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VERTEBRATE REPRODUCTIVE CYCLES

Vertebrate Reproductive Cycles

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PREFACE

IT is the purpose of this book to present a brief but up-to-date account of our knowledge of the sexual physiology of the vertebrates. During the past generation a whole library has been written around this subject, and therefore in such small space it is impossible to do more than introduce the main facts and theories. For those who would read further, references are made throughout the text to the more important reviews and original papers, and these are listed at the end of the book. Indeed, it is hoped that this introduction to the subject may even stimulate a few of its readers to venture further and to make their own observations in this field. Particularly is it to be hoped that more zoologists will pay attention to the problems of vertebrate reproduction for, while veterinary and medical men are studying the patterns of mammalian reproduction in considerable detail, the richest results will undoubtedly come to those who can take the broader view and think in terms of the evolution of physiological mechanisms.

This book was begun in the University of Sheffield and completed in the University of Utrecht. It is a great pleasure to acknowledge the encouragement and friendly criticism received in Sheffield from Professor L. E. S. Eastham and Dr. E. T. B. Francis, and in Utrecht from Professor G. J. van Oordt and his various colleagues. Since many of the fields of research here reviewed have been investigated in Professor van Oordt's department, it is particularly fortunate that opportunity has been found to make a protracted visit to Utrecht. This has been made possible by grants from the Royal Society of London and the University of Sheffield, and also by the extraordinary generosity and hospitality of the Dutch

zoologists. To all these my most grateful thanks are offered.

It is also a pleasant duty to recall the debts due to Professor E. A. Spaul, who has criticized the manuscript, to Mr. T. G. Onions, who has given invaluable assistance throughout, to Dr. S. A. Peyton, the Librarian of the University of Sheffield, who worked hard to obtain copies of the more obscure references, and to Dr. L. D. Brougersma of the Rijksmuseum in Leiden, who helped with the scientific names listed at the end of the book.

Finally, it is especially pleasant to have this opportunity to thank my wife for her constant help and encouragement during the whole enterprise.

W. S. BULLOUGH

UTRECHT
September, 1949

PREFACE TO SECOND EDITION

DURING the ten years that have elapsed since the first printing of this book, research on the subject of vertebrate sexual cycles has been active, especially in the United States. An opportunity has now been taken to revise the original text and to add an appendix that will serve as an introduction to the more modern literature.

In part, this revision is the outcome of a recent Symposium on Photoperiodism held under the auspices of the American Association for the Advancement of Science and the National Research Council and financed by the National Science Foundation of the United States. It was a privilege to be present on that occasion and several of the new ideas now presented were clarified in the debates that then took place.

W. S. BULLOUGH

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CHAPTER I

INTRODUCTION TO CYCLES

ONE of the most arresting and widely known of biological phenomena is the cyclic breeding habit shown by so many animals and plants. Indeed, it is evident that the lives of such organisms are compounded of greater and lesser cycles of growth and reproduction. In the first place there is the major cycle of the life span itself, which passes from fertilization to embryonic growth, through immaturity to maturity, and so to senescence. Sometimes this is the only cycle in evidence, as when an individual breeds only once and quickly dies. This is rare among the vertebrates, but a well-known example is the fresh-water eel which ends its life when it migrates across the Atlantic to spawn in the Sargasso Sea.

In most vertebrates the great cycle of life contains within it a series of lesser cycles, the most obvious of which is the seasonal reproductive cycle. In temperate regions this usually has a duration of one year, and it is common for the major breeding season to be in spring and early summer. However, many species breed at other times of the year, the sheep, for instance, doing so in autumn and the cod in winter. Sometimes this yearly breeding habit is only vaguely defined as when the common dogfish, which spawns most actively in spring, nevertheless lays some eggs in every month of the year.[140] Commonly, however, the timing of a breeding season is precise so that, for instance, unless the weather be very unseasonal, one can say that the British starling will lay its first eggs during the last two weeks of April.[54]

For still greater precision in timing it is necessary to turn to the invertebrates where the classical example is provided by the polychaete *Eunice viridis*, also known as the palolo worm, which lives in the seas around Samoa.[139] This worm spends the whole year hidden in crevices in the rocks, but in each of the months of October and November it spawns at dawn on the day before and the day on which the moon enters its last quarter. So striking is this act of spawning, and so precise its timing, that the natives of Fiji have included it in their calendar.

These yearly breeding cycles affect both sexes equally, although there may be slight differences in timing as when in birds the male commonly attains sexual maturity some weeks before the female. During a breeding season a male is usually able to mate at any time, but in a female still lesser cycles are sometimes evident and the urge to mate is periodic. These cycles appear to be rare among the fishes, amphibians and reptiles. As regards the birds, reference may be made to the fact that a female usually lays only one egg a day and often produces two or more clutches at intervals of about six weeks. However, the phenomenon of the lesser cycle is most clearly seen in non-pregnant female mammals, which, during a breeding season, commonly come into heat at regular intervals. Thus an unmated female mouse experiences a period of heat, when she is ready to mate and to become pregnant, about once every five days. Such a lesser cycle is called an oestrous cycle, the period of heat being known as oestrus, and it is a common phenomenon in both marsupial and eutherian mammals. In a sheep the cycle has a duration of about 16 days, and in the pig, cow, and horse about 21 days.[8] In the case of the great apes it is perhaps not strictly correct to speak of heat in the usual sense, but nevertheless oestrous cycles do occur with a duration of about a month, whence they are also commonly called menstrual cycles.

In this book the seasonal and oestrous reproductive cycles of the vertebrates are examined, and an attempt is made to analyse those factors which are now thought to determine, control, or affect them. However, before proceeding further, it is necessary to make two definitions. The first refers to the term 'breeding season', which is so variously used throughout the literature. Here it is employed in a restricted sense to indicate that period of the year when mating behaviour is evident, and when copulation results in fertilization. It is not used to indicate seasons of incubation, of pregnancy, or of lactation.

Secondly, in view of the looseness with which these terms are commonly used, it is necessary to state that the seasons of the year are here referred to in a precise sense.[9] In northern temperate regions, spring is considered to extend from 21 March to 20 June, summer from 21 June to 20 September, autumn from 21 September to 20 December, and winter from 21 December to 20 March. In the south temperate regions, the timing of spring and autumn, like that of summer and winter, is reversed, while, of course, in the tropics such seasons cannot be recognized.

For definitions of other words used in this book reference may be made to the glossary on p. 105.

CHAPTER II

CYCLES OF REPRODUCTION

I. INTRODUCTION

BEFORE an animal can breed it must first grow to maturity, and between species there is the widest variation in the time taken for this to happen. Among fishes it seems probable that the majority spawn for the first time when they are one or two years old, but the extremes extend from only two or three months in some small tropical species to more than 20 years. Common food fishes like the cod and haddock are mature at about 4 years of age,[116] the hake at about 10 years,[108] and the sturgeon at from 10 to 15 years.[68] The extreme case is that of the European eel, which spawns in the western Atlantic. The young take 3 years to return to Europe where they spend a further 10 to 19 years in fresh-water.[92] So this fish has a total period of immaturity of up to 22 years, which is the longest known with certainty in any animal.

The amphibians on the other hand do not appear to live to great ages, and there is evidence that the common frog and toad spawn for the first time when they are between 2 and 4 years old. The reptiles and birds also tend to avoid extremes. Many common species breed for the first time when about 1 year old. The adder for instance does not do so until it is about 5 years old[188] and some tortoises and turtles may even approach the record of over 20 years held by the eel. Among birds the longest recorded period of immaturity seems to be about 4 years as in the golden eagle, gannet and herring gull. In mammals the range again widens, and no general statement is possible. Extremes are set by the house mouse, which may become pregnant when 6 weeks old, and the

Indian elephant which may not do so until after 15 years.[8] Man, as is well known, also takes some 12 to 15 years.

2. SEASONAL CYCLES IN TEMPERATE REGIONS

After the onset of maturity, seasonal reproductive cycles are evident in most species. These are most clearly seen in the animals living in temperate and sub-arctic regions although, as will be shown, they are also common in the tropics.

In considering these cycles, it must be stressed again that spring and summer are not the only seasons of reproduction. There is no month of the year in which some species of vertebrate does not regularly breed. Indeed, at least one species braves the polar winter for this purpose. This is the emperor penguin, which has developed the astounding habit of laying, incubating and hatching its eggs in the autumn and winter darkness of the antarctic continent in temperatures ranging from $-25°$ to $-55°$ C.[65] By the following spring the young have grown into downy chicks, and are ready to take advantage of that season for their growth to adult stature.

Nearer home, although spring breeding is an almost universal habit among the amphibians and reptiles, autumn is the breeding time of many British fishes, like the bullhead, the salmon and sea trout, and the various species of *Coregonus*. In winter other fishes spawn including the halibut, the cod and the fresh-water turbot.[116] In explanation of these differences in habit it has often been remarked that the breeding season of each species is so timed as to give the maximum advantage to the young during their early period of growth. For most animals this appears to be true, although some cases are not yet adequately explained.

Clearly, the timing of a reproductive cycle to meet the needs of a given species is something that can be achieved by the operation of natural selection. Even to-day such selection can be seen at work in the odd cases of out-of-season breeding that have been described. In the British starling many such reported cases have been reviewed,[54] and it is obvious that the eggs and young have only the slightest chances of survival so that the number of these misfits is kept at a minimum. However, if for any reason it ever became an advantage for the starling to breed in autumn or winter instead of in spring, there is material here from which a new population with new habits could be built.

Spring breeding is an almost universal habit among the birds of temperate regions. These are all rapidly growing species that can pass from a single cell to adult size and structure in the extraordinary short space of 5 or 6 weeks, although large species like ducks and geese may take some weeks longer. Clearly it is greatly to their advantage that all this violent growth and differentiation should occur at a season when food is most abundant and most succulent.

Among mammals the situation is complicated by the habit of allowing the eggs to develop in the uterus for a longer or shorter period of pregnancy. Thus it is not the act of mating but the act of birth which must be timed to take place in a season that provides optimum conditions for the survival and growth of the young. In mammals with only a short period of pregnancy, both breeding and birth may take place in the spring. Among small species this is a general rule, and is seen, for instance, in the wild rabbit, which, with a duration of pregnancy of about 30 days, produces a series of litters between midwinter and midsummer.[42] In larger mammals pregnancy is prolonged so that the breeding season becomes separated from the season of birth. This is shown by ruminants like the deer and sheep, which have an autumn breeding season, a period of pregnancy of about 150 days, and a season of birth in late winter and early spring.[8] With still longer periods of pregnancy the breeding season may move still earlier into the summer. Thus the yak in Russian Asia breeds in July and August, has a gestation period of about 260 days, and a season of birth in the following spring.[8] In the horse pregnancy lasts about 11 months and in the ass about 12 months, so that breeding in one spring is followed by the birth of the young in the next.[8] In such animals the season of mating is only separated by a few days from the season of birth.

Mention must also be made of other factors that prolong the time between mating and birth in some mammals. In bats living and hibernating in temperate regions there is a long interval between copulation and fertilization. This curious state of affairs is well-known in the British horseshoe bats of the genus *Rhinolophus*,[136] and in the little brown bat of North America.[8] Copulation occurs during September and October, and the females retain the spermatozoa in the vagina or uterus until the eggs are produced in April. Pregnancy then begins and the young are born in June or July.

Another factor which has the same effect in causing a wide separation between the times of breeding and of birth is the phenomenon of delayed implantation of the embryo. This was first described by Bischoff, more than a hundred years ago, in the case of the roe deer, which has a breeding season in July and August.[8] The fertilized eggs develop for a few days to produce the blastocyst stages, and these then lie dormant until December. During that month they become implanted into the uterine wall, and growth is rapid until the young are born in May. The same phenomenon is common among the Mustelidae (the badgers, stoats and weasels) in which fertilization usually occurs in summer, the blastocysts remained unimplanted until the following January, and the young are born in March.[104]

Similar delays appear to be rare among the lower vertebrates, and no case has been found among the birds. However, among reptiles mention may be made of the curiously long incubation period of *Sphenodon*, the tuatara lizard of New Zealand.[80] The eggs are deposited in November, in the southern spring, but the young tuataras do not emerge until the December of the following year after an interval of 13 months. Among amphibians it is also known that salamanders commonly practise a form of delayed fertilization similar to that of bats. Copulation takes place during the summer, and the spermatozoa are then stored by the female until they are required for the fertilization of the eggs in the following spring.

3. THE EFFECTS OF LATITUDE

It has been suspected for a long time that the further north one goes from the north temperate regions, or the further south from the south temperate regions, the later in the year is the onset of the breeding season in any particular species or genus. Conversely, the further one goes towards the equator the earlier does breeding commence. There is evidence that this affects all classes of vertebrates, but the only detailed investigation so far made refers to the birds. This was the work of Baker[11] who set out to discover how much earlier the breeding seasons become as one goes away from the pole, and also how far towards the equator this tendency is maintained. A further question that he considered was the manner in which breeding seasons cross over from one hemisphere to the other.

This study had to be restricted to a consideration of egg seasons, the months when living eggs (fresh or incubated) are to be found, since most information is available on this point. In the first place an attempt was made to discover whether for each latitude there are particular times of the year in which birds breed, and the evidence is summarized in Fig. 1. From this it can be seen that in 60° – 70° N. June is the optimum month. From 30°–60° N. it is May, but in 20°–30° N. the egg season spreads out. Just north of the equator all that can be said is that there is a tendency for the greatest number of eggs to be found in the first 6 months of the year. Just south of the equator the reverse is evident, and as one passes deeper into the southern hemisphere the egg season again becomes more sharply defined until in 50°–60° S. the optimum month is December.

It must be stressed that Fig. 1 refers to birds in

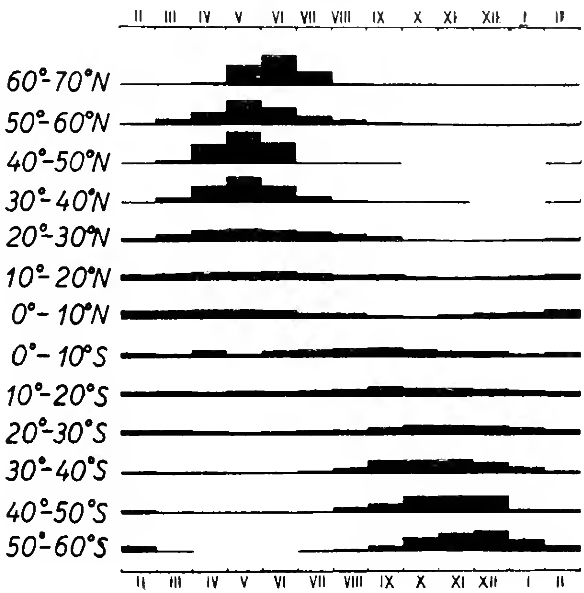

Fig. 1.—Diagram showing the relative numbers of times that each month occurs in the records of the egg-seasons in each 10° of latitude (after Baker). The months are indicated by Roman numerals.

general, and the conclusion must not be drawn that on the equator all birds breed all the time. There are a few records of species which apparently do this, as for example the birds on the tropical islands of Fernando de Noronha and St. Paul Rocks,[145] but generally speaking each tropical species has a well defined annual breeding season.

This becomes clearer when groups of related birds are examined individually. For all groups it is the general rule that as one goes from temperate latitudes towards the poles the egg season becomes later and later at a rate of between 20 and 30 days per 10° of latitude. However, as one goes towards the equator differences become apparent between the different groups. One extreme is set by the Accipitriformes (hawks) and the Coraciiformes (swifts, nightjars, etc.) which lay their eggs earlier and earlier until the equator is reached. The Passeriformes (passerine birds) also do this, though to a lesser extent. The other extreme is set by the typically aquatic birds, the Charadriiformes (waders), Lariformes (gulls), and Anseriformes (ducks), which tend to breed later and later as the equator is approached just as they also do towards the poles.

These points are illustrated in Fig. 2 in which the relation of the sun to avian breeding seasons is also made clear. Breeding in temperate and subarctic regions is generally at a time of increasing or of maximum day length. Similarly at the equator there is a tendency for the breeding season to be at its height some weeks before, or at the time when, the sun passes overhead, and since in this region the sun passes overhead twice a year, there tend to be two discrete breeding seasons. However, on the equator most species breed only once, either with the northward or with the southward swing of the sun. The hawks whose ranges extend from the northern hemisphere do so just before the northern swing of the sun, while those of the southern hemisphere do so just before the southern swing. Only rarely is a species of hawk found that breeds at both times.

With the aquatic birds of the northern hemisphere the egg season becomes later as the equator is approached so that it crosses into the southern hemisphere just before the sun's southward swing. Thus on the equator the northern water birds and the southern hawks breed at about the same time. The reverse is also true when passing from south to north, the southern water birds breeding on the equator at about the same time as the northern hawks. Again it is rare for any species to breed

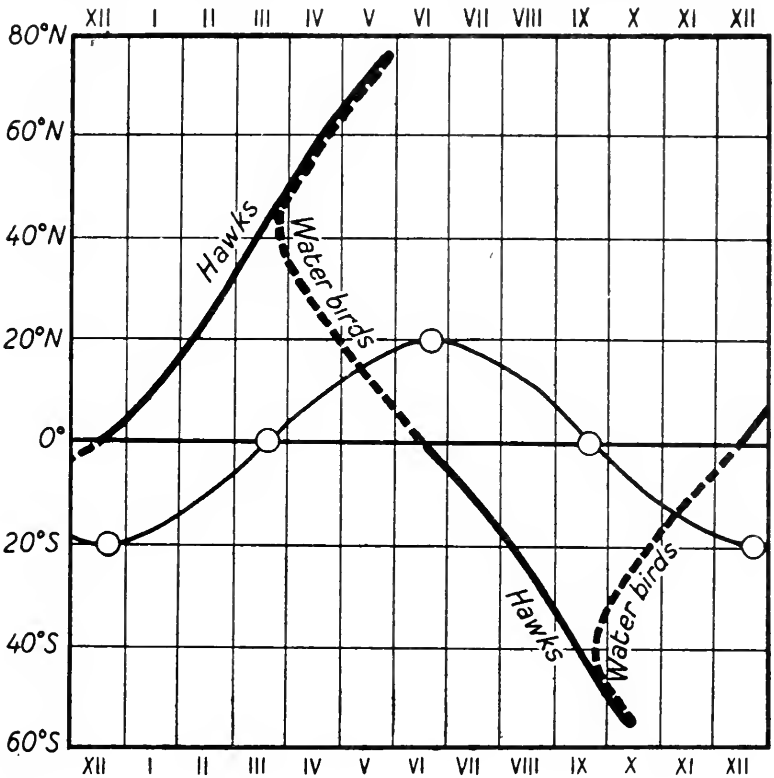

Fig. 2.—Diagram showing the variation with latitude in the start of the egg-laying seasons of hawks and of water birds (after Baker). Also shown are the seasonal changes in the position of the overhead sun. The months are indicated by Roman numerals.

more than once a year, but an example may be provided by the sooty tern of the Ascension Islands which is said to breed with both the northward and the southward swing of the sun.

Of course neither the breeding habits of the northern birds nor those of the southern birds change sharply at the equatorial line. Sometimes they stop short of the line and sometimes they overlap it. An example is provided by the Laysan albatross which, when it breeds north of the equator in Hawaii, lays its eggs at the time of the southern spring like the rest of its kind in that hemisphere.[10]

Finally, it must be pointed out that while much, if not most, egg laying occurs while the days are lengthening, many species do not follow this rule. It is evident as Baker concludes,[11] that neither a very long day, nor yet a rapidly increasing day, is necessary for active reproduction in birds, though, generally speaking, ovulation is rare all over the world when the day length is less than 11 hours. Further discussion of these points is reserved for the next chapter.

4. THE EFFECTS OF DOMESTICATION

So far the evidence put forward has stressed the common rule that reproduction in wild animals is a seasonal phenomenon. However, it is common knowledge that domestic animals frequently depart from this rule by breeding at almost any season of the year. This is particularly obvious in the case of man himself, the animal that invented domestication. The breeding of man is continuous at all times of the year, although some have searched for and have claimed to have detected traces of an old seasonal cycle in statistical analyses of monthly birth records.[83] It has often been suggested that primitive man did experience an annual breeding season in spring, and there are old reports, now largely discredited, that the Eskimo still experiences one to-day.

