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XI—THE CROONIAN LECTURE

Sexual Periodicity and the Causes Which Determine It

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It is a matter of common knowledge that the great majority of animals, both vertebrate and invertebrate, not to mention plants, have a more or less definite season or seasons of the year at which they breed. This time for breeding is generally, though by no means invariably, in the spring and summer, and it is well known that whereas a favourable season as regards warmth and general conditions tends to accelerate breeding an unfavourable one may retard it. So much is known to be generally true, yet the precise factors which determine the sexual season vary in passing from group to group and from species to species or even from breed to breed. WESTERMARCK (1921), confining himself to mammals alone, has pointed out that there is no month of the year at which some species does not have its breeding season, and yet that for the particular species in question the season is most regular. Speaking teleologically, the breeding season is regulated by the times most suitable for the young to be produced and reared. Without disparaging the use of teleological categories which justify themselves as means of generalization and prediction and are very generally used by the naturalist to the great advantage of his work, it is obvious that such a view is no explanation of the physiological causes of sexual periodicity in the individuals of which a species is made up. We still know only a little about these causes. But in view of the general correlation between the seasonal and the sexual cycles it must be assumed that these stand in the relation of cause to effect, unless, indeed, we believe in a pre-established harmony. And nowadays it is not fashionable to believe in pre-established harmonies. Moreover, in countries where conditions are more or less uniform throughout the year, as in some parts of the tropics, *e.g.*, in the Philippines as found by SEMPER (1881), animals of all kinds may breed at any time.* This is not saying that there is no internal rhythm occurring independently of the environment.

In the lower forms of life, especially in those in which there is no nervous system, apart from the alternation of activity and rest associated with the release of the ova and sperms, especially when these are discharged in bulk, the rhythm of reproduction must be controlled metabolically by the direct action of the environment—food, temperature, light, the humidity of the atmosphere, and in water-living animals the chemical composition and hydrogen-ion concentration of the medium. In the higher

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* BAKER (1929) states that in the New Hebrides, where the climate and general conditions are fairly constant and the length of the day only varies by about two hours, there is a breeding season in the giant bat (*Pteropus*) and in the bird *Zosterops*. The lizard (*Lygosoma*) breeds all the year round but is most fertile in November and December. The insectivorous bat, *Miniopterus*, also has a season.

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forms, certain of the external factors act through the intermediation of the nervous system, and the evidence bearing on this subject I propose to discuss presently. Apart, however, from these factors and from the exteroceptive factors which are dependent on the animals themselves—the stimuli of sight, hearing, smell, and sexual contact, as well as lactation and (in birds) incubation—it is evident that sexual periodicity is conditioned by the general environment, just as all vital processes are so conditioned, and that food supply is of prime importance. This latter fact was recognized by Aristotle who remarks that where the weather is warm and fine and food is abundant sheep may have young twice a year. We see a similar effect, partly, in the increased polyoestrum of so many of the domestic animals. The practice of "flushing" sheep, that is, supplying them with extra food—corn, cake, or turnips, or turning them out on a good new ley, rape or mustard, or merely superior pasture, is well known, not merely to increase the crop of lambs, but to hasten forward the sexual season. Flushing, however, will not bring the ewes " on heat " in the middle of the period of quiescence or anoestrum ; it will merely bring them to a higher degree of nutritional activity and so slightly accelerate the time of tupping. The converse effect of a poor nutrition has been described, among others, by Papanicolaou and Stockard (1920), who observed the results of underfeeding in producing a disturbance in the oestrous cycle and the rhythm of ovulation in the guinea-pig. Moreover, it is well known that poverty of nutrition during the Great War was often responsible for transient amenorrhoea and irregularity in the menstrual cycle in women. On the other hand, disturbances in the cycle and even complete sterility may be associated with adiposity, as shown both in women and in the domestic animals. Furthermore, the possibility must not be lost sight of that sexual periodicity is affected by the absorption of vitamin E which may be present in greater quantity in the food at certain seasons of the year. Vitamin E, which is found in most concentrated form in certain plants, especially in seeds (oats, corn, etc.) and in green leaves, has been shown by Evans and his collaborators (Evans and Burr, 1927) to be essential for spermatogenesis in the male mammal and for embryonic development in the uterus of the female, but as to whether its greater abundance at certain seasons is a factor in breeding periodicity is a matter on which at present there is no evidence.

That the generative functions may be inhibited by faulty nutrition or an inappropriate environment is well shown also by the peculiar case of the marmosets at the Lister Institute. These animals not only failed to breed but suffered from rickets, a disease to which this species in captivity is especially liable. It was found impracticable to supply the necessary vitamin D in cod-liver oil owing to the animals' dislike to it, so ultra-violet rays were used as a substitute, and with complete success, for the marmosets acquired perfect health and bred freely, forming a considerable colony (Lucas, Hume, and Smith, 1927). Vitamin D, therefore, or a sufficient supply of ultra-violet rays is a necessary condition for breeding activity, and, as will be shown later, ultra-violet irradiation is a possible factor also in sexual periodicity.

Apart, however, from external factors which condition or regulate breeding, there is undoubtedly in the higher as in the lower animals an inherent reproductive rhythm. Thus, in the dog, at any rate under a state of domestication, the male is capable of breeding at any time of the year, but the female experiences a regular sexual cycle, typically of six months' duration, and which appears to occur independently of any exteroceptive or other external stimuli.* On the other hand, in the nearly related fox, as described by Rowlands and Parkes (1936), there is a single annual oestrous cycle, reproduction taking place in the early part of the year.

The Gonads

Before passing on to the consideration of the stimuli which probably act through the intermediation of the nervous system—and this I propose to do in some detail—it is desirable to state briefly the main known facts concerning the part played by the internal organs in regulating sexual and reproductive rhythm. That the gonads are essential organs in these periodic processes has presumably been recognized ever since castration was first practised. Thus, it is well known that if these organs are removed prior to maturity the sexual cycle never begins, or if this is done after maturity has been reached the cycle stops. Moreover, the gonads in many animals undergo an increase in size at the approach of breeding, and in some, as in most birds and in insectivores amongst mammals, this increase is enormous. In rodents it is often accompanied in the male by the passage of the testes into the scrotum from which they are withdrawn after the sexual season is over. The periodic increase in the size of the accessory sexual organs (prostate, vesiculae seminales, etc.) which, in some mammals such as the insectivores is very great, is also inhibited by castration, and so is the annual growth of certain of the secondary sexual characters such as the antlers in stags. In all the higher animals, to the consideration of which I shall confine myself in this lecture, there is a succession of processes together constituting the breeding phenomena—in birds pairing, nest building, the laying of eggs, incubation, and the feeding and rearing of the young; and in female mammals oestrus, followed by pregnancy and lactation or in some cases, when pregnancy does not supervene, by pseudo-pregnancy. Moreover, in the polyoestrous species of mammals the matter may be complicated by the recurrence of oestrus and the succeeding processes inside the sexual season of the female, so that there is a secondary rhythm within the main sexual cycle.

This brings me to the consideration of the testis and ovary as organs elaborating internal secretions that differ in quantity or in kind in successive phases of the cycle.

The formulation of the idea of internal secretion is usually associated with the name of Claude Bernard (1859), who applied it to the liver, while at a later date the principle became extended and popularized through the influence of Brown-Séquard (1889), although his therapeutic observations on which his conclusions

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* There is, however, a tendency for the heat periods in the bitch to occur in spring and autumn more than at other seasons.

were based were subsequently discredited. It is interesting to note, therefore, that the fundamental principles on which endocrinology is founded were actually first deduced considerably earlier than the time of Brown-Séquard, and that this was done as a result of an experimental investigation on the reproductive organs. For it was as far back as 1849 when Berthold published an account of the effects of the removal and transplantation of the testes in fowls. The experiments showed that whereas castration was followed by the loss of masculinity and the cessation of male sexual activity, testicular transplantation in an abnormal position with the ordinary nerve connexions presumably non-existent resulted in the retention of the sexual characters. The conclusion reached, namely, that the gonads elaborate substances, now called hormones, which are responsible for the development of the secondary sexual characters and the initiation and maintenance of the capacity to breed was many years later confirmed and extended as a consequence of experiments conducted on precisely similar lines, both in the male and in the female. Transplantation of the ovaries into abnormal positions in mammals with continuation of the sexual phenomena was effected by Knauer (1900) and by Halban in 1900, and transplantation of the testes with comparable but less conclusive results was done by Foges in 1903 and by Shattock and Seligman in 1904, and more recently with complete success in various animals by Pézard (1911), Steinach (1920), and many others, sexual potency and the secondary male characters being retained (*cf.* also Monckton Copeman, 1912). In the meantime, Fraenkel (1903) showed that the successful implantation of the fertilized ovum depended upon the corpus luteum, and he formulated the theory that the corpus luteum was the essential ovarian organ of internal secretion and was re-formed in different positions in the ovaries with each cycle. In 1905, mainly as a result of an experimental investigation on the dog and the rat, the theory was put forward that there were two ovarian hormones, one being formed by the follicles, or interstitial cells of the ovary (afterwards called oestrin) and the other being produced by the corpus luteum (afterwards called progestin and progesterone). These were believed to be respectively responsible for the two chief stages of the active part of the oestrous cycle, the period of " heat " (prooestrum and oestrus) and the period of pregnancy (Marshall and Jolly, 1905), and this view is now generally accepted as being within limits substantially correct. It has been shown also that the condition of pseudo-pregnancy which occurs under experimental conditions (as after sterile coition) in such animals as the rabbit (this animal normally ovulating only after the orgasm) is also dependent on the corpus luteum (Ancel and Bouin, 1910, 1911), and the same is true of the bitch in which pseudo-pregnancy takes place in the non-occurrence of gestation (Marshall and Halnan, 1917). In pseudo-pregnancy the uterus undergoes growth and hyperaemia and glandular development in the same kind of way, but not to the same extent, as during true pregnancy, and there is also mammary growth, followed by the secretion of milk.

Further, at the end of pseudo-pregnancy, animals which experience it may display habits and instincts such as are ordinarily associated with parturition at the end of true pregnancy. Thus the bitch tends to prepare a bed as though for the reception of young, the rabbit to pluck its breast of fur and to make a nest, and the marsupial cat to clean out its pouch (Marshall and Halnan, 1917, Hammond, 1925, Hill and O'Donoghue, 1913). These phenomena suggest that the processes occurring at parturition, at least in many species, are functionally correlated with the regression of the corpus luteum which usually occurs at the close both of pregnancy and of pseudo-pregnancy.

In polyoestrous animals (which have a succession of short cycles within the sexual season) the short period of rest which Heape (1900) called the dioestrum is now known in most species to be of the nature of an abbreviated pseudo-pregnancy (but not in the rat and mouse), and Hammond (1927) and Loeb (1911) have shown in the cow and the guinea-pig respectively that extirpation of the corpus luteum from the ovary reduces this period, a new " heat " or oestrus supervening in about two days after the removal of the gland. Furthermore, Snyder (1934) and others, by inducing ovulation in the rabbit in the latter part of pregnancy (through injecting urine of pregnancy containing an anterior pituitary principle), have produced a new batch of corpora lutea in the ovaries, and these have been the means of prolonging the pregnancy for an additional ten days. This is further evidence as to the function of the corpus luteum in maintaining pregnancy. It must be mentioned, however, that in some species (such as man and the horse, cat and rat), the corpus luteum can be removed in the later part of pregnancy without terminating it, and there is some evidence that the endocrine function is taken over by the placenta (Courrier and Gros, 1935, and Selye, Collip and Thomson, 1935).

It must be emphasized that the change over in the cycle from the oestrous phase to the luteal phase is effected by ovulation, after which the ovarian follicles become converted into the corpora lutea. In such animals as the rabbit and the ferret which do not ovulate spontaneously oestrus may continue for many weeks without any luteal phase. In a somewhat similar way in some animals (*e.g.*, mares and cows) with abnormal cystic follicles which fail to rupture, a nymphomaniac condition of oestrus may go on almost indefinitely. On the other hand, the abnormal persistence of the corpus luteum is associated with failure to experience oestrus.

