I

INTRODUCTION

THE study of the reproductive processes in the cow was undertaken with several practical objectives in view.

Veterinarians have for some time past been treating cows for sterility by various empirical methods, some of which have been quite successful at times, but there has been very little work done on the physiology of reproduction in the cow to form a basis for the rational treatment of such cases.

A study of the changes occurring during pregnancy was attempted in the hope that it would serve as a basis for the study of the pathology of the organs in abortion, and that it might also indicate the causes which led to the development of the udder and those which may form the foundation of the genetic differences between good and poor milking cows.

Although artificial insemination has been found useful in mares few attempts have been successful in cows, and it was thought that a detailed study of the reproductive processes in the cow might show the cause of failure and lead to extensions of this method of reproduction.

The experiments were on the whole designed to elucidate problems which if solved would do much to assist the farmer in regulating the management and feeding of his herd for the production of calves and milk.

From a scientific point of view it was thought that a comparison of the processes occurring in the reproductive organs during pregnancy with those occurring during the cycle in the same species would throw light on the processes involved in the cycle, and enable one to realise the significance of these changes.

The similarity between the reproductive cycles in the cow and in woman (the former having a cycle of three weeks and the latter of four weeks), which in both cases culminate in the flow of blood from the vulva, renders the study of reproduction in the cow particularly interesting to those engaged in elucidating problems in human reproduction and the relation of "heat" in animals to menstruation in women.

One of the chief difficulties met with, and probably the reason why such a study has not been undertaken before, is that the cow is an

expensive animal to keep and kill, so that the numbers used for experimental purposes must necessarily be limited. For this reason the experiments made have been precise detailed studies of a few individuals rather than a superficial examination of a large number. The size of the reproductive organs is of great advantage in the study of reproduction, for observations with the naked eye can be made on the ovaries which are not possible in the fresh condition in the mouse or rat, where resort has to be made to staining and microscopical examination. Measurements and weights can also be made and taken to a degree of accuracy which is impossible in a small animal. Moreover, since as a rule only one egg is shed at each ovulation, the process of tracing the corpus luteum during its history, and of experimenting with it, was much easier than if several were shed as in the dog, ferret and rabbit.

Discussions of the sexual life of the cow and other domestic animals have been published by Schmaltz (1) and Kronacher (2) in whose treatises many of the problems investigated have been outlined.

Material.

The material on which this study is based falls under two headings: (1) experimental animals, (2) organs collected from slaughterhouses.

(1) The majority of experimental animals used were cross-bred Shorthorn Heifers of 2–3 years old. Heifers were selected rather than cows so as to eliminate chances of infection of the uterus and organs by contagious abortion or other diseases occasioned by pregnancy. The facilities for keeping the animals were limited and lots of about four only could be accommodated at any one time; this had the advantage, however, that it was possible to keep them all under close observation. The majority came from the Cambridge University Plant Breeding Farm (and my thanks are due to Mr N. Langridge for the assistance he has given me in the selection of these animals), where they had been kept a year or more, and a few were purchased from a dealer direct. All were kept under observation for a month or two before the experiments proper began.

The few cows that were used were not purchased on the market but came direct from farmers in the district from whom an account of their previous history was obtained.

(2) Material was also collected from the slaughterhouses of local butchers (and I have to thank more especially Messrs Warrington and Sons for their assistance in this respect). In the majority of cases, however, the previous history of these animals was not known as most were pur-

chased in the open market; in some cases, however, where the animals came from the University Farm or from local farmers the breeding history of the cow was obtained.

In addition to the foregoing material much information was obtained from experienced stockmen met at the Agricultural Shows (see Appendix I). Many have had a life-long experience in the management of breeding cows and to them my thanks are due for various details which have suggested new lines of research.

Methods.

An attempt has been made to study the oestrous cycle by timing the processes concerned by means of time observations, in much the same way that physiologists have studied muscle-nerve preparations by the use of recording drums.