Whether early man was a seasonally breeding animal or not, his newly acquired habits of living in caves and houses, of using fire for added warmth and light, and of storing food against a famine, have protected him against those extremes of nature to which most other species are subject, and there seems to be some reason to believe that the continuance of such optimum conditions throughout the year may tend to prolong breeding. Certainly the reverse is true, and it is well known that during siege, as in the harsh conditions of the German concentration camps, loss of fertility has frequently occurred.

However, a clearer picture of the effects of domestication may be obtained from a study of the animals that man has tamed. The first of these is the dog, which has been with man for a very long time. Its nearest wild relatives have sharply defined breeding seasons, those of the various northern wolves,[8] like that of the Australian dingo,[117] being in late winter and spring. The English fox is more distantly related, but it too has a discrete breeding season at about the end of January, while the arctic fox breeds a little later in February. In contrast, the domestic dog is far less precise in its breeding habits, and indeed the male is able to mate at any time. The female normally experiences two breeding periods each year, and there is a tendency for one of these to be in spring and the other in autumn. However, both the number of periods per year and their timing are highly variable. It is also interesting to note that there are reports that dogs in the arctic breed only once in the spring, and that conversely foxes and wolves kept in zoological gardens may develop two seasons per year in the manner of the domestic bitch.[107]

The story of the cat is similar. The wild cat of Scotland breeds only in the spring,[8] but with the domestic animal the male can mate at all seasons while the female may experience two, three or four sexual periods each year which are unconnected with the seasons. Similarly the domesticated rabbit, kept warm and well fed, can breed all the year round, while the wild rabbit has a sharply defined breeding season which in Wales lasts from January to June. Brambell[42] sums up his study of the wild rabbit by stating that it differs from the tame animal in the sharp delimitation of its breeding season, in the intensity of its breeding during this season, and in its power of maintaining pregnancy during lactation.

Besides the domestic animals, those other mammals that have come uninvited to live with man in his houses also tend to breed throughout the year. This is true of the house mouse[124] and of the brown rat, although in the latter a greater proportion of the females are pregnant from March to June than at other times of the year.[155]

So all the evidence points to an increase in fertility among those mammals that live in the comparative comfort of men's houses. However, a suggestion of which notice must be taken is that all these species were uniquely constituted in this respect before they were tamed, and in support of this it has been pointed out that most animals when forced into captivity in zoological gardens have tended rather towards sterility.[202] In view of the extreme rarity of continuous breeding among wild animals in temperate regions, this suggestion does not carry great weight, and the sterility of animals in zoos may well be due to the depressing effects of an abnormal life (see also p. 41), effects which the domestic animals overcame long ago if indeed they ever felt them.

It is unfortunate that so few data on this subject are provided by the lower vertebrates. Hens and ducks, being highly bred for egg production, are outside the present argument, while reptiles, amphibians, and fishes are not normally kept indoors.

5. OESTROUS CYCLES

So far in this chapter only yearly reproductive cycles have been considered, and for the male this completes the story. In some species the shedding of the sperm occupies only a few hours or days while in others the supply is continuous over a period of many months, but whether the breeding season is short or long it is possible to conclude that a typical male is ready to breed only once a year.

In a non-pregnant female, however, cycles of lesser duration are commonly found. These are most obvious in the mammals where they are known as oestrous cycles, and are seen as periods of heat, or oestrus, which recur at intervals of days, weeks, or months according to the species. Only during oestrus are the eggs shed from the ovary, and only then does the female become sexually receptive so that fertilization can occur. Thus oestrus is characterized by both structural and behavioural changes. The word itself refers to the behavioural change and is derived from a Greek word meaning a gadfly. By suggesting a resemblance to the agitation caused by the bite of this fly, it indicates the excitement that is often shown by an animal at this time.

In the fishes and amphibians such lesser cycles appear to be rare. Most females shed all their eggs quickly during a period of days or weeks, and then spend the rest of the year in building up a new stock. However, as they come to be studied in sufficient detail some species with prolonged breeding seasons may be found to show lesser cycles. Bretschneider and de Wit[43] have already described a kind of oestrous cycle in the female bitterling, and Jaski[115] has done the same in the little viviparous millions fish. In the former species the cycle is particularly obvious since it involves the periodic growth of a prominent ovipositor. This takes place at intervals of from about 7 to 14 days, and it is only at these times that the eggs are laid.[138]

Among birds it is a common habit for an egg to be laid each day until the clutch is complete, and this may be likened to a 24 hour oestrous cycle. Also during spring and summer some species of birds lay two or three clutches of eggs at intervals of perhaps 6 weeks. However, this clutch cycle does not seem to be comparable to an oestrous cycle since it is now known that the interruption in laying between clutches is due to some appreciation by the female that the nest already contains sufficient eggs or young. If a clutch is kept small by the daily removal of an egg, then many females will continue to lay steadily for a considerable time; in this way a flicker has been induced to lay 71 eggs in 93 days. So while the habit of laying an egg each day may be due to the operation of an internal cyclic mechanism, as in the true oestrous cycle, the habit of laying successive clutches is controlled by external circumstances.

However, the most clearly defined oestrous cycles are those of the mammals. Indeed, it may be better to reserve the term oestrus for use in this class only, and to find other terms to describe the cyclic phenomena of the lower groups. By far the best known and most closely studied oestrous cycle is that of the laboratory mouse, which breeds at all times of the year. An unmated female ovulates repeatedly about once every 5 days from the age of about 3 months to that of about 12 months when old age begins. Such an animal, which experiences more than one oestrous period in a year, is polyoestrous. Of course in a wild mammal, in the absence of pregnancy, the polyoestrous condition lasts for only a limited season, and alternates with a non-sexual season of anoestrus.

A few mammals, whether they become pregnant or not, have only one period of heat per year. Such animals are monoestrous, and this term is sometimes also loosely applied to males and to many of the lower vertebrates. An example is the English fox which ovulates spontaneously in January, and which remains in anoestrus for the rest of the year.

There remains to be considered the special question of the primates (the monkeys, apes and man), which are characterized by the unusual habit of breeding throughout the whole year. Most of them appear to experience a smooth and uninterrupted sexual life extending from puberty to old age.[201]

The females of the lower primates show links with other mammals in exhibiting typical oestrous cycles. This is the case for instance in *Tarsius*, which has a cycle length of about 23 days,[8] and in the platyrhine monkeys. The catarrhine or old-world monkeys are similar except that they also show a periodic bleeding from the uterus caused by a breakdown of the uterine lining.[203] This lining becomes thickened to receive the embryo should fertilization follow ovulation, and in the absence of fertilization it degenerates. All mammals with oestrous cycles show a similar degeneration between successive ovulations, but in the non-primate the process is not usually so drastic and does not involve loss of blood. Thus the difference shown by the catarrhine cycle is one of degree only. It is unfortunate that this cycle is so often regarded as being something unique, and that it has been distinguished by the special name of menstrual cycle. Indeed the name is doubly unfortunate since not all menstrual cycles have an average periodicity of one month. In Azara's capuchin the cycle length is about 16 days, and in the gorilla about 45 days.[8]

The human cycle has an average length of about 28 days, with 97 per cent of cycles lying between 22 and 36 days,[100] and this, of course, is the original menstrual cycle. Within this cycle it is generally agreed that the commonest time for ovulation is at about the middle of the interval between successive menstrual periods, the times when bleeding occurs. However, individual variations from this rule are common, and in extreme cases ovulation may even occur during menstruation.[58] It is to be regretted that no detailed study of this cycle has yet been made.

In conclusion an exception must be mentioned to the general rule that female mammals with extended breeding seasons experience some form of oestrous cycle with periodic and spontaneous shedding of the eggs. In a small number of species, of which the rabbit is the best known, the non-pregnant animal is always ready to mate, and it is the nervous stimulation of the act of copulation that causes the ovary to release its eggs.[101] Thus a non-pregnant rabbit can be regarded as experiencing perpetual oestrus. This is made possible by the development of overlapping crops of eggs, each crop developing, remaining mature for some 7 to 10 days, and then degenerating. Copulation occurring at any time causes the shedding and fertilization of those eggs which are then mature so that pregnancy after mating becomes a certainty.

6. CONCLUSIONS

It has been stressed that within the life span of an individual animal there are usually greater and lesser cycles of reproductive activity, although a few species such as the eel, which breeds only once at the end of its life, may be quoted as exceptions.

In all parts of the world sexual activity is commonly a seasonal phenomenon. The seasonal cycle is normally of a year's duration, but the actual time of breeding varies from species to species, and may be in any month. Within a single species, or group of related species, it also varies widely according to latitude.

The duration of the breeding season also varies widely. In some animals like the common frog all the eggs and sperm are shed in the course of a few days or even hours, while in others like the wild rabbit breeding may be prolonged for six or more months.

One of the two groups of animals in which the breeding season is not clearly defined is that which lives in houses. From man himself to the uninvited house mouse the habit of living a protected indoor life seems to have resulted in an extension of the sexual period until in many cases breeding has become continuous throughout the whole year. The other group which is characterized by continuous breeding is that of the primates (monkeys, apes and man). Man is the one species common to both these groups.

In female mammals with prolonged breeding seasons it is common for an unmated individual to experience a series of lesser cycles, known as oestrous cycles. Similar cycles may also be seen in some of the lower vertebrates. It is only during oestrus, or heat, that the eggs are shed from the ovary, and usually too it is only at this time that the female is willing to receive the male. Female primates experience a form of oestrous cycle that is distinguished by the name of menstrual cycle.

CHAPTER III

THE ENVIRONMENT AND REPRODUCTION

1. THE NATURE OF SEASONAL CYCLES

IT has been stressed that animals tend to breed only at certain times of the year, and the question which now arises is whether the timing of the yearly sexual cycle is achieved by means of an internal physiological mechanism, or whether it is imposed from outside by the influence of the seasons themselves.

A preliminary answer to this question may be given as follows. If the control of the cycle is solely internal then the timing of the physiological mechanism must be as good as that of a perfect clock, and since such a degree of precision is unknown in any biological process, this appears to be inconceivable. Although there is good evidence that internal physiological rhythms do exist, there is, as Baker[14] has said, 'no possibility that annual phenomena can be *wholly* controlled by them in any species of plant or animal', and it is therefore necessary to suggest that some factor in the environment periodically 'puts the clock right'.

2. EVIDENCE FROM THE MOVEMENTS OF ANIMALS

With the question of an internal rhythm momentarily set aside, it is relatively easy to build a *primâ facie* case for the control of yearly reproductive cycles by seasonal changes in the environment. In the first place there is the argument of *reductio ad absurdum* set out above, and in the second there is the evidence provided by the results of animal movements. On this latter point text-figures 1 and 2 may be referred to again. These indicate that any one species of bird, or any related group of species, tends to breed at a certain time of the year. In the northern hemisphere this may involve egg-laying in any month from June in the arctic to January on the equator, while in the southern hemisphere the times are from December to June. Thus on the equator there is a marked divergence of habit, with some northern species breeding about January and some southern species doing so about June. This would appear to act as an effective bar to the interbreeding of northern and southern birds, but clearly the equator means nothing to an animal. It is only an imaginary line which offers no obstacle to movement, and innumerable species must have extended their range across it on innumerable occasions. The existence of identical or related species in both hemispheres is clear proof of this. It follows that a bird which extends its breeding range across the equator, and penetrates deep into the opposite hemisphere must suffer a reversal of its breeding season so that a species which typically breeds in May in the north will come to breed in November in the south.

Of course, as pointed out above, there is evidence that such a reversal does not occur suddenly the moment latitude 0° is crossed. Species from the north may extend some distance south of the equator while still retaining their northern habits of breeding, and the case has been quoted of a southern albatross which breeds in Hawaii in the northern hemisphere at the time of the southern spring.[10]

While such changes must often have happened naturally during the spread of successful species, they have also happened on many occasions due to man's intervention. This has been particularly true during the last hundred years with the settlement of South Africa, Australia and New Zealand by emigrants from the northern hemisphere, and with the foundation and increasing popularity of zoological gardens. The settlers in the southern hemisphere naturally took with them their farm and domestic animals, and for sentiment's sake they also took an astounding variety of wild animals. Captain Cook, who was the first European to set foot in New Zealand, introduced pigs, and those animals which now run wild in the South Island are supposed to be their descendants. Since that day the widest variety of mammals and birds have been taken there, as well as some five species of frogs and toads and several fresh water fishes including the brown trout.[82]

Such animal movements have provided valuable information concerning the control of reproductive seasons, though a great deal of the data has not yet been analysed. The first serious attempt at such an analysis was that of Marshall,[130, 131] and later, together with the Duke of Bedford, he made a further study of the situation as it affects the mammals.[22] The general conclusion arising from these surveys is that any animal with a fixed breeding season in temperate latitudes reverses this season to conform with the new conditions when it is transported to the other hemisphere. Sometimes this reversal is slow as in the case of a pony brought to Scotland from Timor in the southern hemisphere. In its first year it came on heat in the autumn, but afterwards it adjusted itself to breeding in the spring.[130]

It is also reported that when the chital, or spotted deer of India was introduced into Europe, it was at first in danger of extinction because the calves continued to be born in mid-winter when the unsuitable conditions proved fatal, but later they adapted themselves and the young were born at the appropriate season.[130]

Commonly, however, the change in timing is immediate so that individual animals may experience two breeding seasons in the year in which the journey is made. An example of this is provided by the ferrets which were taken from England to the zoological gardens in Pretoria, South Africa, in 1937. The transference took place from the late northern summer to the early southern spring, the animals arriving at their destination in October. In the spring conditions they shortly bred again although it was only six months since their last breeding season in the north. Following this, they became adapted to the southern seasons, and bred at yearly intervals in the southern spring.

Such examples could be multiplied, and it is also interesting to notice that a similar reversal is shown by animals which normally breed in seasons other than the spring. This is true, for instance, for autumn-breeding sheep. Late in 1932, 21 pregnant ewes were transported from England to Cape Province, South Africa, and they lambed after arrival in January 1933. When the southern autumn started in March they again came into breeding condition, and they were mated in May. Thereafter they bred only in the southern autumn.[130]

Following his surveys, Marshall has concluded that the sexual periodicity of mammals in temperate regions is governed by two main factors. The first is an internal gonadal rhythm which is characteristic of the species, while the second is that external environmental factor which determines the precise time of breeding. Normally these two forces act together, but when an animal is transferred to the other hemisphere a conflict arises between them. If the internal rhythm is unusually powerful this may cause some disorganization during the first year, but thereafter the animal becomes adjusted to the new seasons. This shows clearly that the influence of the environment is stronger than that of the internal rhythm.

In the birds, reptiles, amphibians, and fishes the same general conclusion seems to apply. Many common spring-breeding English songbirds have been taken to Australia and New Zealand, and nowadays they all breed in the spring of their new home. Lizards, frogs, and fishes are also known to have experienced the same change.

3. ENVIRONMENTAL FACTORS

Having reached this conclusion it becomes necessary to attempt to analyse the environment in which the animals live, and to distinguish those of its many components which influence the sexual cycle. Of course, since some species are to be found breeding regularly in each season, it can be guessed at once that the same environmental factor is not operative in all cases. Among spring-breeding animals it is possible that an increase in the clemency of the weather, in daylength, in temperature, and in the quality and quantity of the food available may one and all be important, but in the case of autumn-breeding species it appears necessary to think in the opposite terms. In some cases, too, the moon may be suspected of exerting an influence, and in some parts of the world the seasonal rains may be of importance.

Of all these possible factors it seems true to say that until a generation ago only food and temperature were thought to be important, and this was perhaps due to the fact that man himself notices these more than he does any of the others. Certainly the food and temperature theories were widely held, and they can be seen to have influenced the writings of Heape[107] about 1900 and of Zuckerman[202] as lately as 1932. Even to-day, when they have been largely discredited, it must be remembered that breeding cannot be successful unless animals have suitable food and a proper degree of warmth, particularly if they are cold blooded.

Nowadays, being wise after the event, it appears surprising that so little attention was given to the question of daylength, particularly in temperate regions. If one had consciously to choose some environmental variant by means of which a particular season of the year could be regularly observed, it would soon become obvious that nothing else could give such certain results. A spring may be warm or cold, the food supply may vary widely from year to year, but in a particular latitude a given day always has a given length which is longer by a given interval than the day just past.

If this reason were not sufficient for suspecting that daylength might be a critical external factor in controlling seasonal reproduction, then it could have been noted that in some parts of the world poultry farmers had for a long time been using artificial light in autumn and winter in order to stimulate unseasonal egg production.[12] A similar practice was common in Japan whereby from ancient times pet birds, such as *Zosterops*, were brought into spring song in January. The method, known as 'yogai', was achieved by exposing the birds in autumn to some 3 or 4 hours of artificial light after sunset. This again is similar to an old Dutch custom, recalled by van Oordt, whereby many songbirds were caught in autumn with singing decoys. These decoys were put into the dark in May and exposed to light again in August so that by September and October when they were used, they were in full song as in the breeding season.

An analysis of the effect of light on breeding is given in the following section, and the effects of other external factors are considered on p. 36. However, before proceeding, it is necessary to reinforce Baker's warning[19] against the misuse of the term 'exteroceptive' in the literature of this subject. The expression 'exteroceptive factor' has been widely used in preference to the expression 'external factor'. The word exteroceptive was originally coined by Sherrington who used it, in contrast to proprioceptive, to mean 'receptive of external stimuli'. Thus the eye may be properly called an exteroceptive organ, but the light which it appreciates is clearly an external and not an exteroceptive factor.

4. THE EFFECTS OF LIGHT

Although practical men, by rule of thumb, may have discovered long ago the magical influence of light on song and on egg laying in birds, the credit for the first logical approach to the subject belongs to Rowan. His original paper[159] was published in 1925, and years later in 1938 he wrote a review of his pioneer work.[165] His original aim was to obtain information on the mechanism of bird migration, and the first step was to discover whether the gonads of birds could be artificially stimulated to growth in the autumn 'in the belief that if this were possible, and the birds were liberated in such condition, they might migrate north on release'. It will be appreciated from this that he started with the assumption that northward migration in the northern spring is a form of sexual behaviour, which depends for its seasonal recurrence on the development of the gonads. This point is considered on p. 91.

Rowan showed considerable prescience in discarding from the start any consideration of the effect of temperature. His first experiments[160] were made with the common Canadian bunting, *Junco hyemalis*, which he trapped as it was passing through Edmonton, Alberta, in Western Canada, on its southern migration in September 1924. Due to an accident caused by interfering children many of the birds were lost so that the experiment was almost wrecked, but the remaining specimens, all except one of which were males, were maintained in two open-air aviaries. In both of these the birds were fully exposed to the weather, but in one of them two 50 watt electric light bulbs were fitted. From 1 October the experimental birds were subjected to an increasing day-length of 5 minutes per day, which was achieved by switching on these lights at sunset. By the middle of November the testes of these birds were increasing in size, and by the end of December, when the last bird was killed, they were larger than those of the first juncos to arrive in Edmonton in the spring. All this time the control birds were kept in normal autumn conditions and their testes remained at a minimum size.

This experiment demonstrated conclusively the influence which increasing daylength has on the reproductive organs of the junco. As Rowan remarked, what had been done was to repeat on a small scale by means of electric light what happens on a grand scale when animals are transferred from one hemisphere to the other. In both cases increasing light causes what to the affected individuals is an unseasonal sexual development. However, Rowan's experiment demonstrated one other thing with startling clarity, namely the complete lack of effect of temperature on the reproductive cycle of the junco. While this bird is accustomed to breeding in the pleasant warmth of the Canadian spring, these experimental individuals were sexually stimulated in temperatures which fell progressively below freezing point, to a minimum of – 46° C.!

Further experiments of the same kind were carried out between 1925 and 1928[162] using the junco and a variety of other finches. These started with a study of the effects of the intensity of illumination until an optimum was found. After this it was possible to obtain complete maturation of the gonads, with normal histology, in spite of extremely low temperatures that continued for long periods. As a further variation on this theme, Rowan induced full maturation in a group of 30 juncos in late autumn. Then he reduced their daylength from 15 hours to 9 hours, and so caused the gonads to regress again. Finally, he exposed them to the normal increases in daylength during late winter so that by May they came into full breeding condition for the third time in twelve months.

