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The "Sexual Season" of Mammals and the
Relation of the "Pro-œstrum" to Menstruation.

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INTRODUCTION.

THE following paper is concerned with certain phenomena which affect reproduction and which occur in female mammals prior to the fertilisation of the ovum.

The times of propagation of the species and the behaviour of many female mammals during certain portions of the

breeding season have been noted by zoologists, but the changes which take place in the female generative system prior to gestation require examination which it is impossible to extend, with few exceptions, to mammals in the wild state, and almost all that is known on this matter is derived from a study of domesticated mammals and of some few wild animals kept in captivity. But little attention, however, has been paid to the subject at all by scientific students, while the only attempt, so far as I am aware, which has been made to treat it from a comparative point of view is that of Wiltshire, whose "Lectures on the Comparative Physiology of Menstruation" were published in the 'British Medical Journal' (1883).

The subject is of importance in proportion to the light it may throw upon the evolution of the functional phenomena of breeding. To attack such a subject by means of data obtained from the highest groups of animals may seem to many to be beginning at the wrong end of the story, and there is, of course, much truth in that view; but knowledge of the physiology of the lower animals is at present very limited, and information regarding the habits of most of them at times of reproduction extremely scanty;¹ on the other hand, we have available some knowledge of the habits of many classes of mammals and of the variety of sexual phenomena exhibited by them.

The data for a comprehensive comparative account even in mammals does not exist; at the same time there is sufficient material at hand, in my opinion, to permit of a foundation being laid, upon which it will be more easy to arrange facts in the future. It is, therefore, not with any idea of finality, but with the purpose of suggesting a wide field of inquiry, and with the hope of assisting therein, that this chapter on the comparative physiology of breeding has been written.

In the first place, with regard to the terms to be used; at present there is great confusion regarding those used by breeders; the same terms are used for both male and female

¹ In this relation Dr. Lo Bianco's papers in the 'Mith. Zool. Stat. Neapel,' vol. viii, 1888, and vol. xiii, 1899, are of great value.

animals when they should not be so used, the same terms are used for different processes and conditions in female mammals, and it is necessary for a clear understanding of the subject that the limits of their use should be defined, and where needful new terms adopted.

One of the most fertile sources of confusion is, disregard of the fact that the history of the generative phenomena exhibited by female mammals is different when reproduction takes place and when it does not take place; it is essential that this fact should be kept in mind.

The remainder of this Introduction I have devoted to a definition of the terms used in the following pages, and to an endeavour to show wherein they differ or are in accord with those now in use.

Reproductive Period.—I have used this expression to denote the whole of that period in the life of a mammal, whether male or female, during which its generative organs are capable of the reproductive function; and in contrast to the Pre-reproductive and Post-reproductive periods which severally precede and follow it, during which the generative organs are either not fully developed or are degenerate.

The bearing of young, however, is not possible at all times during the reproductive period. In the course of that period there are intervals during which the generative organs of all mammals exhibit, on the one hand special activity, and on the other hand a fallow condition. This variation is periodic, and is due, not to a periodic degeneration from a stable condition, but to the periodic accession of a special stimulus, culminating in sexual desire, and resulting in coition and in gestation in the female when conception takes place.

The periodicity of this stimulus is very variable, and is influenced by many factors of both extraneous and internal origin.

Breeding Season is adopted to denote the whole of that consecutive period during which any male or female mammal is concerned in the production of young, and it is not applicable to any isolated portion of that period.

Although the part which the male takes in breeding is confined to the insemination of the female, while the whole of the rest of the process is carried on by the female, and in spite of the fact that the word "breed" carries with it, in its original sense, as I understand it, the giving of nourishment, and might perhaps in that sense be confined to the female, it is impossible to avoid including the male. The extent of the breeding season of a male depends upon the length of time during which he is preparing for, and is capable of, inseminating a female; while the extent of the breeding season of a female mammal depends upon the extent of the sexual season, during which her generative organs are preparing for conception, plus the time occupied by gestation, or the gestation period.

The term has been used to describe specially the season when mammals copulate, or, again, it has been used to specially designate the period of gestation in the female; but it is not applicable as a definitive of either of these periods separately, and must be used for the whole consecutive breeding period experienced, and in this sense is applicable to both male and female mammals.

The term "breeding" is also frequently used in connection with the rearing of the young after birth, and this has given rise to confusion, inasmuch as while the mother is providing nutriment for young already born, she may or may not be bearing others. It is obviously inconvenient to include the period of suckling in the "breeding season," for which reason I have called it the Nursing Period.

Sexual Season is a term I have used to designate, for both male and female mammals, the particular time or times of the year during which their sexual organs exhibit special activity.

Some mammals experience only one sexual season each year, some experience more than one; in some it is a brief period, in others it occupies a much longer time; in some the sexual season of the female may be interfered with by gestation, in others it is not.

It is a convenience to be able to use one term for this phenomena in both sexes, but it is to be noted in the first place, that the sexual season of an individual male and individual female of the same species is not necessarily coincident, either with regard to time or with regard to extent; and in the second place, that the phenomena exhibited are different in the two sexes. For this reason special terms are used for each sex.

The Male Sexual Season.

Rutting Season.—This term is used to describe all seasons of special activity of the generative organs of the male, during which he is desirous of coition and normally capable of inseminating the female. In some animals these seasons are of short duration and at long intervals; in others the intervals may be shorter or the duration of the season longer; while in others, again, there would appear to be little or no cessation of the generative power.

It is necessary here to remark that the term "rut" (German "Brunst," French "rut") is used by German and French authors frequently, and by some English writers, to designate the conditions obtaining in both male and female mammals during the sexual season. This is an error; it is essentially a word which should be confined to the phenomena exhibited by the male; it has its origin in the Latin word "rugire," to roar or bellow, and is, I believe, strictly applicable only to such animals as stags and boars. There are, however, other male animals to which the term may be applied in its original sense, as, for instance, the bull elephant in a condition of "must," and it will be convenient to extend the use of the term "rut" to the males of all animals which exhibit seasons of special generative activity; to those, on the other hand, who are capable of inseminating the female at all times of the year, the term is not applicable.

The Female Sexual Season.

In the case of the female the activity of her generative

organs and the form which that activity takes is modified by conception, and it is necessary to consider the subject under two heads: (1) when reproduction does not take place, that is in the absence of the male, or when coition does not result in conception; and (2) when reproduction does take place.

Under either of these circumstances the changes which take place in the generative system are both complex and variable, and for purposes of comparative study must be identified.

(1) When Reproduction does not take place.—In the first place we will consider the changes which take place in the simplest form of the female sexual season, and afterwards indicate the nature of the more complicated processes.

Pro-œstrum, or the Pro-œstrous Period, is the term I have adopted to describe the first phases of generative activity in the female mammal at the beginning of a sexual season; it is identical with the period spoken of by the more accurate breeders as the time during which an animal is "coming on heat," or "coming in season." During this period certain changes take place in the generative organs which, while in some animals they are more drastic, in some more complete than in others, are based on the same plan, have the same object, and the same effect in all. They result in a condition which I have called—

œstrus.—This is the climax of the process; it is the special period of sexual desire of the female; it is during œstrus, and only at that time, the female is willing to receive the male and fruitful coition rendered possible in most, if not in all, mammals.

œstrus may be a brief period and exist for only a few hours, or it may extend for days, or apparently even for weeks; it is possible; however, normally, only as a result of the active changes which take place in the generative organs during pro-œstrum.

The period of œstrus is referred to by various writers as "Brunst," "rut," "heat," "season," "brim," or

"œstrum;" as I have before remarked, some of these terms are used also to designate the rutting season of the male, and most of them are used indiscriminately for both the periods of pro-œstrum and œstrus, which I seek now to establish for the female. In comparing, therefore, the writings of former investigators with the statements made in the following paper, it must be recollected that the various terms hitherto used are not necessarily homologous with those used by me, and are not necessarily descriptive of the sexual season or of the breeding season of female mammals, as I understand these processes. Much of the confusion and misunderstanding which exists, regarding breeding phenomena, is due to the indiscriminate use of the terms above noted, and it is essential that their use should be restricted, or given up altogether.

There is one point which I should briefly refer to here. I have said above that œstrus, the period of desire, normally follows pro-œstrum; but there are times when the females of certain, probably of many, mammals are anxious to receive the male without the pro-œstrum having taken place.

This condition may occur in various mammals during pregnancy, and has frequently been noticed in most species of domestic mammals during that period, while it is evident in a considerable number of animals also at other times. This may be called abnormal œstrus. Normal œstrus, as we shall see below, occurs in conjunction with certain changes in the uterine tissue, and this is accompanied by congestion and stimulation or irritation of the copulatory organs; whether the congested condition of the latter organs is in itself sufficient to induce œstrus, or whether the presence of some peculiar substance in the blood, or other influences, are essential for that purpose, is not known; however that may be, congestion is invariably present, and is an essential condition.

So also in abnormal œstrus, congestion of the copulatory organs takes place, but the changes in the uterus which are evident in normal œstrus are apparently absent. When

œstrus occurs during pregnancy it is probably due to a temporary diversion of a superabundant supply of placental blood; when it occurs at other times, the highly nutritious food, with which the animals which experience it appear to be generally supplied, or the condition resulting therefrom, is possibly largely responsible for it.

Metœstrum, or the Metœstrous Period.—If conception does not take place during œstrus the activity of the generative organs gradually subsides during a definite period, which I have called the metœstrum; and this is followed, in the simple form which we are now considering, by a long period of rest.

Anœstrum, or the Anœstrous Period, is the name I have given to this period of rest. It may last two or three or eleven or possibly more months, and during that time the generative organs lie fallow in the non-pregnant female. It is eventually succeeded by a new pro-œstrum, and the four periods, pro-œstrum, œstrus, metœstrum, and anœstrum, constitute what I have designated as the anœstrous cycle.

By some this period of anœstrum is called the non-breeding season, but this is not correct, for although conception cannot take place during this period it may be occupied partially or wholly by the period of gestation, and inasmuch as gestation is included in the breeding season, the anœstrum cannot be considered as a non-breeding season.

We now have to consider a more complicated form of sexual season. In this case the sexual season is ushered in as before, with the pro-œstrum, œstrus follows, and is succeeded by metœstrum, but instead of the anœstrum, a short quiescent period now occurs which I have called the—

Dicœstrum, or the Dicœstrous Period.—This is a brief period lasting only a few days, at the most probably not more than twelve or fourteen days, while in some animals four to six days may be its duration. It is followed at once by a new pro-œstrum, and the four periods, pro-œstrum, œstrus, metœstrum, and dicœstrum, I have designated the dicœstrous cycle.

In those animals which experience the diœstrous cycle the sexual season (when conception does not take place) consists of a series of such cycles, two or more; and may occupy any length of time from one month to the whole year. In the former case it is limited to a definite portion of the year only, while in the latter case it may be coincident with the whole reproductive period [human female, under certain conditions]. But when the recurrence of the diœstrous cycle is limited to a definite portion of the year, the sexual season is, of course, also limited to that period, and there is consequently a period of rest, which is the anœstrum.

In such cases the non-pregnant female experiences a series of diœstrous cycles during the sexual season, at the end of which, instead of diœstrum following metœstrum, the latter is succeeded by anœstrum, which persists until the next sexual season occurs.

In order to distinguish between the two classes of female mammals into which the occurrence or absence of diœstrum divides them, I have called those which experience a single œstrus during each sexual season, or in other words those in which the anœstrous cycle only occurs, monœstrous mammals; while those whose sexual season is occupied by a series of diœstrous cycles, or in other words those who experience a series of recurrent œstri, I have called polyœstrous mammals.

The complication into which an otherwise simple story is thrown is due, therefore, to variation in the quiescent period. In some animals this may be a very brief period, never lasting more than a few days; in others it may occupy from two to eleven months each time it occurs; while in others again both these conditions are experienced at different times of the year.

Functionally, no doubt, these two varieties of the quiescent period are homologous, the one is a modification of the other; and the modification is probably due, as will be shown below, to an increased or decreased power of reproduction. At the same time, for the purposes of the present paper, the difference between them is essential, and their relation to the sexual

season renders it necessary to discriminate clearly between them.

The result of the foregoing may be summarised thus: when the male has not access to the female during the sexual season, or when insemination at that time does not result in the fertilisation of an ovum, pro-œstrum and œstrus are followed by metœstrum and, if the animal be polyœstrous, diœstrum is followed by another pro-œstrum, and such diœstrous cycles continue so long as the sexual season lasts; whereas if the animal be monœstrous, or if the diœstrous cycles of the polyœstrous animal be ended, anœstrum follows, and persists until a new sexual season occurs.

