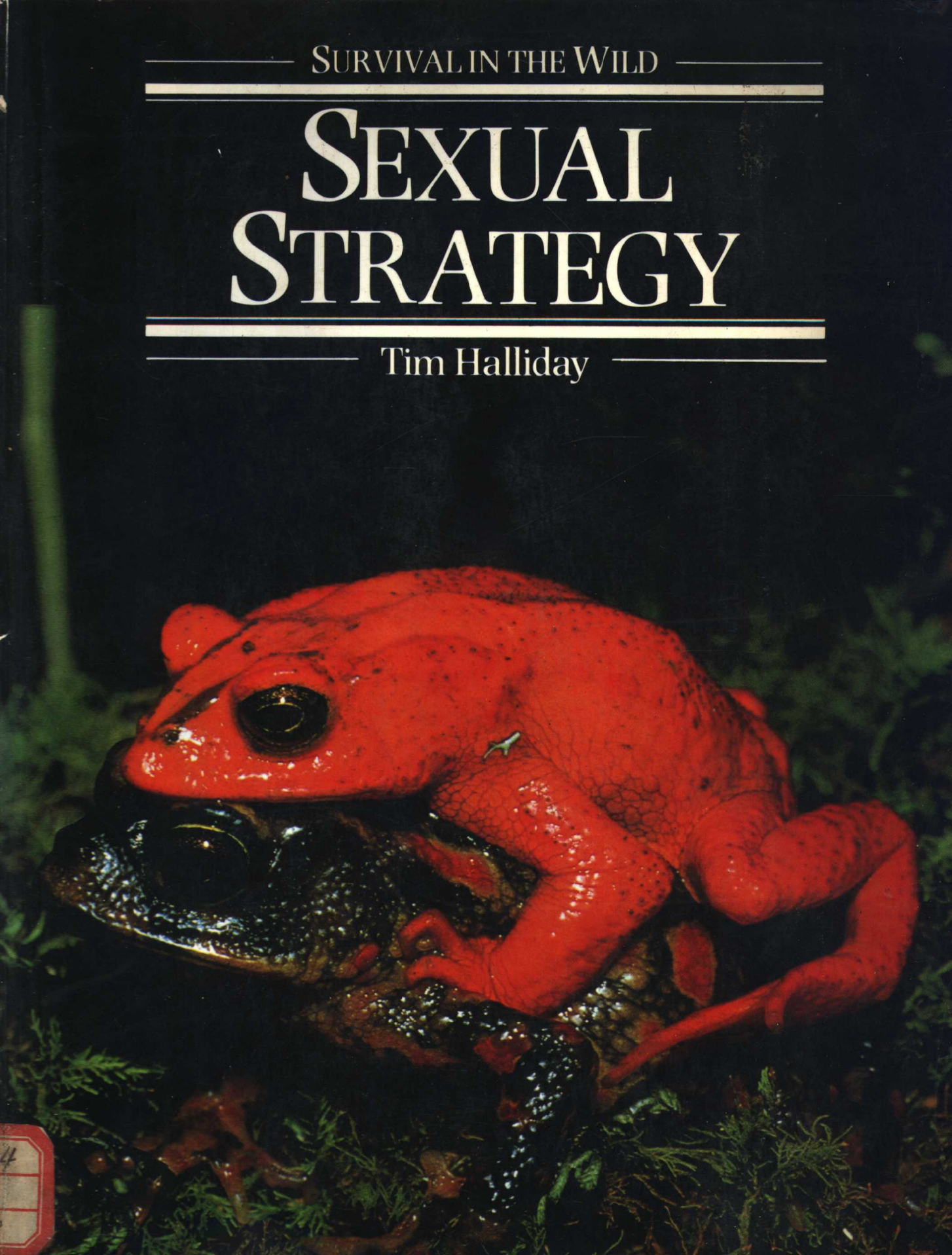
SURVIVAL IN THE WILD

# SEXUAL STRATEGY

Tim Halliday



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*Front cover.* A mating pair of golden toads *Bufo periglenes* from the cloud forest of Costa Rica. The vivid colour of the male contrasts with the darker colour of the female and is an example of extreme sexual dimorphism. *M. P. L. Fogden.*