Later these experiments were repeated using the American crow, and essentially similar results were obtained.[163, 164] About this time other workers were attracted to this field, the first being Bissonnette.[31, 32] He studied the European starling in Connecticut, U.S.A., and found that it too responds by gonad growth to an increasing daylength in late autumn and early winter. This result could be achieved either by means of a progressive daily increase of several minutes, or by a sudden and permanent increase of 6 hours. He also investigated the effects of different light intensities, and found that in the conditions of his experiment there was a progressive acceleration in the rate of gonad growth with light of from 10 watts to 40 watts, but that with higher intensities no further increase occurred.[37]

Since then many species of birds have been studied with essentially similar results, so that it is now known that an increase of daylength causes growth and maturation of the gonads of ducks,[26] mourning doves,[70] pheasants, quail, ruffed grouse,[66] Japanese white eyes,[142] common sparrows,[119] golden crowned sparrows[141] and greenfinches.[77] Conversely it has also been shown in several of these species that a reduction in daylength causes gonad regression.

The first study of the reaction of a mammal to light was that of Baker and Ranson,[12] who found that when the daylength is shortened from 15 hours to 9 hours reproduction almost ceases in the field mouse, *Microtus agrestis*. At about the same time Bissonnette[34] was studying the effect of increasing light on the ferret, which normally breeds from about March to August. Starting in autumn, he increased the daylength of his experimental animals by a single increment of 6 hours. From 6 to 9 weeks later the females were in full oestrus, but, somewhat surprisingly, the response of the males was not so great and the matings which occurred were sterile. Later Bissonnette found that if the daylength was increased by small daily instalments, instead of in one single step, the male ferrets reacted by a full maturation of their testes and fertile matings followed.[35]

In England, Hill and Parkes,[109, 110] also carried out a series of investigations on the ferret, and they corroborated Bissonnette's results. However, they failed to prevent breeding in spring by means of a reduction in the daylength to only 30 minutes. The reason for this failure is obscure because about the same time Marshall and Bowden[133] did cause a stoppage of spring breeding by means of light restriction, and they also quoted the case of a blind ferret (with cataract) which never came on heat although, it fed well and remained apparently healthy for two years. Bissonnette,[36] by light restriction, also prevented the spring breeding of ferrets.

Other mammals which have responded by sexual development to increasing light are the hedgehog,[1] and the raccoon.[39]

The lower vertebrates have not yet been studied so intensively, but similar results have been obtained in some cases. Among reptiles increased spermatogenic activity following artificial illumination has been reported in the case of the lizard *Anolis carolinensis*[69] and of the turtle *Pseudemys elegans*.[59]

However, no amphibian has yet been proved to be sensitive to an increase in light alone, and, as might be expected, the importance of temperature is greater in such cold blooded animals, as it also is among the fishes. In species such as the edible frog[94] and the killifish[60] temperature is of critical importance, and the effect of light is negligible. However, in the case of the little fresh water minnow, it has been found that long days of artificial light in late autumn and winter can induce complete maturation of both testes and ovaries.[47] This result is only obtained if the water temperature exceeds about 10° C., but a high temperature alone is ineffective. Such joint action of extra light and high temperature is also necessary for maturation in the four-spined stickleback.[139]

The studies which have been made on the lower vertebrates are still too few to enable an overall picture to be drawn. In particular it would be interesting to obtain information regarding the reproductive cycles of a variety of marine species living in temperate regions.

5. LIMITATIONS OF THE LIGHT CONTROL THEORY

With all the popularity of a new and stimulating idea, the light theory of the control of vertebrate reproductive cycles gained ground so rapidly during the period 1926 to 1939 that its application was carried too far by many of those who discussed it. A reaction to this state of affairs also developed rapidly. In 1930 Hill and Parkes[109] were already pointing out that the ferret in domestication has a well marked breeding season from April to August, and were finding it 'difficult to imagine what environmental changes take place during April in an artificially heated animal house not particularly accessible to direct sunlight'. In 1934 when they discovered that their ferrets did not experience infertility after a reduction of daylength in winter and early spring, they concluded that the onset of the breeding season is not dependent on the increasing length of day.[110] They even went so far as to suggest that the provision of extra light in winter is an artificial laboratory technique, the results of which do not reflect conditions in nature, and that the breeding cycle is solely dependent on an internal physiological rhythm.

The impossibility of such a rhythm being the sole factor in control of breeding seasons has since been recognized,[14] but further criticisms were also advanced. The first of these referred to the problem of nocturnal and subterranean animals which, it would seem, could not be affected by light. The second was the problem of those animals which normally breed in autumn and winter at times of decreasing or of minimum daylength. The third was that of the tropics where the daylength is relatively constant at all times.

As regards the first of these problems there is still no information, probably because of the practical difficulty of maintaining nocturnal or subterranean animals for any length of time in the laboratory. The question of autumn breeding has, however, been investigated, and it is discussed in the following section. The question of the tropics is considered on p. 34.

6. AUTUMN-BREEDING ANIMALS

The first experimental study of an autumn-breeding species was that of Hoover and Hubbard[111] who in 1937 published their observations on the brook trout of New Hampshire, U.S.A. They subjected numbers of these fish to an artificial summer length of day early in the year, and then, as summer approached, the daily light periods were progressively reduced. The result was that the gonads matured and the fish spawned in an artificial autumn considerably in advance of their normal time.

No similar experiments have yet been performed with amphibians, reptiles, or birds, but as already pointed out very few of these animals are autumn breeders. However, it seems possible that such birds as the emperor penguin of the Antarctic and the kea of New Zealand,[10] which both breed in the southern autumn, may some day be found to be influenced in this way.

With mammals an experiment similar to that of Hoover and Hubbard was carried out by Bissonnette[38] in America, and as a result he found it possible to modify the breeding cycle of the goat. The conclusions reached were that temperature is unimportant to this animal, and that the critical factor which induces, or permits, the onset of oestrus is a shortened daylength. In England Yeates[198] has confirmed these conclusions using the sheep. He exposed animals to an artificial length of day rising from 13 hours in mid-October to 21 hours at the end of January, and because of this they passed out of breeding condition two months in advance of the control animals. Then their daylength was reduced until by the end of June they were receiving only $5\frac{1}{2}$ hours of light per day. The first of these sheep came into breeding condition on 20 May, and within the following three weeks they all did so, including those which had lambed only ten weeks previously.

It can therefore be concluded that, at least in some autumn-breeding species, the seasonal reduction in daylength is the critical factor determining the time of onset of the breeding season.

7. CONCLUSIONS REGARDING THE ACTION OF LIGHT

Some points of primary importance stand out from the above data. In the first place, it is evident that, depending on the species, animals may come into breeding condition as a reaction either to the increasing light of spring or to the decreasing light of autumn. This shows clearly that what an animal appreciates and responds to is not the light *per se* but the *change* in the daylength.

In the second place it is evident that, if reproductive cycles can be regulated by either increases or decreases in daylength, it is probable that these methods of control are merely superficial.[47] Thus there appears to be no theoretical objection to an animal, because of a peculiar mode of life, adopting any suitable external variant to condition its breeding cycle. There seems to be no doubt that this has in fact happened, and other factors which are already known, or thought, to influence breeding in some species are described on p. 36.

In the third place evidence has been mentioned that suggests the existence of an internal physiological rhythm with an approximate periodicity of one year. Although it has been shown that this could not by itself maintain indefinitely the regular periodicity of breeding seasons, there is no doubt of its existence. It can be demonstrated by experiments such as those with ferrets in which the imposition of almost total darkness in winter and early spring does not infallibly prevent the maturation of the gonads,[110] and of those with minnows in which a similar treatment did no more than delay gonad growth.[48]

The theory has therefore been put forward[48] that some if not all vertebrates possess an inherent reproductive rhythm, which is possibly of a more or less vague kind, and which in normal circumstances is rendered more precise in its time of action by the effects of the seasonal variations of the environment. This internal rhythm may be likened to that of an alarm clock which throughout the day and night is a moderate or even a poor timekeeper, but which is automatically corrected each day by the rising of the sun so that the sounding of the alarm is always precisely timed.

It is now known that the strength of this internal rhythm is not always constant, but that it may vary with age and season. As an example it can be mentioned that the gonads of the golden crowned sparrow are resistant to the stimulus of an experimentally increasing daylength until after the month of November.[141] This conclusion is of importance because it suggests an explanation for the peculiar problem of those migrating birds which breed in one hemisphere but not in the other. The common British swallow is a case in point. When the northern summer is over it migrates southwards across the equator into the South African spring. If the bird was at that time sensitive to the influence of increasing daylength it would surely come into breeding condition and nest again. That it does not do so must be regarded as proof that it is then in a resistant state similar to that of the golden crowned sparrow. The gonads of such migratory birds actually begin to enlarge early in the southern autumn as the observations of Rowan and Batrawi have shown.[167] This cannot be in any way related to increasing light, and it must be presumed to be due to the action of the internal rhythm. The birds then move north, and, as they penetrate into the northern hemisphere, it appears that the increasing daylength exerts its influence to bring them into full breeding condition.

8. THE QUESTION OF THE TROPICS

All the experiments, observations, and conclusions so far set out in this chapter refer to the temperate regions. It is obvious, however, that some parts of the tropics offer an intriguing field for research since they experience almost uniform climatic conditions throughout the whole year, and in such countries it has often been observed that some animals can always be found breeding.

The most important work done in these regions was that of the Oxford University Expedition to the New Hebrides in 1933-4, the results of which have been published in a series of papers.[13-19] At Hog Harbour on Espirito Santo where the expedition was based the mean temperature varies by only 2° C. between the hottest and coldest months, the longest day is only $1\frac{3}{4}$ hours longer than the shortest, and there is no dry season, the least wet month having on the average about twice as much rain as the wettest month in England. The land is covered by typical rain forest, and within this it is probably true to say that environmental conditions vary less from month to month than they do anywhere else on land. The two questions which the expedition attempted to answer were whether in such a uniform climate the animals reproduce continually or seasonally, and whether, if breeding seasons are evident, these can be correlated with environmental changes of any kind.

To the first question a clear answer was given. Most of the terrestrial organisms, plants as well as animals, showed marked seasonal changes in their reproductive habits. Only one of the vertebrates studied, the lizard *Emoia cyanura*, reproduced continuously, and even in this species egg-laying almost ceased during two months. At the other extreme the most clearly defined breeding season was that of the insectivorous bat, *Miniopterus australis*. The females became pregnant only during the first few days of September, and afterwards the epididymides of the males were found to be empty of spermatozoa. In Baker's words, 'No animal living in a strongly seasonal climate could have a more sharply defined breeding season. This seems all the more extraordinary when it is remembered that this little bat hangs throughout the period of daylight, till about ten minutes before sunset, in a dark and almost thermostatic cave.'

Of the birds, the golden whistler also has a sharply defined breeding season with most of the egg-laying crowded into one month, and Baker was therefore driven to the conclusion that the various vertebrates studied are at least as seasonal in their reproductive habits as are those in temperate climates.

The second question then remained to be answered, namely what regularly varying factors in the environment are responsible for the timing of these seasons? To this it is not yet possible to give any answer. It was noted that the reptile *Emoia* bred most actively in November and December when the days were at their longest, while the golden whistler behaved in an exactly opposite manner. Thus these two animals may conceivably be influenced by the slight variations in daylength. To *Miniopterus*, which only leaves its dark cave at nightfall, the duration of daylight would seem to be a matter of little moment.

One way in which it has been suggested that light might influence tropical animals is through its quality or its intensity. In the New Hebrides there is, for example, far less ultra-violet light in some months such as June than in others such as December, and perhaps an animal could be conditioned to react to this fluctuation. Again in many other parts of the tropics there are alternating wet and dry seasons with a lower intensity of light at those times when the days are cloudy.

Partly no doubt because of the war, little more has been done in analysing this problem of tropical breeding seasons. However, Marshall[129] has recently published results which show that the fruit bat *Pteropus giganteus*, living in the stable climate of Ceylon, has a single sharply defined breeding season in December. In this it follows the general habit of fruit bats which tend to copulate when the days are getting shorter, even though in latitude 7° N. the contraction in daylength is only slight.

9. THE VARIOUS EXTERNAL FACTORS WHICH AFFECT BREEDING

The suggestion has been made that the environmental control of breeding cycles is a superficial one, and that the widespread response of animals to increasing light in spring has developed merely because it is advantageous for the majority of animals to breed at this time. It is equally possible for an animal to become adapted to respond to decreasing light if for some individual reason this is more expedient. It has also been suggested that tropical animals may react to the quality of light, and particularly to the ultra-violet component. This might explain the two tropical breeding seasons shown by birds (Fig. 2) which can be related to the two seasons of the year when the intensity of the ultra-violet light is at a maximum. It is equally possible that other animals, living in conditions of almost constant daylength, may respond to variations in light intensity as determined by the presence or absence of clouds.

Further, although not nearly enough observations have yet been made on factors other than daylength, it is already possible to suggest a number of other environmental variants which may influence or control the growth and maturation of the gonads. It also seems certain that this number will be increased when more species living in unusual environments are examined.

One factor which may have considerable importance is the light of the moon. From early times it has been supposed to influence the menstrual cycle and breeding habits of man, and, although this has now been disproved, it undoubtedly influences the breeding of some animals. Among invertebrates the remarkable case of the palolo worm has already been mentioned (p. 2), and other instances have been discussed by Fox[91] and Baker.[10] Regarding vertebrates there is still not a great deal of information. However, it is probable that both the Californian smelt, and the New Zealand whitebait spawn only at particular phases of the moon, the process being repeated during two or three successive months, although of course such action by a marine species may be related more to the state of the tide than to the light of the moon.

Regarding the amphibians, reptiles and mammals, nothing appears to be known, although the possibility of an effect cannot be discounted. The breeding of bats may be remembered in this connexion, and it is not impossible that the precise nature of the breeding season of *Miniopterus* in the New Hebrides may be ensured in this way, the effect of the moon being to impart great accuracy to the timing of an internal rhythm with approximately a yearly periodicity.

Among birds there are indications that ovulation in the nightjar, a crepuscular species, is controlled by the moon. Wynne-Edwards has described how the two eggs are laid during the last quarter of the lunar cycle so that the chicks are reared during the next full moon when hunting can continue all night.[197] Similarly, it has been shown[132] that when the eggs of a nightjar are taken a period of three weeks must pass before the bird can lay again. This is unlike the other species which have been studied, and the contrasting case of the flicker has been mentioned in which the steady removal of eggs has resulted in the production of 73 eggs in 93 days.

Another environmental variant which is particularly important in the tropics is rain. In these regions the alternation of dry and rainy seasons is normal, and there is a great deal of evidence that this change in some way controls the breeding habits of many tropical species. Frequently birds breed when the rains begin. An Australian cockatoo, *Kakatoe roseicapilla*, does this, and it may miss a season altogether if the rains fail.[135]

The habit is common among birds in tropical Africa and in India. It is particularly striking in Ceylon where the north-east monsoon affects one side of the island at one time of the year, while the south-west monsoon affects the other side at quite a different time.[10] It has also been suggested that the breeding of the wood swallow of Western Australia is dependent on the rains since it breeds either in February and March, or in June and July, or at both times, according to whether rain falls.[10]

In the lower vertebrates similar conditions are known to prevail in many species. Among reptiles it has been noted for snakes and lizards in Oklahoma,[10] while among amphibians, as might be expected, the habit of relating breeding to rain is very widespread. The North American toad, *Scaphiopus bombifrons*, spawns at the first heavy rain after the middle of spring, and in a season with little rain breeding may be delayed until the end of the summer.[10] Rain also determines the breeding time of the American toad *Bufo cognatus*.[132] An extreme condition is perhaps reached in the Australian desert where after heavy rains frogs such as *Chiroleptes platycephalus* swarm from the ground, where they have lain buried in a state of aestivation, and spawn almost immediately.[90] For fishes there appear to be no data, but it seems probable that the lung fishes, which sometimes also aestivate, may react in the same way as do these amphibians.

No experimental work has yet been done on this problem, and it is not possible even to suggest how the rain may achieve its effect. Indeed it is not even possible to say whether the important factor is the rain itself, or as suggested by Baker[10] the degree of saturation deficiency of the air, or the psychological effect of the existence of ponds or floods, or the increase in food supply which accompanies the development of green vegetation. In all probability the answer is not the same in all species.

The next environmental factor to be considered is that of temperature. Among the warm-blooded birds and mammals it is not known to play any great part in stimulating or preventing breeding, although of course it has a potent effect on food supply, particularly in the case of insectivorous species. It is this lack of food, and not the cold as such, which is the ultimate cause of the migration of so many birds from arctic and temperate regions in the autumn. If one of these birds is kept back by force and its food supply artificially assured then, as in the case of Rowan's juncos,[160] it may survive and be brought into breeding condition in the most extreme arctic conditions. Of course this may not be possible with all species, and certainly birds such as the canary, which come from warmer climates, cannot be stimulated to breeding condition during a Canadian winter.[165]

In cold-blooded vertebrates, the fishes, amphibians, and reptiles, the importance of temperature is obviously great. Towards freezing-point the metabolism of most of these animals is so far slowed down that they become sluggish or even immobile, and in such conditions breeding would clearly be impossible. Animals such as these are perhaps more likely to make use of the rising temperatures of spring to regulate their breeding seasons. Such a mechanism may perhaps be common among those sea fishes which breed in spring and summer because the temperature of the sea varies steadily and is not subject, like that of shallow freshwater, to violent and unseasonable fluctuations. Certainly the marine and brackish water killifish reacts to an increasing temperature by the development and maturation of its testes,[60] and there is some evidence that the same may be true of the fresh water perch[186] and of the three-spined stickleback.[73] Among the amphibians of temperate regions the temperature of the environment may also be a critical factor. This seems to be true of the edible frog[94] and of the American newt, *Triton viridescens.*[139]

In all considerations of gonad growth the question of food looms large. It is well known that if insufficient food of the right kind is available animals may survive, perhaps for long periods, but they do not breed. Whether food supply ever acts as a trigger mechanism in determining the time of the breeding season is, however, another question. Baker has suggested that it may do so, and he has pointed for example to the possible effect in an equatorial rain forest of the seasonal production of fruits which so many animals eat.[10] However, there is little trustworthy evidence on this point, and until more observations have been made it is impossible to do more than speculate.

It appears from what is now known that there are few if any parts of the world which lack some environmental variant by which animals and plants can regulate their breeding seasons. The only region that is perhaps completely seasonless is the very deep sea. Light penetrates into the ocean to a maximum depth of about 3,500 feet, and below this all is absolute and perpetual darkness. There are also no temperature changes, and the water remains near to freezing-point. In these regions it seems possible that fishes may solve the problem by eliminating altogether their old habits of periodic breeding. Of course, this need only be done by one sex. If the female continued to breed in a cyclic manner the times of ovulation could not remain seasonal and would therefore become irregular, but if the male was always capable of shedding spermatozoa the eggs could be fertilized whenever they were laid. Alternatively, the problem could be solved in another way which would provide an explanation for the well-known existence of parasitic males among the deep sea angler fishes. When males and females become fused together in this way the rhythms of their two systems can be synchronized so that maturation in one of them is always accompanied by maturation in the other. Then, however irregular the breeding times, fertilization could always be achieved.

10. PSYCHOLOGICAL FACTORS IN REPRODUCTION

Evidence has been reviewed that suggests the existence of an internal physiological reproductive rhythm which tends to stimulate the growth of the gonads at some particular season of the year, and to this has been added the information that an animal is commonly dependent on some regularly varying environmental factor in order to render the timing of this rhythm more precise. It is now possible to go one step further, for, granted that by these means the gonads have reached potential maturity, yet another set of requirements, psychological in nature, must be satisfied before successful breeding can occur. In the lower vertebrates these are not obvious, although undoubtedly they will be found to exist when these groups are studied in more detail. Already an example is provided by the bitterling. This is a fish with a complex courtship ceremony which must be performed before the female will lay its eggs, and also necessary at this time is the presence of fresh-water mussel into which the egg can be deposited.[44]

Examples of factors of this kind are best understood in birds, and since they have been reviewed in detail by Armstrong[7] it is only necessary to mention a few examples here. When the gonads of a bird are approaching maturity certain needs must usually be satisfied before the gametes are shed and successful copulation can occur. In the first place the immediate environment must be satisfactory. It is unthinkable that a guillemot might be found nesting in the middle of a field, or that a hedge sparrow might lay its eggs on a seashore. The incompatibility of the environment is probably one of the most important of the factors that tend to inhibit breeding among animals in zoological gardens.