Owing to its importance from a practical point of view it was necessary to know exactly the duration of oestrus. While by observation it was generally possible to tell whether a cow was on heat or not, yet it was thought best to apply the test of whether she would actually "take the bull" or not. In order to do this without interrupting the cycle by a pregnancy ensuing, a vasectomised bull was used; such an animal has all the desire and powers of coitus possessed by an entire animal but ejects no spermatozoa.

The bull was kept in a loose box separate from the cows, but, except for a few experiments, within sight of them. To determine whether or no a cow was on heat the bull was turned into an enclosure or covered shed with her and they were kept under observation. It was decided to test the cows at intervals of every two hours, commencing a day or more before the expected heat period was due, and if there was any doubt (as sometimes happened when they were coming on and going off) a period of half-an-hour was allowed before the bull was withdrawn. In this way it was considered that the actual time a cow came on or went off heat could be determined within about an hour. Extracts from the log-book kept are given in Appendix II.

After the experiments had been going on for some time and it was found that the cow was staying on heat 12 hours or more, the bull was not put in at the 4th, 6th or 8th hour after heat began, but was re-introduced at the 10th and subsequent 2 hour periods; in this way his energies were conserved, and the end period of the heat could more readily be determined.

This method has involved continuous observation of the cows over

considerable periods, and my thanks are due to Mr S. J. Tadman, my laboratory assistant, who has shared this work with me, one of us watching by day and the other by night.

This work has been supplemented by a study of the anatomical and histological changes in the reproductive organs of these animals, which were killed at different periods of the cycle and of pregnancy. An accurate reproductive history of the animals was, therefore, obtained before they were killed. The observations were made both in the fresh state and after they had been fixed (for the most part in 10 per cent. formalin solution) and stained (mostly in iron or Delafield's haematoxylin and eosin).

The bull used was operated on when he was about 15 months old, having previously been used to get four heifers in calf. He was killed when about four years old, after the experiments were completed; during this time he remained sexually active, mating on the average about five times a week. His secondary sexual characters were normal, and the testes as far as could be judged were of normal size. The operation was performed by making two small incisions (at the top of the posterior side of the scrotum) through the skin, cremaster muscle and tunica vaginalis, which exposed the vas deferens; a small portion of each of these latter was then removed but the ends were not ligatured and the wound was stitched up.

The testes were sectioned after the animal was killed and were to all appearances normal, both seminiferous tubes and interstitial cells being well developed and the former containing spermatozoa. This result does not agree with Ancel and Bouin's(3) experiments with vasectomised horses and other animals, in which they found degeneration of the seminiferous tubules and hypertrophy of the interstitial cells. They ligatured the vas deferens, however, and thus by causing pressure and inflammation in the tubules may have aided their degeneration in much the same way as the mammary gland atrophies when the products of secretion accumulate within it.

Steinach(4) states that the interstitial cells of the testis undergo hypertrophy after vasectomy and that the seminiferous tissue disappears.

Lipschütz(5) however believes that no actual hypertrophy of the interstitial cells occurs and that whether or no degeneration of the seminiferous portion is found after operation depends on the interval between the operation and the date of killing.

II

THE BREEDING SEASON

Data collected from Milk Recording Societies soon established the fact, as is generally known, that cows will breed at all times of the year. These data which are given in Table I show the percentage of the total number of cows which calve in each month of the year; it will be seen that the time of year that they actually calve depends on local agricultural conditions and is no guide to their natural breeding season, for in the west of England, where grassland prevails, the majority calve in March and April, whereas in the east on arable land, where milk is required for winter supply to the towns, more calve in the autumn, although even here a large number tend to calve in the spring.

Weber (6) found that in domestic cows heat occurred at all times of the year.

Heape (7) states that whereas domesticated cattle breed all the year, in wild cattle the calving season is limited, but in the Zoological Gardens they are capable of breeding at any time of the year.