# Contents

# Foreword

A full understanding of animal species can be acquired only after years of extensive studies in their natural environments. Only in the wild is it possible to discover the evolutionary and adaptive significance of each biological activity. It then becomes apparent that many of the forms, colours and activities of wild animals and plants are adaptive responses to the basic problems of survival: the need to eat, to avoid being eaten, and to mate and reproduce. Each species is beset with a unique set of problems depending on the type of environment in which it lives and on its structure: whether it is in a desert or in a jungle, or whether it is a frog, a tiger or a fly. Each species has evolved its own repertoire of strategies which enable it to survive. A successful individual not only survives but also reproduces to pass its genes on to the next generation. However, only those individuals best adapted to their environment survive, and they transmit the traits which have made survival possible to their offspring, an idea embodied in the phrase 'survival of the fittest'.

It is the aim of this new series *Survival in the Wild* to describe and explain the bewildering diversity of strategies displayed by the living world. Each book selects a biological activity vital to survival and describes the array of physical and behavioural adaptations which have evolved as a result of fierce competition. In an often hostile world, individuals interact with others, as food sources, or potential predators to be avoided, or mates.

The fundamental difference between the sexes, the difference between eggs and sperm, has had a profound effect on the evolution of sexual behaviour, and males and females have evolved very different and often conflicting strategies for reproduction. *Sexual Strategy* examines some of the biological principles that underly the nature of sexual behaviour in animals. The book reflects the fact that in no other aspect of their lives do animals show so much variety as they do in their sexual activities, and describes examples of sexual behaviour in many different kinds of animals. It shows that, beneath this immense variety, there is a set of basic rules that has determined the course of evolution of sexual behaviour.

Tim Halliday has spent several years studying the causal mechanisms underlying courtship behaviour in newts and mate selection in frogs and toads. He is able, therefore, to draw on personal observations and conclusions when discussing the nature of sexual behaviour in animals. In his text, he explains that reproducing is often highly competitive and that, for many creatures, it may involve jeopardizing their own survival: a male cricket who calls to attract a female may also attract a

predator that can kill him. But, as Tim Halliday shows, the risks inherent in reproduction arise not only from predators. Other members of the same species can also pose a serious threat. In many animals, there is intense hostility between members of the same sex and between males and females before, during and after mating. A male mantid may be eaten by a female even as he mates with her, and fighting between male red deer and between male elephant seals for the possession of females can lead to severe injuries. It has become necessary, therefore, to question the belief that reproduction is a cooperative venture whose purpose is the perpetuation of the species, and there are many instances where Tim Halliday does put this belief to the test.