Even if the bird is in its normal nesting locality it is common to find that as a necessary preliminary to breeding it must lay claim to and occupy an area of land from which all other members of its species except its mate are excluded.[112] Then there is the question of the nesting site itself, which is normally situated somewhere within this territory. This too must be acceptable, and if it is not, as for instance in the case of the arctic tern when the ground is waterlogged, then ovulation does not occur and eggs cannot be laid.[122] Similarly, in India and Egypt the kingfisher makes its tunnels into the river banks as soon as the water level has fallen far enough for it to do so, and not until then does ovulation begin.[10]

Further there is the stimulus which the presence of one bird exerts on another. The attachment of a male to a female is often necessary before either of them can reach full maturity. In this connexion it is known that an isolated pigeon does not lay eggs, but if another pigeon, male or female, is introduced, egg-laying begins at once. This effect can even be achieved by putting a mirror into the cage,[72] and thus it can be proved that the stimulus is visual and not tactile, olfactory, or auditory. In many species such mutual stimulation is carried to extreme with the development of peculiar behaviour patterns called sexual displays or courtship activities. Particularly in birds, the failure or faulty performance of these activities can prevent successful mating.

Mutual stimulation is particularly highly developed in colonially nesting birds. This was first demonstrated by Darling who studied the herring gull and the lesser black-backed gull,[79] and it is probably also true of the arctic tern.[51] For a long time it has been the habit of these birds to live and nest in flocks so that nowadays they are incapable of nesting successfully in single pairs. Unless a certain minimum number of nesting birds assemble in a group, the females are unable to lay eggs. With larger and larger groups above this minimum the egg-laying of the various pairs is earlier and more closely synchronized.

All these examples may be considered as instances of the psychological (i.e. nervous) stimulation of a physiological mechanism. Summing up, it may be said that unless all those factors which constitute an animal's immediate environment are felt to be satisfactory, then the purely physiological mechanism of reproduction is inadequate to ensure complete maturity and successful fertilization, so that the production of eggs or young becomes impossible.

II. CONCLUSIONS

The breeding seasons of most vertebrate species are determined by two sets of causes, which have been called by Baker[10] the ultimate and the proximate. The ultimate causes of the timing of a breeding season are the reasons why that time of the year is the most beneficial for this purpose. Probably the most important single reason is that the food supply should be adequate both in quantity and quality to satisfy the extra needs of the young when they appear. As to the mechanism by which such breeding seasons have become genetically fixed, it is generally supposed that natural selection must have been responsible.

The proximate causes which determine the timing of a breeding season are three-fold. First there is the internal reproductive rhythm, which usually has an approximate periodicity of one year. Such a rhythm may be stronger or weaker according to the species and also according to age and season, but that it exists generally there can be very little doubt. The results of experiments such as those with minnows, which when kept in the dark in spring nevertheless come to maturity, are conclusive on this point.

The second of the proximate causes which determine the time of breeding is that environmental variant (sun, moon, rain, etc.) to which the cycle is attuned. These factors have been listed in detail, and it has been stressed that their function is to ensure an accurate timing of the sexual season. Normally the stimulus of the external factor reinforces that of the internal rhythm, but if by experiment they are made to clash then either one or the other may prevail. Usually the external factor is the more powerful and over-rides the influence of the internal rhythm.

The third of the proximate causes is that group of factors in the immediate neighbourhood of the individual animal (the breeding area, the mate, and perhaps the social group), which must also conform to an appropriate pattern before the final act, the shedding of the eggs and sperm, becomes possible. Perhaps it may be objected that this last distinction has been too sharply drawn. The so-called environmental factors and the so-called psychological factors may in fact merge together so that the effect of the moon on ovulation in the nightjar, or of water on the spawning of a desert frog, may be more in the nature of a psychological stimulus. As has been repeatedly stressed much further work on such problems is needed.

CHAPTER IV

HORMONES AND REPRODUCTION

I. INTRODUCTION

DURING the last thirty years the increase in our knowledge of the physiology of vertebrate reproduction has been overwhelming, and to-day it is almost more than one person can do to continue to evaluate the spate of new information that is constantly pouring out in many languages from many countries. In these circumstances the present chapter offers little more than the merest introduction to the subject; it is a picture painted in the broadest outlines. For those who would go further there are many more detailed reviews, of which the most generally useful are the two books of Allen[4, 5] and, more recently, those of Burrows,[63] and Robson,[158] and especially Parkes.[218]

In disentangling the physiological processes that initiate and control reproduction, it is necessary first to consider briefly the structures of certain organs, and then, in more detail, the ways in which these organs function and the influences which they exert on each other and on the body in general. Such influences are usually exerted by means of chemical substances known as hormones, which are formed by internal secretory glands, also called endocrine glands. These substances have been classified by Huxley,[113] who has defined a hormone 'as a chemical substance produced by one tissue with the primary function of exerting a specific effect of functional value on another tissue'. Some of these substances may diffuse directly through the tissues, but the commonly known hormones, including those mentioned below, are transported round the body in the blood and lymph.

At the end of the chapter the question of the external environment is discussed again, and an attempt is made to indicate the manner in which it exerts its effect on the internal physiological mechanism.

2. THE PITUITARY GLAND

The organ which apparently holds the keys to the reproductive processes is the pituitary gland, or hypophysis, and although the details of its anatomy may vary widely, its basic structure and function are much the same in all vertebrates. In the adult it is seen as a glandular mass attached by a stalk to the base of the brain, but a study of its development shows that it is a composite organ formed partly from an invagination of the ectoderm of the buccal cavity (the so-called Rathke's pit) and partly from an evagination of the floor of the forebrain. In the cyclostomes these two components may remain separate throughout life, but in the higher types they are intimately fused together.

In its adult form the organ consists of two main lobes, the anterior and the posterior. The anterior lobe is derived from the anterior side of the buccal invagination while the posterior lobe is formed partly from the posterior side of the buccal invagination (which is also called the intermediate lobe) and partly from the nervous tissue which retains its connexion with the base of the brain (and which is also called the neural lobe). The cleft that separates the simple anterior lobe from the composite posterior lobe is all that remains of the cavity of the buccal invagination, the cavity of Rathke's pit.

The various parts of the pituitary gland secrete a number of hormones, but for present purposes only those of the anterior lobe are important. The cells which compose this lobe are of three kinds, and they tend to be mixed indiscriminately together. According to their staining reactions they are known as acidophils (combining with acid stains), basophils (combining with basic stains), and chromophobes (staining with neither). Hormone secretion is the function of the acidophils and basophils, and when they have completed a secretory phase it is thought that both may revert to the chromophobe condition. It appears that the chromophobe cells form a reserve from which the acidophils and basophils can be developed as they are required.

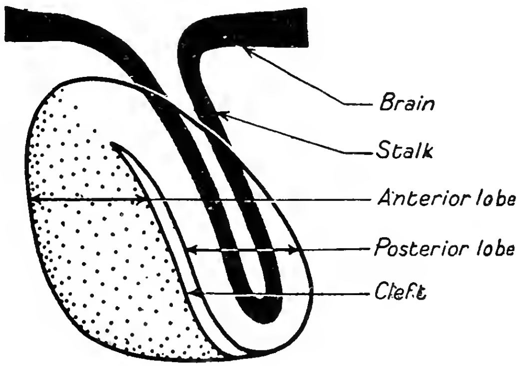

Fig. 3.—Diagram of the structure of a pituitary gland as seen in sagittal section.

The proportion of these three cell types within the anterior lobe varies according to the age and physiological condition of the individual, and from a study of these variations some idea can be obtained of the functions of these cells. The most suggestive evidence is that provided by pathological conditions. Thus it is found that gigantism, or acromegaly, in man is associated with an excessive development of the acidophil cells, while hereditary dwarfism is associated with a complete absence of these cells. Such evidence suggests strongly that the hormone secreted by the acidophils is that which controls body growth.

As regards the basophil cells a curious condition has recently been discovered by Kerr[118] in adult roach parasitized by the plerocercoid larva of the tapeworm

Ligula. For reasons not yet understood, such parasitism is accompanied by a great reduction in the size and numbers of the basophil cells, which in turn is associated with the continuing immaturity of the gonads. Such evidence suggests that the hormone secreted by the basophil cells is that which controls the growth of the reproductive system.

3. THE HORMONES OF THE ANTERIOR PITUITARY

A great deal of effort has been devoted to the extraction of these hormones in as pure a state as possible, but unfortunately they are proteins and the large size of their molecules makes the problem of their analysis extremely difficult. Their structure remains unknown, and although potent extracts have been prepared, it is doubtful whether these even approximate to purity. One of the hormones extracted is that which influences growth, and this will not be mentioned again. The other, which may be a single substance or a complex of related substances, is that which stimulates gonad growth and which is probably derived from the basophil cells.

It is generally believed that there are at least two secretions of the anterior pituitary which stimulate the gonads, and which are therefore known as gonadotropic hormones. Unfortunately most of the research on these substances has been related to the mammals, and relatively little is known of their actions in the lower vertebrates. The effect of one of these hormones on the mammalian ovary is to cause the rapid growth of the follicles containing the eggs, and thus it is known as the follicle-stimulating-hormone, or F.S.H. for short. In males it stimulates particularly the germinal epithelium to cause the production of spermatozoa. It exerts these effects in mammals which are immature,[88, 99] which are in anoestrus,[192] or from which the pituitary has been removed. In pigeons it causes a rapid increase in the size of the eggs in the ovary.[126] Thus the main effect of this hormone appears to be the induction of gonad maturation in both sexes.

The second gonadotropic hormone of the pituitary does not induce this reaction. Its primary function is seen most clearly in female mammals in which, after ovulation, it stimulates the luteinization of the old follicle cells to form the corpus luteum. For this reason it is often known as the luteinizing hormone, or L.H. for short. It is also said to stimulate the growth and function of the non-germinal interstitial tissue in both ovaries and testes, whence it is also known as the interstitial-cell-stimulating-hormone, or I.C.S.H. for short. Its action in the lower vertebrates remains uncertain, but perhaps it functions in similar ways.

When used together F.S.H. and I.C.S.H. reinforce each other. Thus when F.S.H. is injected into 21 day old rats, a given dose induces the ovaries to grow to a weight of about 40 mg. while the same dose with added I.C.S.H. causes growth to about 80 mg.[89] Since I.C.S.H. alone has no effect in these circumstances it is suggested that it acts by sensitizing the gonad to the stimulation of F.S.H. Similarly Lipschütz[127] and others have shown that while F.S.H. does not itself affect the development of corpora lutea, it greatly augments the luteinizing power of I.C.S.H. Indeed it has been suggested that F.S.H. is powerless to stimulate follicle growth in the mammalian ovary unless some I.C.S.H. is also present, and similarly that I.C.S.H. cannot cause luteinization in the absence of F.S.H.[93] At this somewhat confusing point the warning must be issued that the separate identities of F.S.H. and I.C.S.H. in the normal pituitary secretion have not yet been finally established. While it seems probable that they are in fact distinct chemical compounds, the suspicion remains that some yet unrecognized circumstances in the method of preparation of the extracts for experimental purposes may lead to different responses by the gonads to one and the same hormone.[63]

The above observations relate almost exclusively to the eutherian mammals. As regards the lower mammals and other vertebrates almost all the experimental work has involved the injection of pituitary extracts containing both F.S.H. and I.C.S.H. Also in many cases a gonadotropic hormone derived from the placenta has been used instead of that from the anterior pituitary. This substance is much more easily obtained, being prepared from pregnancy urine, and it has a similar biological action to the anterior pituitary hormone. Consequently it is sometimes called the anterior-pituitary-like-hormone, or A.P.L.H. for short. A consideration of its function during pregnancy is out of place here.

Without going into details, it has been found that both the pituitary and the placental gonadotropic hormones are capable of stimulating gonad maturation in the lower vertebrates. This has been demonstrated in immature and anoestrous individuals of species of marsupials,[146] birds,[81, 176, 181] reptiles,[137] amphibians,[61, 62, 168] and fishes.[106, 187] Thus the general conclusion emerges that a hormone of the anterior pituitary gland affects reproduction in all vertebrate classes, and since mammalian extracts were effective in these cases it is evident that this hormone is neither species- nor class-specific. However, it is often found that extracts of pituitaries taken from the same species are more potent than those taken from other species.[150]

It has also been demonstrated in a variety of vertebrate species, including mammals, that when the gonads are mature the actual release of the eggs from the ovary (ovulation), like that of the sperm from the testis (spermiation), is dependent on the pituitary hormones. The release appears to be due to the combined actions of F.S.H. and I.C.S.H., but the precise manner in which it is brought about remains unknown. Since a similar effect is also induced by the A.P.L.H. present in pregnancy urine, this reaction is often used as a test for pregnancy. Until recently the animal most commonly used was the female clawed toad, which lays eggs a a few hours after treatment with pregnancy urine. In the last year or two this test has been superseded by another based on the use of male toads,[95] frogs, and urodels,[151] which react by shedding their sperm.

4. THE TESTIS

The greater part of the vertebrate testis is made up of a mass of spermatic tubules, which are bounded by connective tissue. These tubules, which are woven and twisted together are blind at one end while at the other they converge on to the dorsal side of the testis. There they open into the vasa efferentia, which lead to the vas deferens and so to the exterior. In the teleost fishes the testis is similar in structure, but the ducts are absent.

In a maturing testis the lining cells of the spermatic tubules divide to form spermatogonia, which in turn produce primary and secondary spermatocytes, spermatids, and spermatozoa. Thus a gradient is established with the spermatogonia on the tubule wall and the spermatozoa in the central lumen along which they move slowly towards the ducts. In a rat the time taken for the production of a spermatozoon from a spermatogonium is estimated at about 20 days.

The spaces between the spermatic tubules are filled with blood vessels, lymphatics, connective tissue and the glandular cells of the interstitial tissue.

The testis remains in an immature condition until the hormones of the anterior pituitary gland reach it through the blood stream. Then it is generally thought that the F.S.H. acts primarily by stimulating spermatogenesis within the spermatic tubules, while the I.C.S.H. acts primarily by stimulating the multiplication and growth of the glandular interstitial cells. However, it must be borne in mind that each of these hormones can apparently exert little if any effect in the complete absence of the other.[93]

When stimulated to activity the testis itself acts as an endocrine organ to produce the male hormone, or androgen. This substance is described in the next section, and the only question to be dealt with here is that of its site of formation. For a long time it has been suspected that the interstitial cells, which are glandular in appearance, may be the main source of the testis hormone. The

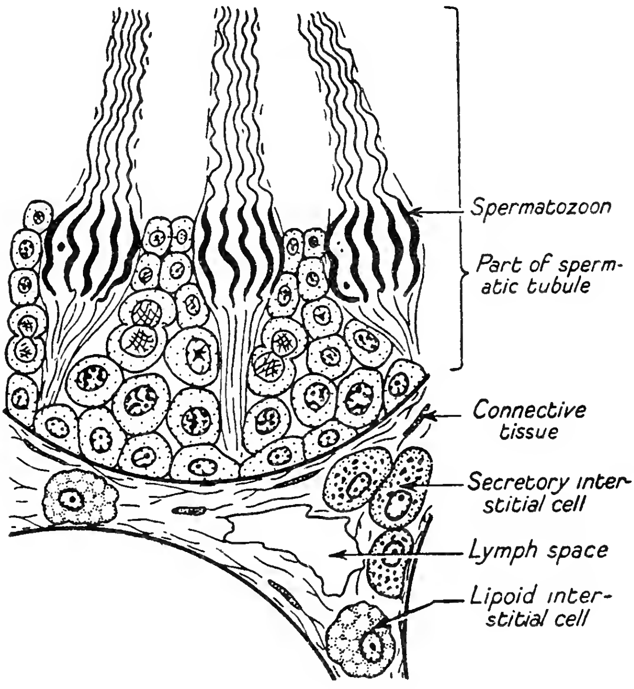

Fig. 4.—The structure of the testis of a chaffinch, showing part of a spermatic tubule and some of the interstitial tissue (after Sluiter and van Oordt).

early work of Benoit[23, 24, 25] supported this view, and showed that hormone secretion in the cock is not interfered with when the spermatic tubules are destroyed by x-rays. Thus, Benoit was driven to assume that the male hormone is formed somewhere in the interstitial cells. Much recent work on this subject has been done by van Oordt and his associates in Utrecht. A re-examination of conditions in the cock[180] has shown that the interstitial cells are of two types; the lipoid cells which store large quantities of fatty material and the secretory cells which do not. It is concluded that the lipoid cells can take no part in secretion, unless perhaps they store the chemical reserves from which the hormone is manufactured.

The evidence regarding the secretory cells is circumstantial and may be stated as follows. When male hormone is being secreted the comb and wattles on the cock's head enlarge considerably so that their size can be used as a quantitative indication of the amount of hormone circulating in the body. An increase in size occurs when normal animals reach maturity and when birds are treated with a mixture of the pituitary hormones, and it is always accompanied by an increase in the number of the secretory cells. Thus the number of these cells present at any time, like the size of the comb and wattles, can be used as a quantitative estimate of the amount of hormone present.

However, even if the main site of male hormone secretion is in the interstitial cells of the testis, the production of this substance is also carried on elsewhere. Even after the removal of the testes some hormone continues to be formed, probably mainly in the adrenal cortex.[63]

5. THE TESTIS HORMONES

The most obvious function of the male, or androgenic, hormones is their stimulation of the accessory sexual organs and secondary sexual characters, and it is by means of these reactions that they are commonly assayed. The main methods used are the rat test and the capon test. Castrated rats or castrated cocks are injected with the test substance which can then be standardized according to the degree of growth of the accessory sexual organs of the former or of the comb and wattles of the latter. There are many known substances which can stimulate such growth, although several of them are synthetic and are probably not found in nature. The actual substance produced in the mammalian testis is thought to be testosterone (Fig. 5). Other androgenic hormones

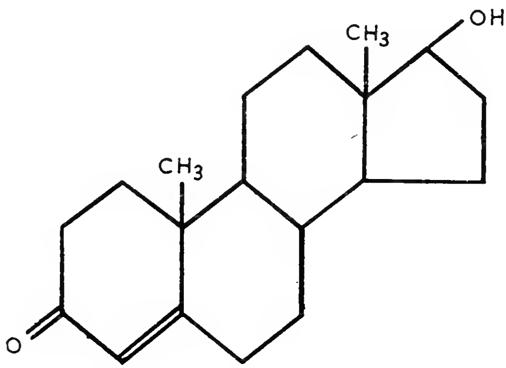

Fig. 5.—The structure of a molecule of testosterone.

have a similar molecular structure, although curiously enough it is sometimes found that the isomer of some particularly potent substance is itself biologically inactive.[63]

It has also been discovered that the normal testis secretes female hormones, also known as oestrogens. The reason for this is still obscure, but evidently the only difference between a male and a female in the formation of these hormones is one of degree. A male typically produces more androgenic and less oestrogenic hormone, while a female does the reverse. It is also important to remember that the effects of the male and female hormones are organ specific rather than sex specific, so that the chief distinction between a male and a female lies not in their hormones but in their possession of different tissues and organs which are competent to react to these hormones.[63] In a male the hormone testosterone stimulates the growth of the ducts which carry the sperm from the testis; the seminal vesicles in which the sperm are stored; the various glands which supply nourishment and fluid for the sperm to swim in; and the penis (if this is present) for the transmission of the sperm to the female. It also induces the growth of those adornments which a male commonly possesses for the excitement and stimulation of the female.

Most of these changes are the result of true growth, that is of cell multiplication by mitosis. It has recently been suggested that this is a fundamental function of both androgenic and oestrogenic hormones, so that the term mitogenic hormone has been proposed to cover them all.[57] It is now also evident that these substances not only stimulate growth by mitosis in tissues and organs related to sex function, but that they may also do this in other tissues as well. So the accessory and secondary sexual tissues and organs, which respond so strongly to the stimulating presence of male hormone, may merely have developed an unusual sensitivity to this substance. It also follows that all tissues and organs have the potentiality of enlargement in relation to sexual processes should a special need arise. In this way there must have originated the comb and wattles on the head of a cock; the thumb pads by which the male frog maintains a grip on the female; and the modified posterior end of the kidney from which, during the breeding season, a male stickleback secretes the sticky substance used in the manufacture of the nest.