We must now consider briefly the evidence based upon the extraction and injection of the hormones of the testicle and ovary. The first experiments with definitely potent testicular extracts seem to have been those of Pézard (1911), who injected the substances intraperitoneally into capons and obtained growth of the comb. Later, McGee (1927) and many others confirmed and extended the conclusions, showing that the growth of the accessory male organs, secondary sexual characters, and periodic sexual phenomena could be induced by the injection of testicular substances. Thus, in the male ground squirrel in which the accessory organs atrophy during the non-breeding season, the injection of testicular hormone will restore them to activity (Wells, 1935). In the female, Allen and Doisy (1924) discovered a definite oestrogenic principle in the ovarian follicles, and it was afterwards extracted from the extra-follicular stroma. Allen and Corner (1929) were the first to derive from the corpus luteum a potent extract (progestin) which not only produced the progestational growth of the uterus in an oöphorectomized female but permitted one which had become pregnant to maintain the foetus in *utero* where it developed until full term.

Thus the main hormones which determine sexual periodicity were obtained in a state of potency, and more recently their chemical composition has been successfully investigated and some of them have been made in the laboratory from other sources than animal tissues.

A whole series of oestrins or oestrus-producing substances are now known to occur (and this has been one of the obstacles encountered in making exact analyses of the chemical factors concerned in the control of the cycle), and several excellent reviews have been written dealing with this subject (DODDS 1934, 1935, A, 1935, B, RUZICKA 1936). Oestrone (ketohydroxyoestrin—$C_{18}H_{22}O_2$) and oestriol (trihydroxyoestrin—$C_{18}H_{18}O_3$) have been isolated from the urine, and also equilenin ($C_{18}H_{19}O_2$) and equiline ($C_{18}H_{21}O_2$). Oestradiol ($C_{18}H_{24}O_2$), the most potent of all the oestrus-producing substances, has been isolated from the ovary and is probably the true ovarian oestrogenic hormone. However, all these substances have been shown to be capable of causing oestrus, but their potency varies considerably. Oestrone is generally taken as the standard, but oestradiol is about five times more potent. The other compounds are less effective. In their composition there is an apparent connexion, as they have the same carbon skeleton as the sterols but differ in the arrangement of the hydroxyl groups round the carbon ring. The active principle of the corpus luteum, named originally progestin and now known to be a diketone called progesterone ($C_{21}H_{30}O_2$), has also been isolated. Substances having the properties normally ascribed to the testicular hormone have been isolated from male urine; these are androsterone ($C_{19}H_{30}O_2$) and dehydroandrosterone ($C_{19}H_{28}O_2$), while another hormone, with the same physiological properties but a slightly different constitution called testosterone ($C_{19}H_{28}O_2$), has been extracted from the testis itself (DAVID, LAQUEUR *et al.*, 1935). Androsterone is three times as potent as dehydroandrosterone, but testosterone is the most active, being twenty times as effective as dehydroandrosterone.*

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* Oestrone was isolated from urine by DOISY (1929), BUTENANDT (1929), and DINGEMANSE and LAQUEUR (1930). Oestriol was also isolated from urine by MARRIAN (1930). SCHWENK and HILDEBRANDT (1933) obtained oestradiol, which is a dihydroderivative of oestrone, by reduction of the ketone group to a secondary alcohol and so obtained a substance five or six times as potent as oestrone. It was afterwards isolated from the liquor folliculi of the ovary, showing it to be a natural production of the animal, by MACCORQUODALE, THAYER, and DOISY (1934). Equilenine and other substances with varying degrees of potency were isolated from urine by GIRARD (1933). Progesterone, an unsaturated diketone, was isolated by ALLEN, W. M. (1932), FELS and SLOTTA (1931), and FEVOLD and HISAW (1932). BUTENANDT (1934) made it also from stigmasterol (a sterol of the soya bean) and established its structure. Androsterone, which is a saturated hydroxyketone, was isolated by BUTENANDT (1931) and has been prepared from cholesterol by RUZICKA (1936). Another male excitant, androstandiol ($C_{19}H_{32}O_2$), has also been prepared by BUTENANDT and by RUZICKA and their co-workers (RUZICKA *et al.*, 1935), but the latter does not occur naturally. The preparation of sex hormones from sterols suggests that in the living animal they may be metabolic derivatives of sterols.

Many synthetic compounds also which resemble oestrin physiologically have been prepared in the laboratory. Some of these bear only a comparatively slight chemical similarity to the true oestrins, the partially hydrogenated phenanthrene nucleus which they possess being the sole character in common. Dodds and Lawson (1936), however, quite recently, have reported that they have now produced synthetic agents without the phenanthrene condensed ring-structure, which, therefore, is not necessary for their activity. The natural sources from which oestrus-producing substances have been obtained include a great many animal and vegetable organisms in which they are formed and generally, at least, in the organs associated with reproduction.

In mammals oestrus-producing substances of different chemical composition, besides being obtained from the ovaries, have been extracted from the placenta, the blood, and (in women, mares, sows, and cows) from the urine, more particularly from the urine of pregnancy, but, as demonstrated by Zondek (1934), the richest known source is the urine of the stallion. It is to be noted that oestrins are not normally obtainable from any source in the body after the extirpation of the gonads excepting from animals with retained placenta. After the placenta is removed none of these substances is to be found. Similarly, the formation of the male hormones is apparently confined to the testes, but, as in the female, there are several naturally produced substances which can be made to cause the sexual phenomena. In view of all these facts it is apparent, as Dodds has pointed out (1935, a, b), that the hormone-producing mechanisms are not very specific in their demands for a chemical excitant, and it is all the more remarkable that the body should, so to speak, go to such trouble to produce the particular active substances which are believed to be responsible for the respective sexual processes of the male and female. At present the most reasonable way of regarding the matter is to suppose that the sexual hormones were originally derivatives from the sterols which are widely distributed in living tissues, that the hormones at first had no particular physiological significance, but that in the course of evolutionary progress the parts of the body concerned, the uterus and the vagina and the male accessory sexual glands as well as the secondary sexual structures, have developed the capacity to respond to the chemical substances which have thus acquired the character of specific hormones in the manner originally postulated by Starling (1935). The mechanism in this respect is, in fact, comparable to that of the regulation of the respiratory movements through the centres in the brain responding to the increased tension in the blood of that simplest and most primitive of all products of metabolism, carbon dioxide. It is interesting to note, further, that the oestrogenic substances which are got rid of in such large quantities in the urine of pregnancy are nearly all in a " combined " form, and possess a very low physiological potency, and that one of these inactive substances has now been isolated and identified by Cohen and Marrian.* This discovery is in agreement with the suggestion that the oestrus-producing substances were primitively of no special physiological significance, and it would seem that after the development of the mechanism involving their

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* As being probably oestriol monoglucosonide (Cohen, Marrian, and Walton, 1935).

use it may be necessary for the organism at certain seasons to take steps, so to speak, to put them out of action. Nevertheless, the oestrins found during pregnancy, though they do not cause oestrus in the animals producing them, may have a functional action on the uterus, both on the mucosa and on the contractility of the muscle as experiments by Robson (1934) and others have shown.

We have seen, then, that oestrus and the corresponding condition in the male are brought about in the individual by the action of chemical substances produced by the gonads. In the female mammal the oestrous processes are followed by a phase due to the hormone formed by the corpus luteum and in pregnancy possibly also by the placenta. In the polyoestrous animal these hormones act alternately until the breeding season is over, the organism then going into a state of sexual rest, but in certain species such as man there is ordinarily no period of quiescence. It is interesting to find that according to Frank (Frank and Goldberger, 1928) the phase of the menstrual cycle at which there is the greatest concentration of oestrins in the blood in man is just before menstruation.* This is in general agreement with the view that menstruation corresponds to the end of pseudo-pregnancy (or pregnancy), and in this connexion it is to be noted that Robson and Henderson (1936) by injecting oestrone or oestriol into a bitch at about this phase (and for some time before) have brought about a uterine condition which resembles histologically that of the menstruating human uterus. In most animals, both in the male and in the female, in the non-breeding season the production of the hormones is much diminished, and this is probably most marked in those vertebrates where the gonads are spent and reduced to a minimum after the discharge of the reproductive products.

The Anterior Pituitary

I must now retrace my steps and consider briefly the part played by the anterior lobe of the pituitary. Heape (1905), some thirty years ago, put forward the theory that some substance is formed in the body in small amounts that is responsible for both growth and reproduction, pointing out that, broadly speaking, reproduction begins when growth ceases or at least slows down. This hypothetical substance he called tentatively the "generative ferment". Hammond (1925) adopted the same idea and used it to explain certain phenomena which had been produced experimentally. For instance, Foà (1901) found that immature ovaries when grafted into a previously oöphorectomized adult underwent a rapid development in the mature somatic environment. Conversely, it had been shown that adult ovaries when transplanted into young immature females lost their adult histological characters and had no perceptible endocrine activity. The mechanism of compensatory hypertrophy of the ovary was similarly explained, as well as the fact that a third engrafted ovary does not add to the number of mature follicles in the animal, the three ovaries together

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* According to Zuckerman (1936, a), the actual menstrual discharge is associated with a fall in the oestrin content, but there is a lag in the effect of 7 to 14 days represented by the period between ovulation and the beginning of the discharge. This succession of phases, he claims, can be imitated experimentally by injection of oestrin into oöphorectomized monkeys.

producing about the same number of follicles as is ordinarily produced by two (*see* LIPSCHÜTZ, 1927). On this view of a somatic control of the ovary it was supposed that the problematic generative substance was limited in amount, and limited also in its effect upon the gonad. Subsequently HEAPE withdrew the idea of the substance being a ferment and tended to identify it with vitamin E, while HAMMOND identified it with an active principle in the anterior pituitary gland. Bearing on the same point are the experimental results of PARKES (1929), who found that the ablation of the ovarian follicles in the young mouse before puberty or even in the embryo in the uterus, while it completely eliminated the cyclical histological changes in the ovary after maturity, did not destroy the other manifestations of the oestrous cycle. These experiments suggested that the cycle in the mouse, although dependent upon the presence of the ovary, is regulated by some other factor or factors external to it.

That there was a functional correlation between the anterior pituitary and the sex organs had long been known to clinicians, and sterility and various abnormal conditions and aberrations on the part of the sex organs have been found associated with hyper- and hypo-pituitarism, as described by FRÖHLICH (1901), CUSHING (1932), and many other investigators. In recent years the functional correlation between the anterior pituitary and the gonads has been definitely established, and it has been shown that in the absence of the anterior pituitary the gonads in the young fail to develop and in the adult undergo atrophy. The first experiments dealing with the problematical hormones were those of EVANS (EVANS and LONG, 1922), who showed that simple saline, and more particularly NaOH extracts of ox pituitary, caused the ovarian follicles of rats to become converted into luteal tissue. Shortly afterwards two groups of workers, ZONDEK and ASCHHEIM (1927) in Germany and SMITH and ENGLE (1927) in U.S.A., obtained striking results from the implantation of pieces of anterior lobe tissue into young rats and mice, the ovaries of these animals undergoing marked development followed by ovulation and the formation of luteal tissue and the corresponding oestrous and post-oestrous changes in the accessory organs.

It has been supposed that there are at least two gonad-stimulating hormones produced by the anterior pituitary, since, speaking generally, alkaline extracts have produced marked lutealization and the implantation of pituitary tissue has brought about oestrous conditions. The precise converse of these results has, however, also occurred, so that it is still uncertain whether there are really two anterior pituitary hormones controlling the two main stages of the cycle or only one reproductive hormone formed by the pituitary. Indeed, it is held by some that there is one principal gonadotropic hormone formed by the pituitary, which is probably produced in varying quantity depending upon the external environment and the stimuli derived therefrom, but the question is still an open one.*

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* BELLERBY (1933), basing his conclusions on the results of different methods of extraction, whether by acid or by alkali, is of opinion that there is probably only one anterior pituitary gonad-stimulating principle. Thus ovulation in *Xenopus* could be induced by the hormone obtained in both these ways. The anterior pituitary principle which causes ovulation in the rabbit, referred to below, is probably the same hormone.