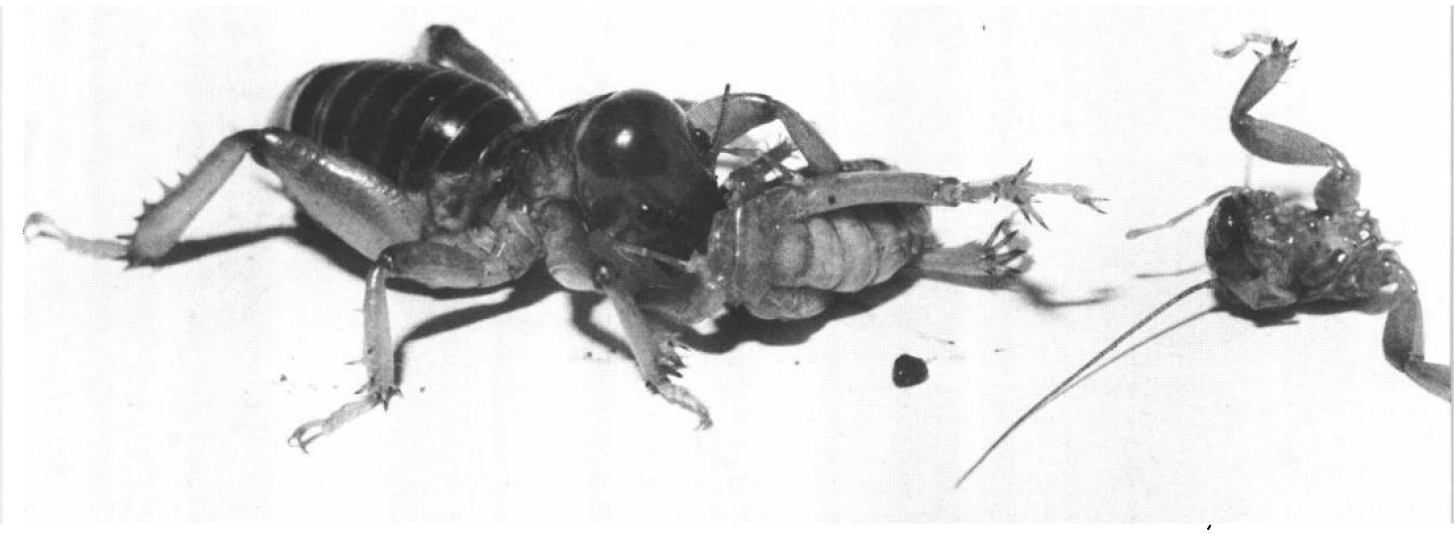
In the course of writing this book, Tim Halliday has received help from a number of people either in conversation or in their published work in books and journals. He would like particularly to thank Carl Gerhardt and Steve Arnold for information imparted during useful discussions, Beverley Dugan, Ron Rutowski, Peter Stacey and Diane Williams for allowing him to quote unpublished work, and Nick Davies and Carolyn Halliday for reading the manuscript and for making valuable suggestions.

# 1 Introduction

This book is about the behaviour that precedes, accompanies and follows the act of mating in animals and man. The word 'strategy' implies that such behaviour is part of a tactical plan towards some specific goal. What is that goal? For a long time biologists, naturalists and the public at large have been content with the explanation that when animals mate their purpose is to 'perpetuate the species'. If this was really their aim, males and females would, by mating, be acting cooperatively towards a common goal. However, the most cursory examination of the sexual behaviour of animals reveals countless examples in which males and females treat each other with great hostility and are clearly not behaving cooperatively. Female spiders and mantids often eat their mates; male sticklebacks are frequently very aggressive towards females; male lions and langur monkeys kill the young of the female members of their social groups before they mate with them. Such apparently antisocial patterns of behaviour hardly seem designed to 'perpetuate the species' and we must seek other kinds of explanation for their evolution. This book examines many examples of the sexual behaviour of animals and seeks to explain their evolution in terms of certain basic biological principles.

The word 'strategy' also has other connotations. To label a sequence of behaviour as a strategy might suggest that it is planned and controlled by deliberate, rational thought, as it would in a human context. When we use the word in relation to the behaviour of animals we are not implying that they use the same kind of thought processes that humans do. Strategy is a convenient label for animal behaviour patterns which are directed towards a clear goal, such as obtaining a mate. It carries no implications about the internal mechanisms that control the behaviour of animals.

Before we can understand the function of sexual behaviour we must examine the purpose of sex itself. Sexual reproduction, in which single cells from two different individuals combine to form new individuals, is but one of a number of mechanisms by which animals reproduce themselves, but it is by far the most widespread. The evolution of sex is still a problem that puzzles biologists and it is discussed in the first chapter of this book. Another basic factor that will be examined is the evolution of gender; that is, the division of individuals into two distinct sexes, males who produce vast numbers of sperms and females who make relatively very few eggs. Differences in gender between individuals lead to differences in behaviour, most importantly in the form of parental care shown by males and females.



Harmony and conflict between mates. The Magellan penguins of both sexes incubate their eggs in a communal site (left). A male Jerusalem cricket (above) has mated with a female but has failed to make his escape and is being devoured by her.

