ANALYSIS OF VARIATION IN THE SEXUAL CYCLE AND SOME OF ITS COMPONENT PHASES, WITH SPECIAL REFERENCE TO CATTLE[1]

By A. B. Chapman, *assistant in genetics*, and L. E. Casida,[2] *assistant professor of genetics, Wisconsin Agricultural Experiment Station*

INTRODUCTION

Normally there is a periodicity of the reproductive processes of female mammals, and this more or less regular recurrence of sexual phenomena is primarily under hormonic control. It has been shown that the rhythm of the ovarian processes can be disturbed experimentally. It has also been shown that some animals exhibit marked variation in the length of the cycle associated with concurrent physiological disturbances, both functional and pathological. But, in addition to these variations there is also considerable variation which has not been explained on the basis of the above factors.

An attempt has been made in this study of the sexual cycle and its component phases to isolate that part of their variation which is associated with determinable factors.

DATA STUDIED

The records on dairy cattle were taken by the herdsman (a university graduate) of the Pabst Farms, Oconomowoc, Wis. These cattle were Holstein-Friesians and were under uniform management and feeding conditions throughout the 10 successive years covered by these records. The records were kept with unusual accuracy, and the cattle were observed daily. Ovarian changes as shown by rectal palpation, the flow of blood or mucus from the vulva, infections, etc., were recorded. The records on the oestrous cycles of swine were taken, under the direction of Dr. F. F. McKenzie, at the Missouri Agricultural Experiment Station, by a trained investigator who recorded the lengths of the period in hours. In the test for oestrus a vasectomized boar was used. The published records utilized were, as far as possible, accurate records of normal individuals.

SEXUAL CYCLES

GENERAL VARIATION

Examination of the literature makes it evident that the scarcity of accurate records has left the general impression that the length of the sexual cycle is relatively invariable in normal individuals of most species. A study of the more accurate data shows to what a surprising degree this supposition is in error.

[1] Received for publication June 6, 1936; issued May, 1937. Paper from the Department of Genetics (no. 200), Wisconsin Agricultural Experiment Station. This work was supported in part by a grant from the Graduate School.

[2] The authors wish to express appreciation to Dr. L. J. Cole, at whose suggestion this work was initiated and carried out; to the management of the Pabst Farms for allowing free access to their records; and to Dr. F. F. McKenzie for the loan of the swine records of the Missouri Agricultural Experiment Station.

Journal of Agricultural Research, Washington, D. C.

Vol. 54, no. 6
Mar. 15, 1937
Key no. Wis.-81

Table 1 shows the frequency distribution of the oestrous cycles for the cattle. The same is shown in more detail in figure 1. The total frequency, the mode, the mean and its standard error,[3] and the standard deviation are given in the table.

TABLE 1.—*Oestrous-cycle lengths in clinically normal cattle* [1]

Length (days)	Number	Percentage of total
4–16	34	4.9
17–27	416	60.3
28–33	34	4.9
34 or more	206	29.9
Total	690	100.0

[1] Summary: Total cycles, 690; mode, 21; mean, 32.1±0.8; standard deviation, 20.5. Cycles within the 4- to 33-day range, 484; mode, 21; mean, 21.4±0.2; standard deviation, 4.4.

The distribution of the oestrous-cycle lengths of the clinically normal cattle (as defined below) shows a much wider variation than has been reported before, but the distribution is quite similar in form to that of other data within the range of variation given by other authors.

The variation in the intervals between heats which may be attributed to careless observations is slight. Extremely short and "silent" heat periods are probably responsible for what might be termed "observational error." The multimodality is, in all probability, largely due to these two factors, i. e., failure in observing oestrus when of very short duration or of subthreshold expression.

Table 2 presents the statistics of sexual-cycle lengths of several other species. It is to be noted that the oestrous cycles of cattle used in this study showed significantly greater variation than the sexual cycles observed in other species.