A few examples will render the foregoing somewhat more clear. Among monœstrous mammals is the wolf, which, in the wild state, experiences only one sexual season at a particular time each year; in her case pro-œstrum and œstrus are followed, when conception does not take place, by metœstrum, and the whole of the remainder of the year is occupied by anœstrum. She therefore experiences a single anœstrous cycle each year.

Another monœstrous animal is the domestic bitch; but in her case, in the absence of gestation, the anœstrous cycle may recur two, three, or even four times each year.

Among polyœstrous mammals the mare may be taken as an example; during a certain portion of the year, of variable extent, she undergoes a series of diœstrous cycles when she is not pregnant; this portion of the year is her sexual season; when it is over anœstrum occurs and lasts until the commencement of the same time the following year.

The human female, who is also a polyœstrous mammal, under certain circumstances has a continuous series of diœstrous cycles throughout the year when she is not pregnant, and is thus subject to a sexual season during the whole of her reproductive period.

(2) When Reproduction does take place.—In this case the pro-œstrum is followed by œstrus, during which period insemination occurs and the ovum or ova are fer-

tilised; gestation results and persists until parturition takes place.

After parturition there may be a considerable interval of rest; this interval may occupy only what remains of the anœstrous period which the same animal would experience in case it had not borne young, or it may persist during a nursing period which extends beyond the normal limits of such anœstrous period, or it may be even still further prolonged. On the other hand, parturition may be followed almost immediately, and in spite of the nursing period, by pro-œstrum, œstrus, insemination, and renewed gestation. While finally, the same animal may at one time of the year exhibit a recurrent gestation, while at another time of the year its generative organs may continue fallow for the remainder of that interval which represents the anœstrous period.

Such briefly are the different types of breeding phenomena exhibited by female mammals during their reproductive period; the following account will show that they all conform to one plan, and that the variability, which altered conditions of life induce therein, clearly indicates the origin of these types. On this account the subject is likely to be of considerable interest to students of variation, and the collection of facts which bear thereon is urgently needed.

The Sexual Season of Male Mammals.

It is unnecessary to do more than mention here that males may be divided into two classes: those which rut (stag), and those which do not rut (dog). Rutting males have a special sexual season; those which do not rut experience sexual capability all the year round.

The sexual season of some males in captivity¹ is capable

¹ Information regarding wild animals in captivity, unless otherwise stated, has been obtained from certain keepers in the Zoological Gardens of London, whose statements appear to me to be reliable. The reference given in the text is (Zoo.).

of modification similar to that of certain females under the same conditions; for instance, wapiti stags under natural conditions have a special limited rutting season, but in captivity (Zoo.) they rut all the year round except during the season when they cast their antlers and until those structures grow again.

When rutting exists it is probably excited by similar influences to those which induce the advent of œstrus in the female; on the other hand, when the sexual season of a male is a permanent characteristic, either all the females of that species have a sexual season all the year round or individual females have different times for their sexual season.

As examples of these two conditions it may be pointed out that the camel in the Zoological Gardens of London ruts at much the same time as the female camels experience œstrus in Mongolia, namely, early in spring (Prejevalsky, 1876), although in the Gardens there are no female camels; while the sexual passions of the dog, on the other hand, are excited by œstrus of the bitch and may be called forth at any time of the year.

At the same time the proximity of the two sexes may stimulate both œstrus and rutting. The stimulation of œstrus is noticed in some of the larger carnivora in the Zoological Gardens by the presence of the male, while I have noticed rut in *Semnopithecus entellus*, in the Calcutta Zoological Gardens, stimulated by the female; and rut in the domestic rabbit stimulated by a doe under the influence of œstrus.

It is interesting to observe that while the sexual activity of domestic mammals (Müller, 1838) and of wild animals in captivity (Heck, 1899) may be more frequently exhibited, it is not so violent as is shown by animals in the wild state.

For the purposes of this paper, this is all that need be said specially, regarding the generative phenomena exhibited by the male; although the activity of his generative organs may be to some extent influenced by the presence or absence of the

female, the general scheme of his reproductive period, and breeding, sexual or rutting season, remains the same.

The Breeding Season of Female Mammals.

The breeding season of mammals should rightly be considered after the sexual season has been discussed, but, owing to the fact that the term "breeding season" has been so universally used to designate the sexual season as well as the gestation period of breeding mammals, it is necessary to say a few words here in order to make the following account clear.

The occurrence of a breeding season depends upon the occurrence of a sexual season, and those factors which influence the former, influence also the latter, and will be treated under that head. The same is true for the recurrence of both the breeding and the sexual seasons.

The recurrence of the sexual season may be interfered with by the bearing of young, both gestation and nursing may so interfere, but that does not remove a consideration of the question, under such circumstances, out of the realm of the sexual season; the effect of these processes, of bearing young and of nursing young, on the sexual season, must be considered in relation to that period, and must not be supposed to have relation only to the remainder of the breeding season.

Questions regarding the breeding season of mammals concern what happens during both the sexual and the gestation periods jointly, and, as I have before stated, the expression is a term used to define the period passed through by an animal which experiences both these processes; it is not applicable as an expression or term which may be used for the occurrence of either of them separately, nor for the effect one of these processes may have upon the other.

A breeding season may include only one sexual season and one gestation period; this is true for all monœstrous mammals, of which the bitch will serve as an example, and it may

be also true for certain polyœstrous mammals, as, for instance, the mare, under certain circumstances. On the other hand it may include several sexual seasons and several gestation periods, a condition to which only certain polyœstrous mammals can attain, of which the rat is an example.

The time occupied by a breeding season is very variable, from a few weeks (bitch) to several months (mare), and even more than a year (elephant). There may be only one breeding season in the course of several years, as shown by the walrus (Bell, 1874), elephant, and probably rhinoceros (Willoughby, 1889). There may be one breeding season each year (mare) or more than one (domestic bitch and cat).

The result of a breeding season may be the birth of one young one (mare usually), one litter of young ones (bitch), or many litters (rat).

There may be great variation in the period of gestation of different species of the same order of mammals. For instance, among Rodents, the rat goes twenty-one days in young, the rabbit thirty-two days, the guinea-pig sixty-three days. Among Equidæ, mares carry their foals eleven months, asses from three hundred and fifty-eight to three hundred and eighty-five days, and Burchell's zebra over thirteen months (Tegetmeier and Sutherland, 1895). Among Ovidæ the Barbary wild sheep goes from twelve to fifteen weeks in young (Zoo.), while the domestic sheep in this country averages about twenty-one weeks.

There may even be variation in the period of gestation in varieties of one species; for instance, Merino sheep average 150·3 days' gestation, while Southdowns average 144·2 days (Darwin, 1875), and different breeds of cows apparently vary from 277 to 288·75 days' gestation (Varigny, 1892).

The supply of food available may influence the length of time occupied by gestation. A correspondent who is a sheep-breeder informed me that his ewes, when run on poor land, experience an appreciably longer gestation period than those run on rich land; and I am strongly inclined to think investigation will show that the supply of food, and the

quality of that food, have very marked effects not only upon breeding seasons and gestation periods, but upon fertility generally, upon the mother and upon the foetus (Latarte, 1891).

It is with such questions as these that the consideration of the breeding season as a whole is concerned; with them the following paper does not deal, and it is obvious that before they can be profitably discussed, not only the sexual season, but the gestation period must be examined separately.

The Sexual Season of Female Mammals.

In dealing with this subject we have to discriminate between mammals under three different conditions: namely, wild animals in a state of nature, wild animals in captivity, and domesticated animals; and this is necessary, because the generative system of wild animals is affected by the conditions attending captivity, because the effect of captivity is not necessarily the same as the effect of domestication, and because wild animals cannot be examined so closely as the others and less is known about them.

In dealing with wild animals in captivity it is necessary to bear in mind the fact that good food, warmth, and shelter have a very great effect on the increase of the generative powers of some animals, while on others a strange climate, confinement, want of violent exercise, and probably the absence of opportunity for periodic gorging of freshly killed food, or of a sufficient variety of food, have the opposite effect.

As an example of the former the deer and cattle in the Zoological Gardens may be quoted, as an example of the latter some of the larger carnivora will stand.

In dealing with domesticated animals we do not know what the original conditions were, and we have to take the facts as they stand. At the same time we may assume that animals which do not show themselves to be prolific under domestication are rarely domesticated, and that a very long

course of artificial selection, added to the plentiful supply of food, with warmth and shelter inseparable from domestication, has no doubt greatly increased their power of reproduction.

As has been already stated, there are two forms of sexual season evident in female mammals; the monœstrous, in which there is only a single œstrus at one or more particular times of the year (bitch), and the polyœstrous, in which there are two or more concurrent diœstrous cycles at a particular time of the year (mare).

The sexual season may be influenced by the climate of the region in which the animal lives, by the seasons of the year when these are of marked variation, and by the supply of food, or possibly by the nature of the food, obtainable. These may be called climatic influences.

It may also be influenced by special nervous, vascular, and secretory peculiarities of the individual and by its habits of life. These may be called individual influences.

It may also be influenced by the length of gestation, the claims of the newly-born offspring on the mother (i. e. nursing), and by her powers of recuperation. These may be called maternal influences.

Such influences may affect the time of year when the sexual season occurs, its recurrence, and its duration. The influences which affect the time of year when the sexual season occurs, concern both monœstrous and polyœstrous mammals, and are essentially governed by climatic considerations, including the supply of food. The recurrence and duration of the sexual season on the other hand are affected either by climatic, individual, or maternal influences, and are also experienced both by monœstrous and polyœstrous mammals, though in a somewhat different way by each.

In order to understand this difference it is necessary to examine briefly what occurs in these two classes of animals. Among monœstrous animals there are a variable number of sexual seasons each year, one or more, each composed of a single œstrous of variable duration. So that the result of the

different influences which affect the sexual season may be either to increase or decrease the periodicity of that season, or to increase or decrease the duration of each one.

Among polyœstrous animals there is usually one sexual season per annum, which is composed of two or more diœstrous cycles, and the result of these influences on such animals may be, either to increase or decrease the number of consecutive diœstrous cycles in any one sexual season, or to increase or decrease the duration of each cycle.

The effect of these influences in both cases is to increase or decrease the reproductive power of the animals, and they act in monœstrous animals by affecting both the periodicity and duration of the sexual season, in polyœstrous animals chiefly by affecting the duration, but in two different ways, namely by increasing or decreasing both the number of consecutive diœstrous cycles and the duration of the œstri which occur therein.

Modification of the periodicity of the sexual season, therefore, is chiefly found among monœstrous animals; while modification of its duration is common to both monœstrous and polyœstrous animals. It would seem possible to simplify these conditions if it were assumed that the polyœstrous arose from the monœstrous condition; if it were assumed, in point of fact, that polyœstrum is simply a condition arrived at by the concentration of several monœstrous sexual seasons.

There might seem to be some reason for this when such animals as the red deer, for instance, are considered; in the wild state this animal is apparently monœstrous, while in captivity it is polyœstrous, at any rate in this country.

But it may equally plausibly be argued that monœstrum is simply decentralised polyœstrum. There are instances among domesticated animals of monœstrous animals with a tendency to polyœstrum (bitch), and of polyœstrous animals with a tendency to monœstrum (mare). So also among wild animals there are instances of animals which are monœstrous in one climate and apparently polyœstrous in another (*Sciurus vulgaris*) (compare Bell, 1874, and Lataste, 1887).

I doubt if, in the present state of our knowledge of the subject, it is possible to determine which is the original of these two conditions. The behaviour of animals in captivity and under domestication inclines one to believe that monœstrum is the original form ; then, again, it is the simplest form, and on that ground may be thought the more archaic. But, on the other hand, it is the lower animals which are the most prolific breeders, and, for many reasons, we may perhaps expect the ancestral mammal to have been more prolific than wild animals are now.

If this should be true, the increased capacity for reproduction, shown by domesticated animals, would indicate reversion to ancestral powers, due to the removal of such obstructions as must be inseparable from the struggle for existence. Thus all we can be certain of is the close similarity between these two forms of sexual season.

A further complication is introduced by certain breeds of domesticated sheep and by pigs ; these are polyœstrous animals when domesticated, and they may also exhibit more than one sexual season each year. Such a condition appears to be exceptional, and I have not included this form of variation in the foregoing account for that reason ; but I am quite prepared to believe a more exact knowledge of what takes place among domesticated animals will show a similar variation among individuals of other classes of animals.