Moreover, the condition of pregnancy (and also probably of pseudo-pregnancy) must be supposed to react upon the anterior pituitary, and in the absence of such a condition the mammary glands are not built up in the natural state, though they can be experimentally by the injection of oestrin followed by anterior pituitary extract, even in castrates. It has been commonly supposed that the basophil cells of the anterior pituitary are the source of the gonadatropic follicle-producing hormone (and SEVERINGHAUS (1934) considers it to be definitely proved), though with some there is still doubt about this matter (*cf.* LANGDON-BROWN, 1935). WOLFE, PHELPS, and CLEVELAND (1934) have described a cyclic rhythm in the predominant cell type at different stages of the oestrous cycle in the rat, the basophil cells being more numerous at oestrus and the acidophil cells during pregnancy and pseudo-pregnancy. Castration in both sexes has a marked effect upon the anterior pituitary, large, clear cells called castration cells making their appearance, and in correlation with this there is said to be an increase in the gonadotropic hormone content of the gland which may be inhibited by the injection of oestrin (HOHLWEG and DOHRN, 1931); furthermore, with two mice grafted together so as to be in circulatory union, one being a castrate and the other a female, it has been found that the female is maintained in a state of continuous oestrus through the hyperactivity of the pituitary of the castrate (MARTINS, 1931).* For such reasons it has been suggested that anterior pituitary activation is periodically arrested when greater amounts of oestrus-producing hormones are secreted into the blood until such time as the diminution of the gonadotropic hormone reduces the secretory activity of the ovaries (MOORE, 1935). In this way the ovario-pituitary rhythm is supposed to be regulated; that is to say, when the level of oestrus-producing substances falls the pituitary responds with an increase of gonadotropic follicle-producing hormone, and when the level rises the pituitary output is reduced. This explanation, however, if it be true, can only apply to the short or dioestrous cycle in polyoestrous animals such as the rat. It cannot apply to the alternation between the sexual and non-sexual or anoestrous seasons, for during the anoestrum the whole reproductive system goes into a state of prolonged rest which should perhaps be regarded as a result of exhaustion consequent upon activity. This is seen also in birds in which the pituitary makes no attempt at any time to maintain an adjustment, the ebb and flow of follicle-stimulating and ovarian hormones being approximately coincident.

In the bird, however, as described by WITSCHI (1935), the reactions to the various gonadotropic substances are not quite the same as in mammals. The follicle-stimulating substances appear to be far more potent in their effects upon the bird's gonads than those which in the mammal tend to cause lutealization. WITSCHI found that in the finches on which he worked, the most perfect results were obtained from the injection of pregnant mare's serum, which contains an anterior pituitary-like principle, the hens ovulating and laying eggs. This happened even in cases where

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* For further information and references, *see* article by SEVERINGHAUS, ENGLE, and SMITH in ALLEN'S "Sex and Internal Secretions" (1932), also MOORE and PRICE (1932), SEVERINGHAUS (1934), and MOORE (1935).

the birds otherwise never lay in captivity (in the African weaver birds), while in the males there was full spermatogenesis.

Walton and I (unpublished) found that by injecting an anterior pituitary principle made from human placenta into female white-fronted geese (a species which does not breed in this country, not even in captivity, or only very seldom) the ovaries could be induced to grow and produce good-sized follicles, but the birds did not lay, possibly because the surroundings were not sufficiently suitable.

Gonad-stimulating substances (anterior pituitary-like principles) have been obtained from human urine, especially during pregnancy, which correspond physiologically more or less to the two anterior pituitary principles, as well as in large quantities from the placenta (Zondek and Aschheim, 1928, Zondek, 1931), and from blood serum (as already indicated), but their physiological action, although similar, is not identical (Collip, 1932, Cameron, 1935). Moreover, substances have been extracted (Bellerby, 1929, Friedman, 1929), both from the pituitary and from the urine which cause ovulation, and others have been obtained from the pituitary which appear to act directly on the mammary gland, promoting growth and also secretion (Corner, 1930, Asdell, 1932, Riddle, 1935). Extracts of urine of pregnancy (and sometimes anterior lobe extracts) often give rise to haemorrhagic follicles in the ovary and these are unruptured; sometimes also the follicles may become lutealized without the ovum being discharged.

The chemical composition has not been determined in the case of any of these anterior pituitary substances, and in no instance have they been obtained in crystalline form. In the absence of further evidence it seems probable that many of these substances, which have slightly varying biological properties, are products of metabolism or chemical derivatives of one or two gonad-stimulating hormones in just the same kind of way as there is a number of oestrus-producing substances that are probably derived from the principal hormone of the ovary, or certain of the anterior pituitary-like principles may be formed in the placenta from which they have been obtained. As shown by Catchpole, Cole, and Pearson (1935), whereas some of these substances are excreted in the urine there are others which after circulating in the blood are destroyed somewhere within the body.

Here it may be mentioned also that Riddle has extracted from the anterior lobe a substance (which he considers to be a distinct hormone) which produces full development of the crop-gland in the pigeon at any time in the cycle and in both male and female and also in castrated birds (Riddle and Braucher, 1931). It is obtained from a definite fraction and does not produce the effects which characterize the growth and gonadotropic hormones of the pituitary. This substance, which he calls prolactin, also causes the incubation instinct in fowls and the associated regression of the ovary, besides producing active lactation in mammals (provided that the mammary glands are already fully developed) and exciting the various maternal instincts associated with the feeding and care of the young (Riddle, 1935). It appears to be a different substance from that which may stimulate mammary growth, as described by (Corner 1930). Here we have a definite example of a substance which presumably existed as a product of metabolism before it became a hormone and to which various other organs—the crop gland, the ovaries, and the mammary glands, came to respond in the progress of evolutionary life. Anyway, it existed before the main vertebrate stem divided into birds and mammals, though in some of the more primitive forms it may already have possessed a function. As we have seen in the pigeon, it appears to control a certain stage in the cycle. In the rat the release of prolactin at parturition may result from afferent stimuli occurring during that process.

We have now seen that the gonads through their respective hormones act upon the accessory organs and other tissues concerned in the sexual cycle, and that the anterior pituitary gland acts similarly by its hormone or hormones upon the gonads. We have seen, further, that in the female there may be secondary or dioestrous cycles within the major cycle and that these also are dependent upon the ovarian hormones which are successively produced. Further, the duration of the corpus luteum depends partly, at any rate, on the anterior pituitary, as shown especially in such species as the rat. As to whether the ovarian hormones react upon the anterior pituitary at certain stages in the cycle we have no completely satisfactory proof, but it is almost certain that such an influence exists. The castration effect must be regarded as definitely proved.

As to whether the suprarenal and the thyroid exert any effect on the oestrous cycle in any way other than that they may be supposed to condition it, there is no clear evidence. The facts have been well presented by Smith (1932), who supplies many references. Deanesly (1928) has shown that in the rat and mouse a high percentage of animals survive after adrenalectomy and that the cycles are normal or slightly lengthened. Most other recent investigators have got similar results. The evidence as to the thyroid is also unsatisfactory. According to Benoit (1934), however, this gland plays a part in determining the periodic testicular growth in the drake. The conclusions are based on the results of injections of thyroid hormone as well as on the effects of removal of the thyroid.

We may now consider the evidence as to the existence of the exteroceptive or other stimuli which regulate the gonadotropic activities of the anterior pituitary.

Effects of Light and Ultra-Violet Irradiation

The first to show experimentally that light was a cause of cyclical reproductive activity was Rowan (1926, 1930), who conducted an investigation upon the migratory junco finch of America. By exposing the birds in mid-winter in Canada to ordinary electric light he obtained an increase in the size of the gonads comparable to what occurs with the increase of daylight in spring. Warmth was clearly not a factor in the process since the birds were kept at the temperature of the outside environment which was very cold. The results were confirmed with crows and canaries, and Bissonette (1933) extended them to the European starling, for which he found that intensity and wave-length, as well as daily periods of light, are factors in promoting sexual activity, while the method of increase of light also played a part. Moreover, BISSONETTE (1932), as a result of researches in Cambridge, made the important discovery that with increased illumination by electric light (200-watt bulbs) in mid-winter and therefore at the time of the normal anoestrum ferrets came into full oestrus with typical vulval swelling in 38 to 64 days. In the male ferret the response was less complete, for although the accessory organs developed and mating took place, owing to the incompleteness of spermatogenesis the matings were followed by sterility. At the same time, BAKER and RANSON (1932), at Oxford, showed that the oestrous cycle in the vole could be modified by varying the rations of artificial light though food and possibly other factors might alter the response. Furthermore, the effect of illumination with ordinary electric light in producing oestrus in the ferret was fully confirmed by HILL and PARKES (1933). These investigators showed also that the anterior pituitary is bound up with the sexual photoperiodicity since hypophysectomized animals are unaffected by artificial lighting and go into permanent anoestrum unless injected with pituitary extracts. This is in conformity with what we know about the function of the pituitary in other animals and with the experimental results of pituitary implants and the injection of extracts.

The question as to whether the acceleration of the recurrence of the cycle is brought about by general light and heat radiation or whether the effect is due to stimulation by definite portions of the spectrum was then investigated by BOWDEN and myself (MARSHALL and BOWDEN, 1934). It was found that for the ferret heat rays and the near infra-red were inactive. The effect begins with the red radiation and extends throughout the visible to the near ultra-violet. Pairs of ferrets were subjected, further, to the same total quantity of radiation from incandescent lamps, but in one case it was concentrated into two hours, and in the other spread over 16 hours. The results were similar in each. The ferrets which were subjected to ultra-violet remained on heat for a longer time than the others, although the irradiation had for some months been discontinued; that is, they remained on heat for five or six months after irradiation ceased. The following year the results were similar, and this year they are so far similar again.* Further, ferrets which were subjected to incomplete darkness did not come on heat, but individuals which had already begun to come on heat entered into full oestrus and remained in that state for a normal period. A blind ferret (with cataract) did not come on heat at all, although kept under observation for two years, during which time it was apparently healthy and fed well. HILL and PARKES, however, found that in ferrets subjected to darkness there

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* The two ferrets subjected in the spring to ultra-violet irradiation have been continuously on heat since February, while those brought on heat by other rays "went off" after several weeks, but are now (after the manner of normal ferrets) on heat a second time (20 July, 1936). The two ferrets irradiated with ultra-violet light finally "went off" heat at the end of the summer, behaving like those similarly treated in previous years, and in contrast to those treated with light which "went off" much earlier (6 October, 1936).

was on the average some lag in the times of onset of oestrus but this was slight. Bissonette (1935), on the other hand, found that by employing hoods or curtains or otherwise reducing the light received there was a definite arrest of the cycle, that with ferrets already on heat treatment by darkness led to regression, and that in general the onset and duration of oestrus could be regulated artificially by changes in the duration or intensity of the light to which the ferrets were exposed. Further, Bissonette (1936) found that severing the optic nerves of ferrets frees the cycle from the influence of the seasons and sexual activity can occur at abnormal times (June to November or July to December instead of March to August). In all the experiments on ferrets warmth may be ruled out as a factor in the periodicity—the controls as well as the results of infra-red radiation show this—while food may also be excluded since the irradiated ferrets ate no more than the normal animals.

It seems probable that the great fecundity of the marmoset colony at the Lister Institute, where these animals were induced to breed after irradiation with ultra-violet light was not merely the result of improved health due to the anti-rachitic effect of the treatment, but that the rays may have had a stimulating influence also on the anterior pituitary, promoting the secretion of the gonadotropic hormone. Miss Margaret Hume, to whom I am indebted for unpublished information, states that some of the marmosets produced an excessive number of foetuses which in certain cases could not be born and that even the mother of the colony started having triplets instead of the normal two. These results of ultra-violet treatment are probably comparable to those associated with super-ovulation in mice when injected with anterior-pituitary extracts.