TABLE 2.—*Statistics of sexual-cycle length of species other than cattle* [1]

Species	Reference	Cycles	Mode	Mean	Standard deviation
		Number	*Days*	*Days*	*Days*
Sheep	(*12*) [2]	65	16	16.57±0.10	0.77
Do	(*41*)	590	16	16.58± .03	.72
Do	(*34*)	226	17	17.04± .05	.74
Swine	([3])	66	21	21.36± .22	1.77
Do	(*20*)	71	21	20.99± .30	2.54
Horse	(*35*)	594	21	22.79± .12	4.44
Man	(*3, 11, 17, 18, 19, 21, 33*)	2,323	27	27.94± .10	4.73
Baboon	(*46*)	72		31.40± .62	5.24
Monkey	(*8, 15*)	623	28	28.34± .27	6.72

[1] Most of these statistics and those of other tables were calculated from the original data as reported by the investigators referred to.
[2] Reference is made by number (italic) to Literature Cited, p. 433.
[3] McKenzie, F. F. Unpublished data on swine at the Missouri Agricultural Experiment Station.

CLINICAL ABNORMALITY

Deviation from the generally accepted length of the sexual cycle is commonly thought to be associated with definite abnormalities, functional or pathological. As a rule, these associated conditions are discussed in general terms, and the limits of the variations in the cycle

[3] The standard error, rather than the probable error, is reported in all cases.

length indicative of them are not specified. It is well known that cystic follicles and persistent corpora lutea are common causes of markedly disturbed periodicity in the sexual cycle.

In order to determine whether variability in cycle length is associated with subsequent clinical abnormality, the records of the cattle were divided, on the basis of the herdsman's observations, into two groups, "clinically normal" and "clinically abnormal." The former included those showing no cystic follicles, retained corpora lutea, or other deviations from the normal; the latter, those which had a record of cystic follicles or persistent corpora lutea in at least one calving interval, but were normal in other respects. The oestrous cycles in both these groups were again divided into two classes; one, "noncopulatory", in which the oestrous cycles were not preceded by service; the other, "copulatory", in which at the beginning of the cycle there was a potentially fertile service (infertile mating with a male of good general fertility).

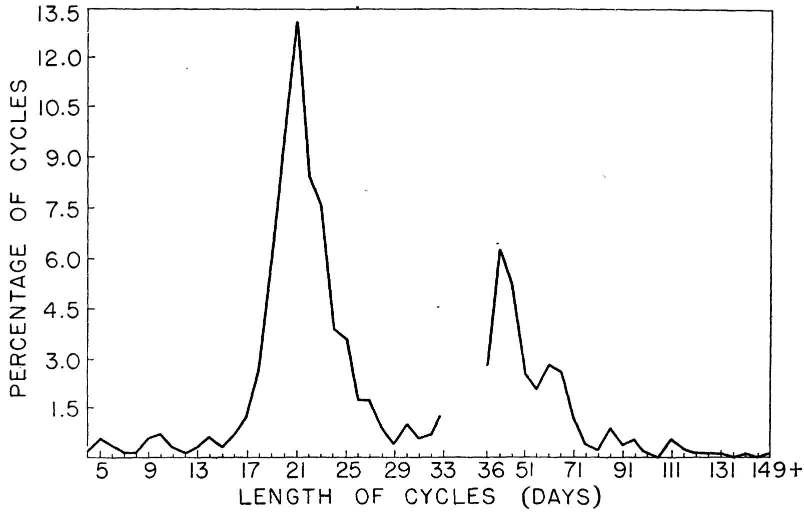

FIGURE 1.—Frequency polygon showing variation in length of the oestrous cycle in clinically normal cattle. The 4- to 33-day range is plotted by 1-day intervals; thereafter the points are plotted on the midpoints of 5-day classes.