Variation in the periodicity of sexual seasons is brought about by an increase or decrease in the persistence of the œstrum, and has nothing to do, necessarily, with variation in the œstrus cycle itself ; while, on the other hand, variation in the duration of a sexual season is brought about by an increase or decrease in the number of consecutive diœstrous cycles (polyœstrous mammals), or by an increase or decrease in the persistence of the œstrus (monœstrous and polyœstrous mammals), the œstrum being only secondarily affected in consequence thereof.

The effect of an increase in the periodicity of sexual seasons may be twofold ; it permits of reproduction at differ-

ent times of the year, and, when gestation is of sufficiently short duration, of reproduction more than once a year. An increase in the duration of the sexual season may also have two effects; it gives increased opportunity for successful coition, highly advantageous to those animals which live an isolated life, while, among animals which experience a sufficiently short period of gestation, it gives them opportunity for reproducing several times in each season. On the other hand, a decrease in the periodicity or duration of the sexual season has an opposite effect.

It would seem highly probable that the method of increasing or decreasing the opportunities of reproduction varies with the habits of animals, the claims of maternity, and the climate in which they live. The different methods are not necessarily peculiar to particular groups or classes of animals, and they may vary, within limits, in the same species in different localities and in the same individual under different circumstances. Climatic and maternal influences may be observed in wild, captive, and domesticated animals; but individual influences can only be noted in the two latter classes, and especially in domestic mammals.

It has been freely stated, originally by Aristotle and subsequently by numerous biologists, that the sexual seasons are governed by the requirements of the newly born young; in other words that the season for conception is regulated by the length of gestation and the time of year which is most favourable for the birth of the young; and it is argued, that the different times of the year during which the sexual seasons of similar animals occur is sufficient ground for that view.

I cannot agree with this opinion; if it were so, why should some bats experience a sexual season in the autumn and not produce young until about June (Beneden, 1880, and others, see below), although not more than two months are required for gestation and these animals are active for that length of time in the spring, before parturition takes place? Again, why should roe deer, in Germany, have their sexual season

in early autumn, when the embryo does not develop beyond the segmentation stage until the following spring? (Bischoff, 1854). Why should the seal take eleven to twelve months for gestation, while a large dog only requires three months? If there was a great difference in the size of these animals the variation might to some extent be accounted for, but it is not so. It is true that the newly born seal is a far more perfect animal than the newly born puppy, but it cannot be that the whole of the difference in the time of gestation, namely, eight to nine months, is required for the extra development of the more perfect seal embryo, other factors being equal.

Again, how is it that an unusual change of climate will affect the sexual season of an animal? This is constantly observed among domesticated animals, and a very marked case is recorded of cows, in Skye, after an exceptionally severe winter (Youatt, 1834).

And how is it that the sexual season, for instance, of the fox (Bischoff, 1863) and red deer (Cameron, 1900), is modified in accordance with the nature of the country in which it lives, whether high or low ground, in accordance with the age of the animal, and probably also in accordance with its bodily condition?

There seems to me ample reason for the belief that the sexual season is governed directly by the influences detailed above—climatic, individual, and maternal; and that variation in the rate of development of the embryo, in the length of gestation, and in the powers of nursing, are quite sufficient to provide for the launching of the young at a favourable time of the year.

The origin of the sexual season is another matter; for a solution of this question a comparative study of the phenomena in the lower animals is necessary.

That it is the result of a stimulus which may be effected through the alimentary canal is demonstrated by the effect upon ewes of certain stimulating foods; the sexual season of ewes may be thus forced by "flushing" them, as it is called by flockmasters.

In the same way it is stated that a quart of milk, drawn

from a cow "in season" (i. e. during œstrus), but which has not had the bull, will, if drunk by another cow, bring on the sexual season of the latter (Youatt, 1834).

That it is associated with a stimulus which is manifested by exceptional vigour and exceptional bodily "condition" is demonstrated by the pugnacity of the males at such times, by the restless activity of the females, by the brilliant colouring of such widely divergent animals as, for instance, annelids, amphibia, birds, and mammals, by the condition of the plumage of birds, and of the pelage or skin of mammals.

That it is associated with nutrition, and that it is a stimulus which is gradually collected, is indicated by the increased frequency of the sexual season among domesticated mammals as compared with nearly allied species in the wild state.

That it is manifested by hypertrophy and by congestion of the mucous tissue of the generative organs, and of various other organs, such as the wattles and combs of birds, the crest of the newt; and by the activity of special glands, the affection of all of which may be exceedingly severe, is true.

These, and many other similar facts, are well known, but they do not assist in the elucidation of the origin of the function.

The most that they do is to show that the sexual instinct is seasonal, and that nutrition, whether affected by external or internal factors, plays an important part in its manifestation.

The Periodicity of the Sexual Season in Monœstrous Mammals in the Absence of the Male.

In the absence of gestation most mammals would appear to experience at least one sexual season per annum, under natural conditions, but there is great variation in the periodicity of the sexual season in captive and domesticated mammals, the variation being extended not only to varieties of a species, but also to individuals of that species under domestication.

Among certain wild animals which are known to undergo parturition only during a very circumscribed time, the monœstrous condition may be assumed as probable, and the periodicity of the sexual season calculated; but it must be

recollected that without accurate observation, during the absence of the male, it cannot positively be asserted that such animals are monœstrous.

In the case of the bitch, in Danish Greenland the bitch generally experiences only one sexual season per annum, though sometimes she may have two (Rink, 1877).

In this country, as a rule, the bitch has two sexual seasons each year, one in the spring and one in the autumn, but there are wide variations to this rule. She may have only one sexual season per annum, or it may occur every eleven, ten, nine, eight, seven, six, five, or four months (Stonehenge, 1887). It seems probable the sexual season recurs less frequently in breeds of large dogs as a rule; a correspondent (Dr. Inmann), who breeds St. Bernard dogs, informs me this is his experience, and I have had information from other breeders of large dogs, mastiffs and bloodhounds, which shows there is an obvious tendency in this direction; at the same time it does not appear to be by any means a universal rule. Again, while the spring and autumn are the usual times when the sexual seasons of dogs occur, the sexual seasons of each bitch have a more or less exact periodicity peculiar to herself.

Finally, the sexual seasons of any bitch may be interfered with to the extent even of complete cessation, if she is systematically prevented from breeding.

The bitch may be considered a case of extreme variation in the periodicity of the sexual seasons of a monœstrous domesticated mammal. The normal two sexual seasons experienced in this country are reduced usually to one in Danish Greenland, probably owing to the effect of climatic influences, while the variations which exist in this country indicate the effect of individual influences, which are largely stimulated by artificial selection and domestication.

The wolf, jackal, and fox are monœstrous like the dog, and in captivity in the Zoological Gardens they show two sexual seasons per annum, like the normal dog in this country.

Bears are also monœstrous, but they have only one sexual season per annum in the Zoological Gardens.

Badgers also are probably monœstrous, but there is great uncertainty regarding their breeding (Harting, 1888; Denwood, 1894).

The same is true for the Barbary wild sheep; they are said to be monœstrous and to have one sexual season per annum in captivity in this country (Zoo.).

The red deer, fallow deer, and roe deer are probably monœstrous in the wild state; they have only one sexual season of very limited duration (Bell, 1874). The same may be said for the ibex, Markhor, Barasingh, and *Hemitragus jemlaicus* in Cashmir (Laurence, 1895), possibly also the American bison (Allen, 1876), and various other species of *Bos*, *Ovis*, and *Capra* (Lydekker, 1898); also the black-tailed deer in Montana (Roosevelt, 1893), and several antelopes (Sclater and Thomas, 1900).

The truth regarding these animals is not, however, known; their monœstrous condition is rendered probable from the known very limited sexual and calving seasons, but it is by no means certain.

The genus *Sorex*, some of the *Mustela*, *Myoxus avelanarius*, *Arvicola amphibius*, and *Sciurus vulgaris*, in this country (Bell, 1874) are probably monœstrous in the wild state, as are also the wild cat and the fox, and they have only one sexual season.

Phoca vitulina, *P. hispida*, *P. grœnlandica*, *Cystophora cristata*, and *Halichœrus gryphus* have all a very limited sexual season, occurring once only in the year, and it is highly probable they also are monœstrous (Bell, 1874, and Turner, 1875).

Variation in the periodicity of the sexual season of various domesticated animals, in comparison with nearly allied species in the wild state, has been observed in a few cases.

The cat in the wild state has one (Hamilton, 1896)—some say two (Mivart, 1881), though this seems doubtful—sexual season per annum, while the domestic cat may have three or four sexual seasons each year.

The sow has only one sexual season in the wild state in

France (Beever, 1870), but it is not clear whether she is monœstrous or polyœstrous; when domesticated, however, she is polyœstrous (Fleming, 1878; see also Aristotle).

Certain wild sheep, *O. argali*, *O. burrhel*, *O. poli*, have only one sexual season per annum, and are probably monœstrous (Prejevalsky, 1876); whereas domesticated sheep are polyœstrous, and may have such an extended series of diœstrous cycles that they are capable of producing young almost at any time of the year; such, for instance, are Dorset Horns in the south of England and Hampshire Downs in some parts of Ireland (compare also Aristotle). As a rule, however, sheep in this country have a much more limited polyœstrous season,—as, for instance, the Scotch black-faced sheep, which has only two recurrent periods of œstrus (Cameron, 1900).

Variation in the periodicity of the sexual season of wild animals, as compared with individuals of the same species in captivity, has been noted in but few cases. Some of the large carnivora in the Zoological Gardens exhibit great irregularity in their sexual seasons, but too little attention has been paid to the subject in these animals to allow of more being said than that, in some cases, their generative activity appears to have been stimulated, in others checked.

The wolves in the Zoological Gardens have two sexual seasons, while the Tibet wolf (*L. chanco*) has only one (Prejevalsky, 1876) in a wild state; in New Mexico also, I am told by a keen sportsman familiar with the country, wolves bear young only once each year (W. Ruston). The same is true for the foxes in the Zoological Gardens; they have two sexual seasons, while the Tibet fox (Prejevalsky, 1876) and the English fox (Bell, 1874) have only one in the wild condition.

The wild cat, on the other hand, in captivity does not experience more sexual seasons than when in a feral state, namely one (Hamilton, 1896); and the tame cat, when it becomes wild, has apparently only one sexual season, whereas the same animal under domestication has from two to four sexual seasons per annum.

Among the deer in the Zoological Gardens their generative activity appears to have been universally stimulated—they will be referred to under the heading of "Duration of the Sexual Season in Polyœstrous Mammals,"—for it would seem that their normal (as I have considered it) monœstrous sexual season is increased by the conditions of captivity until it may become a continuous polyœstrous sexual season.

The Barbary wild sheep, on the other hand, does not appear to be affected by captivity; it exhibits a single monœstrous sexual season only, each year (Zoo.), and that is probably its condition in the wild state if we may judge from what is known of *O. argali*, and *O. burrhel* in Tibet (Prejevalsky, 1876).

It is with some hesitation I have included among monœstrous mammals deer, sheep, and pigs in the wild state; their retention in this class is doubtful; but if these animals were omitted there remains a remarkable series of examples of the variability of the sexual season of monœstrous mammals under various conditions.

The Duration of the Sexual Season in Polyœstrous Mammals in the Absence of the Male.

The duration of the sexual season in these animals depends upon two factors, the length of the diœstrous cycle and the number of times it recurs. Both factors may be different in different species of animals, and either may be different in different individuals of some species, or variable in the same individual at different times.

Knowledge of polyœstrum in animals in a wild state in this country is limited to certain rodents. The rat (*M. decumanus*), mouse (*M. musculus*), and the rabbit in this country are known to experience a recurrence of the diœstrous cycle. It is probably recurrent also in *M. minutus*, *M. sylvaticus*, *M. rattus*, *Arvicola agrestis*, *A. glareolus*, and *Lepus timidus*; while possibly *Mustela vulgaris* and *Lepus variabilis*, under favourable circumstances, may also experience a recurrence of the diœstrous cycle, judging from the account given of them by Bell (1874).

In Southern Europe and Algiers polyœstrum is apparently usual amongst rodents (Lataste, 1887). It appears to be ascertained for *Sciurus vulgaris* living in that part of the world—though the same animal is probably monœstrous in this country—for *Eliomys quercinus*, *Gerbillus hirtipes*, *Dipodillus campestris*, *D. simoni*, *Meriones shawi*, *M. longifrons*, *Mus musculus*, *M. rattus*, *M. decumanus*, and to be probably true also for several other species.

The animals on which these observations were made by Lataste were kept in captivity, but there is good reason to think that the conditions under which they were kept did not interfere with their habits in this respect.

Among domesticated animals polyœstrum occurs in horses, cattle, sheep, and pigs. While for wild animals in captivity it has been observed (Zoo.) in the gayal and bison; in wapiti, axis and red deer; in the gnu, eland, nilghau, and waterbuck; in *Gazelle dorcas*, in giraffes, in elephants, and probably in kangaroos.