In the meantime, Kirschbaum's (1933) experiments on the sparrow showed that artificial lengthening of the day brings about a precocious development of the sex glands, especially in the male in winter, and Witschi (1935) repeating the experiments obtained the same effects. Moreover, Cole's (1933) researches with the mourning dove of America and experiments upon mejoros, turkeys, guinea fowl, pheasants, quail, and grouse, conducted on the same lines, led to similar results (*see* Bissonette, 1936). In the experiments upon ducks by Walton and myself, artificial lighting in the spring accelerated the cyclical change, as was shown by the birds displaying courtship phenomena, the drakes fighting, and the occurrence of the seasonal eclipse in April instead of at the usual time in July. But in these experiments, probably as a result of otherwise unsuitable conditions, the birds did not lay. Benoit also has shown that light has a pronounced effect in stimulating the testis of the drake, both immature and mature birds being affected. When a hood was used to cover the eyes the effects did not supervene. Benoit (1934), therefore, at first concluded that the stimulus must pass through the eyes and optic nerves and brain and thence to the anterior pituitary, but in his later experiments, just published (Benoit, 1935), he severed the optic nerves or removed the eyeballs. Under these conditions the effect of lighting still led to acceleration, yet hooding of the eyes and the region around them had an inhibitory effect. Benoit concludes that there must be some other receptor organs in this region, but the matter remains obscure.

According to the recent observations on sparrows by Ivanova (1935), the plucking of the feathers of irradiated birds resulted in a greater augmentation of testicular growth than in birds with feathers, but the latter also underwent an increase. There is probably considerable species variation, and though the eyes normally receive stimuli which are transmitted through nervous paths to the anterior pituitary, the effects in some animals are conveyed by alternative paths. In this connexion, Hogben's observations on the result of irradiation on the pituitary of the Cape clawed toad are not irrelevant, although in this case the effect was shown in another function of the gland. Hogben found that in *Xenopus* the secretion of the melanophore hormones of the pituitary is stimulated through colour vision. " In the eyeless animal, the melanophores are neither fully expanded nor fully contracted. The dark background response (fully expanded melanophores) is caused by photoreceptors in the fundus of the eye which reflexly stimulate the pars intermedia (of the pituitary). These receptors are most sensitive to light from the red end of the spectrum and are hardly affected by blue-green rays. On the other hand, the photoreceptors of the white background response are located in the periphery of the retina ; they are not sensitive to red light and appear to control the activity of the pars tuberalis. On this view, the two responses are separate entities and the secretion of two different hormones of the pituitary is differentially controlled by different wave-lengths " (Hogben, private communication to Miss Whetham, Whetham, 1933). These results are interesting as showing that in some animals at any rate the activity of the pituitary gland is directly affected by irradiation through the retina. Moreover, it was found that in blinded toads (*Xenopus*) the ovary was under-developed (Hogben, Charles, and Slome, 1931).

It may again be remarked that increases in light have no effect if the pituitary is removed (as shown by Hill and Parkes for the ferret), and further, that the same effects as those produced by light can be evoked at any season of the year by the injection of the gonad-stimulating principles.* Again, Bissonette (1936) has shown that the pituitaries of stimulated ferrets undergo histological changes similar to those of castrated animals, large clear cells being produced. The effects of stimulation, however, are not permanent, for the animals eventually go into a state of sexual rest in spite of the continuance of the stimulating agents used.

It must, of course, be freely admitted that all animals do not respond to an increase of light ; there are exceptions both among mammals and among birds. Young and his collaborators found that the cycles in guinea-pigs are but little affected by changes in light or by darkness (*see* Dempsey and others, 1934), and Moore and his collaborators (Moore, Simmons, and others, 1934), adopting similar methods, did not obtain any alterations in the sexual cycles of the spermophile. That there is variation in passing from species to species is shown also in birds, for whereas the Adélie penguin in the Antarctic breeds in the warmest and lightest time of the year the Emperor penguin lays its eggs in the dark. In some species of mammals the

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* The possibility must always be borne in mind, however, that light may sometimes act by producing chemical changes in the skin and not through receptor organs.

gonads begin their annual development in winter before the days begin to lengthen, and in birds which migrate from the southern hemisphere to the northern the periodic enlargement commences before the migration starts, and in crossing the Equator the birds pass to countries where the days are shorter. In the African weaver finch, to take an instance, the breeding season is in the autumn. These birds must presumably react to diminution and not to increase in light. Witschi (1935) records that he has kept these birds at Iowa under constant food conditions and that their autumn breeding seasons are most regular; also that young birds without exception fell into line with their adult companions, even though they had travelled widely in different parts of the country. With tropical birds living where there is little or no variation in the length of day, seasonal breeding may still occur, as recorded by Bannerman (1930, 1931, 1933) and others, and it is suggested that it is determined by the recurrence of the rains and various ecological factors. These factors may also act through the intermediation of the nervous system upon the anterior pituitary.

The outstanding fact remains, however, that in nearly all animals breeding phenomena occur in response to seasonal change, and in the vast majority of these (but not in all), as shown by observations under both natural and experimental conditions, the principal stimulus is increase of light. Changes in temperature and food are generally eliminated by control observations, though in some cases these factors not merely condition the phenomena but play a part in determining the sexual cycle.

The general conclusion is reinforced by statistical studies of the times of breeding of the domestic animals. In view of the practice adopted by poultry keepers of using artificial light to increase and extend the time of egg production, Miss Whetham undertook a statistical investigation based on available records to ascertain if there were any relation between egg production and variation in daylight in different latitudes, and found that there was a correspondence which though not absolute was nevertheless definite. Similarly, in the case of horses, although in the more domestic breeds (*i.e.*, in the " better bred " or more improved types) the dioestrous cycle may recur for a great part of the year, there is a definite tendency for foaling to occur in the spring. Dr. Hammond, to whom I am indebted for the information (at present unpublished) based on his statistical researches upon the records obtained from the stud books of different countries, has constructed frequency curves with peaks showing when foaling was most common. In Canada, as with Britain, there is a very pronounced peak in May. In the United States, which extends far down towards the Tropics, where the seasonal differences are less, there is for the whole country a definite peak also in May but not so pronounced as in Canada. In Australia and New Zealand there are very marked peaks in October and November respectively, in the spring of these countries. In South Africa there are only slight peaks in September and again in November. In India, where comparatively speaking conditions are much more uniform, there is only a slight peak in March. The gestation period being eleven months, the service peaks are in all cases a month later than the foaling peaks. The results as a whole undoubtedly suggest a correlation between the sexual season and the incidence of daylight. HAMMOND noted, further, that with the Shetland pony, which is comparatively primitive, the service and foaling peaks were more pronounced than with the more improved breeds. It may be recorded, further, that COSSAR EWART imported a pony from the Island of Timor, which is in the southern hemisphere, into Scotland and found that whereas in the first year it came on heat in the autumn, which synchronizes with spring in Timor, it afterwards adjusted itself and underwent recurrent oestrus in the spring in Scotland.

The usual sexual season for sheep, especially for the hill breeds, is autumn, as also is the case with deer, these animals being among the exceptional species which appear to respond to diminution rather than to increase in daylight. In the southern hemisphere their breeding season is in actual time the exact reverse of what it is in Europe. But what is more interesting is that Dr. ROUX (1936), to whom I am indebted for supplying me with unpublished information, found that individual sheep on being transported from Britain to South Africa adjusted themselves to the reversed seasons, coming into line with others that were born and bred in South Africa, thus showing that the major cycle is definitely determined in sheep by external stimuli rather than by an inherent reproductive rhythm. The behaviour of these animals was clearly comparable to that of EWART's Timor pony. ROUX states, further, that the sheep were fed uniformly and consequently nutrition could not have been a factor in the rhythm.* (*See* Postscript.)

OTHER EXTEROCEPTIVE FACTORS

I pass on now to consider the evidence as to the part played by exteroceptive stimuli arising from the relations between the sexes and the relations between the mother and her offspring in controlling or modifying the phases of the sexual cycle.

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* I am indebted to the Marquess of TAVISTOCK for kindly supplying me with the following important information about the breeding habits of foreign birds in captivity :—" Tropical birds, such as doves and finches, that breed for the greater part of the year in their own country often attempt to do so in this, usually with fatal results to the hens and young. In some cases, however, the cold, short days and restriction of highly-vitamized food will affect their general health adversely to a sufficient degree to discourage breeding.

A few species succeed in rearing their young successfully even during our winter—the lovebirds, *Agapornis personata*, *fischeri*, *lilianae*, and *nigrigenis* being noteworthy examples. Some Australian lorikeets (*Trichoglossus*) will also breed successfully in mid-winter, as will the budgerigar, zebra finch, etc.

The emu shows little willingness to adapt itself to our seasons, usually laying in mid-winter. Only exceptionally do pairs defer breeding until the spring.

The rheas, however, always adapt themselves to our seasons and, as a rule the ostrich does likewise. Birds from North Australia are markedly more inclined to stick obstinately to their own breeding season (October). The hooded parrakeet (*Psephotellus cucullatus*) and BROWN's parrakeet (*Platycercus venustus*) are a case in point. Only after some years and a good deal of encouragement (by the removal of nests in autumn and their return in spring) can some pairs be induced to adopt our seasons and their English-bred offspring are as inclined to spring-moulting and autumn-breeding as their parents even when spring-bred themselves. BROWN's parrakeets often have two moults in this country ; one in May when they would naturally moult in Australia ; and another in August when they would moult if they had adopted our seasons."

The best-known examples of this kind of phenomenon are probably those supplied by the rabbit and the ferret, and also by the ground squirrel, and under certain circumstances by other animals which normally only ovulate in response to the stimulus set up by coition or by the orgasm. Sterile coition in the rabbit and ferret is followed by pseudo-pregnancy with mammary development and secretion. The stimulus therefore causes a switch over from the oestrous or follicular phase to the luteal phase. Moreover, the switch cannot be effected in the absence of the pituitary, whereas, on the other hand, it can be brought about by the injection of anterior pituitary or anterior pituitary-like extracts (FEE and PARKES, 1929). The presumption is that ovulation is due normally to a nerve reflex but the stimulus apparently may be carried by several nervous paths. Thus, it is not necessarily started from the vagina and vulva, since FEE and PARKES have shown that local anaesthesia of these parts does not inhibit ovulation after coition. Ovulation can likewise occur after complete thoraco-sympathectomy (CANNON and his pupils, 1929), and in the absence of any nerve pathway to the ovaries (HINSEY and MARKEE, 1932); also after ovarian transplantation to an abnormal position (ASDELL, 1926, FRIEDMANN, 1929). It can also occur in the rabbit after cervical sympathectomy (pseudo-pregnancy following) (VOGT, 1933, HATERIUS, 1933). Nerve fibres have been found in the pars intermedia by CROLL (1928) and others, but their source and origin have not been traced. LOEWI (1935), in his Ferrier lecture given to the Royal Society a year ago, remarked that the anterior pituitary appears to receive its messages humorally and transmits them in the same way.

VERNEY and I (1936) have found that the natural method in the oestrous rabbit can be imitated by a strong electrical stimulation of the central nervous system,

Parrakeets from Southern and Central Australia adapt themselves to our seasons at once. If imported in winter they moult soon after arrival and again in August; after that in our late summer and autumn only. In the case of grass parrakeets (*Neophema*) and Bourke's parrakeet, conditions of captivity appear to induce much greater prolificacy and several broods may be reared. In a wild state, these species appear at most only double-brooded and apparently usually single-brooded." (*See also* TAVISTOCK, 1935.)