The cycles in the calving intervals prior to the occurrence of clinical abnormality, in cows which eventually become at least temporarily abnormal, were analyzed for indications of abnormality which they might show. Cycles reported as less than 4 days in length are possibly due to continuous oestrus and are therefore omitted. Those of more than 33 days are thrown into one class (table 3) as being abnormally long on the basis of the normal distribution curve and not likely to yield more information by finer classification. This class is probably in large part due to those factors mentioned above as "observational errors." Of the remainder (those of 4 to 33 days), the distribution curve shows the range of greatest concentration to be from 17 to 27 days. This range includes 62.2 percent of all cycles and 86.8 percent of the cycles less than 34 days in length.

TABLE 3.—*Comparison of noncopulatory oestrous cycles of clinically normal and clinically abnormal cattle* [1]

Length of cycles (days)	Clinically normal		Preceding clinical abnormality	
	Number	*Percent*	*Number*	*Percent*
4–16	28	6.0	12	11.3
17–27	289	62.2	43	40.6
28–33	16	3.4	7	6.6
34 or more	132	28.4	44	41.5
Total	465	100.0	106	100.00

[1] Summary: Total cycles, χ^2, 877.68; *P*, <0.01. Cycles within the 4- to 33-day range, χ^2, 10.01; *P*, <0.01.

The test of the difference between the early cycles of cows which became cystic or had retained corpora lutea in later calving intervals, and those of cows which were clinically normal throughout life, was made by means of the χ^2 test of independence as given by Fisher (*10*). In this case (for the range 4–33 days) the difference between the means is not statistically significant[4], but the differences between the distributions tested by χ^2 are highly significant. The reason for the nonsignificant mean difference is that the cycle lengths in the calving intervals preceding the clinical abnormality are concentrated at the two extremes, thus balancing each other, to the extent of making the mean of this group almost identical with the mean of the clinically normal group.

Among the clinically abnormal cows there were 10 which had 5 or more noncopulatory cycles preceding the calving interval in which the abnormality occurred. None of the 10 had as many as 62 percent of these cycles in the 17- to 27-day range, whereas 52 percent of 42 normal cows had at least 62 percent of their 5 or more cycles lying in a similar range.

These facts suggest that extreme variation in the length of the oestrous cycles of a cow is an indication of ovarian abnormality. Presumably, there is disturbed periodicity in the ovarian rhythm before the derangements can be recognized by means of rectal palpation of the ovaries. Irregularity in cycle length may therefore be taken as warning of impending breeding difficulty.

INFERTILE SERVICE

The marked effect of service (copulation) on ovarian behavior is well known in certain animals. In the ferret, cat, and rabbit it serves as a stimulus to ovulation. Furthermore, in those animals, as well as in the rat and mouse, an infertile copulation is succeeded by pseudopregnancy.

The present data afford opportunity for the study of the effect of unsuccessful service by a presumably fertile bull on the length of the oestrous cycle (table 4). Only clinically normal cows were used in testing the significance of the difference between the noncopulatory and copulatory oestrous cycles. Over the entire range and even over the restricted range (4–33 days) the copulatory cycles are significantly longer, on an average, than the noncopulatory. Similarly, the χ^2 test

[4] The word "significant" is used throughout in a statistical sense. If differences of the size given would occur less than 5 percent of the time by chance alone they are arbitrarily considered significant; if less than 1 percent of the time, highly significant.

based either on the tabular classification or on the reduced range points to a highly significant difference between the two distributions. Hammond's data (*13*) do not show increased cycle length when the cycle is preceded by mating with a vasectomized bull. In McKenzie's swine data [5] 8 cycles preceded by service with a potentially fertile male were significantly longer and more variable than the 45 cycles preceded by service with a vasectomized male (mean difference 4.43±1.77 days.) Similar observations on sheep were reported by Terrill (*41*).