If the male hormone is primarily a mitosis stimulator, it remains to be determined whether it also exerts this influence in the testis itself. It has been generally believed that the testis, like the ovary, depends for its development and function only on the hormones of the anterior pituitary. Recently, however, this view has been challenged by Gaarenstroom and de Jongh[93] and by Bullough.[57] It appears that in the complete absence of the pituitary hormones, testosterone is able to maintain the production of spermatozoa,[76] and similarly in the annually breeding ground squirrel it can cause the precocious development of spermatozoa in young animals and their unseasonal development in adults.[190, 191] Among fish it has been used to cause the precocious maturation of the testes of the millions fish,[87] and their unseasonal development in the minnow.[50]

It has also been shown that quantities of F.S.H. which are beneath the threshold required to promote testis growth, produce a strong reaction if given together with I.C.S.H. or with testosterone.[93] It may therefore be suggested that the influence of the anterior pituitary is exercised partly by the direct action of F.S.H. and partly by the indirect action of I.C.S.H. which causes the production of male hormone. Thus in normal circumstances spermatogenesis may be the result of the action of the F.S.H. combined with the mitogenic stimulus of the testosterone.

Male hormone also has the action of checking the secretion by the anterior pituitary of its gonadotropic hormones, and in this way a balance is maintained between the two glands.[63] If a lack of testosterone develops, the anterior pituitary is able to secrete maximum quantities of its gonadotropins. As a consequence the testis production of testosterone rises, and as a further consequence the secretion of gonadotropins diminishes. One way in which this mechanism can be demonstrated is by castration. When the testes are lost the gonadotropic output of the anterior pituitary rises unchecked to a maximum, and abnormally large quantities of these hormones are excreted with the urine where they can be assayed.[63]

This introduces a final point, the question of the fate of the testis hormones. These substances are not stored, and are quickly inactivated by destruction in the body and by excretion in the urine. It is now known that the main site of destruction is in the liver,[30, 78] and that even the excreted fraction is first converted into such substances as androsterone which are biologically less active.

6. THE OVARY

The vertebrate ovary is a solid organ encased in connective tissue and covered by a thin sheet of cells. These cells form the germinal epithelium, which is

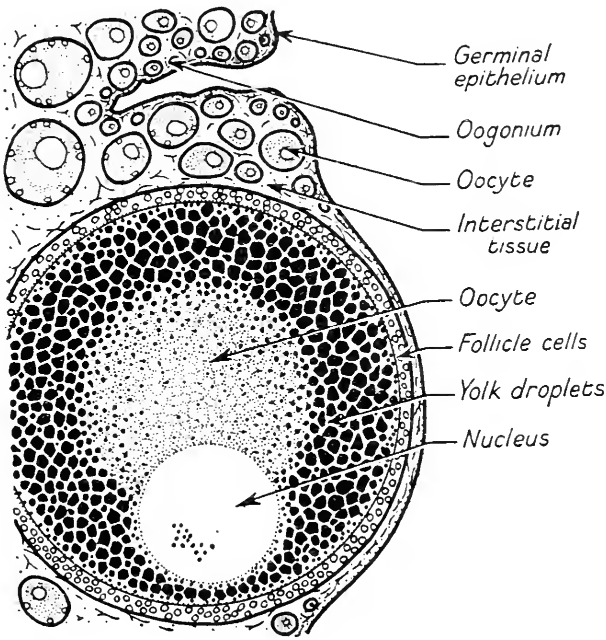

Fig. 6.—The structure of the ovary of a starling, showing a yolk-filled primary oocyte.

continuous with the peritoneum, and they are highly important since from them the ovary is replenished with eggs. The centre of the organ is filled with a matrix of fibrous connective tissue through which run blood vessels and lymph spaces, and in which are embedded the growing eggs. Each egg is enclosed in a group of follicle cells, and between the follicles are numbers of interstitial cells similar to those in the testis.

There are two types of vertebrate ovary which are distinguished by the different degrees of development of the eggs and follicles. In the egg-laying vertebrates the egg is large, due to the inclusion of masses of yolk, and the investing follicle is thin. In the marsupial and eutherian mammals, on the other hand, the egg is microscopic, since it contains no yolk, and it is the follicle that is large. In all ovaries the sheath of follicle cells must burst when an egg is shed. In the lower vertebrates this involves the simple tearing of a thin sheet of cells, but in the higher mammals the follicle is far bigger than the egg which it encloses. Such a follicle becomes distended not by the egg but by the development of a cavity, the antrum, into which fluid is secreted. Follicles with antra are called Graafian follicles, and when fully charged with fluid they burst to release the egg into the body cavity.

After the bursting of a follicle the disorganized cells reform into a group and swell into a structure known as the corpus luteum. This structure is particularly obvious in the mammals where its function has been closely studied.

The cycle of egg production in the ovary starts with the division of one of the cells of the germinal epithelium. Of the two cells thus formed, one passes into the ovary by penetrating the connective tissue.[3, 50, 52, 54, 57] Within the ovary it is known as an oogonium, it acquires a sheath of follicle cells, and it grows without division into a primary oocyte. In the egg-laying vertebrates the main function of the follicle cells is to pass yolk into the primary oocyte until it is greatly distended, but in higher mammals their function is to pass fluid into the antrum. Apparently in all vertebrates it is common for the final divisions of the primary and secondary oocytes (with the shedding of polar bodies) to take place in the oviduct after ovulation.

The effect on the ovary of the follicle-stimulating-hormone of the anterior pituitary is seen particularly in the later stages of the growth of the primary oocyte and of its follicle. In the pigeon injections of this hormone cause the rapid growth of the largest oocytes,[126] while in mammals such as rats and monkeys, it causes the rapid enlargement of the Graafian follicles.[158] In no case,

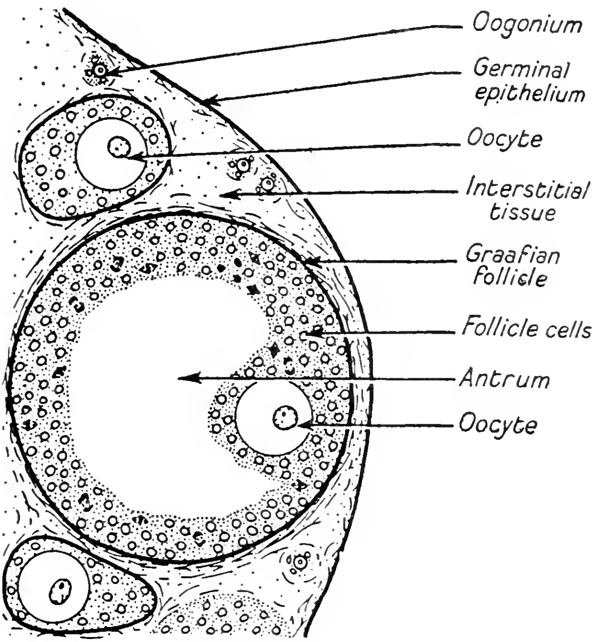

Fig. 7.—A section of the ovary of a mouse to show the developing oocytes and follicles.

however, do these hormones appear to affect the growth of the oogonium or that of the primary oocyte in its earlier period of growth. The approximate stage at which the primary oocyte becomes susceptible to the influence of F.S.H. is, in the egg-laying vertebrates, the time when yolk droplets begin to be deposited in the cytoplasm, and, in the mammals, the time when the antrum forms inside the mass of follicle cells. Thus it is possible to divide the growth of the primary oocyte into two phases; the primary phase before either yolk or antrum appears and before a response is possible to the presence of F.S.H., and the secondary phase after the appearance of yolk or antrum and after the development of a sensitivity to F.S.H.

It is not yet known whether any hormone affects or controls the growth of the oogonium and of the primary growth phase of the primary oocyte.

The second effect produced in the ovary by the anterior pituitary hormones is the stimulation of the production of female hormone. Such a hormone is also known as an oestrogen since its presence in sufficient quantity causes the onset of heat, or oestrus. It is usually thought to be the F.S.H. which induces the secretion of this substance, while it is the I.C.S.H. which causes the growth of the interstitial tissue. If this is true it would appear that hormone secretion in the ovary, unlike that in the testis, is not the function of the interstitial cells. This is an unexpected conclusion and further study of the point is clearly needed, particularly since the interstitial cells of the ovary have a similar glandular appearance to those in the testis.[179]

Various attempts have been made to locate the source of the ovarian hormone and, as regards the mammals, one well-known theory is that the site of secretion lies in the theca interna, which is one of the cell layers in the follicle wall.[71, 144] However, even if this is true it seems certain that the hormone can also be secreted elsewhere. If all the ova and follicles of the mouse are destroyed by X-rays, the oestrous cycle, which depends on oestrogen production, continues unchecked.[154] Thus the interstitial cells may also secrete female hormone, as in the male they are thought to secrete the male hormone.

Among the egg-laying vertebrates there is no evidence as to which is the glandular region of the ovary. However, since in these ovaries the follicle cells have a primary function of supplying yolk to the growing oocytes it

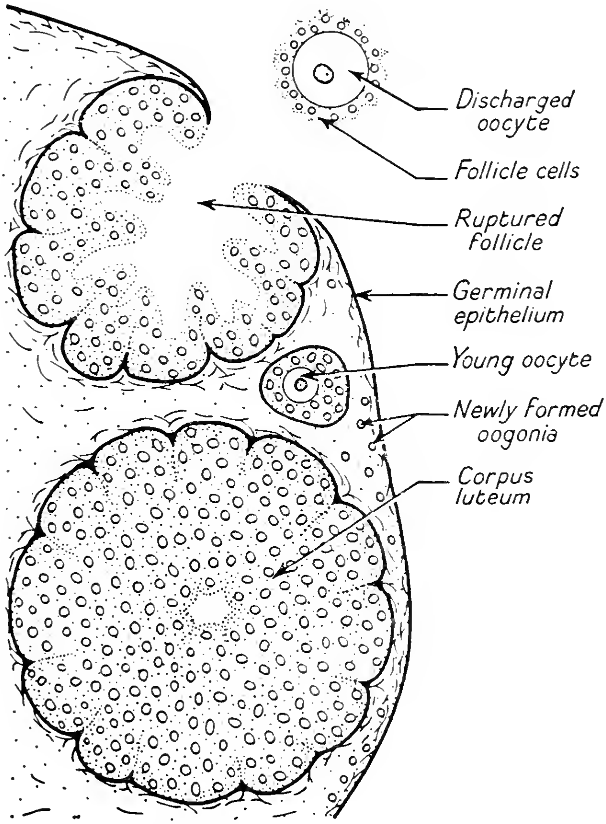

Fig. 8.—A section of the ovary of a mouse to show the method of formation of a corpus luteum.

seems improbable that they can also have an endocrine function.

The third way in which the pituitary hormones affect the ovary is after ovulation when the corpus luteum is being formed, and it is generally considered that this process is stimulated by I.C.S.H. Once formed, the corpus luteum is itself an endocrine gland. In the mammals the hormone that it secretes is known as progesterone, the functions of which are described on p. 65. In the lower vertebrates the only information available is that concerning the bitterling in which it has been suggested that the corpus luteum produces a hormone called oviductin.[44] This is discussed on p. 66.

7. THE OVARIAN HORMONES

The most important hormones produced by the vertebrate ovary are those known as the female or oestrogenic hormones. It is thought that the substance

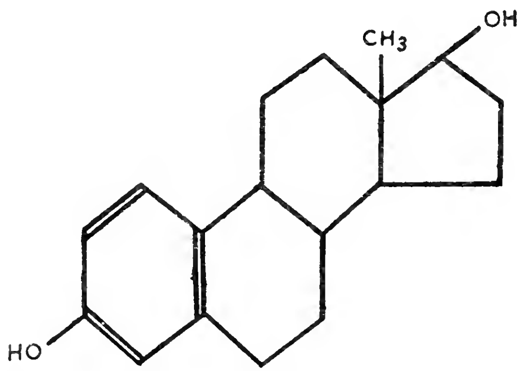

Fig. 9.—The structure of molecule of oestradiol.

actually secreted by the mammalian ovary is oestradiol, and this is the most active natural oestrogen known. Other oestrogens occurring naturally in the body are oestrone and oestriol, which are perhaps formed from oestradiol by oxidation. A variety of other chemically related substances have been synthesized, and many of these induce similar physiological effects. However, oestrogenic activity does not seem to be the property of this type of molecule alone, and other oestrogenic substances which are apparently chemically unrelated have been manufactured in the laboratory and used in medical practice.

The method of standardisation of such oestrogens gives an indication of their normal function. Solutions to be tested are usually injected into mice from which the ovaries have been removed, and the effect is looked for in the cellular content of the vagina. The typical action of these substances is to cause the growth of the Müllerian duct system.

Indeed, a fundamental effect of oestradiol on the body, like that of testosterone, may be the stimulation of cell division, whence these substances have also been called mitogenic hormones.[57] However, those organs which are especially sensitive to oestrogenic stimulation are the oviducts of the egg-laying vertebrates and the vagina, uterus, and mammary glands of the mammals. Consequently, it is these organs which have been mostly studied, and only recently has it been realized that a variety of other tissues, such as the epidermis and the lining of the oesophagus, may react in much the same way. The degree of reaction of various tissues to the presence of oestrogens may vary widely, but as in the male it is evident that most, if not all, body organs have the potentiality of enlargement in relation to sexual processes should special need arise. It must have been in such a manner that the mammary gland was evolved in those vertebrates which suckle their young.

It has also been realized only recently that oestrogens have important functions to fulfil inside the ovary itself.[6, 55, 93] As usual, conditions are best understood in the mammal, and they may be summarised as follows. When the follicle-stimulating-hormone of the anterior pituitary induces rapid growth of a Graafian follicle, part of this growth is achieved by mitosis and part by the secretion into the antrum of the follicular fluid.[53, 55] It is well known that this fluid has a high oestrogen content, and it is evidently this that stimulates the mitotic activity of the follicle wall. The theory can therefore be advanced that while the pituitary induces the active secretion of follicular fluid and of oestrogen, it is the oestrogen that causes the real growth of the follicle.

This conception of the action of the oestrogenic hormone is still a new one, but another of its actions is now well established. When a Graafian follicle bursts to release the egg within it, the follicular fluid is also spilled from the ovary. As it oozes out, the oestrogenic hormone which it contains comes into contact with the germinal epithelial cells on the ovary surface, and there is a burst of mitosis. In the germinal epithelium of one mouse ovary as many as 2,000 cell divisions may occur within a period of $9\frac{1}{2}$ hours,[6] and this results in the production of a new crop of oogonia, which pass into the ovary to start their cycle of growth.[3, 52, 57] Thus whenever eggs are shed from the ovary a new cycle of egg production starts.

In the egg-laying vertebrates there is, of course, no follicular fluid, but the egg-laying period, when oestrogen production is probably at a maximum, is also a time of high mitotic activity in the germinal epithelium. Among fishes this has been seen in the minnow,[50] among amphibians in the common frog,[96] among birds in the starling,[54] and among marsupials in the opossum.[86]

One final point about the oestrogens is that, like testosterone, they have a depressing effect on the rate of pituitary secretion. However, it is said that unless excessive quantities are present, the immediate effect of oestradiol is to depress the production of F.S.H. only, while that of I.C.S.H. increases.

The second substance produced by the normal ovary is the male hormone testosterone, which has already been described. At the moment its function in the female is unknown. Sometimes, in pathological cases, excessive quantities are produced, and in this way a hen may develop such secondary sexual structures as a comb and wattles, while a woman may grow a beard and develop a deep voice. However, in many such cases the hormone responsible is not testosterone, but the male-like hormone of the adrenal cortex. This cortical hormone also has a close chemical relationship with the natural androgens and oestrogens.

A third hormone secreted by the ovary is that formed

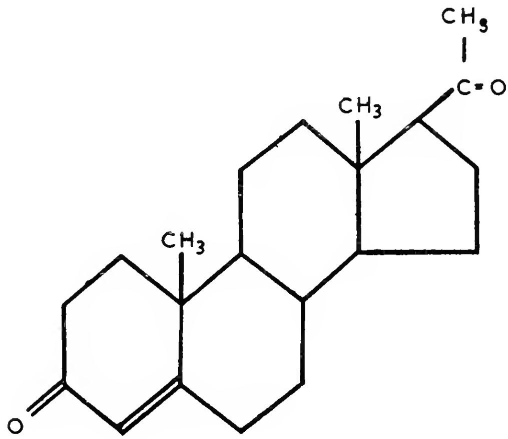

Fig. 10.—The structure of a molecule of progesterone.

in the corpus luteum. Again the situation is best understood in the mammals, and indeed it is often held that true corpora lutea are peculiar to these animals. The corpora-lutea-like bodies in the ovaries of the egg-laying vertebrates are often described as functionless, though this has recently been seriously challenged.[44]

The substance produced by the mammalian corpus luteum is called progesterone, and it has a molecular structure similar to those of the androgens and oestrogens. Of course, its action does not begin until after the bursting of the Graafian follicle, that is after the oestradiol has exerted its full effect. At this moment progesterone takes over to maintain and increase the uterine growth already accomplished. Thus progesterone maintains the uterus in a condition suitable for the implantation of the embryo should fertilisation occur. If there is no fertilisation the secretion slackens and finally ceases, but if an embryo implants itself in the uterus the corpus luteum persists and enlarges.

In pregnancy a second effect of progesterone usually becomes apparent, namely the suppression of any further ovarian activity. This it is able to do because, like testosterone and oestradiol, it has a depressing effect on the secretion of gonadotropic hormone by the anterior pituitary. However this is not the case in all species and it is known that, in the horse and cat,[218] ovulation may continue during pregnancy.

In the egg-laying vertebrates bodies which resemble the mammalian corpora lutea, both in method of formation and in structure, have been seen in all classes. The first attempt to ascribe a physiological function to them was made by Bretschneider and de Wit,[44] who used for this purpose females of a common fresh-water fish, the bitterling. The value of this female as an experimental animal rests in its possession of a long ovipositor, which becomes longer or shorter according to the presence or absence of hormones in the body. It has been found that the most important substance stimulating ovipositor growth is a hormone, which has been called oviductin, and which, though formed in the corpora lutea, is probably not identical with progesterone. However, in this species ovipositor growth must be stimulated *before* ovulation so that the organ is ready for use when the eggs are shed. Consequently it is not the post-ovulation corpora lutea which are important, but the corpora lutea atretica which result from the breakdown of some of the growing oocytes.

It is considered possible that oviductin may be the key substance which stimulates the final growth of the oviducts of the egg-laying vertebrates, and that in all of them it is produced before ovulation in corpora lutea atretica. Thus the pre-ovulation corpus luteum may exert its most important function in the lower vertebrates, while the post-ovulation corpus luteum is most important in mammals. Where exactly in this sequence the production of oviductin ceases and that of progesterone begins has not yet been investigated, and of course the two may overlap. The chemical relationships of these two substances are still unknown, but their biological relationship appears to be close since both seem to exert their main influence on the final stages of oviduct development.

A final word may be said regarding the fates of these various substances within the body. Oestradiol, secreted by the ovary or introduced by injection, quickly disappears. Probably it is partly oxidized to the less active oestrone and oestriol which are excreted by the kidneys.[64] Oestradiol itself is rarely found in the urine,[63] and perhaps the greater part of it is destroyed in the liver, as also is testosterone. As regards progesterone little appears to be known, but it is certainly destroyed quickly and some is excreted in the urine in the relatively inert form of pregnanediol.

8. THE OESTROUS CYCLE

This brief survey of the hormones affecting vertebrate reproduction is now complete, but it is still necessary to fit together the facts that have been given to indicate the sequence of physiological events within the reproductive cycles. The two main cycles to be considered are the yearly seasonal cycle which is common to most vertebrates and the shorter oestrous cycle which is peculiar to the female mammal. It is proposed to consider this oestrous cycle first.