Mr. DAVID LACK informs me that the cases of the black swan, the *Cereopsis* goose, and the emu (*see* above), which have been quoted as examples of birds which retained their southern hemisphere breeding seasons in England, were based on mistaken evidence as to their breeding seasons in Australia. ZUCKERMAN states that many species of mammals which have bred in the London Zoological Gardens (*e.g.*, polar bears, reindeer) have retained their original breeding habits, but none of the animals cited came from the southern hemisphere. On the other hand, according to PYCRAFT (1913), the Chital or spotted deer from India, on being introduced to Europe, was at first in danger of extinction owing to the calves being born at an unsuitable season (in mid-winter) and consequently dying, but the animals afterwards adapted themselves to the new conditions and bred freely at an appropriate time. ZUCKERMAN says on the authority of SCHUSTER that several mammals living in East Africa breed at any time of the year, and also on the authority of STEVENSON-HAMILTON, that the evidence suggests that the lion has no demarcated breeding season. It may be noted further, that the goat in South Africa, like the sheep, has reversed its breeding times to conform to the seasons of the southern hemisphere. (For further information and references *see* MARSHALL and BOWDEN (1934) and ZUCKERMAN (1932).)

and ovulation followed by pseudo-pregnancy produced. The stimulus was equally effective whether applied through the brain or through the lumbo-sacral part of the cord. In a few animals, however, haemorrhagic follicles were produced instead of corpora lutea, but it is to be observed that this also often happens after injecting anterior pituitary-like principles. Further, ovulation did not supervene until 17 to 24 hours later instead of the usual interval of 10 hours, and pseudo-pregnancy might be a day or two shorter than usual. It is clear, however, that an electrical stimulus could switch the cycle over from the oestrous to the luteal phase. Friedgood and Pincus (1935) found that ovulation could supervene after stimulation of the cervical sympathetic ganglia, but, as in our experiments, there was a delay of 12 to 14 hours beyond the normal interval, the result in this respect being in agreement with our observations. Friedgood and Pincus's experiments are remarkable in view of the fact recorded above that ovulation can occur in the rabbit after complete cervical sympathectomy. One may, perhaps, interpret the results on the assumption of more than one nervous path and more than one mechanism for the initiation of the processes. Haterius (1934), however, could not produce ovulation after cervical sympathetic stimulation.

Harris (1936, b) has succeeded in producing ovulation in the rabbit and ferret after local stimulation of the hypothalamus, but it is just possible that the effect was due to an extension of the stimulus to nerve endings in the pituitary itself. There was a long delay—30 to 40 hours, before ovulation occurred, and in some cases instead of ovulation taking place haemorrhagic follicles were formed or luteal tissue without the discharge of the ovum, in just the same way as often happens after the injection of anterior pituitary-like principles.

In the rat, unlike the rabbit, ovulation takes place spontaneously, but a prolongation of the life of the corpora lutea with consequent pseudo-pregnancy can be induced by sterile coition or on artificially stimulating the cervix uteri by mechanical or electrical means (Long and Evans, 1922, Shelesnyak, 1931). Meyer, Leonard, and Hisaw (1929) found that general and spinal anaesthesia inhibited the occurrence of the pseudo-pregnancy which otherwise follows electrical stimulation of the cervix. Bacq and Brouha (1932) found that sympathectomy had no effect on the cycle in the female rat and they do not mention the occurrence of pseudo-pregnancy. Harris (1936, a) found that electrical stimulation through the brain of the oestrous rat, after the manner of Verney and myself for the rabbit, caused definite pseudo-pregnancy, and deciduomata could be induced to form in response to a mechanical stimulus introduced in the uterus. The observations show very clearly that the switch over from the oestrous to the pseudo-pregnant condition in the rat must be due to a change in the anterior pituitary and not merely to the corpus luteum which is formed in any case, whether a stimulus is applied or not. Selye and McKeown (1934) have shown that mechanical stimulation of the nipple without the withdrawal of milk (as after the removal of the galactophores) in both rats and mice, also produces a prolongation in the duration of the corpora lutea, but the stimulus must be continued if this effect is to be produced. The well-known fact that suckling is normally essential for the continuance of lactation in mammals is similarly to be accounted for on the assumption that exteroceptive stimuli are conveyed from the nipples to the anterior pituitary by nervous paths. And the further fact that menstruation in women in about 60% of cases is inhibited by suckling is perhaps also relevant.

General evidence of a functional correlation between the hypothalamus and the gonads is furnished by the described effects of hypothalamic lesions in inducing the symptoms of dystrophia adiposo-genitalis. Smith (1930) has included genital atrophy among the results of injury to the tuber cinerum in the rat, but according to Cushing (1932) the gonadal effect may be an instance of interference with the hypophysial blood supply or with its nerve supply. Cushing, however, after a discussion of the clinical and other evidence, strongly emphasizes the essential unity of the diencephalo-hypophysial mechanism.

Lastly, Theobald (1936), has collected evidence showing that drugs such as morphine as well as psychical factors (suggestion, etc.) may affect the rhythm of the menstrual cycle in women, and he suggests that the results are transmitted through a centre in the hypothalamus, but further evidence is required before such a conclusion can be established.*

Instances have been given above from among mammals showing that the succession of the phases of the cycle in some species may be modified by exteroceptive stimuli acting through the intermediation of the nervous system upon the anterior pituitary gland. Cases of the same kind of phenomena are also very common among birds. There is no luteal phase in birds, but as we have already seen, there occurs from the beginning of the season of reproductive activity a succession of phases which manifest themselves in the bird's behaviour, and which often grade into one another and to a certain extent overlap. There is, of course, much species variation, but speaking generally the order is as follows : Movement to the breeding area which may consist of migration over long distances, this occurring contemporaneously with the periodic development of the gonads, the taking up of territories (where this is done), pairing, sexual display, coition, nest building (during which display and coition are usually repeated), and in the female ovulation and egg laying, and then, sometimes for one and sometimes for both sexes, incubation, and the feeding and rearing of the young. Here I may quote Eliot Howard (1935) :—" No one doubts that the generative organs determine sexual activity, though all may not agree that prooestrum and

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* Sir Flinders Petrie has suggested to me that the lunar cycle in women may have become " fixed " in primitive people by the custom of promiscuous dancing, etc., at the full moon, the idea being that these influences may have acted exteroceptively (*cf.* Ellis, Havelock (1900), who notes that various persons have made similar suggestions). It must be mentioned, however (as perhaps against this idea) that some of the lower Primates have a lunar menstrual cycle. In the chimpanzee the cycle is 35 days (Elder and Yerkes, 1936). In the baboon, according to Gillman (1935), it varies from 29 to 63 days, the variation being produced partly by seasonal variation and partly by emotional disturbances. Here we have a suggestion of the cycle in a lower primate being modified by exteroceptive factors.

oestrus in a bird depend upon ovarian processes comparable with the uterine changes in a female mammal, or, indeed, that these phases are really there ; what some may doubt is the wider view that behaviour which custom thinks a matter of mind is in some way determined by changes in the body. True, no change in testis or ovary, or hormone in the blood stream, has yet been found to correspond with territory, with building shells, or with care of young. But from point to point, consider the events. In the spring a male shuns his own kind and makes himself public ; singing, if a song bird ; drumming on a dead branch, if a pied woodpecker ; wandering in air like a butterfly or dancing in it like a moth, sparrow-hawk, godwit, curlew, with slow flapping flight, redshank and dunlin with vibrating wings, each after his kind ; moreover, he defies intruders, threatens attacks, fights until one or other yields ; and before a mate finds him he builds a nest, if a whitethroat ; or a platform, if a waterhen, and broods upon it ; or, like a lapwing, bores hollows in the ground to enjoy it, or merely carries stuff in its beak to drop it anywhere." In each species there is a characteristic succession of phases in both sexes, and this, as Howard supposes, must be related to internal change. The study of bird behaviour has already become a large subject, and following upon Hudson (1919), Selous (1928), Julian Huxley (1914), Eliot Howard (1929), and others, as a result of the intensive watching of birds in a state of nature have made important observations upon the relations of the sexes. But concerning the physiological causes which are responsible for the successive phases we have little knowledge beyond those endocrine factors which I have already recorded. Here I confine myself to some further matters where there is direct evidence as to the effects of exteroceptive stimuli in altering the succession of the physiological processes which constitute the cycle.

The first point I wish to refer to is one which is well known to all ornithologists. For any one species the number of eggs in the clutch is generally constant within narrow limits, that is to say, there is a tendency to lay a definite number of eggs and then to brood over them. If, however, the eggs are withdrawn shortly after being laid, many birds will go on laying, making an attempt, so to speak, to lay up to the right number, and the incubation phase in the cycle is postponed in correlation with the repeated ovulation. One of the best-known examples of this is the case of a wryneck, a species that normally lays 7 or 8 eggs and which, in this instance, laid 42 eggs as a result of the daily withdrawal of the egg deposited. The incident was repeated in the next year when the wryneck again laid 42 eggs, before its ovary was exhausted (Yarrell (1882), Kirkman (1911–13)). Similarly, it is recorded that a swallow, by having one of her eggs taken from her daily, was induced to lay 19 eggs (Ray 1848). Jesse (1842), mentions similar observations upon the blackbird, the lark, and the long-tailed tit. About the lark he says, " if only one or two eggs are allowed to remain in the nest, the bird will go on to lay for a time indefinite, but if there are three she will sit. The usual number of eggs in a lark's nest is five." Witschi (1935) found that for the house sparrow whereas the normal number of eggs is four or five in a clutch, by removing the eggs daily, the bird may lay up to 50 eggs in succession and often 12 to 19 on consecutive days. On the other hand, if the full clutch is allowed to remain, the ovary rapidly regresses during incubation through degeneration of the larger eggs, a result which occurs, according to Riddle, through the secretion of the anterior pituitary hormone prolactin. In the case of the common fowl, as is well known, as a result of domestication and prolonged artificial selection, the maternal habit of broodiness may be bred out, while the bird has become a veritable factory of egg production. Since in the fowl, and therefore presumably in most birds, there is an interval of only about a day between ovulation and the laying of the egg, it follows that in the cases just cited the repetition of ovulation must be the result of exteroceptive stimuli, though whether the stimulus is derived from perception by the eye, or through tactile perception by the ventral surface of the body, is uncertain. In any case, presumably, the stimulus must pass through the intermediation of the nervous system to the pituitary and so interfere with the normal course of succession in the sexual cycle, the incubation phase being postponed for a long period or indefinitely. Moreover, if the nest of the bird is removed along with the clutch, the nest building may be repeated and the succeeding egg-laying and incubation periods are deferred accordingly, ovulation being resumed in due course. The succession of the phases, therefore, is not merely a matter of cyclical endocrine control (Chance, 1936).*

So far we have been considering the exteroceptive factors responsible for the continuance of ovulation after the process has once started. The question as to the initiation of the first seasonal ovulation which I have reserved for longer consideration is another matter. Like mammals, birds in respect of ovulation fall into two categories, (1) those that ovulate spontaneously when the ovaries are in the appropriate condition, and (2) those that require an additional stimulus which is usually provided by the male. The common fowl and the pheasant are examples of the first kind ; the pigeon is an example of the second. Concerning the pigeon, Harper, in a paper published in 1904, writes as follows : " When a pair ready for mating is put together, egg-laying ordinarily ensues at the end of a rather definite period, at the least eight days. The female functions are held in abeyance till the proper stimulus is received from the mate. The maturing of the egg is so exclusively a female function that it seems odd at first thought that an apparent exception should occur to the rule. Of course, we know that the final maturation of the egg, or the giving off of the polar bodies, awaits in most animals the act of fertilization. But here the effect is produced upon the egg by the entrance of sperms. How mating and the act of copulation (which is repeated at frequent intervals every day at this time) could influence the ripening of the egg in the ovary is another problem. In this connexion the curious fact must be mentioned that two female pigeons placed in confinement may both take to laying eggs. The function of ovulation is in a state of tension, so to speak, that requires only a slight stimulus, ' mental,' apparently in

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* By removing the complete clutch, Chance obtained " repeat layings " in the blackcap, carrion crow, raven, dunlin, and golden plover. Further, the house sparrow, garden warbler, kestrel, and merlin could be induced to lay three complete clutches, and the red-backed shrike four clutches, but there was some reduction in the normal number of eggs in the fourth clutch.

this case, to set the mechanism to working. At any rate, it is impossible to regard the presence of sperm in the oviduct as an essential element of the stimulus to ovulation, although it may have an important influence in the normal case. Our attention is directed to the various and complex instincts of the male which come under the head of courtship, both before and after mating is effected, as furnishing a part of the stimulus to the female reproductive organs." HARPER proceeds to describe a curious habit which is common among pigeons before copulating. The male bird regurgitates some secretion in its throat, presumably from the crop gland, and this is taken up by the bill of the female in much the same manner as the young take their food. " It is easy to see that here may be one of the sources of indirect stimulation to the female reproductive organs." Numerous observations on the pigeon have been made likewise by WHITMAN (1919), who speaks of posturing as self-stimulating. Confirmatory observations have also been made recently by MARTINS (1935). That the display is accompanied by a high emotional disturbance in all birds that show it is very apparent.