In its most complete form polyœstrum occurs in certain monkeys and in the human female; probably most monkeys are similarly affected, and possibly also lemurs; in these animals there is a regularly recurrent series of diœstrous cycles throughout the year.

The Duration of the Diœstrous Cycle varies from five days (exceptional in rodents, Lataste, 1887) to as much as two months (exceptional in mares, and in various wild animals in captivity from time to time, Zoo.).

The usual length of the diœstrous cycle for rodents is ten to twenty days, and in other animals in which the phenomena has been observed from three to four weeks. In the rodents observed by Lataste (1887) the diœstrous cycle was usually ten days, and in the rat and mouse in this country the same may be said to be approximately true. In the domestic rabbit, however, I find great variability; while some individuals exhibit œstrus every three weeks fairly regularly, others do so every ten days; on the whole I think ten to fifteen days is the usual length of their diœstrous cycle.

In the domestic mare and cow three to four weeks, and in the domestic sheep and pig two to four weeks is said (Fleming, 1878) to be the length of the diœstrous cycle, while another authority (Ellenberger, 1892) regards three to four weeks as the usual time for all these animals.

In wild cattle, deer, and antelopes in captivity (Zoo.) three weeks is the usual time. In monkeys it appears to be about one month in duration (Heape, 1894, 1897, Keith, 1899). In the human female, while twenty-eight days is the normal length of time occupied by the diœstrous cycle, it is frequently experienced every three weeks or every five weeks, while occasionally even shorter or longer periods are known. Aristotle is represented to have made the extraordinary statement that few women menstruate every month, while most menstruate every three months. It would seem possible that the opposite is what he meant; at the same time it should be remarked that various observers (Wiltshire, 1883) have recorded their opinion that the women of certain tribes in different parts of the world menstruate only at long intervals (see also Ellis).

The recurrence of the Diœstrous Cycle is also very variable; exact knowledge on this point is not possible for wild animals; only those under observation, captive or domestic, can supply the requisite information.

The known limitations of the sexual season among certain wild animals, however, admit of a fairly accurate idea being gained of the recurrence of their diœstrous cycles, although not accurately enough to enable one to determine with certainty whether an animal is monœstrous or polyœstrous. For instance, the American bison (Allen, 1876) experiences a sexual season from some time in July until some time in August. In the Cashmir ibex it persists during parts of November and December. In the Markhor and *Hemitragus jemlaicus* in Cashmir it occurs in December, while in the "Barasingh" in that country from September 20th to November 20th it has been observed (Laurence, 1895).

In Scotland the red deer's sexual season lasts three weeks,

during September and October, according to Cameron (1900) six weeks, while in this country September is the sexual month for the fallow deer, and July and August the time when the roe deer will receive the male.

In all these cases there can be little over three weeks during which copulation takes place, and the extremely limited period during which parturition occurs strongly corroborates the view that this is the extent of the usual time during which sexual intercourse is possible. The fact that in captivity three weeks is the usual period which intervenes between two œstri in such animals, and the extreme probability that individual females do not all experience œstrus at exactly the same time (Cameron, 1900), predispose one to believe that they are monœstrous in the wild state; but, if the limit of time for coition is three weeks, there is still just time for the females to undergo two diœstrous cycles, and it is this possibility which prevents positive assertion on the matter.

Among captive animals (Zoo.) not more than two diœstrous cycles have been observed in the gnu during one sexual season. Gazelle dorcas has two or three; the giraffe about three; while the eland, nyghau, and waterbuck have a series of diœstrous cycles, each lasting three weeks, during May, June, and July each year.

The gayal and bison, the axis and wapiti deer, on the other hand, experience a continuous series of diœstrous cycles all the year round, at intervals of about three weeks.

The hippopotamus at present in the Gardens is an old animal; for long she showed no signs of a sexual season, but lately she has done so at irregular intervals; no doubt in her case captivity has checked the generative function, for a former specimen which bore three young while there is said to have exhibited monthly sexual excitement (Wiltshire, 1883).

Among wild rodents in this country, recurrent diœstrous cycles last about two months, probably, in *Lepus variabilis*; about three months, probably, in *Arvicola agrestis*; from four to six months, probably, in *Mus minutus*; about nine

months in *Mus rattus*; and even longer, perhaps, in *Mus musculus* and *M. decumanus*.

Bell (1874) appears to think that, under favourable circumstances, the diœstrous cycles may continue all the year round in these latter animals and in the rabbit, but I am inclined to think such a condition is unusual in this country among wild rodents, since it is exceptional to find any of them pregnant during the winter months.

Among domesticated animals the period during which the diœstrous cycles recur, in the absence of the male, lasts from one month to as many as eight months for the mare, about five to six months for the rabbit, from one to three months for the sheep (with certain exceptions), and about two months for the pig. So far as the domestic rabbit is concerned, no doubt, if they are kept warm, carefully fed, and their breeding carefully regulated throughout the spring and summer, they may exhibit œstrus also in winter, but it must be recollected that here we are treating of œstrus independent of pregnancy, which is a very different matter.

Among certain monkeys, probably in most of them, the diœstrous cycle recurs all the year round (Geoffroy, St. Hilaire and Cuvier, Ehrenberg, 1833, Numan, 1838, Heape, 1894, 1897, Keith, 1899; compare also Rengger, 1830, Sutton, 1880, and Ellis). In the human female, as a rule, this is also the case; there appear, however, to be exceptions to this rule, for instance, the women of the Esquimaux peoples living between the seventy-sixth and seventy-ninth parallel do not always menstruate during the winter months. It is said (Cook, 1894) that not more than 10 per cent. of these women menstruate during the long dark winter months, and it is possible to imagine that the peculiar conditions of life they experience during that time may well be responsible for their peculiarity. If this be so, a true anœstrous period may be experienced by women.

Rink's (1877) account of the origin of these people, if correct, precludes the probability that the occurrence of an anœstrous period is a racial characteristic, and emphasises the view that it is a variation due to climatic conditions.

It is held by some writers, several of which are quoted by Wiltshire (1883), that the women of various savage tribes exhibit the menstrual flow only at intervals of several months; and the same author remarks on the fact that girls at puberty in this country menstruate only at intervals of three, four, or six months; and that it may be this condition is an indication of an ancestral habit. Ellis also quotes various authors who state that menstruation takes place at long intervals in women of Lapland, Greenland, the Faroe Islands, Tierra del Fuego, and among the Guaranis of Paraguay.

The effect of captivity or domestication on the duration of the sexual season in mammals is very remarkable.

As has been already pointed out, wild sheep have only a very limited sexual season per annum (*O. argali*, burrhel and poli, in Tibet, Prejevalsky, 1876), a condition which is maintained by the Barbary wild sheep in captivity in this country (Zoo.); whereas the domestic sheep has a much longer sexual season, and in addition has for many centuries (Aristotle) been capable of reproducing twice in each year under favourable circumstances.

Again, the wild goat has a very limited sexual season (Lydekker, 1898), whereas the domesticated goat will receive the male at almost any time (Low, 1845). A more remarkable example is that of certain deer in captivity (Zoo.). Wild red deer have a special sexual season, extending little over three weeks (Bell, 1874), and including certainly not more than two diœstrous cycles; whereas in captivity (Zoo.) the sexual season of these animals extends over most of the year, and consists of an extensive series of diœstrous cycles.

A similar condition prevails with the wapiti deer in the wild state (Roosevelt, 1893), while in captivity (Zoo.) the possibility of pregnancy at any time of the year is only prevented by the fact that the male does not rut during the casting and growth of his antlers; and it is asserted that park-fed wapiti stags in America are able to beget offspring even after their horns are shed (Caton, 1881).

Wild cattle in captivity (Zoo.) are also capable of reproduction at any time of the year, and they also experience a remarkable increase in the recurrence of their diœstrous cycles, from what we are led to infer, by the limited calving season, is the case among similar animals in the wild state.

Among domesticated mammals similar modifications are evident, not only in animals of different species, but in individuals of the same species, as, for instance, in cattle and horses.

Mares may have only one period of œstrus in the year, in which case they are purely monœstrous animals, but this is a rare condition; rarely, also, they may have two diœstrous cycles, but usually they have many. In the latter case œstrus may recur every three weeks, or the interval may be longer. As a rule among thoroughbred mares the history of the sexual season shows a series of diœstrous cycles, each occupying about three weeks and recurring throughout the spring and often until the early autumn, as many as seven or eight months being in some cases thus occupied.

Although these animals—horses, cattle, and deer—either in captivity or under domestication, experience such an extensive increase in the consecutive recurrence of the diœstrous cycle, it is not a condition natural to them; it is due, in all probability, to the care and attention paid to them by man; in the same way, it may be argued, that the stimulated power of reproduction evinced by certain rodents is also due to the advantages derived from their intimate relations with the luxuries of civilisation (rat and mouse).

The only animals, so far as is at present known, which experience a continuous series of diœstrous cycles in a state of nature are certain monkeys.

The fact that it is possible to induce such an enormously increased capacity for œstrus in any animals, prepares one to consider the regular recurrence of the diœstrous cycle in monkeys, and in the human female also, as a very slight step in advance; and when the whole of the evidence is considered,

it will, I believe, be found that the regularly recurrent diœstrous cycles of the Primates are strictly homologous with the more or less regular diœstrous and anœstrous cycles of the lower animals.

The Sexual Season in Monkeys.—The consideration of this subject introduces a further complication, and that is, while monkeys may have a continuous series of diœstrous cycles, they are not all of them fitted for reproduction at all times of the year.

Some monkeys in tropical countries may be in a condition to become pregnant at all times of the year; though this is by no means certain it is not an impossible fact, but others are certainly not so. For instance the chimpanzee and gorilla are said to have a special sexual season in West Africa (Garner, 1896).

Semnopithecus entellus, from the jungles on the south bank of the Hugli, has a definite time for reproduction (Heape, 1894); and *Macacus rhesus*, the area of whose geographical distribution is very large, apparently produces young at different and definite times in different districts (Heape, 1897).

There is every reason to believe, however, that these animals experience regular recurrent diœstrous cycles throughout the whole year.

If the diœstrous cycle of a monkey is homologous with the anœstrous cycle of a dog—and that this homology exists will be apparent when the question is considered from a histological point of view—it is obvious that we are naturally led to suppose that an increased number of œstri should result in an increased number of opportunities for pregnancy, precisely as in the case of the mare, deer, etc. But this is not so, and the result is that there exist certain mammals which, while they exhibit a continuous recurrence of the diœstrous cycle, have a circumscribed season for conception.

As I have shown elsewhere (Heape, 1894, 1897), this result is due to the fact that, although menstruation recurs regularly, ovulation does not; or, in other words, that ovula-

tion is not necessarily coincident with the œstrus in these animals.

This opens up a wide question, which I hope to treat of in a separate paper, but it is necessary to refer to it here in order to point out, that the limited season for conception in some monkeys is no reason for regarding their diœstrous cycle as in any way different from that of other animals.

Briefly, we may say that both ovulation and œstrus are due to stimulating influences. But they are not necessarily coincident in the lower animals, and they are not necessarily both induced by the same means, nor at the same time.

In the virgin domesticated rabbit I find that ovulation does not occur in consequence of œstrus alone; while various observers have shown that in the bat ovulation may occur at quite a different time of year from œstrus, in some cases probably as much as six months may intervene between the two functions in this animal (Benecke, 1879; Eimer, 1879; Fries, 1879; Beneden and Julin, 1880).

Again, as I have already noted, there may be abnormal œstrus in many animals, it may occur during gestation and be independent of ovulation; while finally, it is quite certain that many animals which usually experience ovulation during œstrus, sometimes fail to become pregnant at that time in consequence of the failure of the function of ovulation.

Such being the case, it may truly be said the period of œstrus is not invariably identical with the period of ovulation; the two are separate functions, possibly closely associated, but also possibly widely divergent.

In monkeys we have an instance of animals in which the rhythm of ovulation may be different from the rhythm of œstrus, but it must not be supposed, on this account, that either of these processes is not homologous with the same process in other animals in which the rhythm may be identical. It would seem as if the sexual activity of these animals had been developed more than, and out of proportion to, the ovarian activity; or, in other words, that their sexual powers were greater than their powers of reproduction.