The typical oestrous cycle begins with the active secretion of the gonadotropic hormones of the anterior pituitary. This secretion commences either because the animal has grown to maturity or because of the onset of the breeding season, and it is thought that at this early stage it is the follicle-stimulating-hormone which is produced in the greatest quantities. As a result a few of the half-developed follicles surrounding the primary oocytes are stimulated to rapid growth. This growth is the result of two processes: first the secretion of liquid into the follicular cavity, or antrum, so as to cause the mechanical enlargement of the follicle in a manner resembling the blowing up of a balloon; and second, the

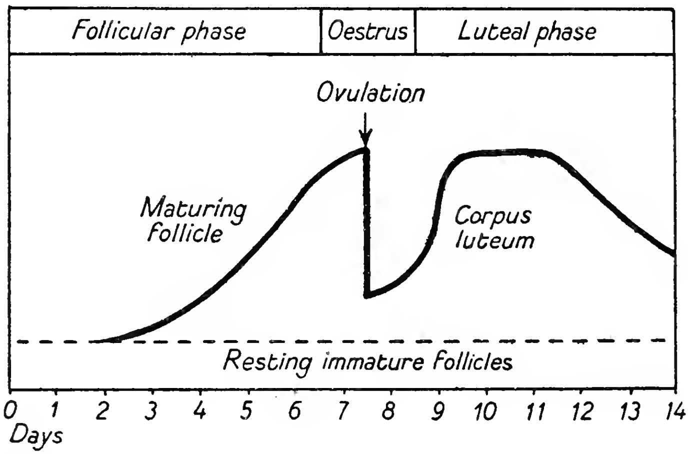

Fig. 11.—Diagram illustrating the changes in follicle size which occur during a typical oestrous cycle. The length of such a cycle may vary from about 5 days in the case of the mouse to about 3 weeks in the case of the pig and the horse.

action of oestradiol (contained in the follicular fluid) which induces active cell division in the follicle wall. For a time these two processes keep pace, but ultimately the mechanical process of distension proceeds faster than that of growth by cell division. At this point, in some way not yet understood,[105] the anterior pituitary hormones cause the follicle to burst to release the follicular fluid together with the egg, which at this time is still a primary oocyte.

During this period of rapid follicle growth, which in the mouse ovary lasts for about 3 days and in the human ovary for about 2 weeks, the rate of secretion of oestradiol rises to a maximum. This causes the growth and distension of the vagina and uterus, and, as described in the next chapter, it also commonly changes the whole behaviour of the animal so that it becomes ready and eager to mate.

As the rate of oestrogen secretion reaches a maximum it reacts on the pituitary to depress the rate of production of F.S.H., and, so it is said, to increase the rate of secretion of I.C.S.H. Thus about the time of ovulation the supply of F.S.H. and of oestrogen is diminishing, and the I.C.S.H. is then mainly responsible for the luteinization of the cells of the ruptured Graafian follicle to form the corpus luteum. In most species the corpus luteum immediately begins to secrete progesterone, but the rodents are peculiar in that the corpus luteum does not become functional unless pregnancy ensues.

Progesterone exerts a variety of influences at this time. In the first place it stimulates the final build-up of the uterine lining ready for the implantation of the embryo should fertilisation occur. In the second, it inhibits any further production of F.S.H. by the anterior pituitary and so it may prevent the growth of any more ovarian follicles. Thirdly it is also said to facilitate the excretion of any remaining oestrogen via the kidneys. If the animal becomes pregnant the activity of the corpus luteum is usually prolonged, and the uterus continues to grow in size to accommodate the enlarging embryo.

In the absence of pregnancy, however, the activity of the corpus luteum quickly wanes so that, with neither oestradiol nor progesterone present in sufficient quantities to inhibit it, the anterior pituitary can once more begin to secrete its follicle-stimulating-hormone to begin another cycle. At this moment, when the concentrations of oestradiol, progesterone, and the pituitary hormones are all at a minimum, the uterus and vagina cease their growth, their blood vessels contract, and many of their cells undergo resorption so that both organs shrink rapidly to a minimum size.

In the menstrual cycle of the monkeys, apes, and man the same events take place in the same sequence. At the end of a menstrual period the F.S.H. begins to be secreted by the anterior pituitary with consequent

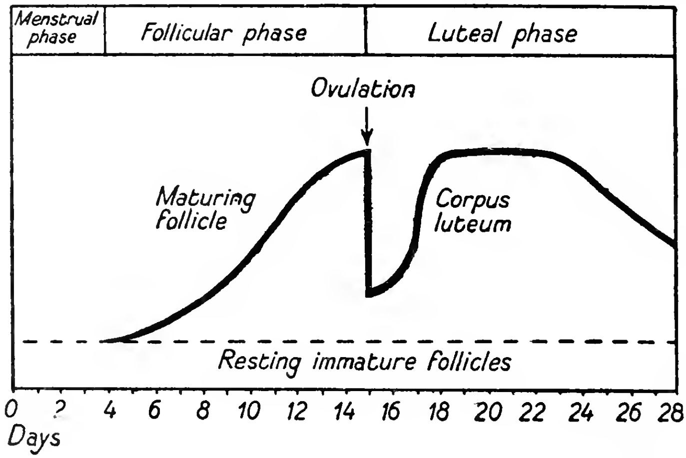

Fig. 12.—Diagram illustrating the changes in follicle size which occur during a typical human menstrual cycle. In monkeys and apes the average length of the menstrual cycle varies from about 16 days in a capuchin to about 45 days in a gorilla.

oestrogen secretion and follicle growth. After ovulation progesterone maintains the uterus in readiness for the implantation of the embryo should fertilisation occur. Finally, in the absence of fertilisation, the production of progesterone slackens and the uterus, having neither oestradiol nor progesterone to maintain it, undergoes destructive changes. During this time the breakdown of the uterine wall is so active that capillaries are ruptured and a flow of blood escapes through the vagina.

In a human cycle in which ovulation occurs half-way between menstrual periods the phase of follicle growth lasts for about 12 days, that of corpus luteum activity for about 12 more days, and that of tissue destruction in the uterus (the menstrual period) for about 4 days. However, man is peculiar in that the widest variation exists in the time of ovulation within the cycle, although in any one individual this time is perhaps fairly constant. Thus the follicular and luteal phases may be longer or shorter than 12 days. A case has even been described in which ovulation took place regularly during the menstrual period,[58] which was perhaps due to the failure of the corpus luteum to secrete progesterone and so to delay uterine breakdown.

9. THE SEASONAL CYCLE

A seasonal cycle of reproduction is found in most vertebrates and in both sexes, and like the oestrous cycle its internal control has been thought to be centred in the anterior pituitary gland (but see p. 102). Marked changes have been described in the histology of this gland at the onset of the breeding season, one of the best surveys being that of Moore,[143] who studied the ground squirrel. During anoestrus the anterior lobe of the pituitary is reduced in volume, its cells consist mainly of small chromophobes, and no gonadotropic hormone can be detected. With the approach of spring the anterior pituitary increases in size, there is a marked production of basophil cells, and the presence of gonadotropic hormone can be demonstrated. At the close of the breeding season the reverse changes occur. Similar variations in the anterior pituitary have been described in the case of the dog,[193] the wood-chuck,[156] and the Virginian oppossum.[193]

With the formation of the basophil cells and the consequent rise in the output of gonadotropic hormone, the testes and ovaries are stimulated to develop. In the testes this is seen in an increase in the number of glandular interstitial cells, which begin to secrete the male hormone testosterone. In the first place this hormone acts on the testis itself to cause, or assist, the process of spermatogenesis. In the second it circulates in the blood stream to stimulate the growth of accessory sexual organs, which include such structures as the vesicle gland (the so-called seminal vesicle), and of the secondary sexual characters, which are usually seen as adornments of various kinds.

In a male the secretion of testosterone is not cyclic, but a balance is struck between it and the rate of secretion of the pituitary gonadotropin. This balance remains relatively steady until after all the spermatozoa have been shed. Then the activity of the anterior pituitary quickly ceases, and that of the testis perforce follows suit as the glandular interstitial cells are reduced in numbers.

The changes occurring at the onset of the breeding season of a female mammal with only one oestrous cycle in a year are those already described on p. 67. The only difference is that no further cycle begins until after many months of anoestrus.

In the egg-laying vertebrates the effect of the seasonal pituitary stimulus is two-fold. In the first place it causes the growth of the primary oocytes by the deposition within them of large quantities of yolk, and in the second place it induces the secretion by the ovary of the oestrogenic hormone. This hormone, by stimulating cell division, causes the enlargement of the oviducts and of any secondary sexual character which may be typical of the species.

10. THE PROBLEM OF INTERNAL REPRODUCTIVE RHYTHMS

These accounts of the reproductive cycles and of their hormonal control have so far included no consideration of the mechanisms which determine their timing. This is actually a double problem since in the first place there is the question of the method of timing of the internal reproductive rhythms, and in the second there is the question of the method by which environmental changes are able to influence and control reproductive physiology.

With reference to the first question, two cycles have been described which can operate independently of environmental control. The first is the oestrous cycle which in animals such as rats and mice continues unchecked (except by pregnancy) throughout the whole year. The average length of cycle is fixed and typical for each species, but so far it has been impossible even to hazard a guess at the way in which this is achieved. It was once thought that the rhythm could be accounted for merely in terms of a see-saw action between the pituitary stimulation of the ovary on the one hand and the ovary inhibition of the pituitary on the other. However, the same relationships between pituitary and gonad exist in the male where there is no vestige of an oestrous cycle, and clearly some other explanation must be sought.

An exactly similar difficulty must be faced regarding the problem of the internal reproductive rhythm which lies behind the seasonal cycle. While the final control of such cycles is usually exercised by the external environment, it is nevertheless necessary to suggest that somewhere inside the body there exists some tissue or organ that experiences a physiological rhythm with a periodicity of approximately one year.

It is usual to sidestep these difficulties by suggesting that both the oestrous and seasonal rhythms depend on the periodic activity of the anterior lobe of the pituitary or more probably of the hypothalamus (see p. 102).

II. THE INFLUENCE OF THE ENVIRONMENT

Finally, although our knowledge of the subject is still only slight, it is necessary to discuss the manner in which external environmental changes are able to affect the physiology of reproduction. Most of the analyses that have so far been attempted relate only to one factor, that of increasing light. However, there is also some evidence of the manner in which the so-called psychological factors operate, and this also bears on the problem.

In the first place it is necessary to reconsider the original experiments of Rowan in which he stimulated maturation of the gonads of the junco by means of increasing light in autumn.[159-162] At that time he thought that the light *per se* could not be the critical factor involved, and he suspected that the stimulus to the gonads came from the extra exercise which the birds were able to enjoy. He therefore carried out an investigation without the use of extra light in which, by means of rotating perches, the birds were kept awake and moving for hours after the winter darkness had fallen, and again the result was an increase in testis size over that of the normally sleeping controls.[161] The experiment was repeated by Bissonnette,[31] who used the starling, but neither this nor any other species subsequently examined has responded in like manner. However, although it has been impossible to confirm Rowan's results, it is important to remember, as always in this work, that a factor which is of critical importance for one species may be unimportant to another. Thus the stimulus of spring to a junco may be through its increasing wakefulness (i.e. through the increased activation of its proprioceptors) while to a starling it may be through the increasing light itself.

All the later attempts to analyse the effect of increasing light have been made on the assumption that it is the light itself which exerts the stimulus. In the first place attempts were made to discover which wavelength is most effective, and again contradictions arose. The starling was found to react most to the longer waves of red light and to be relatively unresponsive to green, blue and ultraviolet,[33] while the ferret was found to be most responsive to the short ultraviolet waves, although it also showed some response to the whole of the visible spectrum.[133] Again the experiments showed that animals differ widely regarding the factors to which they have become attuned.

The next step in the analysis was to study the pathway along which the action of the light passes into the body. This problem was considerably simplified by the obvious expectation that the only organ capable of appreciating increases in light is the eye, while the one internal organ which must be stimulated is the anterior pituitary gland. The problem was therefore to discover the route between them.

To prove the importance of the eye itself a number of experiments were performed, the first being those of Benoit.[27-29] He worked with the duck and showed that the removal of the eyeballs did not inhibit the growth of the gonads in spring. However, when ducks were kept in darkness the spring gonad development was slower than usual, and if hoods were placed over the head a similar result was obtained. From this last observation he concluded that the region round the eyes of a duck is also light sensitive so that if either the eyes or this surrounding region is left exposed the gonads mature at their normal rate. It now appears that the duck, a bird that is highly bred for domestic purposes, is an unsuitable animal for such work since it apparently possesses a powerful inherent reproductive rhythm by which it is able to achieve breeding condition in the complete absence of external stimulation. A similar criticism applies to the work of Ivanova[114] who used the sparrow, which moreover has only a diffuse breeding season.

More reliable results have been obtained from the ferret. In this species the internal rhythm is not so strong, and in the absence of light in spring sexual development is either prevented or greatly delayed.[133] Experimentally it has been shown that the cutting of the optic nerves has the same effect in eliminating or delaying the onset of heat. Thus the importance of the eye has been confirmed, and it is evident that the pathway of stimulation lies along the optic nerve. In the higher vertebrates, with bodies covered with feathers or fur, there is little possibility of other light receptors being involved, and Benoit's observations on this point must be regarded with scepticism. However, among the lower vertebrates other light sensitive organs may be found, and indeed Scharrer[170] has shown that blinded minnows are still capable of appreciating changes in light intensity.

More recently attempts have been made by Clark *et al*[67] to trace further the course of the stimulus as it passes from the eye to the anterior pituitary gland. In the first place they confirmed that in the ferret the first part of the path lies in the optic nerve. Then they proceeded to make experimental lesions in the brains of female ferrets, and they found that not even the removal of the complete visual cortex could prevent the development of oestrus at the usual time. The conclusion drawn was that the visual stimulus depends on impulses passing either to the ventral nucleus of the lateral geniculate body, or to the subthalamus via the accessory optic tracts.

The problem has recently been tackled again by Thomson and Zuckerman[185] who have once more confirmed that the stimulus is a nervous one which enters the brain via the optic nerves.

The important conclusion arising from this work is that the secretory activity of the anterior pituitary is modified by nervous stimulation, and this is confirmed by a study of the psychological factors affecting reproduction. In the birds, which have been most extensively studied in this connexion, the eyes again appear to play a dominant role. The stimulus to breeding which is afforded by the sight of the nesting place, the mate, and sometimes the social group has already been described (p. 41), and this aspect of the problem is well summarised by Marshall[130] in the following words: 'It has been shown that the gonad-stimulating hormone of the pituitary will cause ovarian development and ovulation in birds, and that sexual posturing or even the mere association of two individuals will initiate nest-building and ovulation. There is a presumption, therefore, that sexual posturing produces stimuli which act upon the anterior pituitary through the hypothalamus, and so effects the necessary synchronisation between the sexual processes of the male and female birds. Herein then, in all probability, lies the biological or race-survival value of sexual display and of the adornment which in many species is taken advantage of to render the display more effective. Those birds which have brighter colours, more elaborate ornamentation, and a greater power of display must be supposed to possess a superior capacity for effecting by pituitary stimulation a close degree of physiological adjustment between the two sexes so as to bring about ovulation and the related processes at the most appropriate times.'

Finally it remains to consider the effect of copulation on ovulation since this too demonstrates the important influence of the nervous system on the anterior pituitary. While this nervous mechanism is probably present in most mammals, it is best seen in such a species as the rabbit. Here it is so highly developed that ovulation always occurs automatically after copulation. The act of mating initiates a train of events, the first step in which is the passage of a wave of nervous excitation to the brain and so to the pituitary. The anterior lobe then begins to discharge its stored gonadotropic hormone which induces ovulation within 24 hours. If the connexion between the pituitary and the brain is cut ovulation does not occur,[45, 46] and, of course, the same is true if the pituitary is removed altogether. Conversely, ovulation can be induced without copulation if gonadotropic hormone is injected.

This effect can also be obtained experimentally by inserting a glass rod into the vagina, or even by the mere sight of a male. It is amusing to recall that when the ovulatory mechanism of the rabbit was first being studied Villemin is reported[21] to have expressed his complete disbelief that a female would ovulate on being merely ogled by a male in a nearby cage, but apart from the floweriness of the language this may indeed happen!

These examples of nervous stimuli to the secretory activity of the anterior pituitary are all taken from the birds and mammals. As Burrows[63] says it is probable that such stimuli play a greater role in the higher vertebrates, although there is plenty of evidence that they are important in the lower forms as well. In man himself the balance between nervous state and reproductive capacity is also well known to medical men, and one of the commonest causes of the stoppage of the menstrual cycle is said to be nervous shock.

12. CONCLUSIONS

To draw together the evidence recorded in this chapter is a particularly difficult task, but by omitting details and ignoring controversy it may be attempted as follows.

The most fundamental point which has been established is that the anterior pituitary is a control centre of the reproductive processes, although it is perhaps itself under the control of the hypothalamus (see p. 102). The pituitary is undoubtedly the intermediary between the external environment and the nervous system on the one hand and the maturation and proper functioning of the gonads on the other. In all cases which have been studied the influence of the external environment reaches the anterior pituitary through the eyes, the optic nerves, and the brain, but as other species with other habits come to be studied other sense organs will undoubtedly be found to be involved.

The pituitary hormones stimulate the gonads in two ways. First they cause them to secrete their own hormones (androgens in the testis and oestrogens in the ovary), and second they work together with these hormones to induce the maturation and escape of the germ cells.

The gonad hormones may also exert a powerful stimulus to cell division throughout the body, and thus they cause the growth of the accessory sexual organs and secondary sexual characters without which successful breeding could not occur.

In conclusion a word of caution is perhaps not out of place. In handling such an abundance of evidence, most of it inconclusive and much of it contradictory, it is impossible to do more than to pass a personal opinion as to what is significant and reliable. Another, judging the same case, may be found to lay stress on different parts of the narrative and even in some particulars to arrive at different conclusions. In such a field of research, which is still being exploited so vigorously, the future still holds all the final answers.

CHAPTER V

SEXUAL BEHAVIOUR

I. INTRODUCTION

FOR a very long time it has been clearly understood that a close connexion exists between the state of the reproductive system and the behaviour in which an animal indulges. It is obvious to any layman that as an animal reaches maturity its activities and interests change, and similar changes are also strikingly obvious during the course of a reproductive cycle which is characterized by alternating periods of gonad growth and regression. As regards the oestrous cycle, changes are evident in the behaviour of a bitch when it comes on to heat, and as regards the seasonal cycle an example can be given in the sudden urge to nest-building that seizes a bird when its gonads are nearing maturity. Conversely it will be remembered that throughout the whole of recorded history the striking effects of castration on both beasts and men have been widely understood, and even as regards the female Aristotle could write 2,000 years ago that 'the ovaries of sows are excised with the view of quenching their sexual appetites'.[184]

Of course, the behaviour shown by an animal is simply the outward sign of an internal activity of the nervous system, and therefore cyclical behaviour changes must be regarded as reflections of cyclical changes in the nervous state. So while towards the end of the last chapter the effects of nervous activity on breeding condition were discussed, it is now necessary to reverse the process and to examine the effects of breeding condition on nervous activity. Although this is a relatively modern study, striking results have already been obtained, and recommended reviews for further reading are those by Young[200] who deals especially with female mammals, Bullough[56] who considers the case of the birds, and Beach[21] whose book is comprehensive.

2. THE GONADS AND SEXUAL BEHAVIOUR

When the anterior pituitary gland becomes active to induce the growth of the gonads, this growth is accompanied by a steady increase in nervous tension. At first this may result only in the development of apparently confused and incomplete behaviour patterns as when a bird excitedly visits its nesting hole for the first time, but is then unable to do more than stand in evident uncertainty as to what the next move should be. Ultimately when the gonads are approaching full maturity, and when environmental and psychological conditions are satisfied, these behaviour patterns crystallize into successful courtship activities, which end in copulation and may be accompanied by such other activities as nest-building. The compelling nature of this increased activity is often referred to as the sexual drive, and its strength is 'expressed in quantitative terms that describe sexual activities with respect to frequency of occurrence, vigour and persistence'.[183]

Increases in the sexual drive associated with increased nervous tension are evident in a female rat on the approach of oestrus. Only when the development of the ovarian follicles is nearing completion will she receive the male, and at this time she will actively seek him, even if this involves crossing an electrically charged grid which has been laid between them.[189] The frequency of her movements at this time are amazing, and can be measured by keeping her in a revolving drum with a counting mechanism attached. In this way it has been shown that a rat which is not on heat may turn the drum some one or two hundred times in a six-hour period, but that during oestrus the same animal moves so rapidly that the drum may make some 4,000 revolutions in the same period.[183] This is one of the quantitative methods available for measuring sex drive, and indeed, until simpler techniques became available, it was used for determining the degree of maturation of the ovarian follicles.