The Marquess of TAVISTOCK, to whom I am much indebted for giving me the benefit of his extensive experience of birds of all kinds in a state of captivity, states that apart from gallinaceous birds he has very seldom known egg-laying to occur in any species excepting in the presence of the male. Spontaneous ovulation, in his experience, is non-existent or most rare in species which normally mate for life. It may occur, however, in unmated swans and with various kinds of cranes when two females live in abnormally close association. Otherwise, Lord TAVISTOCK informs me, these birds never lay unless mated. The conditions are clearly comparable to those seen in the pigeon. The mere presence of another individual provides an exteroceptive stimulus which acts on the pituitary and starts the nest-building and ovulating stage of the cycle.

THE MEANING OF SEXUAL DISPLAY

In view of such facts as these it is easy to see that sexual display and courtship phenomena generally probably serve an important function in producing the necessary synchronization of the male and female reproductive processes without which procreation cannot be accomplished. Such a view has been put forward by ELIOT HOWARD, and adopted by PYCRAFT (1913), and also by HUXLEY (1914), who has studied sexual posturing in the great crested grebe. HOWARD says that the purpose of posturing is the provocation of sexual reaction by mutual stimulation, HUXLEY refers to it as having an aphrodisiac action, and BEEBE (1931), supposes that it has " a slow indirect effect upon the nerves ". Here I suggest for it a more precise physiological signification.

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 exteroceptive stimuli which act upon the anterior pituitary through the hypothalamus, and so effects the necessary synchronization 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 the 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. Upon the basis of this theory we may, if we like, construct an hypothesis as to the evolutionary development of the display and the acquirement of adornment and of the aesthetic sense, comparable to Darwin's theory of sexual selection, and without encountering the main objections to which that theory is open. DARWIN (1871) applied his theory generally to all cases of sifting in relation to pairing and more especially to those involving the preferential but not necessarily conscious choice by the female of that particular male which by his superior beauty and more effective posturing was most attractive to her. Moreover, DARWIN made use of the argument that unless the female is influenced by the male so as to select him, the display of the males before her is meaningless. In the light of the theory of mutual stimulation postulated here, the display is not meaningless at all but subserves a definite purpose. According to this theory, it is not the female which selects the male; it is the pair which have the highest capacity for mutual stimulation which are, so to speak, selected by Nature for the perpetuation of the race. Nevertheless, that sexual selection occurs in some species, such as the ruff and the blackcock, would seem probable in view of the observations of SELOUS (1928), and it also appears to take place on occasion with various species of ducks. Yet as a generalization of wide application the theory fails. WALLACE (1889) on various grounds, rejected it, and MORGAN (1903) advanced no fewer than twenty reasons as to why it cannot be true. Some of the objections are supported by ELIOT HOWARD as a result of his researches on the warblers, and by BEEBE from his observations on the pheasants. But I do not wish to go into the objections here except to refer to what appears to me to be an outstanding one, which I can myself confirm, namely, that many birds are already paired before they begin their display. Thus, the rook undergoes considerable sexual posturing every breeding season, although the evidence shows that the male and female pair for years together, if not for life (YEATES, 1934). Professor RAVEN (1936), to whom I am greatly indebted for much relevant information, tells me that at the herring-gull colony on Godfrey Island off St. Ives the birds may remain paired for years. His informant was Mr. J. W. LEWIS, one of the lighthouse keepers, who kept careful watch for eight years and reported on the birds, many of which he knew individually. And herring-gulls undoubtedly show some display. The gannet also displays elaborately, as will be recollected by those who have seen HUXLEY's remarkable film (1935); yet KIRKMAN states that the gannet pairs for life. So also grey-lag geese are known to be paired before the breeding season, and other species of geese are said to pair for life (PYCRAFT, 1923). There are, as is well known, a great many other birds which do this, and HUDSON (1919) has shown that even in gregarious species like the starling, there is evidence that the birds pair for life; yet most species, if not all, show some sort of display. HINGSTON (1933) states that ducks pair off within the flock during the winter, whereas they may be seen displaying in the spring. In the warblers, buntings, and other passerine birds which form territories in the spring, the male takes up his position and then the female follows him, and it is not until the birds have already associated in pairs that posturing begins and it often takes place during the time of nest building. Sometimes, as Lord TAVISTOCK has found with birds in captivity, coition precedes nest building, and it is probable that in such cases where it takes place so long before the laying of the eggs its significance lies in stimulation rather than in fertilization, for the process is repeated later and often more than once while nest building is proceeding. A further point of interest is that sexual stimulation by display is often mutual, as seen in the simultaneous bobbing up and down of the head by both the drake and the duck, and in the far more elaborate display by both male and female during the courtship of the great-crested grebe, as described by HUXLEY.

The biological advantages of securing an effective synchronization of the male and female reproductive processes, and more particularly in relation to the time of ovulation, become very apparent when one considers the high degree of temporary infertility which animals may show in cases where the correlation concerned is imperfect. It is known that in some mammals ovulation is not always coincident with oestrus. Thus, DEANSLEY (1935) has shown that in the stoat ovulation cycles may precede oestrous cycles, that is to say, that outside of, or early in, the sexual season, the female stoat may ovulate on successive occasions before the oestrous periods commence. The same lack of correlation occurs also in the sheep, as has been shown by GRANT (1933), but in both these species at the later periods of the sexual season ovulation takes place within the phase of oestrus. These are instances of "disharmony" in functional adaptation, of which the reproductive system affords other examples. Moreover, at the end of the sexual season in the sheep, it sometimes happens that oestrus occurs without ovulation, as though the stimulating power of the ewe were insufficient to induce the process in the absence of the ram (MARSHALL, 1922). Nevertheless, the degree of sterility in the sheep from all causes, as estimated by HEAPE (1906), is not more than 6·76%.* In the horse, on the other hand, there is an exceptionally high degree of sterility, the reports of the Royal Commission on Horse Breeding showing that in any one year as many as 40% of mares in this country fail to have foals. Statistical information subsequently obtained points to the percentage of sterility being at least as great in recent years (according to SANDERS (1926), 50%). What is almost certainly the explanation of this unduly high percentage of temporarily or permanently sterile mares has been supplied by HAMMOND (1935), as the outcome of his studies on the oestrous cycle. Unlike the sheep, which has an oestrous period of a day or less, the mare often remains in a

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* This percentage figure includes abortion.

condition to receive the stallion for fully a week and sometimes for even longer. Ovulation generally occurs towards the end of the period, and most commonly about 24 hours before the end. Since, assuming that the released gametes of the horse are capable of conjugating for approximately the same duration of time as with the rabbit (in which the times have been ascertained experimentally), that is, for about 30 hours for the spermatozoa and six hours with the ova, it follows that service (which may take place at any time within the limits of oestrus) is often sterile, owing to the gametes losing their power of conjugation before it is possible for them to meet. This most frequently happens to the spermatozoa when the mare is served early in oestrus and many hours or even days before ovulation.

Thus, the importance of an effective synchronization between certain of the sexual processes is illustrated negatively by the condition which we find in an animal under domestication and not subject to the influence of natural selection. And we may conclude that in birds, if not in other animals, the significance of sexual adornment and display lies in their race-survival value, the pair of birds which are most effective in mutual stimulation having an advantage over the others in the perpetuation of the species or variety ; that is to say, we are dealing with a special case of natural selection.*

Conclusion

I may now sum up. Speaking generally, there is an internal rhythm of reproduction depending primarily upon the alternation of periods of rest and activity ; in correlation with this rhythm hormones are periodically elaborated by the gonads and act upon the accessory organs and secondary sexual characters. But in the higher animals, the internal rhythm is brought into relation with seasonal changes and other external environmental phenomena, these not merely conditioning the metabolic processes (as they do also in all or most of the lower animals, as well as in plants) but, in part at any rate, acting exteroceptively through the nervous system and probably through the hypothalamus upon the anterior pituitary and thence upon the testis or ovary. In the bird and in the male mammal the hypophisial and gonadal levels of activity tend to rise and fall together, but in the female the matter is complicated by the occurrence of pregnancy (or pseudopregnancy) and in polyoestrous species by the repetition of short dioestrous cycles within the sexual season. In these female cycles there are two main phases, the oestrous or follicular and the luteal, and their repetition in the absence of pregnancy is controlled by the pituitary and ovary acting and reacting upon each other. The condition of pregnancy causes the anterior pituitary to react differently and to prolong the duration of the corpus luteum. Apart from pregnancy, however, both the longer and the shorter cycles are liable to considerable modification by exteroceptive stimuli which play upon the pituitary through the nervous system. The

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* Reference may be made here to those species of animals such as the elephant, which lives perfectly healthily in a state of domestication or captivity, and sometimes to a great age without being able to breed. It may well be that this failure in generative function is due to the animals not receiving the appropriate kinds of exteroceptive stimuli.

sequence in the bird's cycle is also frequently interfered with by various kinds of exteroceptive stimuli which control ovulation and the related processes. We may conclude, then, that in all the higher animals sexual periodicity, while conditioned by the environment, is regulated in its successive phases by the combined integrative action of the nervous and endocrine systems.

The primary periodicity is a function of the gonad, the anterior pituitary acting as a regulator, and the internal rhythm is adjusted to the environment by the latter acting on the pituitary, partly or entirely, through the intermediation of the nervous system. The further fact, however, must not be overlooked, namely, that in the absence of the anterior pituitary the functions of the gonad fail, so that the pituitary, in common with the other endocrine organs, conditions the metabolic processes which are essential for reproduction.

POSTSCRIPT

Exactly parallel to the case of the sheep which, on being imported into South Africa, adjust themselves to the southern hemisphere seasonal cycle, is that of the red deer which were introduced into New Zealand. I have not been able to find any published records relating to the importation of the deer, but Lord LATYMER (1936), to whom I wish to express my indebtedness, has kindly given me some important information. Red deer were first sent to Otago about fifty years ago. Lord LATYMER was informed in New Zealand that the first calves were dropped in November, about two years after the mothers had been turned out, but that the change over may begin almost immediately after arrival. Now the rut begins about 20 March (in autumn) and the calves are dropped in the following November or December. Lord LATYMER states that deer have been imported into New Zealand from various sources besides Scotland—from Warnham Court and other English parks (the Rakaia herd being descended from Central European deer)—but that now, wherever they came from, they all begin roaring about the third week in March. As is well known, red deer, like Scottish and other breeds of sheep, in Europe rut in autumn when the daylight is diminishing.*

* I am indebted to Dr. ROUX for further information concerning a flock of Southdown sheep transported to a farm near Cradock, Cape Province, South Africa. A breeder imported 21 Southdown ewes which arrived on the farm towards the end of January, 1933. The ewes were in lamb and the first ewe lambed down on 23 January. The others lambed within one month of that date; only one ewe out of 21 was not pregnant. The lambs were duly weaned and the ewes put to the ram on 21 May, 1933. The ewes began to lamb on 15 October; all the ewes lambed. The ewes were put to the ram again on 20 April, 1934, and they lambed in September, 1934, except two, which were late; these lambed on 15 November and 14 December. The ewes were put to the ram again towards the end of March, 1935 and the first lamb was born on 27 August; all lambed within 40 days. The ewes were put to the ram again about the middle of March, 1936; they started to lamb on 13 August, and within 19 days all the 21 ewes had lambed. Thus the ewes lambed regularly during the spring months in South Africa. Southdown sheep in Britain have only one breeding season a year, lambing in spring. It is apparent from the record given above that the ewes lambed regularly also in the spring in South Africa. Thus the conversion of the time of the sexual season was very rapid since it took place immediately after the first lambing in South Africa.