The ideas on this subject which have for so long prevailed and which even now are taught, namely, the identity of "menstruation"¹ and of œstrus with ovulation, would make this view impossible; but since it is known that, in various animals, either "menstruation" or œstrus may take place without ovulation, and that ovulation may occur without the coincidence of "menstruation" (Leopold and Mironoff, 1894) or of œstrus (bat), the possibility of isolating these functions is demonstrated. Thus it is no longer impossible to suppose that, while they are both due to similar stimulating influences, one of them may be developed in excess of the other. In this respect monkeys stand in an intermediate position between the lower mammals and man.

The Sexual Season in Man.—In the human female this question of the simultaneity of ovulation and œstrus ("menstruation," as it has been wrongly called) has given rise to wide discussion. I have referred to the question somewhat fully elsewhere (Heape, 1894, 1897, 1898), and have shown that the majority of modern writers on the subject are in favour of the view that the two functions are not necessarily coincident in the human female, the correctness of which conclusion it seems to me impossible to doubt.

With regard to the existence of a special limited sexual season or seasons, it is interesting to note that there is some evidence of such in the human female; evidence both of a time in the past when such special seasons were common to all, and of a time in the present day to which certain peoples confine such matters and during which most peoples exhibit special generative activity.

Here again we are upon the edge of a very wide field of research which it is impossible to do more than touch. I may, however, briefly draw attention to certain facts which in my opinion throw some light upon the matter.

Feasts, similar to the erotic feasts which were indulged in by the ancients—Babylonians, Phœnicians, Egyptians, Greeks, and Romans (Ploss, 1887),—were still practised to

¹ "Menstruation" is used here in its original sense.

some extent in the sixteenth century in Russia (Kowalewsky, 1890 and 1891), and in some parts of India at a much more recent date (Rousselet, 1876), while such customs as "gwneyd Bragod" (Owen, 1886) and possibly our own "bean feasts" may not improbably be the modern representatives of these ancient customs in our own country.

Again, it is worthy of note that the erotic feasts of more civilised peoples are not greatly dissimilar to the sexual feasts and dances of the savage peoples of Australia, Polynesia, West Africa, South America, New Britain, and West Asia (Ploss, 1887). Apart from the fact that many of them surely have some reference to phallic worship, as in the case of the maypole, the origin of these feasts—shrouded as they are in the mists of ancient customs now but little understood, and of laws long since forgotten, complicated as they are by customs, religions, and laws of a later growth—is not definitely known.

It is indeed a matter of the greatest difficulty to trace, justly, the true relation and likeness of any one of these customs to another, however similar they apparently may be. At the same time the universality of such customs is very remarkable, and may, I think with some justice, prepare one to believe that in prehistoric times man was impelled to indulge, if not wholly, at least more freely, in sexual intercourse at certain seasons rather than at other times of the year.

Hill (1888) attempts to trace the apparent survival of a human pairing season, by the customs of the Hindus and the proportions of births in each month of the year; while Westermarck (1891) records customs and statistics which certainly point even more strongly in the same direction. Ploss (1887) also gives many valuable statistics for Russia, Germany, Italy, and France; and Haycraft (1880) does the same for Scotland. It is remarkable that the statistics brought forward by these authors in all cases show a considerable rise in the birth rate at certain seasons. In Scotland, Haycraft points out that from 1866 to 1875 a marked

increase of births occurred with striking regularity in April, showing that a maximum of conceptions takes place in July.

Hill says that ten years' statistics of the district in which he lived in India show that the maximum of conceptions occurs in December, when food is cheapest and the salubrity of the country at its best; while the minimum of conceptions occurs in September, towards the end of the hot season, when food is most scarce and malaria rife.

Ploss shows that in Russia the maximum of conceptions takes place in autumn, in Germany during May and December, while in Italy and France May is the month responsible for most conceptions. This author also points out that in Russia religion affects the birth-curve, and he traces the cause to fasting seasons.

Westermarck goes very fully into this matter, and has collected a great many facts bearing upon it which are of great interest. The sexual instinct in civilised man, he concludes, has two special seasons of activity—spring and autumn, but it is most active towards the end of spring as a rule, in the south of Europe this activity being most marked somewhat earlier than it is in the more northern countries.

Illegitimate births, it is remarked, are comparatively more numerous in early spring, and this, it is suggested, is due to an increase of sexual instinct during May and June.

These conclusions are interesting inasmuch as they indicate a season or seasons which may be the original sexual seasons; but it is the evidence he produces of the sexual seasons of more savage peoples which is of special interest here.

Some of the Indians of California are stated to have a regular sexual season, spring being a literal St. Valentine's Day with them.

The Watch-and-dies of West Australia and the Tasmanians have sexual feasts in the middle of spring-time.

The Hos, an Indian hill tribe, have a similar feast, which becomes a saturnalia during which absolute sexual freedom is indulged in, in the month of January; while among the Santals, another hill tribe, marriages mostly take place in

January. Among the lower castes of the Panjas in Jeypore a festival in January is kept up for a month, during which promiscuous sexual intercourse is allowed. The Kotars, a tribe in the Neilgherries, have a similar feast marked by similar licence and debauchery; and the same may be said for the Keres in New Mexico, the Hottentots, and some tribes near Nyassa.

In New Caledonia November (that is late spring) used to be the time when marriage engagements were made, and among the Rajputs of Mewar the last days of spring are dedicated to the god of love.

Among the Kaffirs of Cis-Natalian Kafirland more children are born in August and September than in any other month, and it seems probable this is due to certain feasts during which there is unrestricted intercourse between the unmarried people of both sexes.

Among the Bateke—Stanley Pool—most children are born in September and October—the season of the early rains,—and it is said the same is the case among the Bakongo.

In Chili the maximum of births occurs in September.

Dalton (1872) gives an account of the Miris, an Indian hill tribe, which shows that at one season of the year sexual relations between the unmarried are specially countenanced and indulged in.

My friend Mr. Caldwell tells me that the Queensland natives with which he was brought in contact have a distinct sexual season in September (that is spring), and that they cannot be prevailed upon to do any work for some weeks at that time of the year.

Cook (1894) records that the Esquimaux which inhabit the country lying between the seventy-sixth and seventy-ninth parallels, exhibit a distinct sexual season, which recurs with great intensity at the first appearance of the sun, and that little else is thought of for some time afterwards: an account which is in agreement with statements made by Bosquet (1885) regarding other Esquimaux.

Finally Man (1882) notes that the children of the natives

of the Andaman Islands are said to be born mostly at a particular time of the year—during the rains.

I have not done more here than simply to indicate the bearing of a very considerable literature which deals specially or incidentally with this subject; one section of this literature demonstrates by means of statistics, for countries where such are available, an excessive birth rate in special seasons; the other shows that the habits and customs of the less civilised peoples indicate that their sexual and reproductive functions are specially stimulated at definite times of the year.

While there is some variation in the season for special sexual activity indicated by the above statements, spring is obviously the most usual time. Hutchinson (1897) seeks to show that the time of marriage among certain widely divergent people is largely governed by times of agricultural plenty; for economic reasons this might reasonably be expected, though the evidence he brings forward is not at all conclusive. But it does not seem to me to be an important point. Many reasons, religious or otherwise social, may have arisen to interfere with such a rule, supposing it ever was a rule. The importance of the evidence consists in the proof that any time is or was specially conducive to sexual disturbance, and this, I think, has been proved. (See also Laycock [1840] and Ellis's very interesting résumé of this question.)

The wide variation in the time of the year during which the sexual season of the lower mammals occurs in different parts of the world, renders it not surprising that there should be wide variation in man also in this respect, in different geographical areas.

However that may be, the fact remains that there is much evidence in favour of the view that special sexual seasons were, at one time, universally experienced by the various races of man, a fact of great importance from a comparative point of view.

But not only is there evidence of a circumscribed period for reproduction in the ancestral human being, and in those

peoples who occupy a low position in the scale of civilisation, but there is also evidence that the latter produce smaller families.

In some cases this is ascribed to the practice of infant marriage, to the strain of child-bearing on a mother who requires for herself all the nourishment she is capable of assimilating; but comparatively small families are usual in many savage peoples whose women do not become mothers at a very early age (Westermarck, 1891).

In these cases the result is probably due not only to prolonged lactation, or to infant mortality, but to inability to produce more children; for, as the practice of polygamy shows, the advantage of large families is fully recognised, and each individual woman will be required to reproduce as frequently as possible.

It would seem highly probable, therefore, that the reproductive power of man has increased with civilisation, precisely as it may be increased in the lower animals by domestication; that the effect of a regular supply of good food, together with all the other stimulating factors available and exercised in modern civilised communities, has resulted in such great activity of the generative organs, and so great an increase in the supply of the reproductive elements, that conception in the healthy human female may be said to be possible almost at any time during the reproductive period.

We have come to believe that it is to the regular monthly menstrual periods, which the human female generally experiences, that this great reproductive power is due. But the evidence of a regular menstruation with a limited conception period in monkeys, shows that this is certainly not so. As in monkeys, so in man, these two functions are not necessarily equally developed.

I think it may fairly be stated that an increase in the frequency of menstruation is not necessarily a sign of an increased power of reproduction among women, and that there is no indication that women who menstruate every two or three weeks are more prolific than those who menstruate

every month; in fact, the reverse is probably true, and the excessive activity of the menstrual organ, if it is not developed at the expense of the reproductive power, in many cases results in lessened fertility.

We are here doubtless in the region of pathological conditions, since when there is a considerably increased menstruation, either by increase of the amount of the menstrual flow or by decrease of the intra-menstrual period, it is accompanied by exhaustion and the evils which result therefrom.

If the above be true, it would appear that civilised woman has reached the limits of reproduction compatible with her mode of life, and it may be concluded that increased reproductive power will not arise until her powers of assimilation are increased to a sufficient extent, and until the products of that assimilation are devoted more exclusively to the reproductive function.

The Duration of the Œstrus in Monœstrous and Polyœstrous Mammals in the Absence of the Male.

There is very little known regarding this point except in certain domesticated animals. The œstrus of monœstrous mammals may last a short or a long time. In the Barbary wild sheep in captivity (Zoo.) it only lasts a few hours. In the bitch it lasts a variable time, variable both in different individuals of the same species and in the same individual at different times. The winter œstrus of the bitch does not last so long as the summer œstrus in certain breeds; a well-known breeder (Dr. Inman) has assured me this is the case with his bitches. The usual time is probably from seven to nine days.

A most careful observer, however, tells me that a bitch which he had for many years usually remained in a condition of œstrus for nine days, but sometimes it persisted in her for fourteen days. Other breeders have informed me they have had bitches undergoing œstrus for even a longer period than this, but it is undoubtedly an exceptional experience.

In certain bloodhounds a well-known breeder (Mr. Brough) has observed œstrus to last twenty-one days, but only very exceptionally, and not as a characteristic of any particular bitch.

There can be little doubt the persistence of œstrus in bitches may be influenced by their temperament, by their food, and by the particular conditions of existence experienced by each bitch.

Wolves, jackals, and foxes in the Zoological Gardens have about the same duration for œstrus as the average bitch, from seven to nine days. In the cat œstrus lasts nine to ten days (Hamilton, 1896); in tigers in captivity (Zoo.) for eight days at the longest. In bears, on the other hand (Zoo.), œstrus appears to last continuously for two to three months; it must be recollected, however, that this occurs with females kept together with males under conditions which, while they may very probably excite sexual feelings, do not result in gestation.

Among wild animals the duration of the œstrus can only be assumed by comparison with other individuals of the same species in captivity; although the duration of the sexual season may be inferred from the known season during which parturition takes place, the duration of the œstrus cannot be so determined.

Among polyœstrous mammals there is not such great variation in the duration of œstrus, since, instead of a long period of œstrus, these animals exhibit a recurrence thereof; still there is some difference apparent: the domestic sheep has œstrus for only a few hours, say twelve hours; the cow for not more than twenty-four hours as a rule; while antelope, deer, and wild cattle in captivity (Zoo.) closely imitate domestic cattle and sheep in this respect.

The mare endures œstrus probably for a slightly longer period as a rule, but this depends very much on the temperament of the individual mare, and the conditions under which she is kept.

The elephant in the Zoological Gardens has persistent œstrus for probably three to four days.

In monkeys the œstrus has not usually been carefully noticed, but I am assured that the Moor macac in confinement (Zoo.) has a definite œstrus which lasts two or three days; and in a few other monkeys a similar condition has been from time to time noticed (Ellis).

In the human female there is not wanting evidence of a similar condition (Aristotle; Martin, 1888; Haycraft, 1880), and on this point information has been supplied to me by various experts, which leads me to think it will probably be found that those women who are most robust, and who suffer least from the enervating effects of civilised life, experience a condition comparable to that of œstrus in the lower mammals (confer also Ellis).

The Effect of Maternal Influences on the Sexual Season and on Œstrus.