Mayo-Smith (8) found that in man the largest number of conceptions occurred in the summer months, and the time of maximum number varied with the climate, in Greece the maximum occurring in April, whereas in Sweden the maximum did not occur until June.

Statistics collected from various authorities are appended to this table (I) and they confirm the above conclusions; in particular there are large differences between Ayrshire and Denmark in the time of year cows usually calve.

In order to determine the readiness with which cows would breed at different times of the year the average length of time was calculated between the times cows calved and their next fertile service. Data on this point are shown in Table II. The average time is 97 days but cows which calve in May are, on the average, served within 76 days, whereas those which calve in September are not, on the average, served until 135 days after calving, and there is a gradual and steady rise and fall between these two extremes. In order to calve on the same date in the following year a cow should be served 85 days after calving. The average interval before service throughout the year varied in different districts, being as high as 105 days in Penrith, and as low as 89 days in Norfolk.

Table I. *Percentage of cows which calve in different months of the year.*

Milk Recording Society or District	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total No. of cows
S.E. Essex M.R.S.	12·9	10·2	8·8	6·5	5·9	8·0	8·0	6·9*	7·3*	6·4	9·5	9·6	1157
Norfolk M.R.S.	11·0	13·3	11·2	9·4	7·0	6·2	8·6	5·9*	5·0*	5·6	7·4	9·4	1799
N. Somerset M.R.S.	10·6	9·9	13·5	11·1	6·3	4·7	5·5	4·7*	8·1*	11·1	7·7	6·8	844
Penrith (Cumberland) M.R.S.	10·9	11·3	21·2	17·4	9·6	5·3	3·8	2·0*	1·8*	4·6	4·8	7·3	1463
Av. 4 M.R.Socs.	11·3	11·5	13·8	11·3	7·4	6·1	6·6	4·8*	5·1*	6·4	7·2	8·5	5263
Essex(9)	9·6	12·4	7·4	5·1	6·1	9·8	10·8	7·9	4·7	8·8	7·3	10·1	1418
Yorkshire (10)	10·5	10·7	12·0	10·3	8·0	5·6	5·0	6·6	8·7	7·7	6·6	8·3	484
Ireland (10)	10·2	13·4	14·9	14·6	8·8	3·1	2·6	5·6	5·4	9·1	6·3	6·0	811
Ayrshire (11)	9·7	16·7	24·4	16·8	7·1	2·6	1·0	2·1	4·6	4·8	4·5	5·7	3893
Denmark (12)	7·6	9·5	11·8	9·6	7·1	5·6	2·9	5·0	7·1	10·5	12·8	10·5	1472
Germany (13)	18·1 with Dec.	40·5		16·2		6·4		6·7		12·1		with Jan.	10960

* Too low as service dates not given in records.

Table II. *Interval between calving and fertile service for cows calving in different months of the year.*

Milk Recording Society	Days ± the average interval. Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Average interval days
S.E. Essex	−3	− 7	−10	−19	−27	+ 1	− 1	+10	+32	+23	+ 5	+ 2	103
Norfolk	−3	− 4	− 9	−12	−13	−15	−14	+ 4	+26	+30	+11	+ 1	89
N. Somerset	−8	− 6	− 5	−17	−13	− 1	+ 4	− 7	+20	+21	0	+15	92
Penrith	−5	−12	−14	−24	−31	−16	−12	−11	+74	+48	+ 7	+ 3	105
Av. of 4 societies	−5	− 7	− 9	−18	−21	− 8	− 6	− 1	+38	+30	+ 6	+ 5	97

This table (II) shows that although cows will breed at all times of the year, yet there is an optimum time—during the summer months May–July—when the reproductive force is at its maximum, and conversely that during the cold weather of the winter months—November to January—the reproductive powers are at a minimum. That there is an optimum temperature rather than that high temperatures shorten the interval is indicated by the fact that for cows calving in July the interval is much less in the more northern districts of Norfolk and Penrith than in the southern ones of Essex and Somerset.