DR. ZUCKERMAN (1936, B) informs me that the spotted deer of India (referred to on the authority of PYCRAFT as having changed its breeding season in captivity in Europe) breeds throughout the whole year and has no season for changing its coat. Dr. ZUCKERMAN states also that with the Thar (*Hemitragus jemlaicus*) in the Zoological Society's Gardens the breeding season as the years went on gradually became later. In the twenty-years period from 1891 to 1910 the peak of births as shown in frequency curves was in the end of May and in the following twenty-years period from 1911 to 1930 it was in the first half of July.*

LACK (1933, B) states that with the Arctic terns on Bear Island the time for ovulation and egg-laying seems to be controlled by the condition of the nesting site. If this is not in a fit state breeding is postponed although the gonads are fully developed, and in a late season the regression of the gonads may set in before the site has become suitable. LACK concludes that with this species, therefore, breeding is controlled partly by the nervous system.

MURPHY (1936) in a book just published on the oceanic birds of S. America, states that in the Atlantic equatorial isles Fernando de Noronha and St. Paul Rocks, the majority of the fowl apparently has no breeding season, for eggs and young may be found in any month of the twelve, but that the sooty tern is an exception. With this species there is evidence that the nesting season on Ascension begins a little earlier in each successive year, and that the change in time is sufficient to make the birds breed on the average four times within three years. It would seem as if in this species breeding periodicity depended entirely upon an internal sexual rhythm unaffected by seasonal exteroceptive factors. MURPHY also records some facts about the periodic breeding of certain species of penguins which are in striking contrast to the great majority of birds. The Peruvian and African penguins, that is, the two members of the genus *Spheniscus* which, coming presumably from the south, have invaded warm-temperate and tropical environments, may have two broods of young, nearly the whole of the year being occupied in breeding operations. KEARTON (1930), says that the African penguins have mating seasons in February and in September. According to LEVICK (1914), the black-footed penguins in the Zoological Gardens can breed several times a year. It would appear that the penguins are almost or quite unique among birds in having freed themselves from external seasonal influences. In this respect they are comparable to the domestic dog among mammals. MURPHY also gives many instances of sea birds of various kinds which seem to have a " continuous breeding season " under uniform conditions.

BAKER (BAKER and BAKER, 1936), in a recent paper on vegetable cycles (with special reference to the New Hebrides), shows that trees and plants are similar to

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* Lord TAVISTOCK informs me that the spotted or " Axis deer does *not* adapt itself to our seasons. No *tropical* deer does. As the Axis breeds and sheds its antlers at *all* times of the year, spring- and summer-born fawns do better in Europe and have more chance of survival, unless protection is afforded, than winter ones. In Europe this deer grows a winter coat and sheds it in spring in the normal way." Lord TAVISTOCK suggests that the later breeding of the Thar as the years went by was probably a nutritive effect.

animals in that they sometimes have specifically inherent flowering and leaf-bearing cycles which are independent of the environmental periodicity, or they may adjust themselves to the seasons, the latter condition being more usual.

The following additional observations pointing to courtship as a factor in ovulation in birds should also be referred to. HUXLEY (1923) states that the red-throated diver undergoes mutual sexual display which he interprets as being of a stimulating nature. The birds are already paired up in the winter months long before the display, and they possibly pair for life. Lastly, HUDSON (1920) records that with the Argentine cow-bird, which like the cuckoo has the parasitic habit of laying in other birds' nests, the males may be seen wooing the females from the beginning of September until the end of January, and in correlation with this extended period of courtship without nest-building or incubation, the number of eggs produced is phenomenally large (probably from 60 to 100), many of the eggs being dropped on the ground and wasted.

Further observations by the Marquess of TAVISTOCK on the breeding habits and periodicity of certain species of birds in captivity are recorded above in a footnote (p. 439).

As to whether the formation of gonadotropic substances (anti-hormones), such as have been produced experimentally in the serum of animals by COLLIP (1924) and others, plays any part normally in the periodicity of oestrus, is a question upon which there is at present no evidence. (*See also* ROWLANDS, 1936.)

REFERENCES

ALLEN, E. (1932). "Sex and Internal Secretions," London.

ALLEN, E. and DOISY, E. A. (1924). 'Amer. J. Physiol.,' vol. **69**, p. 577.

ALLEN, W. M. (1932). 'J. Biol. Chem.,' vol. **98**, p. 591.

ALLEN, W. M., and CORNER, G. W. (1929). 'Amer. J. Physiol.,' vol. **88**, p. 340.

ANCEL, P., and BOUIN, P. (1910). 'J. Physiol. Path. gén.,' vol. **12**, p. 1.

ANCEL, P., and BOUIN, P. (1911). 'J. Physiol. Path. gén.,' vol. **13**, p. 31.

ARISTOTLE. "Historia Animalium." (Thompson's translation.) (1910.) Oxford.

ASDELL, S. A. (1926). 'Ph.D. Thesis,' Cambridge. Unpublished.

ASDELL, S. A. (1932). 'Amer. J. Physiol.,' vol. **100**, p. 137.

BACQ, Z. M., and BROUHA, L. (1932). 'Arch. Int. Physiol.,' vol. **35**, p. 250.

BAKER, J. R. (1929). "Man and Animals in the New Hebrides," London.

BAKER, J. R., and BAKER, I. (1936). 'J. Linn. Soc. (Zool.),' vol. **39**, p. 507.

BAKER, J. R., and RANSON, R. M. (1932). 'Proc. Roy. Soc.,' B, vol. **110**, p. 313.

BANNERMAN, D. A. (1930–31–33). "The Birds of Tropical West Africa," vols. **1**, **2**, and **3**. London.

BEEBE, W. (1931). "Pheasants, Their Lives and Homes," New York.

BELLERBY, C. W. (1929). 'J. Physiol.,' vol. **67**, Proc., p. xxxiii.

BELLERBY, C. W. (1933). 'Bio-chem. J.,' vol. **27**, p. 2025.

BENOIT, J. (1934). 'C.R. Acad. Sci. Paris,' vol. **199**, p. 1671.

—— (1935). 'C.R. Acad. Sci. Paris,' vol. **201**, p. 359.

Benoit, J., and Aron, M. (1934). ‘C.R. Soc. Biol. Paris,’ vol. **116**, p. 221.

Bernard, C. (1859). ‘Leçons sur les Propriétés Physiologiques,’ Paris.

Berthold, A. A. (1849). ‘Arch. Anat. Physiol.,’ p. 42.

Bissonette, T. H. (1932). ‘Proc. Roy. Soc.,’ B, vol. **110**, p. 322.

—— (1933). ‘Quart. Rev. Biol.,’ vol. **8**, p. 201.

—— (1935). ‘J. Exp. Biol.,’ vol. **12**, p. 315.

—— (1936). ‘J. Hered.,’ vol. **27**, p. 171.

Brown-Séquard, C. E. (1889). ‘Arch. Physiol.,’ vol. **1**, p. 651.

Butenandt, A. (1929). ‘Naturwissenschaften,’ vol. **17**, p. 879.

—— (1931). ‘Z. angew. Chem.,’ vol. **44**, p. 905.

Butenandt, A., Westphal, U., and Cohler, H. (1934). ‘Ber. deuts. chem. Ges.,’ vol. **67**, p. 1611.

Cameron, A. T. (1935). “Recent Advances in Endocrinology,” London.

Cannon, W. B., Newton, H. F., Bright, E. M., Menkin, V., and Moore, R. M. (1929). ‘Amer. J. Physiol.,’ vol. **89**, p. 84.

Catchpole, H. R., Cole, H. H., and Pearson, P. B. (1935). ‘Amer. J. Physiol.,’ vol. **112**, p. 21.

Chance, E. P. (1936). “Some Observations on Egg Collecting,” privately printed.

Cohen, S. L., Marrian, G. F., and Watson, M. (1935). ‘Lancet,’ 23 March, p. 674.

Cohen, S. L., and Marrian, G. F. (1935). ‘Bio-chem. J.,’ vol. **30**, p. 57.

Cole, L. J. (1933). ‘Auk.,’ vol. **50**, p. 284.

Collip, J. B. (1932). ‘Trans. Roy. Soc. Canada,’ vol. **26**, p. 1.

—— (1934). ‘J. Mount Sinai Hospital,’ vol. **1**, p. 28.

Copeman, S. Monckton. Unpublished, quoted by Swale Vincent, 1912. “Internal Secretion and the Ductless Glands,” London.

Corner, G. W. (1930). ‘Amer. J. Physiol.,’ vol. **95**, p. 43.

Courrier, R., and Gros, R. (1935). ‘C.R. Soc. Biol. Paris,’ vol. **120**, p. 5.

Croll, M. (1928). ‘J. Physiol.,’ vol. **66**, p. 316.

Cushing, H. (1932). “Pituitary Body, Hypothalamus and Parasympathetic Nervous System,” Springfield and Baltimore.

Darwin, C. (1871). “Descent of Man,” London.

David, K., Dingemanse, E., Freud, J., and Laqueur, E. (1935). ‘Z. physiol. Chem.,’ vol. **233**, p. 281.

Deanesly, R. (1928). ‘Proc. Roy. Soc.,’ B, vol. **103**, p. 523.

—— (1935). ‘Phil. Trans.,’ B, vol. **225**, p. 459.

Dempsey, B. W., Myers, H. J., Young, W. C., and Dennison, D. P. (1934). ‘Amer. J. Physiol.,’ vol. **109**, p. 307.

Dingemanse, E., de Jongh, S. E., Kober, S., and Laqueur, E. (1930). ‘Deuts. med. Wschr.,’ vol. **56**, p. 301.

Dodds, E. C. (1934). Goulstonian Lectures. ‘Lancet’ (5, 12 and 19 May), p. 931, p. 987 and p. 1048.

—— (1935, a). “Harvey Lectures,” p. 119.