Gender and parental behaviour are two basic ingredients in the evolutionary recipe that determines the form of sexual behaviour. To them we must add a third ingredient, the nature of the environment. The form that mating and its associated behaviour takes is constrained by the many other vital activities that animals must undertake in order that they and their offspring may survive. They must find food, often in competition with other members of their species, and they must avoid death at the hands of predators. Each species is beset by a unique set of such problems. For example, male newts, who court females at the bottom of ponds, have to do so while holding their breath between ascents to the surface to take in air. Many aspects of their complex mating behaviour appear to be adaptations to this basic constraint on their sexual activity.

If the perpetuation of the species is not the goal of sexual strategy, what is? The modern theory of biological evolution sees natural selection as a process in which those individuals who leave the greatest numbers of descendants in subsequent generations pass on their heritable characteristics at the expense of less fecund individuals. The 'aim' of sexual strategy is thus to maximize the number of an individual's descendents. While males and females, as individuals, may share this goal, their sexual strategies for achieving it will be different because of the many differences between them associated with gender. Females typic-

ally produce a limited number of eggs and invest a great deal of energy and resources in the production, nourishment and care of each potential offspring. Males, in contrast, produce enormous numbers of sperms and tend to be somewhat profligate with them, seeking to mate with as many females as possible rather than directing a great deal of parental care towards offspring. There are, of course, many exceptions to this pattern of sexual behaviour and some of these will be explored in this book.

In writing a book of this kind one is able to draw upon an enormous number and variety of examples of patterns of animal sexual behaviour and I have been forced to be highly selective. I have tended to use a lot of examples from amphibians, partly because these are animals with which I am very familiar. However, I feel that the inclusion of many amphibians in this book is justified on the grounds that they often provide very good illustrations of particular biological points and also because they have recently become the object of much exciting research throughout the world.

In seeking to find basic biological rules underlying the reproductive behaviour of animals, the question arises, to what extent are such rules applicable to man? Speculation about the evolution of human sexuality is fraught with difficulties and pitfalls, not least because man is so variable in his sexual and social behaviour, suggesting that his habits are largely the product of his culture. In a somewhat cynical view of the sexual ethics of contemporary western man Dorothy Parker wrote in 1944:

*Woman wants monogamy;*
*Man delights in novelty,*
*Love is woman's moon and sun;*
*Man has other forms of fun.*
*Woman lives but in her lord;*
*Count to ten, and man is bored.*
*With this the gist and sum of it,*
*What earthly good can come of it?*

While this poem expresses sentiments offensive to modern attitudes to the sexual and social role of men and women, it most elegantly expresses the essential conflict of interests that exists between the sexes of the vast majority of species. To what extent this conflict is present in man and, if it is, whether it is the product of biological evolution or of our culture, are questions which will be discussed in the final chapter of this book.

# 2 Sex



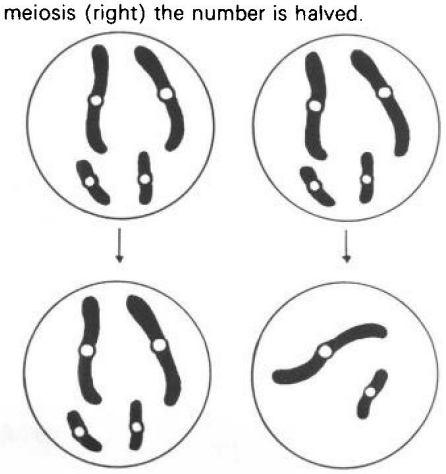
It is characteristic of living organisms, whether they are bacteria, plants or animals, that during their lives they grow, reproduce and die. During an individual's lifetime, reproduction may occur once, several times or more or less continually, depending on the species. There are many ways of reproducing and this book is about only one method, sex.