Maternal influences may or may not completely disorganise the sexual season; this depends upon whether or not they interfere with its recurrence or with that of œstrus.

Gestation.—Gestation may or may not interfere with the recurrence of one or other of these factors. In the dog it does not do so, because the dog has only one œstrus during each sexual season, and the period between two sexual seasons, i. e. the anœstrum, is longer than the period of gestation. In the elephant it does do so, because the gestation period is longer than the anœstrous period. So also with badgers this appears probable (Denwood, 1894). In camels, whose gestation occupies thirteen months, the sexual season is interfered with by gestation, and is on that account put off for another year. The camel conceives every two years (Swayne, 1895). In the rat, on the other hand, gestation does not interfere with the recurrence of the sexual season, but does interfere with that of œstrus, because the rat has a series of diœstrous cycles in each sexual season, and she may also undergo a series of gestation periods during that time, and because the maternal generative cycle (twenty-one days) is longer than the diœstrous cycle (ten days).

But whenever gestation occurs it encroaches upon, if it does not entirely absorb, the anæstrum; that is to say, it reduces the period during which the generative organs would lie fallow if the sexual season were a barren one. Thus in the case of the mare, a barren sexual season may consist of a series of diœstrous cycles lasting for as long as six months, in which case the anæstrum lasts six months also, after which another sexual season again begins.

A reproductive sexual season, however, results in a period of eleven months' gestation; interfering not only with the diœstrous cycles which would have recurred if conception had not taken place, but also absorbing practically the whole of the anæstrum; for, nine days after parturition, the majority of mares again experience œstrus.

Nursing.—Nursing also may or may not interfere with the recurrence of the sexual season and of œstrus. The rat suckles her new-born litter of young while pregnant with another litter; so also does the domestic rabbit and guinea-pig, and probably many rodents. The mare also, as a rule, readily becomes pregnant while suckling her newly born foal. Here, however, there is some evidence of variation, for I am informed, by a breeder of large shire horses in the west of England, that many of the mares in his stud become pregnant only once every two years; the drain on the system, in consequence of gestation and nursing, in these large animals being, apparently, too great to admit of the immediate recurrence of another sexual season. Another breeder of shire horses, however, assures me that he gets a foal each year from his mares.

On the whole there is some reason to believe that, unless these large mares are exceptionally carefully tended, they are liable to miss bearing annually, from time to time.

A few instances may be given here of animals in the wild state which do not bear young every year. The grizzly bear in British Columbia bears young only every second year (Somerset, 1895). The wild yak in the Tibetan desert only produces a calf every second year (Prejevalsky, 1876), and

the same is probably true for the Greenland musk ox (Lydekker, 1898); while the walrus, which goes nearly twelve months with young, nurses her calf or provides it with food for two years (Bell, 1874), and during that time *anæstrum* appears to persist.

Similar evidence of variation is to be found in the human female. Among the Esquimaux in high latitudes children are nursed from four to six years, and women bear children about every four years (Cook, 1894). It is not uncommon to hear of women of various tribes purposely prolonging the nursing period in order to avoid too frequent breeding. The Waganda women nurse their children until two years of age, and live apart from their husbands from the time of conception until the child is weaned (Felkin, 1885). The Andaman Island native women nurse their children as long as they can (Man, 1882). On the other hand, it is recorded that among the North-west Central Queensland natives nursing may go on for three, four, or five years, and a mother is frequently seen with two children of different ages at the breast (Roth, 1897). Among more civilised women menstruation is frequently in abeyance during the nursing period, nevertheless many women menstruate while lactation is still possible. Such a possibility is not confined to women among menstruating animals. I have seen a monkey, *Macacus cynomolgus*, in the gardens of the Zoological Society at Calcutta, which menstruated regularly while still suckling a young one.

The whole question of lactation and its relation to sexual phenomena, more especially gestation, is of great interest, all the more perhaps when it is remembered that virgin bitches frequently secrete milk in sufficient quantities to interfere with their work (foxhounds), while mules have been known to nurse successfully the foal of a mare; but for our present purpose sufficient has been said, and in conclusion it may be argued that when nursing encroaches upon the sexual season, the recurrence of the latter depends upon the vigour of the mother and her powers of recuperation.

The Pro-œstrum.

The pro-œstrum, as I have already stated, is the forerunner of œstrus. Evidence of it is to be seen in each of the large groups of the Vertebrata, fishes, amphibia, reptiles, birds, and mammals (Wiltshire, 1883), and it must be regarded in all of them as a sign of the preparation of the generative system for the sexual act.

Pro-œstrum is usually associated, in the minds of breeders, with reproduction, to an extent which entails the supposition that the same stimulus which incites the former also causes the latter; but the fact that pro-œstrum may occur normally without the concurrent production of ova shows that the two functions are not always interdependent, and that what serves as sufficient stimulus for sexual desire is not necessarily sufficient for reproduction.

A consideration of these relationships belongs rather to the study of ovulation than to the subject-matter of the present paper. I would merely remark here that while the ovary probably does participate to some extent in the excitement evidenced by pro-œstrum, this function in mammals must be considered as evidence mainly of sexual rather than of reproductive power.

Pro-œstrum is first evident in the tissue of the external generative organs and the surrounding parts, and while it increases in intensity there, it extends to the uterus; during this time certain changes (to be mentioned below) take place in the uterine tissue, and they are followed by the subsidence of the disturbance, first in the uterus and finally in the external generative organs.

The length of time during which pro-œstrum lasts is extremely difficult to determine; there seems to be considerable variation in different animals, and in the same animal at different times; but that may be due to variation in the intensity of the external evidence rather than to variation in the duration of the pro-œstrum itself.

In the rabbit I have observed this period lasts, probably,

one to four days; in the bitch seven to twelve days (Stonehenge, 1887); in the chimpanzee six to eight days (Keith, 1899). In cattle and sheep the external evidence of pro-œstrum is difficult to determine, and œstrus appears to follow very quickly upon the former, about one day after or less. Pigs, on the other hand, exhibit external signs of pro-œstrum somewhat longer, while mares are very variable in this respect.

A further consideration of the subject is divided into the external and internal evidence of pro-œstrum.

The External Evidence of Pro-œstrum in Mammals.—The first sign of pro-œstrum noticed, in the lower mammals, is a swollen and congested vulva, and a general restlessness, excitement, or uneasiness. There are other signs familiar to breeders of various mammals, such as the congested conjunctiva of the rabbit's eye, and the drooping ear of the pig, which are considered by some as even more reliable indications of the probability or capability of conception than is afforded by the vulva alone. Many monkeys (Heape, 1894, 1897, Keith, 1899) exhibit congestion of the face and nipples, as well as of the buttocks, thighs, and neighbouring parts; sometimes they are congested to a very marked extent, and in some species a swelling, occasionally prodigious, of the soft tissues round the anal and generative openings, which is also at the time brilliantly congested, indicates the progress of the pro-œstrum.

The Pro-œstrous Discharge and Menstrual Flow.—Following the swelling and congestion of the external generative organs, there is, in most animals, a discharge from the generative canal. The discharge may consist merely of mucus from the uterine glands and from the glands of the cervix and from those in the neighbourhood of the vaginal orifice, of the products derived from the breaking down of epithelial tissue, and of fragments or small masses of pavement epithelium from the vagina; such a discharge is usually to be seen in the rat and mole.

In addition, fragments or small masses of columnar uterine epithelium may be observed in various animals. Again, to

the above, blood may be added for a large number of animals, some of which rarely, some frequently, and some always suffer from a loss of blood. While, finally, more or less compact masses of uterine stroma tissue are included in the discharge of the Primates and some of the lower mammals. Blood has been observed in the discharge during pro-œstrum in the mare, ass, cow, sheep, goat, pig, cat, rabbit (Aristotle; Ellenberger, 1892; Fleming, 1878; Wiltshire, 1883), and rat (Lataste, 1887); it is also recorded as having been observed in marsupials (Wiltshire, 1883); in the bitch it is almost invariably present, and so also it would appear to be in *Pachyuromys duprasi*, *Dipodillus simoni*, *Meriones shawi* (Lataste, 1887), and in *Tupaja javanica* and *Tarsius spectrum* (Stratz, 1898). In most of these animals there is only enough blood to tinge the discharge more or less, but in the bitch, and probably *T. javanica* and *T. spectrum*, there is a flow of blood almost as concentrated as that recorded for monkeys (Heape, 1894, 1897).

It has been recorded for a large herd of highly bred Alderney or Jersey cattle in the south of England, that a discharge of blood is of regular recurrence among them (Wiltshire, 1883); but so far as I can learn this is exceptional, although its occurrence in individuals is by no means rare. It has been suggested that bleeding in the lower mammals during pro-œstrum is confined to domesticated species, but this is not true (Lataste, 1887; Stratz, 1898; Wiltshire, 1883); at the same time it is not improbable that the circumstances attending domestication tend to increase the flow of blood from the uterus, and that highly bred domesticated animals are more liable to experience it than those which are hardier, less carefully attended to, and less luxuriously fed.

The pro-œstrous discharge, then, varies in quality in different animals, and not only is this true, but it varies at different times in the same animal, both as to quantity and quality. There is ample evidence of this in various human tribes (Holder, 1892, Ellis) and in individuals. Among

domesticated animals, mares, cows, sheep, and rabbits do not always experience a loss of blood; further, individual animals of these species sometimes experience a much more profuse flow than at other times, or they may experience a profuse flow only rarely or not at all.

The Internal Phenomena of Pro-œstrum.—It will be convenient first to abstract the account I have given elsewhere (Heape, 1894) of the changes which take place in the uterus of the monkey during pro-œstrum, and then to compare these changes with those which occur at that time in the human female on the one hand, and in the lower animals on the other.

A. Period of Rest.—Stage I. The resting stage. This is the period before pro-œstrum occurs, and at that time the uterine mucosa is a shallow bed, opaque, white, and anæmic.

B. Period of Growth.—Stage II. The growth of stroma. It is now that pro-œstrum first becomes apparent; the uterine stroma thickens, hypertrophy takes place, and it becomes semi-transparent, soft, and flabby.

Stage III. The increase of vessels. The growth of the stroma tissue is rapidly followed by an increase in the number and size of the vessels of the stroma, the whole becomes richly supplied with blood, and the surface is flushed and highly vascular. This process goes on until the whole of the uterine stroma becomes tense and brilliantly injected with blood.

c. Period of Degeneration.—Stage 4. The breaking down of vessels. The walls of the superficial vessels now break down, and the blood contained therein is extravasated throughout the superficial portion of the mucosa.

Stage V. The formation of lacunæ. The extravasated blood becomes gradually collected in lacunæ, which at first lie within the stroma, but gradually become enlarged and project as rounded hillocks, bounded superficially by the uterine epithelium, into the cavity of the uterus.

Stage VI. The rupture of lacunæ. The superficial mucosa cells, isolated or in patches, now begin to degenerate; they

are cut off, as it were, by the extravasated blood, from the deeper mucosa cells, and they shrivel up and die. Soon the uterine epithelium follows suit and, with the degeneration of its cells, loses its continuity and ruptures, thus allowing the blood hitherto contained to pour into the uterine cavity.

Stage VII. The formation of the menstrual clot. With the blood which is poured out from the ruptured lacunæ is mixed also degenerated epithelium cells, isolated or in strings; and as the tissue below is laid bare, the extravasated blood in the deeper parts of the mucosa, together with stroma tissue and the superficial portion of uterine glands, also collects in the uterine cavity, and the whole forms therein a more or less dense clot. Some of the blood and degenerate uterine tissue oozes out through the os uteri to the vagina and thence to the exterior while the process is in progress, but there is frequently left behind until a later stage a clot, which in some cases entirely fills the uterine cavity.

D. Period of Recuperation.—Stage VIII. The recuperative stage. While the clot is still within the uterus, a new epithelium begins to grow over the, now much reduced, uterine stroma. At the same time new capillary vessels are formed, the extravasated blood which still remains in the tissues is collected therein, and brought back into the circulatory system. During this period the clot is expelled, and subsequently the uterus assumes again the appearance first described, and eventually becomes again at rest. It is at or towards the close of this period that œstrus normally occurs.

For the human female the histology of pro-œstrum (menstruation) has never been so fully worked out in healthy normal uteri. Many observers have described isolated specimens, and most of them have had recourse to material which has either been obtained some time after death, or from individuals suffering from diseases which may well have produced pathological changes in the uterine tissue. Then, again, the extent of menstruation varies in different peoples and individuals, and in the same individual at different times. The amount of the menstrual flow and the quality of that flow also

varies, to such an extent, indeed, that, while some women lose a large amount of blood at each pro-œstrum, others sometimes and some never lose any at all. It is not surprising, therefore, to find that while some observers hold that no change takes place in the uterine tissue during pro-œstrum, others state that highly specialised decidual tissue is formed at that time; while some deny that even a portion of the uterine epithelium is lost by denudation during pro-œstrum, others maintain that the whole of the mucosa layer is discarded during that process.