TABLE 4.—*Comparison of copulatory and noncopulatory oestrous cycles in clinically normal cattle* [1]

Length of cycle (days)	Noncopulatory		Copulatory	
	Number	*Percent*	*Number*	*Percent*
4–16	28	6.0	6	2.7
17–27	289	62.2	127	56.4
28–33	16	3.4	18	8.0
34 or more	132	28.4	74	32.9
Total	465	100.0	225	100.0

[1] Summary: Total cycles, mean for noncopulatory 30.8±0.9 and for copulatory 34.9±1.5, the mean difference being 4.1±1.8, P being 0.02, χ^2 being 11.5, and $P<0.01$. Cycles within the 4- to 33-day range, mean for noncopulatory 21.2±0.2 and for copulatory 22.1±0.4, the mean difference being 0.9±0.4, P being 0.04, χ^2 being 10.3, and $P<0.01$.

These records on cattle, sheep, and swine point to greater average length of copulatory cycles (cycles preceded by potentially fertile mating) as compared with cycles following definitely sterile service (mating with a vasectomized male) or no mating at all. These differences must be ascribed to a temporary reproductive disturbance at the time of, or subsequent to, service. Such disturbance might result in failure either in fertilization or implantation or in early resorption of the embryo. Without more evidence than is at present available it is not possible to decide which of the alternatives is correct.

INDIVIDUALITY

Some investigators have pointed to the marked individual regularity of the sexual cycles; others have stressed their distinct irregularity, but no one has given a definite measure of this individual "repeatability" tendency. By analysis of variance a definite measure of the repetition of characteristic sexual cycle lengths per individual can be made. Only clinically normal cows are considered in the following discussion, and copulatory and noncopulatory cycles are treated separately.

In the first two analyses given in table 5 the entire and 4- to 33-day ranges of noncopulatory oestrous-cycle lengths of the cows were used. These wide distributions do not show any significantly inherent periodicity of oestrus. When, however, the central class (17–27 days) of cycles is analyzed it is found that, on an average, each animal has a very definite individuality in cycle length. The noncopulatory cycles show a modified squared correlation ratio [6] (η^2) of 0.41 for the restricted range (17–27 days). This figure indicates that 41 percent of the observed variance would disappear if all the oestrous cycles were those of one individual rather than many individuals; in other

[5] MCKENZIE, F. F. Unpublished data on swine at the Missouri Agricultural Experiment Station.

[6] This constant differs from the more commonly known correlation ratio in that it allows for the loss of degrees of freedom incurred by dividing the data into arrays and calculating the variations within each such array.

words, if "individual" is "held constant", the total mean square (4.4) is reduced 41 percent (to 2.6). This "repeatability" tendency is masked by more influential factors when the range is not restricted to this class of greatest concentration of cycle lengths. Unidentified abnormality and observational error are probably the main factors in this masking effect.

TABLE 5.—*Analysis of variance in oestrous-cycle lengths clinically normal cattle*

Type of cycle	Range	Source of variation	Degrees of freedom	Sum of squares	Mean square	*P*	η^2
	Days						
Noncopulatory	(1)	Individual	73	29,817	408.4	>0.05	0.02
		Remainder	391	138,739	354.8		
		Total	464	168,556	363.3		
	4–33	Individual	65	1,412	21.7	>0.5	.02
		Remainder	262	5,084	19.4		
		Total	327	6,496	19.9		
	17–27	Individual	60	648	10.8	<.01	.41
		Remainder	216	557	2.6		
		Total	276	1,205	4.4		
Copulatory	17–27	Individual	26	194	7.5	<.01	.19
		Remainder	70	277	4.0		
		Total	96	471	4.9		

1 Entire.

TABLE 6.—*Individuality of sexual-cycle length in cattle, sheep, swine, horse, monkey, baboon, and man*