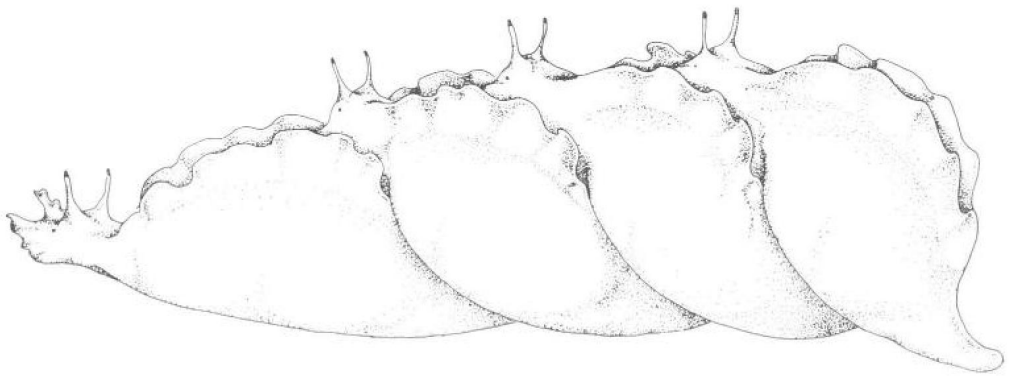
**The mechanisms of reproduction**

There are two essential features of sex that differentiate it from other forms of reproduction. First, individuals produce sex cells called gametes by a special sort of cell division called meiosis. Most cells in the body contain pairs of chromosomes; in meiosis these separate. As a result, each gamete contains only half the number of chromosomes of the other cells in the body, and therefore only half the genetic make-up of its parent. Second, gametes from two individuals fuse, producing a new individual whose genetic make-up is made up half and half from each parent. In the great majority of sexually reproducing species there are two types of gamete, female and male. Female gametes are relatively large and immobile, are produced in small numbers and are called ova or eggs. Male gametes are very small and mobile, are produced in vast numbers and are called sperms.

In man, and in a great many species, individuals are specialized to produce either eggs or sperms and are likewise referred to as female or male. However, a number of species of animals and, to a greater extent, plants are capable of producing both types of gamete within the same individual. Among animals, individuals that can produce both male and female gametes are called hermaphrodites. In some species individuals are hermaphrodites throughout their lives, in others they begin life as one sex and change to the other when they reach a particular age. In the Indo-Pacific reef-living cleaner fish *Labroides dimidiatus* individuals gather in groups of which all but one are female; the male is always the largest fish in the group. If the male is removed from a group the largest of

The two types of cell division. In mitosis (left) the number of chromosomes remains the same but in meiosis (right) the number is halved.





Four sea-slugs, *Aplysia brasiliana*, in a copulatory line. In this mating formation the animal at the back is usually male, the one at the front female, and the animals in between hermaphrodites. Each gives sperm to the animal in front.

the females quickly changes her gender and becomes a male. The reverse process occurs in another marine fish of the Indian Ocean, the anemone fish *Amphiprion akallopisos*, which lives in groups of which all individuals are male except for the largest who is a female, who was previously a male. In sea-slugs, the situation is even more complicated. In one North American species, *Aplysia brasiliana*, individuals are capable of being male, female or hermaphrodite. Mating may involve only two animals, either one male and one female or two hermaphrodites, or anything up to 20 animals in a mass containing any combination of males, females and hermaphrodites.

It is important to remember that sex, with all its variations, is only one method of reproduction. Many animals and plants show forms of reproduction that involve neither the production of gametes nor the involvement of two individuals. Such forms of reproduction are called asexual and, as with sexual reproduction, they show considerable variety. The simplest form of asexual reproduction, shown by many protozoan organisms, is to divide into two. A number of animals, like *Hydra*, can reproduce by growing buds which eventually detach themselves as fully formed individuals. Many species produce eggs, as if they were sexual species, except that these develop into adults without being fertilized. This condition is called parthenogenesis, which means 'virgin birth'. There are two kinds of parthenogenesis, differing in the form of cell division that produces the eggs. In aphids, for example, eggs are produced by the normal method of cell division called mitosis, in which there is no halving of the chromosome number. Each egg, therefore, contains a full and unchanged set of parental genes. In bees, as in other sexual species, the eggs are produced by meiosis. However, unlike the eggs of typical sexual species, they are capable of developing into bees without being fertilized. These unfertilized eggs become males or drones, while the fertilized bee eggs become females, *ie* workers or queens.