A cow does not usually come on heat immediately after she calves. Weber(6) has published in tabulated form the literature on this point, and he himself found that it varied from 3 weeks in cows with intense heat periods to 4–7 weeks in cows with feeble heat periods. In our investigations only one definite case has been experimentally obtained, and in this the first heat period occurred 49 days after calving in March. Information obtained from stockmen (see Appendix I(4)) shows that the time of first heat after calving may vary from 9 days to 6 months, but the usual time is 3–4 weeks if the cow is milked, and rather longer—

about 3 months—if the calf is suckled. They also stated that conditions which tended to reduce the nutrition of the animal, *i.e.* poor feeding and heavy milking, lengthen the interval between calving and subsequent first heat period. Hammond and Sanders (14) have shown that the time of fertile service after calving varies with the age of the cow, being shortest in the prime of life—3rd–4th calf—and longer both before (during growth) and after (during senile decay) this period, and that this may have a nutritional basis.

Bonhote's (15) theory of the reproductive season depending on the state of vigour of the animal is also founded on the amount of nutrition available at different times of the year. Probably temperature affects the nutrition of the animal through its heat loss as well as through the foodstuffs available.

Schmid (16) investigated the frequency with which the first heat period of heifers and the first heat of cows after calving occurred in the different months of the year and found that the highest proportion fell in the spring and autumn months. His data are however open to the criticism, as pointed out above, that these things are determined by agricultural conditions. He also determined the frequency with which conception occurred in the different months of the year, and found that whereas the maximum number of first heats occurred in March and July, the optimum months for conception were May and September. This we believe is again the result of agricultural practice, for it is generally inadvisable to serve a lactating cow at the first heat for if this is done the milk production is decreased (see (14)).

Age of Puberty.

No experimental work has been undertaken on the age at which the first heat period occurs, but enquiries have been made from a number of experienced herdsmen who had exhibits at the London Dairy and Smithfield Shows (see Appendix I (1)) and from their replies it was evident that the age varied considerably with the breed and with the nutrition given, well fed animals coming on heat earlier than poorly fed ones. Both breed and feed are known to affect the rate of maturing of the animal generally and it is probable that the effect on the sex organs is secondary to that of general nutrition.

The average age of puberty for all breeds under normal conditions of feeding is about 9 months old, but it may vary from 5 to 15 months.

Craig (17) states that the average age is 12–18 months, but that heifers have taken the bull at 5–9 months old, while Ellenberger (18)

places the age at 9–12 months and Werner (19) and Hansen (20) at 6–9 months. Dechambre (21) and Curot (22) believe that heat first appears at 12 months old. Schmaltz (1) states that it varies considerably with the breed, Steppe cattle not becoming pregnant before the fourth year.

Eckles (23) from replies given by herd owners states the average age at first heat to be as follows: Jerseys, 8 months; Guernseys, 11 months; Friesians, 11 months; and Ayrshires, 13 months. He also obtained opinions as to the age at which breeders preferred their heifers to calve for the first time, which was as follows: Jerseys, 23 months; Guernseys, 26 months; Friesians, 27 months; and Ayrshires, 29 months. Experiments made by him showed that early calving checked the growth of the animal and that this occurred not during gestation but during lactation.

Experiments with rabbits (24) have shown that the age of puberty is influenced by the time of year at which the animal is born.

III

THE OESTROUS CYCLE

1. Periodicity and Rhythm.

It is known that all mammals (with few exceptions) exhibit a periodicity or rhythm in their times of "heat," the length of time between the "heat" periods—the oestrous cycle—varying with the species. In the majority of animals this is known only in a general way and few records of exact times exist. Investigations of the length of the cycle in the horse, cow, sheep and sow have been made but none to within the accuracy of a day.