The question has been somewhat fully discussed by me in a former paper (Heape, 1894), where an account is also given of the more important literature of the subject. Here it is only necessary to add the conclusions arrived at, which are that in all essential points the menstruation or pro-œstrum of the human female is identical with that of monkeys. More recently I have described (Heape, 1898) two menstruating human uteri, the first of which shows congestion and is closely comparable to Stage IV of the monkey, while the second shows denudation, and appears to be practically identical with Stage VII of the monkey.

A slightly earlier condition of denudation in the human uterus has been described and figured by Minot (1892), and again supports the view above expressed.

Among lemurs, Stratz (1898) has described what he calls bloody "menstruation" for *Tarsius spectrum*. I gather that, in this animal, denudation of the epithelium of the uterus takes place and that Stage VII exists; but there is no proof that denudation extends to the stroma tissue, and therein possibly lies the difference between lemurs and monkeys, otherwise there can be little doubt of the homology of the process in these two animals.

Stratz has also described the existence of a blood-clot and a "menstrual"¹ flow in *Tupaja javanica*, and here again the

¹ The use of the term "menstrual" flow, as it is here used, to denote a flow of blood from the uterus, without regard to the periodicity of that flow, is to be deprecated.

tissue contained in the clot apparently consists only of desquamated epithelium.

Retterer (1892) has given a more detailed account of what happens during the pro-œstrum of the bitch. During period A, of rest, Stage I, the mucosa of the uterine horns is firm, pale, and of a thickness of .3 to .5 mm.; but with the commencement of pro-œstrum, period B, there is a well-marked Stage, II, in which the mucosa grows rapidly to three or four times its original thickness, and becomes soft and spongy. Stage III is also well marked, and the mucosa becomes injected with numerous vessels distended with blood. Then period C occurs, and Stage IV is marked by the breaking down of the vessels and extravasation of the blood in the mucosa tissue. Lacunæ are formed, Stage V, which, during Stage VI, rupture, and pour the contained blood into the uterine cavity.

So far the similarity of the progress of the pro-œstrum in the bitch is practically identical with that of monkeys, but there is no blood-clot formed, and Retterer's account renders it doubtful whether any denudation, even of epithelium, takes place. He himself thinks not. I have myself worked out the history of the pro-œstrum of the bitch to some extent, and have satisfied myself that Retterer's account is true in all essential details.

I have also failed to find any area of the uterine mucosa which has been denuded of epithelium, and do not believe that this process occurs to any extent; at the same time, where lacunæ rupture there must be loss of epithelium, though I think denudation is confined to these spots.

The pigmentation of the uterus, described by Altmann (1878), is further evidence of the probability that much of the extravasated blood is not discharged into the uterine cavity, but is retained in the uterine tissue and absorbed from thence.

The homology of this process in the bitch with that already described for monkeys is absolutely certain, and if nothing more were known, would establish the identity of the pro-

œstrum in these animals; or, in other words, the homology between the pro-œstrum (so-called "heat") of the lower mammals and the menstruation of the Primates.

The absence of Stage VII, the menstrual clot, is not to be wondered at in a large bifid uterus; the denudation of tissue in sufficient quantity to form a clot would be a very severe operation in such a comparatively large organ.

The only other paper dealing with this subject, for the bitch, with which I am acquainted (Johnstone, 1888), treats of what the author calls the "corpuscular development" of the mucosa of the bitch during the pro-œstrum, but I do not gather the author has satisfactorily demonstrated the truth of the view he advocates (see also Johnstone, 1895).

Pouchet's description of the changes in the uterus of the sow during pro-œstrum shows the existence of Stages II and III (Wiltshire, 1883); he does not describe the breaking down of vessels or the formation of lacunæ, but his description of the histology of the uterine discharge shows that it contains, besides mucus, both blood and uterine epithelium. Stage IV, therefore, is assuredly represented, and there can be little doubt that Stages V and VI are also passed through, since there must have been rupture of the uterine tissue in order that pieces of it should be contained in the discharge.

Ellenberger's (1892) account of the changes which take place during pro-œstrum in domestic mammals includes Stages II and III; he also does not describe Stages IV, V, and VI, but he records the presence of both blood and epithelial cells in the discharge, and these stages must therefore have been passed through, although denudation is in all probability very slight. Fleming (1878) adopts the view that, among ruminants, the blood which finds its way to the exterior exudes from the cotyledons; while Ellenberger describes pigmentation there, and states it is caused by the blood left behind in that tissue after pro-œstrum has occurred.

Bonnet (1892) also describes Stages II and III in various domestic mammals during pro-œstrum, but he also adds

Stage IV for ruminants, horse and pig, and where external bleeding is seen in these animals the occurrence of the equivalent of Stages V and VI is essential.

Kazzander (1890) notes the existence of extravasated blood (Stage IV) in the sheep's uterus during pro-œstrum, at a period before external bleeding is noted; so that when the latter occurs, a condition equivalent to Stage VI is passed through by this animal. Both this author and Bonnet (1880, 1882), whom he quotes, describe pigmentation in the uterine mucosa of the sheep, and consider it is due to the extravasated blood which is not discharged during the pro-œstrum.

Lataste (1887) describes desquamation of uterine epithelium in several Muridæ, and states that it takes place independently of pro-œstrum (or, as he calls it, "rut"), during which Stages II and III are noted, and at the close of which a bloody discharge (which he calls "menstruation") is evident. Stages IV, V, and VI are therefore probably also passed through in the case of these animals.

I find it difficult to determine exactly what this author means, but I gather it is his opinion that in these animals there is a periodic shedding of uterine and superficial vaginal epithelium, and that this precedes and is independent of the pro-œstrous discharge (p. 163); if this be so it is quite different from anything which has been already described for any other of the lower mammalia, and is comparable only to that somewhat rare phenomenon, exfoliation of the vagina, in the human female. The same author declares (1893) there is a rhythmical transformation of the epithelium of the vagina in certain of the lower mammalia, which is in connection with rhythmical generative changes; he describes the denudation of this epithelium, and its recuperation from the lower layers.

The subject has been very rarely investigated in the lower mammals, and still more rarely has it been attacked from a histological point of view; isolated specimens have been described with more or less detail, but no attempt has been made to work out the history of the process by any one, so far as I know, but Retterer.

For this reason the evidence available is fragmentary, but it is remarkably consistent; and although further researches may, and probably will, show variations in detail, the broad fact of the homology of the internal process of pro-œstrum in all mammals is sufficiently demonstrated.

This we may summarise as follows: the uterus of all mammals during the quiescent period is comparatively anæmic, and its mucosa is a thin layer; it has at that period the appearance of lying fallow.

During pro-œstrum hypertrophy of the mucosa first takes place, and is followed by congestion, which results usually in the rupture of the superficial vessels and consequent extravasation of the blood into the surrounding tissue; in some cases this extravasated blood finds its way into the cavity of the uterus and thence to the exterior, with either more or less denudation of the superficial mucosa, while in other cases there is no external hæmorrhage, and the extravasated blood is absorbed in situ. While, therefore, neither the discharge of blood nor the extravasation of blood is an essential feature of the pro-œstrum, the hypertrophy and congestion of the mucosa is invariably present in all mammals, a condition which we may confidently expect to find also in the lower Vertebrata.

The Period of Œstrus.

The period of normal œstrus, as I have stated in the introduction to this paper, occurs as a result of pro-œstrum.

As a rule breeders regard œstrus (the period of desire) as an attendant condition of pro-œstrum rather than as a result thereof; where there is no discharge evident there is some excuse for this view, especially as, even when a discharge does occur, œstrus may happen before the discharge completely ceases. Œstrus, however, is possible only after the changes due to pro-œstrum have taken place in the uterus. A wave of disturbance, at first evident in the external generative organs, extends to the uterus, and after the various phases of pro-œstrum have been gone through in that organ,

and the excitement there is subsiding, it would seem as if the external organs gain renewed stimulus, and it is then that œstrus takes place. If the uterine changes are confined to Stages II and III, that is simply hypertrophy and congestion of the mucosa, œstrus rapidly follows the first external signs of pro-œstrum; but if more elaborate disturbance takes place in the uterus, the period of œstrus is delayed.

Thus it is during the subsidence of the uterine disturbance that œstrus takes place. The period during which the discharge continues is not, however, a true indication of the permanence of the uterine disturbance. In comparatively large uteri, especially in those which extend as long horns from the corpus uteri, the area of denudation or hæmorrhage may be situated far from the vagina; and the products of that hæmorrhage and of denudation may take a considerable time to find their way to the exterior; this is especially the case where there is little blood and much mucous discharge.

We have seen above that in the monkey, Stage VIII, a new epithelium is formed over the surface of the newly denuded uterus before the blood-clot is evacuated; and in the same way, before the discharge from long-horned uteri reaches the exterior, the uterine disturbance is largely allayed, and renewed stimulus may be supplied to the external generative organs.

In all animals which have been investigated, coition is not allowed by the female until some time after the swelling and congestion of the vulva and surrounding tissue is first demonstrated, and in those animals which suffer from a considerable discharge of blood, the main portion of that discharge, if not the whole of it, will be evacuated before sexual intercourse is allowed.

Thus in *Pachyaromys duprasi*, which experiences hæmorrhage, coition is not allowed during the flow (Lataste, 1887).

Bitches, except rarely, receive the dog only after bleeding is over (Stonehenge, 1887), although a mucous discharge, which frequently continues after the discharge of blood

ceases, may be still in progress at the time coition is permitted by the bitch (Millais).

The Moor macæ in the Zoological Gardens has a definite œstrus, which always occurs shortly after the menstrual discharge ceases, and which lasts for two or three days; and there is strong reason for believing this is also the case with various other monkeys, as, for instance, the orang-utang (Ellis).

The human female frequently experiences œstrus with marked strength after menstruation is over (Martin, 1888), more especially, it would appear, in those individuals who do not suffer from excessive menstruation,—in other words, in those whose generative system is least disturbed by the consequences of civilisation and social life. This special time for œstrus, in the human female, has very frequently been denied, and no doubt civilisation and modern social life do much to check the natural sexual instinct where there is undue strain on the constitution, or to stimulate it at other times, where extreme vigour is the result.

For these reasons a definite period of œstrus may readily be interfered with, but the instinct is, I am convinced, still marked. Ellis quotes various authors who hold a similar view, but they do not all agree as to the time when œstrus occurs; if, therefore, the views which I have advocated here are correct, it would seem probable that abnormal œstrus has been mistaken for true œstrus in many of these cases.

Summary and Conclusion.

Introduction.—After criticising the terms commonly used to denote the various stages of the “sexual season” of mammals, I have defined the terms used in the present paper.

Female mammals are divided into two classes, “monœstrous” and “polyœstrous” mammals, and I have explained that, in the absence of the male, “pro-œstrum,” “œstrus,” and “metœstrum” are followed by “diœstrum” in polyœstrous mammals, during the recurrence of the “diœstrous

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cycles," and by "anæstrum" in monœstrous mammals always, and in polyœstrous mammals at the close of the sexual season.

The difference between the diœstrous or anœstrous cycles in the absence of the male, and the "maternal generative cycle" when œstrus is followed by insemination, fertilisation of the ovum, and gestation, is drawn attention to.

The occurrence of abnormal œstrus is noted.

The Breeding Season of Mammals is merely touched upon; inasmuch as it concerns what happens during both the sexual season and the gestation period jointly, its full consideration is not possible in this paper.

The Sexual Season of Male Mammals.—Males are divided into two classes, those which have a special sexual season, "rut," and those which are sexually capable all the year round. The influence of captivity is touched upon, and it is shown that, while sexual activity is not so violent in captive animals as in those in the wild state, it may be much more frequently or continuously exhibited.

The Sexual Season of Female Mammals.—This is considered in wild mammals in a state of nature, in those which are captive, and in domestic mammals; and the effects of climatic, individual, and maternal influences are drawn attention to.

Among monœstrous mammals the effect of these influences may be to increase or decrease the periodicity or the duration of the sexual season, while among polyœstrous mammals the effect may be to increase or decrease the number of diœstrous cycles in each sexual season or the duration of each cycle; the effect in both classes of animals being to increase or decrease their reproductive power.

It is pointed out that the knowledge at present available throws no light on the origin of the sexual season; but that it is due to a stimulus which appears to be gradually collected, that it is associated with nutrition, and is manifested by exceptional vigour and bodily "condition" seems assured.