Dodds, E. C. (1935, b). ‘Ergbn. Physiol.,’ vol. **37**, p. 264.
Dodds, E. C., and Lawson, W. (1936). ‘Nature,’ vol. **137**, p. 976.
Doisy, E. A., Veler, C. D., and Thayer, S. (1929). ‘Amer. J. Physiol.,’ vol. **90**, p. 329.
Elder, J. H., and Yerkes, R. M. (1936). ‘Proc. Roy. Soc.,’ B, vol. **120**, p. 409.
Ellis, Havelock (1900). “Studies in the Psychology of Sex,” Philadelphia.
Evans, H. M., and Burr, G. O. (1927). ‘Mem. Univ. California,’ vol. **8**.
Evans, H. M., and Long, J. A. (1922). ‘Proc. Nat. Acad. Sci. Wash.,’ vol. **8**, p. 38.
Ewart, J. C. (1908). Personal communication. *See also* Marshall, 1922. “Physiology of Reproduction.”
Fee, A. R., and Parkes, A. S. (1929). ‘J. Physiol.,’ vol. **67**, p. 383.
Fels, E., and Slotta, K. H. (1931). ‘Klin. Wschr.,’ vol. **10**, p. 1639.
Fevold, H. L., and Hisaw, F. L. (1932). ‘Proc. Soc. Exp. Biol.,’ N.Y., vol. **29**, p. 620.
Foà, C. (1901). ‘Arch. Ital. Biol.,’ vol. **35**, p. 364.
Foges, A. (1903). ‘Arch. ges. Physiol.,’ vol. **93**, p. 39.
Fraenkel, L. (1903). ‘Arch. Gynäk.,’ vol. **68**, p. 438.
Frank, R. T., and Goldberger, M. A. (1928). ‘J. Amer. Med. Assoc.,’ vol. **90**, p. 106.
Friedgood, H. B., and Pincus, G. (1935). ‘Endocrinology,’ vol. **19**, p. 710.
Friedman, M. H. (1929). ‘Amer. J. Physiol.,’ vol. **90**, p. 617.
Frohlich, A. (1901). ‘Wiener klin. Rundschau,’ vol. **150**, p. 883.
Gillman, J. (1935). ‘S. Afric. J. Sci.,’ vol. **32**, p. 342.
Girard, A. (1933). ‘Bull. Soc. Chem.,’ vol. **15**, p. 562.
Grant, R. (1933). ‘Trans. Roy. Soc. Edin.,’ vol. **58**, p. 1.
Halban, J. (1900). ‘Mschr. Geburtsh. Gynäk.,’ vol. **12**, p. 496.
Hammond, J. (1925). “Reproduction in the Rabbit.” Edinburgh.
—— (1927). “The Physiology of Reproduction in the Cow.” Cambridge.
—— (1935). “15th Internat. Physiol. Congress, Leningrad and Moscow.” Summary of Communications, p. 142.
Harper, E. H. (1904). ‘Amer. J. Anat.,’ vol. **3**, p. 349.
Harris, G. W. (1936, a). ‘J. Physiol.,’ vol. **87** Proc., p. 61.
—— (1936, b). Personal communication.
Haterius, H. O. (1933). ‘Amer. J. Physiol.,’ vol. **103**, p. 97.
—— (1934). ‘Proc. Soc. Exp. Biol., N.Y.’ vol. **31**, p. 1112.
Heape, W. (1900), ‘Quart. J. Micr. Sci.,’ vol. **44**, p. 1.
—— (1905). ‘Proc. Roy. Soc.,’ B, vol. **76**, p. 260.
—— (1906). “The Breeding Industry,” Cambridge.
Hill, J. P., and O’Donoghue, C. H. (1913). ‘Quart. J. Micr. Sci.,’ vol. **59**, p. 133.
Hill, M., and Parkes, A. S. (1933). ‘Proc. Roy. Soc.,’ B, vol. **115**, p. 14.
Hingston, R. W. G. (1933). “The Meaning of Animal Colour and Adornment,” London.
Hinsey, J. C., and Markee, J. E. (1932). ‘Proc. Soc. Exp. Biol., N.Y.,’ vol. **30**, p. 136.

Hogben, L. T. (1933). Personal communication to E. O. Whetham, *q.v.*

—— Charles, E., and Slome, D. (1931). 'J. Exp. Biol.,' vol. 8, p. 345.

Hohlweg, W., and Dohrn, M. (1931). 'Wiener Arch. innere Med.,' vol. **21**, p. 337.

Howard, H. E. (1929). "Introduction to the Study of Bird Behaviour," Cambridge.

—— (1935). "The Nature of a Bird's World," Cambridge.

Hudson, W. H. (1919). "Birds in Town and Village," London.

Hudson, W. H. (1920). "Birds of La Plata," vol. **1**, London.

Hume, E. M. M. (1936). Personal communication.

Huxley, J. S. (1914). 'Proc. Zool. Soc.,' p. 491.

Huxley, J. S. (1923). 'J. Linn. Soc. (Zool.),' vol. **35**, p. 253.

—— (1935). "The Private Life of the Gannets." Film.

Ivanova, S. (1935). 'Arch. exp. Path. Pharmak.,' vol. **179**, p. 349.

Jesse, E. (1842). "Gleanings in Natural History," London.

Kearton, C. (1930). "The Island of Penguins," New York.

Kirkman, F. B. (1911–1913). "The British Bird Book," London.

Kirschbaum, A. (1933). 'Anat. Rec.,' vol. **57**, Suppl., p. 62.

Knauer, E. (1900). 'Arch. Gynäk.,' vol. **60**, p. 322.

Lack, D. L. (1933, a). Personal communication.

Lack, D. L. (1933, b). 'Proc. Zool. Soc.,' p. 231.

Langdon-Brown, W. (1935). "Horsley Memorial Lecture." Cambridge.

Latymer, Lord (1936). Personal communication.

Levick, G. M. (1914). "Antarctic Penguins," London.

Lipschütz, A. (1927). 'Biol. Rev.,' vol. **2**, p. 263.

Loeb, L. (1911). 'Deuts. med. Wschr.,' vol. **37**, p. 17.

Loewi, O. (1935). 'Proc. Roy. Soc.,' B, vol. **118**, p. 299.

Long, J. A., and Evans, H. M. (1922). 'Mem. Univ. California,' vol. **6**.

Lucas, N. S., Hume, E. M. M., and Smith, H. H. (1927). 'Proc. Zool. Soc.,' p. 447.

MacCorquodale, D. W., Thayer, S. A., and Doisy, E. A. (1934). 'Proc. Soc. Exp. Biol., N.Y.,' vol. **32**, p. 1182.

McGee, L. C. (1927). 'Proc. Inst. Med., Chicago,' vol. **6**, p. 242.

Marrian, G. F. (1930). 'Bio-Chem. J.,' vol. **24**, p. 435 and p. 1021.

Marshall, F. H. A. (1922). "The Physiology of Reproduction," London.

Marshall, F. H. A., and Bowden, F. P. (1934). 'J. Exp. Biol.,' vol. **11**, p. 409.

Marshall, F. H. A., and Halnan, E. T. (1917). 'Proc. Roy. Soc.,' B, vol. **89**, p. 546.

Marshall, F. H. A., and Jolly, W. A. (1905). 'Phil. Trans.,' B, vol. **198**, p. 99.

Marshall, F. H. A., and Verney, E. B. (1936). 'J. Physiol.,' vol. **86**, p. 327.

Martins, T. (1931). "Suppl. d. Mem. Inst. Oswaldo Cruz. No. 12," p. 301, quoted by Moore and Price, *see* below.

—— (1935). 'Trans. Dynamics of Devt.,' Moscow, vol. **10**, p. 181.

Meyer, R. K., Leonard, S. L., and Hisaw, F. J. (1929). 'Proc. Soc. Exp., Biol., N.Y.,' vol. **27**, p. 340.

Moore, C. R., and Price, D. (1932). ‘Amer. J. Anat.,’ vol. **50**, p. 13.

Moore, C. R., Simmons, G. F., Wells, L. J., Zalesky, M., and Nelson, W. O. (1934). ‘Anat. Rec.,’ vol. **60**, p. 279.

Moore, C. R. (1935). ‘Amer. J. Obstet. Gynaec.,’ vol. **29**, p. 1

Morgan, T. H. (1903). “Evolution and Adaptation,” New York and London.

Murphy, R. C. (1936). “Oceanic Birds of South America,” New York.

Papanicolaou, G. N., and Stockard, C. R. (1920). ‘Proc. Soc. Exp. Biol., N.Y.,’ vol. **17**, p. 143.

Parkes, A. S. (1929). “The Internal Secretions of the Ovary,” London.

Pézard, A. (1911). ‘C.R. Acad. Sci. Paris,’ vol. **153**, p. 1027, and vol. **154**, p. 1183.

Pycraft, W. P. (1913). “The Courtship of Animals.” London.

—— (1923). *See* Kirkman.

Raven, C. E. (1936). Personal communication.

Ray, J. (1848). “The Correspondence of John Ray,” edited by E. Lankester, London.

Riddle, O. (1935). ‘J. Amer. Med. Ass.,’ vol. **104**, p. 636.

Riddle, O., and Braucher, P. F. (1931). ‘Amer. J. Physiol.,’ vol. **92**, p. 617.

Robson, J. M. (1934). “Recent Advances in Sex, etc.,” London.

Robson, J. M., and Henderson, W. R. (1936). ‘Proc. Roy. Soc.,’ B, vol. **120**, p. 1.

Roux, L. L. (1936). Personal communications.

Rowan, W. (1926). ‘Proc. Boston Soc. Nat. Hist.,’ vol. **38**, p. 147.

—— (1930). ‘Proc. Nat. Acad. Sci. Wash.,’ vol. **16**, p. 520.

Rowlands, I. W. (1936). ‘Proc. Roy. Soc.’ B (*in the press*).

Rowlands, I. W., and Parkes, A. S. (1936). ‘Proc. Zool. Soc.,’ p. 823.

Ruzicka, L. (1936). ‘Nature,’ vol. **137**, p. 260.

Ruzicka, L., Goldberg, M. W., and Meyer, J. (1935). ‘Helv. chim. Acta.,’ vol. **18**, pp. 210, 994.

Sanders, H. G. (1926). ‘J. Agric. Sci.,’ vol. **16**, p. 466.

Schwenk, E., and Hildebrandt, F. (1933). ‘Naturwissenchaften,’ vol. **21**, p. 177.

Selous, E. (1928). “Realities of Bird Life,” London.

Selye, H., Collip, J. B., and Thomson, D. L. (1935). ‘Endocrinology,’ vol. **19**, p. 151.

Selye, H., and McKeown, T. (1934). ‘Anat. Rec.,’ vol. **60**, p. 323.

Semper, K. (1881). “The Natural Conditions of Existence that Affect Animal Life,” London.

Severinghaus, A. E. (1934). ‘Anat. Rec.,’ vol. **60**, p. 43.

Severinghaus, A. E., Engle, E. T., and Smith, P. E. (1932). *In* Allen, E. (1932) (ch. 17).

Shattock, S. C., and Seligman, C. G. (1904). ‘Proc. Roy. Soc.,’ vol. **73**, p. 49.

Shelesnyak, M. C. (1931). ‘Anat. Rec.,’ vol. **49**, p. 179.

Smith, P. E. (1930). ‘Amer. J. Anat.,’ vol. **45**, p. 205.

Smith, P. E., and Engle, E. T. (1927). ‘Amer. J. Anat.,’ vol. 40, p. 159.

Smith, P. E. (1932). *In* Allen, E., 1932 (ch. 15).

Snyder, F. F. (1934). ‘Bull. Johns Hopkins Hosp.,’ vol. **54**, p. 1.
Starling, E. H. (1905). “Croonian Lectures, Roy. Coll. Physicians.”
Steinach, E. (1920). ‘Arch. Entw.Mech. Org.,’ vol. **46**, p. 557.
Tavistock, The Marquess of (1935). ‘Bull. Brit. Ornithologists’ Club,’ vol. **55**, p. 144.
—— (1936). Personal communications.
Theobald, G. W. (1936). ‘Brit. Med. J. No. 3933,” p. 1038.
Vogt, M. (1933). ‘Arch. Exp. Path. Pharmak.,’ vol. **170**, p. 72.
Wallace, A. R. (1889). “Darwinism.” London.
Walton, A., and Marshall, F. H. A. Unpublished.
Wells, L. J. (1935). ‘Anat. Rec.,’ vol. **62**, p. 409.
Westermarck, E. (1921). “The History of Human Marriage,” 5th Ed., London.
Whetham, E. O. (1933). ‘J. Agric. Sci.,’ vol. **23**, p. 383.
Whitman, C. O. (1919). “The Behaviour of Pigeons” (posthumous works), Washington.
Witschi, E. (1935). ‘Wilson Bull.,’ vol. **47**, p. 177.
Wolfe, J. M., Phelps, D., and Cleveland, R. (1934). ‘Amer. J. Anat.,’ vol. **55**, p. 363.
Yarrell, W. (1882). “British Birds,” 4th Ed., London.
Yeates, G. K. (1934). “The Life of the Rook,” London.
Zondek, B. (1931). “Die Hormone des Ovariums u. des Hypophysenvorderlappens,” Berlin.
Zondek, B. (1934). ‘Nature,’ vol. **133**, p. 209.
Zondek, B., and Aschheim, S. (1927). ‘Arch. Gynäk.,’ vol. **130**, p. 1.
—— (1928). ‘Klin. Wschr.,’ vol. **7**, p. 831.
Zuckerman, S. (1932). “The Social Life of Monkeys and Apes.”
Zuckerman, S. (1936, a). ‘J. Physiol.,’ vol. **87**, Proc., vol. **51**.
Zuckerman, S. (1936, b). Personal communication.