The following Table III (*a*) shows the intervals between the commencement of successive oestrous periods in a number of cycles in heifers and cows to an accuracy of about an hour. The length of the normal oestrous cycle in the cow is on the average about 19½ days, but it has varied from 420 hours (17½ days) up to 576 hours (24 days).

The opinion of herdsmen (see Appendix I (2)) is that the length of the cycle may vary from 3–4 days up to 4–5 weeks but that animals with abnormally long or short periods are frequently sterile (see Sterility, p. 184). It was stated also that Jerseys have usually a rather longer period than Friesians and Devons, and two Jerseys which were slaughtered during the course of the experiment were found to have unusually large corpora lutea, but the length of their periods was not experimentally determined.

Küpfer(25) and Zietzschmann(26) both state that the average cycle in the cow lasts 21 days. Schmid(16) found that the variation of the cycle in cows may be much greater than the average 2–4 weeks, the limits of variation quoted by most authorities; the majority he observed had periods of 18–24 days (25·6 per cent. of cases). He found however a rather large number of cases over 24 days and some of these we believe were due to unobserved heat periods as well as to the persistent corpora lutea which he cites as being the main cause.

Struve(27) who observed 38 cows during 249 heat periods found that the time between two periods was rarely more than 28 days or less than 16 days, 80 per cent. of the cases falling between 17 and 23 days, 70 per cent. between 18 and 22 days, and 53 per cent. between 19 and 21 days. The limits of variation were between 8 and 30 days. He also

Table III (*a*). *Variation in the length of the oestrous cycle in the cow at different times of the year.*

Length of cycle in hours, calculated from the beginning of one "oestrus" to the beginning of the next.

	Animal														Individual average		
	No.	Age (by teeth) yrs.	mths.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	As hrs.	As days	and hrs
Heifers	C 1	2	3	?	—	—	—	—	—	—	—	—	502	502	? ?	502	20	22
2–3 yrs.	C 2	2	3	**420**	427	—	—	—	—	—	—	—	422	424	422, 424	**423**	**17**	**15**
old	C 3	2	0	462	—	—	—	—	—	—	—	—	442	456	455, 458	455	18	23
	C 4	2	0	—	—	—	432	470, 440	490, 436	506	—	—	—	—	—	462	19	6
	C 5	1	9	—	—	—	436	428, 458	438, 442	510	—	—	—	—	—	452	18	20
	C 6	2	3	—	—	—	424	412, 456	454, 424	420	—	—	—	—	—	445	18	13
	C 7	2	0	—	—	—	458	436, 474	462, 508	498	—	—	—	—	—	473	19	17
	P 5	2	6	—	—	—	—	—	—	—	—	—	508	**544**	—	**526**	**21**	**22**
	P 6	1	9	—	—	—	—	—	—	—	—	—	432	448	—	440	18	8
	P 7	2	3	—	—	—	—	—	—	—	—	—	464	464	—	464	19	8
	P 8	2	6	—	—	—	—	—	—	—	—	—	456	502	480	479	19	23
Average for heifers:				441	427	—	437	442	457	483	—	—	461	477	448	466	19	10
		About																
Cows	A 2	9	0	—	512	**576** (468)*	552	566	—	—	—	—	—	—	—	**551**	**22**	**23**
	A 3	6	0	—	432	**410** (538)†	422	516* (196)‡	—	—	—	—	—	—	—	**445**	**18**	**13**
	A 4	12	0	—	418	480 452	?§	?	—	—	—	—	—	—	—	450	18	18
	A 5	6	0	—	—	—	—	492, 430	(212)‡	—	—	—	—	—	—	461	19	5
Average for cows:				—	454	479	487	501	—	—	—	—	—	—	—	477	19	21

* Camphor. † Yohimbine. ‡ Corpus luteum squeezed out. § Tubercular. (Figures in parentheses excluded from averages.)

The figures in heavy type show maximum and minimum times.