The Periodicity of the Sexual Season in Monœs-

trous Mammals in the Absence of the Male.—This is shown to be affected by climatic and by individual influences, to be more frequent in domesticated than in wild animals of the same species, and to be variously affected by captivity.

The Duration of the Sexual Season in Polyœstrous Mammals in the Absence of the Male.—The sexual season in these animals is affected by the duration and the recurrence of the diœstrous cycle; as in monœstrous mammals, it is shown to be affected by climatic and individual influences, by domestication and captivity.

It is here that we are first brought into contact with monkeys and man, and I have endeavoured to show that the sexual season which undoubtedly exists in monkeys, exists also in certain human peoples in the present day, while there is some evidence that, in the past, all peoples were similarly affected, and that a definite sexual season was the rule. The fact that, in spite of the regular recurrence of the œstrus, monkeys have only a limited season during which conception is possible, is drawn attention to. It is pointed out that this is due to the fact that the ovary is not active all the year round, and evidence is brought to show that the function of ovulation is also not necessarily coincident with œstrus in various other mammals. This condition is apparently due to the want of sufficient energy for both œstrus and ovulation.

The Duration of the Œstrus in Monœstrous and Polyœstrous Mammals in the Absence of the Male.—Knowledge of this point is practically confined to domesticated mammals and to certain animals in captivity, and the evidence, which a study of these animals renders available, shows that the duration of œstrus is very variable, not only in different species, but also in different individuals of the same species, and in the same individuals at different times.

There is greater variation in this respect among monœstrous than among polyœstrous mammals, as a rule.

The Effect of Maternal Influences on the Sexual Season and Œstrus.—These may or may not completely

disorganise the sexual season, and this depends on whether or not they interfere with its recurrence or with that of œstrus.

The above is true for both monœstrous and polyœstrous mammals, for both gestation and nursing; but whereas gestation interferes with the recurrence of the œstrus, only if it extends over the time which would otherwise be a sexual season, the interference of nursing depends upon the vigour of the mother and her powers of recuperation.

The Pro-œstrum.—Evidence of pro-œstrum is to be seen in all Vertebrata, and is the forerunner of œstrus. It is first noticeable in mammals in the external generative organs, and extends thence to the uterus.

The essential manifestations thereof are first hypertrophy, and secondly congestion of the tissues affected, and this is very usually, indeed probably always, followed by a discharge.

The discharge always consists partly of mucus from the uterus, and partly of desquamated vaginal epithelium and the products of broken-down epithelial tissue.

In some animals always, and in others sometimes, blood is also evacuated, which has its origin from the uterine mucosa, in which case there is always more or less of uterine tissue also contained in the discharge.

There is very considerable variation in the extent of both hypertrophy and congestion of the tissue in various mammals, but it is essential to note that these phenomena are to some extent always present, and are frequently combined with the rupture of the congested vessels in the mucosa, and also, more rarely, with a discharge of blood from, and still more rarely a denudation of, the superficial uterine mucosa.

The evolution of the pro-œstrum in its most advanced form, that is to say the menstruation of the Primates, from the simplest form, as it appears in such animals as the mole, is traced, and menstruation is shown to be identical with "heat."

The Period of Œstrus.—This is possible only after

the active changes due to pro-œstrum have taken place in the uterus ; it is always present, under normal conditions, in the lower mammals at that time, and is much more frequent than in the Primates than is generally supposed.

Conclusion.

The conclusions I draw from the evidence detailed above are then, very briefly, as follows :

A sexual season is common to all female mammals ; its recurrence may be interfered with in consequence of climatic, individual, or maternal influences, and it may be modified by the influences attending captivity, domestication, or civilisation.

The modification brought about by one or other of these various influences is not necessarily the same in different species of the same genus, nor in different individuals of the same species, nor even in the same individual at all times ; but whatever differences there may be, they are merely modifications of the same plan.

The sexual season of all mammals is evidenced by a series of phenomena which constitute, in the absence of the male, one œstrous cycle (monœstrous mammals) or a series of œstrous cycles (polyœstrous mammals) ; animals usually monœstrous may, under certain circumstances, show a tendency to polyœstrum ; in the same way animals usually polyœstrous may show a tendency to monœstrum. These two conditions are very closely related, and the main difference between them is the method by which the reproductive power is increased.

The various constituent parts of an œstrous cycle are invariably demonstrated in all mammals ; there is in all of them a period during which the generative organs are hypertrophied and congested (pro-œstrum), followed by a period of desire for coition (œstrus), which, in the absence of the male, gradually dies away (metœstrum), and results in a period of rest (diœstrum or anœstrum). When this period of rest merely separates two recurrent diœstrous cycles it is brief,

and I have called it the *dicestrum*; but where it serves to separate two sexual seasons it persists for a considerable length of time, and I have called it the *ancestrum*.

The *pro-œstrum* is always associated with hypertrophy and congestion of both external and internal sexual organs and the uterus, and with a discharge from the generative orifice. These phenomena are common to all mammals; they may, however, be further complicated. These complications may include rupture of the congested vessels of the hypertrophied superficial uterine mucosa, and extravasation of the blood contained therein; they may include a discharge of this blood into the uterine cavity, and from thence to the exterior; and even more or less denudation of the mucosa may take place, leading to the formation of a menstrual clot.

The rupture of the vessels of the mucosa and the subsequent phenomena are not experienced by all mammals; they are supplementary to the essential factors of *pro-œstrum*, and occur in part rarely in some animals, in part always in some animals, and in a complete sequence only, so far as is known, in *Primates*.

That the *pro-œstrum* of *Primates* is identical with the *pro-œstrum* of other mammals does not, however, admit of any doubt; there is ample evidence of this in the various intermediate conditions of other mammals, by means of which, and bearing in mind the influence of domestication and civilisation on *polyœstrum*, the evolution of the menstruation of monkeys and of the human female from the *pro-œstrum* of the lower mammals can be surely traced. A further evidence of this is the time of the occurrence of *œstrus*. It is manifested at a certain period after *pro-œstrum*, and has a certain relation to it—that is, it follows and is not coincident with *pro-œstrum* in the lower mammals, as is usually supposed.

In some monkeys the same relation of *œstrus* to *pro-œstrum* obtains, and in others it is probably so, while in the human female there is evidence of a similar condition, especially, probably, among normally strong individuals who lead a healthy life.

Thus the human female may exhibit a sexual season, a pro-œstrum, and a period of œstrus, precisely like any other mammal, and the homology of these processes in all mammals is, in my opinion, established.

A review of the literature which treats of the relation between "heat" or "rut," as it is usually called, and menstruation, resolves itself practically into an enumeration of those who deny there is any ground for comparison, and those who assert they are identical processes. I do not propose to enter into a detailed criticism of the voluminous literature which bears upon the subject, but will content myself with quoting the essence of the most frequent assertions which are made for and against the homology of these processes, and with briefly replying to them.

Those who uphold the homology do so because—

I. There is congestion of the generative organs during both "heat" and menstruation.

II. There may be a recurrence of "heat" as there is a recurrence of menstruation.

III. The discharge during "heat" may be of a menstrual character.

IV. From a phylogenetic point of view the homology is to be expected.

These statements may be disposed of together; so far as they go they are true enough, but they are not in themselves, separately nor collectively, conclusive evidence.

Those who deny the homology do so because—

1. The discharge during "heat" in the lower animals is said to be mucus, while in the human female it is mostly blood.

2. The time of "heat" is said to be the only time the lower animals will permit of coition, while sexual union during menstruation is a very rare occurrence.

3. "Heat" or "rut" is said to occur in both males and females in the lower animals and to depend upon the seasons, whereas in the human species it is said to be not so.

4. After "heat" the female of the lower animals is said

to refuse the male, whereas in the human female sexual desire is not confined to the time of menstruation.

5. "Heat" is necessary to the production of the species in the lower animals, while in woman "desire" is said to be not essential to conception.

6. In the lower animals the ovaries are said to contain ripe ova only during the time of "heat," whereas ripe ova are said to be found in the human ovary at all times without reference to menstruation.

7. There is said to be no proof of the identity of the two conditions.

I think these propositions fairly cover the ground over which those who deny the relationship of what they call "heat" to menstruation have hitherto travelled.

It will be seen at a glance that the denials originate, in most instances, in misconception of the facts, and that many of the errors are due to the misuse of terms.

It will be worth while, however, to answer each of them separately, and the following replies are numbered to correspond with the numbers of the above objections.

1. The discharge in many animals during the pro-œstrum contains blood and sometimes uterine tissue; it is not always solely mucus, and when blood is absent it has been shown that its absence is due to a modification of, and not to any radical difference in, the process.

2. The term "heat" is here wrongly used; it is made to include both the pro-œstrum and the œstrus in the lower mammals, and is compared in that extended sense with the term menstruation, which is an error. The time the lower animals will permit of coition is not during pro-œstrum, which is synonymous with menstruation, but during œstrus, which immediately follows the pro-œstrum. I have shown above that there is not wanting evidence that the same may be true for the human female.

3. Although the time for sexual intercourse among human beings is not universally confined to particular seasons, I have shown that in some cases this is so, and that in all

peoples there is a marked disposition to indulge in sexual intercourse at particular times of the year, which are undoubtedly comparable to the so-called "breeding seasons" of the lower mammals. Further, in certain domesticated animals and certain wild animals kept in captivity the males do not "rut" only at certain times of the year, but are prepared to propagate at all times (dog) or almost at all times (captive cattle or deer) throughout the year.

4. There is some truth in this objection; but it must not be forgotten that, among the lower mammals, while captivity and domestication reduce the violence of the sexual passion, they increase its frequency; and that in civilised woman, in all probability, it is this variation of the function still further exaggerated which is responsible for the difference (see also 2).

5. Here again the objection is largely due to a mistaken use of the term "heat," which in this case is used to denote œstrus.

Menstruation, that is pro-œstrum, in women is as necessary to the production of the species as pro-œstrum in the lower animals can be; the fact that œstrus is less pronounced in the former is true, but it is not altogether absent, and has already been referred to in the replies to propositions numbered 2 and 4.

6. This objection has reference to the question of ovulation, which has not been treated of in this paper; with regard to it I would merely say, that ovulation in certain of the lower mammals is not necessarily coincident with œstrus, while in some of them œstrus and ovulation are quite separate functions. Ripe ova are not found at all times in each human female, and the fact that they may be found at times which are not coincident with menstruation, is merely further evidence that these functions are independent also in women. Further, the degree of independence which these two functions assume is apparently variable in the human female.

7. The answer to this objection is contained in the foregoing paper.

In spite of the fact that the evidence I have brought forward is fragmentary, and notwithstanding that only the fringe of a vast subject has been touched upon, I venture to hope enough has been said to show that the wide variations in the sexual functions exhibited by various mammals are variations in degree, not variations in kind; and I venture to think that the evidence of the homology, not only of pro-œstrum and menstruation, but of each of the various sexual phenomena dealt with in the various types, is incontrovertible.

One word with regard to the future development of the subject. It is the cause of the sexual season which requires determination.

Much stress has been laid upon the rhythmical nature of all breeding processes; this has been carried furthest by Lataste (1887 and 1891), and by Beard in a very suggestive paper on gestation (1897). So far as the sexual season is concerned, its rhythm is no explanation of its origin. It may, I suppose, be asserted that all forces are exerted rhythmically, that is a condition; whereas what is required here is knowledge of the nature of the force itself, and the causes which govern or limit its rhythm.

These are questions for the comparative physiologist, in whose hands, as it seems to me, lie so many of the great biological problems of the day.

Speaking generally, the rhythm of the sexual season and the power of breeding is seasonal, it is governed by external forces which are exerted in consequence of seasonal change, and by internal forces which are dependent upon individual powers; further there is abundant evidence that nutriment, and the capacity for storing nutriment, and the energy resulting therefrom are essential factors.

I differ from those who, like Beard, consider the ovary the seat of the governing power of the breeding function; ovulation and the œstrus cycle are not necessarily coincident, the stimulus sufficient to induce the one is apparently not sufficient in all cases to induce the other, and it would appear that the requisite initiative is independently produced.

I am tempted to suggest the probability that there is present in the blood from time to time what may be called an œstrus toxin, to suggest that its presence is due to the external and internal forces mentioned above, and to relegate to it the power which stimulates the activity of the sexual season, and brings about the actual production of those generative elements which nutrition has enabled the animal to elaborate.

It appears to me that research in this direction would be likely to be rewarded; it would not only be of great theoretical interest, but might well lead to increase of knowledge regarding some of the causes of sterility, and prove of enormous practical value.

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