As regards the seasonal reproductive cycle, which is present in most vertebrates, the correlation between gonad size and and overt behaviour is a close one, as may be illustrated by the case of the British starling.[54] During July and August, when gonad size is at a minimum, song is quiet, nest-hole visiting is rare, and a communal life is the general rule. In September and October gonad growth commences and immediately song becomes loud and prolonged, nest-hole visiting is common, and the birds become associated in pairs. During autumn and winter the gradual growth of the gonads is accompanied by increasing sexual activity, which shows itself in increasing attachment to the nesting site and to the mate, and in an increasing intolerance of the social life. Thus about the end of December communal roosting gives place to nest-hole roosting in pairs, and in mid-February nest-building may begin. By April, when the gonads are fully developed, the sexual behaviour patterns are completely formed so that successful breeding can occur, the eggs can be incubated, and the young can be fed. When the gonads regress in June all such activity ceases, the pairs break up, the birds lose their attachment to their nesting sites, and the communal life begins again.

In contrast to this yearly cycle in the British starling it is significant to notice that in the Continental starling gonad growth does not begin until February and no sexual behaviour is seen until early March.[120] Then the males begin to sing, the birds return to their nesting places, and the social life is discontinued.

Many other such cases could be quoted from all the vertebrate classes to show the relationship between gonad size and sexual activity,[21, 56] but it is sufficient to say here that no exceptions are known.

However, while the activities of most vertebrates may be closely associated in this way with the state of the reproductive system, in the higher mammals, and particularly the great apes, the connexion, though present, becomes a little less obvious. It is clear enough at puberty when the gonads mature and sexual activity becomes intense, but once it has started this activity is maintained almost without intermission until the onset of old age. In the female the significance of the oestrous period is reduced or even lost, although in more primitive primates such as the lemur, *Galago senegalensis mohli*, the female is said to permit copulation only during oestrus in the manner of rats and mice.[128] However, in the rhesus monkey, while the female is most ready to accept the male just before ovulation, copulation may occur at other times as well,[21] and in the chimpanzee the female will receive the male at any phase of the ovarian cycle.[199] Conditions similar to those in the chimpanzee are also found in man, the course of the ovarian cycle having little if any effect on behaviour.

The question of the relation between the gonads and behaviour has also been tackled on an experimental basis and the earliest of such experiments, involving the removal of the gonads, were carried out in pre-historic times, perhaps originally as a reprisal against conquered enemies. It is now known that the results of gonad removal vary with the species, the sex, and also the time at which the operation is performed. In males it is generally true to say that if the testes are removed during immaturity there is a complete prevention of all sexual activity, but that if they are removed from an adult the results are variable. In the lower vertebrates the castration of adults usually eliminates or greatly depresses sexual activity, and many examples from the fishes, amphibians, and reptiles are listed by Beach.[21]

In birds, too, it is known that castration disrupts or eliminates song, courtship display, and other mating activities. This has been demonstrated in the case of the ruff,[152] and of the turkey.[153, 177] However, such experiments are sometimes complicated by unexpected secondary effects. Perhaps the most surprising case was that reported by Riddle,[157] who studied pigeons which were congenitally without gonads and which nevertheless developed 'complete and emphatic masculine behaviour'. This observation naturally led him to deny that, in this species at least, male behaviour depends on the state, or even the presence, of the gonads. However, an explanation of this curious state of affairs is possible. It will be remembered that in the absence of the gonads the anterior pituitary gland tends to become overactive, to which the adrenal cortex responds by abnormal growth.[121] It has already been remarked that, when excessively active, the adrenal cortex exerts a male-like influence which may easily account for the male behaviour and so rob the observations of their apparent significance.

Mention must also be made of mammals in which castration sometimes fails, at least for a time, to prevent or depress sexual activity. Occasionally such failure may also be related to the induced hyper-activity of the adrenal cortex, but there is a further complication which arises in these animals, particularly if they are adult at the time of operation. When the testes are removed from adult mice or rats there is a lessening of the desire to mate, but this effect does not become apparent until weeks or even months have passed. In man this delay may be much longer.[21] The reason for this seems to be that these animals, having experienced sexual activity before the operation was performed, possess a clear memory which, together with the strong, if unconscious, desire to imitate the actions of others and to maintain a position in the social group, is sufficient to preserve sexual interest and activity for a considerable time. Such a tendency is particularly strong in man.

Ovary removal in the female has similarly depressing effects on mating behaviour. If the operation is carried out when the animal is young the appearance of sexual activity is prevented altogether, and if it is carried out when the animal is adult then such activity disappears completely in the great majority of cases. The effect is more clearly defined than that obtained by castration in the male, and it has been demonstrated in all vertebrate classes. Even in the case of the mammals the effect is clear cut, and, again unlike the male, it develops immediately after the operation instead of appearing gradually. However, as usual, the case is confused in the human by psychological and social factors, so that the removal of the ovaries results in little if any loss of sexual activity.[21]

Before leaving this subject, a curious reaction which sometimes follows the removal of the ovaries of birds must be mentioned. Most birds possess only the left ovary, and, when this is taken away, interesting behaviour changes may follow. In a hen, the first reaction is normal with a loss of interest in the nests, the cessation of cackling, and the disappearance of the normal female reactions when approached by a cock.[97] Later, however, the bird may start to develop male plumage and a comb, and to crow and otherwise show male behaviour. This result was baffling until it was found to be associated with the development of the rudimentary right gonad. Apparently, when the left ovary is removed the secretion rate of gonadotropic hormone from the anterior pituitary rises unchecked to a maximum to stimulate the growth of this normally quiescent organ. In these circumstances, for reasons which have not yet been fully explained, the growth is commonly bisexual and results in the appearance of both oocytes and spermatic tubules to form an ovo-testis. It is when the spermatic tubules appear that the male behaviour develops and the bird crows regularly.

This introduces the interesting subject of sex reversal, a process which has been reported commonly in all the lower classes of vertebrates. Although the reason need not concern us here, such a change, when it occurs spontaneously, is always in the direction female to male, and is associated with the sudden appearance of spermatic tissue in the ovary. Among fishes such spontaneous reversal has been described in the minnow[49] and in the swordtail,[21] and it is sometimes so complete that the pseudo-male animal produces spermatozoa and successfully fertilizes other females. Among amphibians a series of cases of intersexual frogs and toads has been reviewed by Crew.[74] The 'males' which resulted from this change were able to mate normally, but of course, since they were genetically females, all their offspring were females too. In birds sex reversal is also well known, and again Crew[75] has reviewed a series of examples in the case of the domestic fowl. These observations show clearly that as testicular tissue develops male behaviour also appears until finally the birds are able to crow and to copulate with other hens.

Thus it becomes obvious that male and female behaviour is in no way genetically fixed, but that each is capable of considerable modification by circumstance. Indeed, male behaviour on the part of females is apparently normal in some cases, as in the British starling[54] and the British robin[123] in autumn. In these birds it has been suggested that its curious appearance at this time is related to a transient excessive secretion of androgenic hormone from the ovary and its biological significance has been discussed.

In the mammals the sexes are more stable so that true reversals are extremely rare. However, many instances of pseudo-reversal are known, which are caused by an abnormal growth of the adrenal cortex in otherwise normal females. This overgrown and overactive tissue exerts a male-like influence to cause the development of male secondary sexual characters and of male behaviour. Commonly reported cases of sex reversal in man are usually due to this, and when the adrenal overgrowth is cut away, the ovaries are able to exert their influence once more so that a reversion to the female type follows.

3. HORMONES AND SEXUAL BEHAVIOUR

Consideration must now be given to the effects of the gonad hormones on behaviour since almost all those who have correlated the condition of the gonads with sexual activity have done so on the assumption that this activity is due to the actions of these substances on the nervous system. As long ago as 1903, when the study of hormones was still very much in its infancy, Bouin and Ancel[40] concluded that it is the gonad interstitial tissue which, '*par sa sécrétion interne, tient sous sa dépendance l'ardeur genitale*'. Also, as long ago as 1910, Steinach[182] suggested that courtship and copulatory behaviour were dependent on the 'erotization' of the nervous system by the gonad hormones, but attempts to prove this had to wait until these substances had been analysed and manufactured in a pure state.

Actually the first attempts to induce behaviour changes by chemical means were made not with the gonad hormones but with extracts of the anterior pituitary. It was found that these extracts, when injected into newly-hatched male chickens, caused them to crow when only 9 days old and to attempt to copulate when only 13 days old.[81] Later it was found that normal courtship activities could be induced in the same way in the lizard *Anolis carolinensis* in winter,[85] as well as in the anoestrus horse,[102] cat,[194] and dog.[125] It is now evident that such stimulation is obtained at second hand through the induced activity of the animal's own testes or ovaries.

Attempts to by-pass the gonads and to induce a direct effect on behaviour were next made with the gonad hormones themselves and from the beginning the effects of the injection of male hormone were dramatic. In most of these experiments the synthetic testosterone propionate was used because it is biologically more active than the naturally occurring testosterone. When it is injected into animals which are immature or in anoestrus it induces a rapid development of male behaviour. Under its influence the non-breeding tree frog gives the typical breeding croak and shows male copulatory behaviour[98]; the castrated male lizard, *Anolis carolinensis*, develops sexual activity[147, 148]; month-old chicks of the black-crowned night heron develop a guttural voice and indulge in territory defence, nest building, all male courtship ceremonies, copulation, and brooding[149]; and a variety of mammals, immature, anoestrous, or castrated, show similar behaviour changes.

It is interesting to discover too that these powerful and drastic results are produced in female as well as in male animals. A striking example of this is described by Shoemaker[178] who injected female canaries with testosterone propionate, and found that they suffered a complete suppression of female behaviour. After a few days they were singing loud and long in the manner of males, and were indulging in normal male courtship behaviour.

One effect of the male hormone that deserves special mention is its stimulus to personal aggressiveness which in turn leads to social dominance in a group. This has been studied extensively, the original observations being those of Schjelderup-Ebbe[175] who concluded 'that there exists among birds a definite order of precedence or social distinction'. What he found in so many bird flocks has since been noted in groups of fishes, reptiles, and mammals. In each case one individual in a group has precedence over all the others so that it may bully and drive them away without retaliation, while the others can be numbered according to their positions on a declining scale. Particularly in birds this scale has come to be known as the peck order.

In attempting to explain this hierarchical system, Schjelderup-Ebbe suggested that such factors as strength, age, sex, and season are probably all important factors in determining the position of an individual in the peck order. The first experimental analysis of the problem was that of Allee and his co-workers[2] who attempted to change the peck order by means of hormone treatment. Since then it has become obvious that personal aggressiveness and effectiveness in combat are in direct proportion to the amount of male hormone present in the body, and that this is the most important single factor determining an individual's position in the peck order. Experimentally the effects of injections of testosterone propionate are once again extremely dramatic so that low-ranking hens can be made to rise rapidly to the top of the order. The same result has been obtained in experiments with many diverse species, and in all cases the treated animals showed an increase in bodily vigour and in willingness to fight. No similar effect is induced by the female hormones, and it would therefore appear that dominance within a flock is due mainly to the degree of maleness of the various individuals. This conclusion can be applied to females as well as to males since it will be remembered that the normal ovary secretes male hormone.

Most of these observations and experiments have been made with domesticated or caged animals. It seems probable that among wild animals, such as the starling, which live a social life during their non-breeding season, it is the increase in aggressiveness and intolerance accompanying the growth of the gonads that causes the breakup of the flocks at the beginning of the breeding season.[54, 120]

As usual it is dangerous to apply these conclusions directly to man himself. While aggressiveness and social dominance among both men and women may bear some relation to the hormone testosterone, it is obvious that other factors, psychological and social, are also involved.

Investigations involving the injection of a female hormone, such as oestradiol, into female vertebrates have also produced striking changes in sexual activity. Female behaviour has been induced out of season and after the removal of the ovaries in all the lower vertebrates which have been examined, and the effect is particularly clearly defined in mammals.[21] Oestrogens have been used to bring farm animals on to heat, and to increase their willingness to receive the male. In this way cattle which had never bred successfully before were induced to become pregnant.[103] Treatment with oestrogens induces the activity and excitement of oestrus in immature mammals and also in mammals, such as ferrets, from which the ovaries have been removed.[134] In the rhesus monkey the results are similar[20] and apparently a reaction can even be obtained in the chimpanzee.[84] However, the human subject again gives no clear response, and any effect that may be induced is obscured by the psychological reaction of the patient to suggestion.

It is important to add that the female hormone is without any definite effect on the behaviour of the normal adult male, even when it is administered in very large quantities. It has, however, been reported that such large quantities have a depressing effect on male behaviour, and for this reason oestrogens have been used for suppressing excessive sex function in men.

The hormone progesterone from the corpus luteum is also said to exert a depressing effect on sexual activity, so that in female rabbits and monkeys it may reduce the willingness to mate.

The general conclusion emerging from these data must be that the state of the nervous system, and thus the response which it provides to certain situations, is powerfully affected by the gonad hormones in the blood stream. With an excess of male hormone the behaviour is typically male, while with an excess of female hormone the behaviour is typically female. Thus it is evident that sexual activity is hormonally and not genetically determined.

4. THE SPECIAL PROBLEM OF MIGRATION

The subject of animal migration has always captured the public interest, and particular attention has been given to the regular and spectacular movements of birds. A consideration of the problem is relevant here because migratory movements are a form of sexual behaviour, and the flow and ebb of the tide of animals for the purposes of breeding forms one of the most remarkable cycles of sexual activity known.

However, the analysis of this problem, particularly from an experimental point of view, is hampered by extraordinary difficulties. Observations and experiments must be made in the field, and in this case the field is some hundreds or even thousands of miles long. The simplest starting point is from the observation that the spring movements of birds towards their breeding areas may be related to the growth of their gonads. Sometimes these movements are only short as when the curlew travels some 40 or 50 miles from the seashore to the high moors, but sometimes they are extraordinarily long as when the arctic tern travels more than 10,000 miles from the Antarctic to the Arctic. In those species which have been examined it has been invariably found that the gonads begin their seasonal growth just before the birds begin to move.[167] So it seems that there may be a general correlation between spring migration and increasing gonad activity, and possibly the reverse movement in the autumn may be related to decreasing, or minimum, gonad activity.

Clearly the experimental examination of this thesis presents almost overwhelming difficulties and the efforts of those who have tried can only be considered as valiant. The pioneer in this work was again Rowan[163] who started with the Canadian juncos. After he had modified their reproductive cycle by means of artificial light in autumn, he released the birds together with the untreated controls. Each day food was put out for them because, of course, none at all was naturally available in the snow-bound countryside at that time. By means of this food he was able to retrap the birds, and in this way most of the untreated controls were repeatedly taken showing clearly that they felt no overpowering urge to leave the district. However, of the birds with stimulated gonads some 80 per cent. were never seen again, and Rowan concluded that they must have attempted an unseasonable migration.

Attempts to follow the movements of such birds were then made by repeating the experiments with a larger and more conspicuous species, the American crow.[163, 164, 166] The gonads of the experimental birds were stimulated by light treatment, and then all the birds, experimental and control, were released in mid-November. This release was timed to coincide with a public holiday, and sportsmen who then went out with guns were asked to keep a special watch for the birds, which, to add to their distinctiveness, had their tails sprayed with gold paint. Many birds were recovered and many more were observed but not shot. All those belonging to the untreated control group were found to have moved south as though they had attempted a late but otherwise normal autumn movement. Of the experimental birds some had also moved south, but as many again had travelled north. Of the latter, that which had gone the farthest had flown some 100 miles in 7 days, and there were also reports of two flocks being seen after 9 days on the shore of the Lesser Slave Lake some 200 miles to the north. All the north-bound birds that were recovered came from the experimental group, and thus there was reason to believe that a reversed migration had been induced in some, but not all, of the stimulated birds.

Confirmatory results were later obtained by Wolfson[196] who worked with the Oregon junco in its winter area. He subjected the birds to extra light in autumn, and then, when the gonads were maturing, he released them together with the untreated controls. He too found that these controls could be repeatedly trapped in the immediate neighbourhood of the laboratory, and that the experimental birds vanished. Only one of the latter was subsequently recovered, but this, significantly enough, had travelled 200 miles north in 10 days.

Thus there is at least a *primâ facie* case that the basis of the spring migratory movements of birds lies in the activation of the gonads, and, from what has been said earlier in this chapter, that the effect on the nervous system is achieved through the intermediary of the sex hormones. Clearly much work remains to be done before this can be firmly established, but it is the simplest and most probable explanation of the facts as they are known to-day.

As regards the autumn movement in the opposite direction there is relatively little information. In some species this movement takes place when the gonads are shrinking, but perhaps in most it commences only after they are fully regressed with sex hormone secretion at a minimum. Some experimental observations made in autumn are based on the fact that, towards migration time, those birds which migrate at night become more and more restless, particularly during the hours of darkness. This restlessness has been called the migration urge, and when it reaches a maximum, it interferes with sleep and ends in the movement to the winter quarters. Using female redstarts, Schildmacher[171, 172] found that this autumn restlessness can be eliminated by injections of oestrogens. Later he also eliminated it by inducing gonad growth in the Continental robin by means of extra light,[173] and in winter he found it possible to induce a precocious spring migration urge by the same means.[174]

Attempts to influence migration have also been made by means of castration experiments, but it has been found that both the spring and autumn movements may be completed normally by birds in this condition. This would appear to contradict conclusively the present thesis that migration is a form of sexual behaviour, but it must be remembered that, even in the absence of any other urge, the flock instinct may be sufficient to induce the few experimental birds to accompany the mass of their fellows.[56] This is an important point which has usually been overlooked and which is liable to affect any experiments in which attempts are made to inhibit normal movements.

So once again the psycnological or social factor must be introduced into this question of sexual behaviour, and once again the warning is necessary that, at least in the higher vertebrates, the hormones alone cannot furnish the full explanation of the problem. However, while a theory of migration based entirely on hormonal considerations may prove to be quite inadequate, such a theory may at least be of value in providing some foundation on which our future knowledge can be built.

5. CONCLUSIONS

The evidence summarized above emphasizes the dependence of sexual behaviour on the presence of active testicular tissue in the male and of active ovarian tissue in the female. Thus cyclical changes in gonad activity are usually accompanied by cyclical changes in overt behaviour.

It has been shown that the gonads exert their influence through the intermediary of the hormones which they secrete. Consequently the appearance of male behaviour can be induced by injections of testosterone, while that of female behaviour can be stimulated by oestradiol. If the gonads are removed sexual activity diminishes rapidly in the female and more slowly in the male, the partial maintainance of activity in the latter being perhaps related to a compensatory oversecretion of the male-like hormone of the adrenal cortex. In any conflict between the male and female hormones, due to congenital abnormalities or to experimental conditions, it is the male which is dominant and male behaviour only is seen.

Because of the weight of this evidence Stone[183] has concluded that the 'hormones of the gonads appear to be a *sine qua non* for the organization of sexual behaviour'. However, there is still very little evidence as to what parts of the central or sympathetic nervous systems are affected or as to how they become eroticized to produce this result.

Also unanswered is the difficult question, which looms so large in the higher mammals, of the part played in sexual activity by non-hormonal factors. As Beach[21] concludes, the 'evidence already available shows that as we consider first the lower mammals, then those of intermediate phyletic status, and, finally, the higher primates including man, we find that the relative importance of hormonal effects to normal sexuality grows progressively less apparent, while the magnitude of extra-physiologic influence becomes increasingly evident. The description and interpretation of this evolutionary shift in emphasis is a basic task that will provide the only solid foundations upon which our understanding of human sex life can rest'.

Finally, it may also be mentioned that, while attention has been concentrated on the effects of the gonad hormones, there is reason to believe that other hormones may also be found to exert an influence on breeding activities. In particular it appears that maternal behaviour may be induced by an anterior pituitary hormone, distinguished by the name of prolactin. It is this substance which is considered to be responsible for inducing the secretion of 'milk' from the wall of the pigeon's crop, and it has been described as causing the appearance of parental behaviour in several fishes, birds and mammals. A full review of these results, which do not yet seem to be conclusive, is given by Beach.[21]

CHAPTER VI

GENERAL CONCLUSIONS

THE data summarized in this book relate to the two best known sexual cycles, namely the short oestrous cycle, which is most clearly seen in female mammals, and the long seasonal cycle, which is common to most vertebrates in all parts of the world. The information now available indicates that these are controlled by two distinct mechanisms. The first is that inherent physiological rhythm which is in complete control of the oestrous cycle and in partial control of the seasonal cycle. The second is that physiological rhythm which depends for its development on external environmental changes, and which usually exercises a dominant control over the seasonal cycle.