This picture of the variety of methods of reproduction is made even more complicated by the existence of many species that can reproduce both sexually and

asexually. Many plants reproduce asexually by sending out suckers or runners and sexually by flowering. *Hydra* is capable of reproducing, not only by budding, but also by producing eggs and sperms. Another variation is shown by hermaphrodite animals or plants that fertilize themselves. Inasmuch as such organisms produce gametes by meiosis they are behaving like sexual species, but in fertilizing themselves they are like asexual species in that there is no combining of genes from different individuals. Many plants are self-fertilizing hermaphrodites, but this mode of reproduction is very rare among animals.

What are we to make of this variety of methods of reproduction? Can we say that one method is better or more efficient than another? This is unlikely because if one mode of reproduction were better than the others we would expect it to have replaced all these others during evolution. The answer seems to be that the variety of reproductive methods is a reflection of the

**Below** Changing sex. Two stacks of slipper limpets *Crepidula fornicata* attached to the same stone. (three on the left and six on the right). The older, larger individuals at the bottom are females; the younger, smaller individuals at the top of the stacks are males.

variety of environments in which animals and plants live. Just as different species of animals vary in their methods of obtaining food or avoiding being eaten by a predator, according to the nature of these features of their environment, so it seems that their methods of reproduction are adapted to environmental factors. There are two basic modes of reproduction, sexual and asexual. The question we must now answer is, under what environmental conditions is each of these methods the more effective? To answer this question we must look more closely at the products of sexual and asexual reproduction. These two processes differ not only in terms of the mechanisms they involve, but also, and most importantly, in the nature of the offspring that they produce.

The end results of any reproductive process is the formation of new individuals. Asexual reproduction produces individuals that are exact replicas of their parents since they have inherited their parent's genes in an unaltered form. By contrast, sexual reproduction involves re-shuffling of each parent's genes during the formation of gametes, followed by the fusion of gametes from different parents. As a result every individual offspring is genetically unique, differing both from its parents and from its brothers and sisters. An essential feature of the theory of natural selection is that during reproduction individuals produce many more offspring than can possibly survive. The resulting struggle for survival can be compared to a lottery, in which each individual offspring represents a ticket whose number is its genetic make-up. In asexual reproduction all the offspring of any one parent carry the same number, that of their parent. In sexual reproduction every offspring carries a different number. Which form of reproduction is more likely to be successful in life's lottery depends on the predictability of the environment.

Any individual who has survived long enough to reach reproductive age must carry a combination of genes that makes it a good survivor, since it has survived while most of its fellows of a similar age have perished. If it lives in a stable environment it would seem that the strategy that would best insure the survival of its offspring is to give them the same good, proven combination of genes. This can be achieved by asexual reproduction. To reproduce sexually would create offspring with combinations of genes that might or might not be suited to the environment. Most will be unsuited and will perish. However, if the environment is unstable, the conditions in which reproducing adults have proved themselves able to survive will not be the same conditions as those that will be faced by their offspring. Thus the survival prospects of genetically identical, asexually produced offspring are likely to be small. By contrast, reproducing sexually creates varied offspring, of which at least a few are likely to be well-suited to the uncertain environment in which they will have to struggle to survive.

The argument that sexual and asexual reproduction are adaptations, respectively, to unstable and stable environments, is supported by many of those species that are capable of both. *Hydra* and *Daphnia* are both small inhabitants of freshwater ponds and pools that are liable to dry up during the course of a year. While the pond is full, and conditions are good, both animals reproduce asexually, *Hydra* by budding and *Daphnia* by parthenogenesis. However, when the pond begins to shrink, conditions deteriorate and both creatures switch to sexual reproduction, producing fertilized eggs. They are contained within drought-resistant coverings so that they are able to survive until the environment once again becomes favourable. A single *Hydra* can produce both eggs and sperm but in *Daphnia* the switch to sexual reproduction involves the production of some exclusively male individuals.

The tiny protected eggs that are produced during sexual reproduction in