As regards the basic mechanism of inherent sexual cycles little or nothing is yet known. Oestrous cycles are genetically fixed, and have a periodicity that is peculiar to each species. It has been suggested that the physiological rhythm on which these cycles must be based may be centred in the anterior lobe of the pituitary gland, but it is more probable that it may be centred in some part of the nervous system which dominates the pituitary gland (see p. 102).

The control which the nervous system may exercise over the activities of the pituitary gland can be clearly shown by an analysis of the seasonal cycle. In an animal such as the ferret which breeds in spring the stimulus of the increasing daylength enters the eyes and passes in the form of nervous activity through the optic nerves and the brain to the pituitary gland. In other species a similar nervous activation of the pituitary may be achieved in other ways. In the sheep it is probable that the eyes are also important but the stimulus is the result of decreasing daylength; in the junco the nervous activity may emanate from the proprioceptors in the muscles; in some frogs it may be due to the presence of water on the skin; in the killifish it may start with the sensation of the increasing temperature; in birds it may be reinforced by the nervous excitement of courtship displays, and in the rabbit by that of copulation itself. So it may be concluded that external circumstances exert their effects on the physiology of reproduction through the intermediary of the nervous system, and that the type of external stimulus to which the nervous system is attuned may differ widely in different species.

Once the anterior pituitary gland has been activated it secretes the gonadotropic hormones which stimulate the gonads. These in turn secrete hormones which have the primary function of increasing the rate of cell division throughout the body. By the combined actions of the pituitary and gonad hormones the eggs and spermatozoa grow to maturity, and by the unaided action of the gonad hormones the accessory sexual organs and the secondary sexual characters develop.

The gonad hormones also have a powerful effect on the nervous system to induce the development of sexual behaviour. Such behaviour is often remarkably complex, particularly in birds which may perform extraordinary courtship ceremonies. The proper and energetic performance of these ceremonies is necessary to the success of breeding, the effect being obtained through a further nervous stimulation of the anterior pituitary. Thus the sequence of events comes full cycle, the nervous activity induced by the environment being followed by still greater nervous activity associated with courtship activities. In this way the stimulus to the anterior pituitary is maintained and increased until gonad maturation is complete.

So, with the difficult problem of the inherent physiological rhythm set aside, the story of the sexual cycle of the vertebrates resolves itself into three parts.

First there is the effect of the external environment on nervous activity, second there is the effect of nervous activity on the internal secretion of those hormones which induce gonad maturation, and third there is the effect of the hormones on that further nervous activity which is seen externally as sexual behaviour. Only the broad outlines of these relationships are known, and the whole subject remains a fascinating one for further research.

CHAPTER VII

APPENDIX: RECENT RESEARCH

1. INTRODUCTION

RESEARCH into the details of the physiological mechanisms controlling the vertebrate reproductive cycles stopped almost completely during the war. Since then, and since the first edition of this book was written, new details have been discovered and described, although our overall picture of these mechanisms has not significantly altered.

It has been confirmed that certain species may respond by gonad maturation to increasing daylength in spring (see p. 25) or to decreasing daylength in autumn (see p. 31), or in the case of such amphibians as *Rana temporaria* to changing temperature (van Oordt and van Oordt[219]), or in certain reptiles to what has been called 'behavioural thermoregulation' (Bartholomew[204]), or in certain tropical birds to the onset of the rainy season (Marshall and Disney[217]). It has therefore become increasingly obvious that the external environmental factor which is primarily responsible for the onset of sexual maturation may be quite different in different species and consequently that the effects of the environment must be felt through different sense organs in different species. A general conclusion is that in all cases the external stimulus must be translated into nervous messages passing to the brain, and that therefore the brain may form an important link in the reaction.

Modern research thus falls into two main categories: that concerned with further and more detailed investigations into those external factors which control the timing of the various vertebrate breeding cycles, and that concerned with the role of the brain in the chain of physiological events which lead ultimately to gonad maturation.

2. EXTERNAL FACTORS AND BREEDING CYCLES

New observations have recently been made on fishes, reptiles, and birds. In the fishes it has been shown that variations in temperature and light, separately or in combination, may have a critical effect according to species (see review by Harrington[210]), and although information on the reptiles continues to be very inadequate, a similar conclusion may perhaps also be drawn in this group. In his review Bartholomew[204] has also drawn attention to the critical importance of considering the behaviour of reptiles in the wild. He points out that, because these animals are cold blooded, each species tends to seek out the environmental temperature that suits it best. To take a simple illustration, a lizard may appear above ground only for an hour or two in the early morning and late evening. By night it may burrow away from the cold and by day it may burrow away from the heat. Thus it avoids any great temperature variation and its exposure to daylight may vary inversely with the temperatures of the day. Consequently, as Bartholomew concludes, 'the complications imposed on the analysis of reptilian photoperiodism by behavioural temperature regulation are formidable'.

However, most of the more recent work has related to the birds of temperate regions in which reproductive cycles are mainly, if not entirely, controlled by variations in daylength (Wolfson;[221] Farner[206, 207]). It has been confirmed that there are normally at least two phases in the typical avian reproductive cycle. The first has been variously called the recovery period (which may be considered as the final period of the previous cycle or the preparatory period (which may be considered as the first period of the next cycle) or the refractory period (see p. 33) (because at this time the system cannot be stimulated to further activity). It is perhaps best to use the last name so as to emphasise the distinction between this phase and the second phase of the cycle, the so-called progressive phase, during which the bird can respond by maturation to the stimulus of natural or artificial increases in daylength.

However, the importance of increasing daylength in inducing sexual maturity in the birds of temperate regions has recently been questioned. Jenner and Engels[212] and Kirkpatrick and Leopold[213] have suggested that the observed stimulus actually arises from the shorter dark period. They have shown that, without increasing the number of hours of light per day, a stimulus to gonad maturation can be obtained by splitting the long dark night period into two shorter periods. However, Farner *et al*,[208] Hammond[209] and Marshall[216] have all expressed doubt that the dark period has any active role to play. Farner[207] has suggested that during the light period there may be a very rapid synthesis of some stimulatory substance which decays only slowly during the dark period. His data suggest that only about one minute in light is necessary for the synthesis of this substance to equilibrium, while several hours of darkness are needed for its decay to minimum concentration. Thus splitting the long dark period by only a short period of light may induce a long-acting stimulus.

It is evident that these modern results do not radically alter the general theory of the environment control of vertebrate reproductive cycles. It is unfortunate that no proper analysis has yet been attempted of the reproductive cycles of animals that breed at times other than the spring or that are nocturnal or subterranean, and not nearly enough work has yet been done on tropical species. Until these deficiencies have been made good our knowledge of this whole subject must continue to be very one-sided.

3. THE ROLE OF THE HYPOTHALAMUS

As already indicated, whatever the nature of the environmental factors that influence or control the breeding cycles of vertebrates, their influence must first be translated into nervous stimuli which then pass to the brain. In the case of light entering the eyes to stimulate the growth of the gonads, the pathway of the stimulus through the optic nerves to the brain has long been recognised (see p. 75).

The most important recent development has been the suggestion that, within the brain, the hypothalamus may be a region of special significance in connexion with breeding cycles. The stimulus from the sense organs may pass first to this region and thence via the pituitary gland to the gonads (Donavan and Harris[205]). It is also considered possible that inherent reproductive cycles, which are not influenced by external changes, may be controlled from the hypothalamus. Such cycles may have a periodicity of about a year (see p. 71) or they may be the shorter oestrous rhythms seen in polyoestrous mammals (see p. 67). It is no longer thought probable that rhythms of this sort are situated in the pituitary gland.

The hypothalamus is well developed in all vertebrates, and when it is damaged or stimulated, changes may occur in temperature regulation, sugar and fat metabolism, the rhythm of waking and sleeping, and in sexual activity (Donovan and Harris[205]). In particular, experimental lesions in this region may cause either gonad atrophy or constant oestrous with ovulation.

It is suggested that effects of this kind on gonad activity must be mediated through the pituitary gland, and that the message passing from the hypothalamus to the pituitary must be hormonal in nature. This hormone, which has not yet been extracted, evidently passes with the blood through the hypophyseal portal vessels that run lateral to the pituitary stalk. The theory of Thomson and Zuckerman[220] that the message may continue to pass in the absence of these vessels seems doubtful, especially in view of the observation of Harris and Jacobsohn[211] that sexual cycles do not recommence in hypophysectomised animals unless a new pituitary is grafted into place beneath the hypothalamus and unless this new pituitary is revascularised by the portal vessels. The presence or absence of a nervous connexion between the hypothalamus and the pituitary is evidently unimportant.

Finally, it has been questioned whether the wakefulness that can be induced by experimental stimulation of the hypothalamus may be in any way comparable with the restlessness of the sexually stimulated bird about to migrate (Farner;[206] and see p. 93); whether the obesity that may be induced by lesions of the hypothalamus (Long[215]) may be basically similar to the fat deposition that is also seen in birds about to migrate (Farner;[206] Koch and de Bout[214]); and whether indeed the hypothalamus may prove to be the site of the seasonal migratory urge and of the post-breeding refractory period.

Experiments involving the hypothalamus are especially difficult to devise and to carry out, but it is becoming increasingly evident that a thorough knowledge of this region of the brain will be necessary before a full explanation can be given of the mechanism of control of vertebrate reproductive cycles, whether these are linked to the external environment or whether they are entirely internal.

4. CONCLUSIONS

Evidently the external world may exert its influence on the reproductive cycles of the vertebrates through the nervous reactions of a wide variety of sensory end-organs, and the effects of all this nervous activity may be co-ordinated within the hypothalamus. However, the nervous impulses arise not only from the initial reaction to a single external factor, such as increasing daylength, but also from an appreciation of such environmental factors as the presence of a mate and of a suitable breeding place, of courtship behaviour, and of copulation itself (see p. 76). Thus the main stimulus to gonad maturation may result from an initial but prolonged stimulus to one particular type of sense organ, but for full maturity with the shedding of eggs and sperm many more repeated stimuli from a variety of sense organs may be necessary.

The long, steady, and mounting 'pressure' exerted by the nervous impulses reaching the hypothalamus may cause that region of the brain to secrete more and more of the hormone which evidently induces the secretion of gonadotropins from the anterior pituitary gland, and finally as the gonadotropin blood concentration also rises, the gonads reach their full maturity.

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GLOSSARY

Aestivation. A state of torpor in which some animals spend the hot dry months of summer.

Androgen. A hormone (e.g. testosterone) secreted primarily by the testis, or a substance with similar physiological properties prepared artificially.

Anoestrus. The period of sexual inactivity between breeding seasons, particularly in female mammals.

Antrum. The fluid-filled cavity which forms inside the ovarian follicle of a marsupial or eutherian mammal.

A.P.L.H. The anterior-pituitary-like-hormone secreted by the placenta and usually obtained from human pregnancy urine.

Autumn. A term here used in a restricted sense to indicate the period 21 September to 20 December in the northern hemisphere, or the period 21 March to 20 June in the southern hemisphere.

Breeding season. The period of the year when mating behaviour is evident, and when copulation results in fertilization.

Corpus luteum. The solid body which forms from the torn remnants of the ovarian follicle after the escape of the egg at ovulation.

Corpus luteum atreticum. The solid body, similar to a normal corpus luteum, which forms from the ovarian follicle when an egg is resorbed.

F.S.H. The follicle-stimulating-hormone secreted by the anterior lobe of the pituitary gland.

Germinal epithelium. The epithelium which covers the surface of an ovary and from which the oogonia are formed.

Gonadotropin. A general term covering the hormones F.S.H., I.C.S.H., and A.P.L.H. which stimulate the activity of the gonads.

Graafian follicle. An ovarian follicle possessing an antrum.

Heat. The period of sexual excitement that develops in most female mammals when the eggs are about to be shed from the ovaries. Also known as oestrus.

Hormone. A substance secreted by an organ or tissue for the purpose of exerting a specific effect of functional value on some other tissue.

I.C.S.H. The interstitial-cell-stimulating-hormone secreted by the anterior lobe of the pituitary gland.

L.H. The luteinizing-hormone which is apparently the same substance as I.C.S.H.

Luteinization. The process of differentiation by which the cells of the ovarian follicle are transformed into those of the corpus luteum.

Menstrual cycle. The oestrous cycle of the higher monkeys and apes. It is characterized by a period of bleeding from the uterus at the end of each cycle, and in one species (man) it has an average periodicity of about a month.

Menstrual period (*menstruation*). That period at the end of a menstrual cycle when the uterus is reduced in size and when bleeding occurs.

Migration. The annual movement of animals to another locality in order to breed there, and the annual return when the breeding season is over.

Mitogen. A hormone which acts as a general mitosis stimulator, and which, according to its influence on vaginal growth or on comb growth in capons, can be further classified as an oestrogen or an androgen.

Monoestrous. Having only one oestrous period each year.

Oestradiol. The main hormone secreted by the ovary.

Oestrogen. A hormone (e.g. oestradiol) secreted primarily by the ovary, or a substance with similar physiological properties prepared artificially.

Oestrous cycle. The sequence of changes in the reproductive system of a female mammal, namely pro-oestrus (period of increasing activity), oestrus (when the female is ready to mate and when the eggs are shed from the ovary), metoestrus (period of declining activity), and dioestrus (period of quiescence).

Oestrus. The period when a female mammal is sexually aroused, when copulation occurs, and when the eggs are shed from the ovary.

Oviductin. A hormone which, it is suggested, may be secreted by the pre-ovulation corpora lutea of the bitterling, and perhaps also of other lower vertebrates.

Ovulation. The release of the eggs from the ovary.

Polyoestrous. Having more than one oestrous period each year.

Progesterone. The hormone secreted by the corpus luteum of the marsupial and eutherian mammals.

Puberty. The time when an animal is first able to reproduce.

Spermiation. The release of the spermatozoa from the testis.

Spring. A term used in a restricted sense to indicate the period 21 March to 20 June in the northern hemisphere, or the period 21 September to 20 December in the southern hemisphere.

Summer. The period 21 June to 20 September in the northern hemisphere, or 21 December to 20 March in the southern hemisphere.

Testosterone. The main hormone secreted by the testis.

Winter. A term used in a restricted sense to indicate the period 21 December to 20 March in the northern hemisphere, or 21 June to 20 September in the southern hemisphere.

LIST OF SPECIES MENTIONED

Adder	*Vipera berus* (L.)
Angler fish, deep sea	*Ceratias holboelli* Kr.
Albatross, Laysan	*Diomedea immutabilis* Rothschild
Ass	*Equus asinus* L.
Bat, lesser horseshoe	*Rhinolophus hipposideros* Bechstein
—— greater horseshoe	*Rhinolophus ferrum-equinum* Schreber
—— little brown	*Myotis lucifugus* Le Conte
Bitterling	*Rhodeus amarus* Bloch
Bullhead	*Agonus cataphractus* L.
Burbot	*Lota vulgaris* Cuv.
Bush-baby	*Galago senegalensis* Geoffroy
Canary	*Serinus canarius canarius* (L.)
Capuchin, Azara's	*Cebus azarae* Rengger
Cat, domestic	*Felis catus* L.
—— Scottish wild	*Felis sylvestris* Schreber
Cattle, domestic	*Bos taurus* L.
Chaffinch	*Fringilla coelebs* L.
Chimpanzee	*Pan satyrus* L.
Chital	*Cervus axis* Erxleben
Cockatoo, Australian	*Kakatoe roseicapilla* (Vieillot)
Cod	*Gadus morrhua* L.
Crow, American	*Corvus brachyrhynchos brachyrhynchos* Brehm
Curlew	*Numenius arquata arquata* (L.)
Deer, roe	*Capreolus capreolus* L.
—— spotted	*Cervus axis* Erxleben
Dingo	*Canis dingo* Blumenbach
Dog, domestic	*Canis familiaris* L.
Dogfish, common	*Scyliorhinus caniculus* (L.)
Dove, mourning	*Zenaidura macroura* (L.)
Duck, domestic	*Anas* sp.
Eagle, golden	*Aquila chrysaëtus chrysaëtus* (L.)
Eel, European	*Anguilla vulgaris* Turt.
Elephant, Indian	*Elephas maximus* L.

Ferret	*Mustela furo* L.
Flicker	*Colaptes auratus luteus* Bangs
Fowl, domestic	*Gallus gallus* (L.)
Fox	*Vulpes vulpes* L.
Frog, common	*Rana temporaria* L.
—— edible	*Rana esculenta* L.
—— tree	*Hyla cinerea* (Schneider)
Gannet	*Sula bassana* (L.)
Goat, domestic	*Capra hircus* L.
Goose, domestic	*Anser* sp.
Gorilla	*Gorilla gorilla* Wyman
Greenfinch	*Chloris chloris chloris* (L.)
Grouse, ruffed	*Bonasa umbellus umbellus* (L.)
Guillemot	*Uria aalge aalge* (Pont.)
Gull, herring	*Larus argentatus argentatus* Pont.
—— lesser black backed	*Larus fuscus fuscus* L.
Haddock	*Gadus aeglefinus* L.
Hake	*Merluccius merluccius* L.
Halibut	*Hippoglossus vulgaris* Flem.
Hedgehog	*Erinaceus europaeus* L.
Heron, black-crowned night	*Nycticorax nycticorax hoactli* (Gmelin)
Horse	*Equus caballus* L.
Junco, Oregon	*Junco oreganus oreganus* (Townsend)
—— slate coloured	*Junco hyemalis connectens* Coues
Kea	*Nestor notabilis* Gould
Killifish	*Lebistes reticulatus* Peters
Kingfisher, Indian	*Ceryle rudis* (L.)
Man	*Homo sapiens* L.
Minnow	*Phoxinus phoxinus* L.
Monkey, rhesus	*Macaca mulatta* Zimmerman
Mouse	*Mus musculus* L.
Mussel, fresh-water	*Anodonta fluviatilis* L.
Nightjar	*Caprimulgus europaeus europaeus* L.
Opossum, Virginian	*Didelphis virginiana* Kerr
Palolo worm	*Eunice viridis* Gray
Penguin, emperor	*Aptenodytes forsteri* G. R. Gray

Perch	*Perca fluviatilis* L.
Pheasant	*Phasianus colchicus* L.
Pig	*Sus scrofa* L.
Pigeon, domestic	*Columba livia livia* Gmelin
Quail, valley	*Lophortyx californica californica* (Shaw)
Rabbit, common	*Oryctolagus cuniculus* L.
Raccoon	*Procyon lotor* L.
Rat, laboratory	*Rattus rattus* L.
—— brown	*Rattus norvegicus* Erxleben
Redstart	*Phoenicurus phoenicurus phoenicurus* (L.)
Roach	*Leuciscus rutilus* L.
Robin, British	*Erithacus rubecula melophilus* Hartert
—— Continental	*Erithacus rubecula rubecula* (L.)
Ruff	*Philomachus pugnax* (L.)
Salmon	*Salmo salar* L.
Sheep	*Ovis aries* L.
Smelt, Californian	*Leuresthes tenuis* (Ayres)
Sparrow, common	*Passer domesticus domesticus* (L.)
—— golden crowned	*Zonotrichia coronata* (Pallas)
—— hedge	*Accentor modularis modularis* (L.)
Squirrel, 13-lined ground	*Citellus tridecemlineatus* Mitchill
Starling, British	*Sturnus vulgaris britannicus* Bullough
—— Continental	*Sturnus vulgaris vulgaris* L.
Stickleback, three-spined	*Gasterosteus aculeatus* L.
—— four-spined	*Apeltes quadracus* (Mitchell)
Sturgeon	*Acipenser sturio* L.
Swallow, common	*Hirundo rustica rustica* L.
—— wood	*Artamus melanops* Gould
Swordtail	*Xiphophorus helleri* Heckel
Tern, arctic	*Sterna macrura* Naumann
—— sooty	*Sterna fuscata* L.
Toad, common	*Bufo bufo bufo* (L.)
—— clawed	*Xenopus laevis* Daudin
Trout, brook	*Salvelinus fontinalis* Mitch.
——brown, or sea	*Salmo trutta* L.
Tuatara	*Sphenodon punctatum* Gray
Turkey, bronze	*Meleagris gallapavo* L.

Whistler, golden	*Pachycephala pectoralis* (Latham)
Whitebait, New Zealand	*Galaxias attenuatus* (Jenyns)
White eye, Japanese	*Zosterops palpebrosa japonica* Temminck and Schlegel
Wolf, European	*Canis lupus* L.
Woodchuck	*Marmota monax* L.
Yak	*Bos grunniens* L.

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