Species	Reference	Range	Cycles	Individuals	*P*	η^2
		Days	*Number*	*Number*		
Cattle	(*13*)	(1)	59	15	<0.01	0.58
Sheep	(*34*)	(1)	226	24	<.01	.20
Do	(*12*)	(1)	62	14	>.05	.09
Swine	(2)	(1)	36	15	≐.04	.37
Horse	(*35*)	(1)	38	10	≐.02	.28
Monkey	(*6*)	<50	109	10	(3) ≐.01	------
Do	(*15*)	<50	514	32	<.01	.06
Baboon	(*46*)	(1)	71	9	>.05	.10
Man	(*3, 11, 17, 18, 19*)	(1)	1,493	88	<.01	.03
Do	(*3, 11, 17, 18, 19*)	19–36	1,406	86	<.01	.43

1 Entire.
2 McKenzie, F. F. See footnote 5, p. 421.
3 In this group there is greater similarity between the mean cycle lengths of different individuals than between cycle lengths of a single individual. These are cycles of young postpuberal monkeys, which, as is pointed out later, are known to have more variable cycle lengths than mature individuals.

Table 6 summarizes the results obtained by a similar analysis of published records for a number of species. Hammond's records of heifers, (*13*), reported to the accuracy of an hour and with a range of 17½ to 24 days, give additional evidence of inherency of oestrous periodicity in cattle. The analysis of Quinlan and Maré's (*34*) and Grant's (*12*) records for sheep, the Missouri records for swine, and Satô and Hoshi's (*35*) for horses, brings out the same tendency in these species. Likewise in the menstrual cycles of man, monkey, and baboon there is distinct evidence of individuality. Detailed analyses of these are given by Chapman.[7]

7 For detailed tables of all the data discussed in this paper, reference is made to the following: Chapman, A. B. Analysis of variation in the sexual cycle and some of its component phases Unpublished manuscript on file in the Univ. Wis. library.

This measure of individuality of sexual cycles includes, in addition to the genetic, all other effects on the cycles of an individual which tend to make them more similar to each other than to the cycles of other individuals. It is impossible to say definitely how much of the variation in the sexual-cycle lengths is a permanent or genetic characteristic and how much is due to uniformity of other influences acting on the individual.

AGE

Long and Evans (*24*) and Parkes (*31*) have shown that the earlier cycles of the rat and mouse are longer than those of the more mature animal, whereas Stockard and Papanicolaou (*38*) state that the length of the cycle in guinea pigs tends to increase with age. Hammond (*13*) reports an indication of increased cycle length with age (as judged by the teeth) in cows. Krallinger (*20*) points out a similar relationship in swine. McKenzie and Phillips (*26*), Grant (*12*), and Terrill (*41*) state that no age effect was noticeable in sheep. Satô and Hoshi (*35*) made similar observations on horses. Engle and Shelesnyak (*9*), reporting on the length of the menstrual cycle in man, and Corner (*6*) and Hartman (*15*), on that in monkeys, point to a decrease in variability as menstrual life increases.

In order to study the association between age and cycle length in cattle, the noncopulatory oestrous cycles, i. e., those not preceded by service, were arrayed by calving interval and analyzed for calving interval effect within the restricted range. All calving intervals over the fifth were classed in one group. There was a definite increase in the means from the first to the sixth-and-over calving interval (table 7). This age trend was shown to be significant by analysis of variance. Likewise, comparison of the heifers and cows reported by Hammond indicates an increase in the length of cycle with increasing age, though his numbers are insufficient to establish a significant difference. Five percent of the variance in both sets of data is associated with calving interval or age variation.

TABLE 7.—*Association between age and length of non-copulatory oestrous cycles in clinically normal cattle* (*17 to 27-day range*)

Calving interval no.	Cycles	Mean length of cycles	Standard deviation	Calving interval no.	Cycles	Mean length of cycles	Standard deviation
	Number	*Days*	*Days*		*Number*	*Days*	*Days*
1	22	20.4	2.1	5	13	22.4	2.2
2	103	21.6	2.1	6 and over	39	22.7	2.1
3	57	21.6	2.0				
4	26	21.9	2.1	Total or average	260	21.7	2.1

The standard deviation of the oestrous-cycle lengths for each calving interval is given in table 7. It is obvious that there is no significant change in variability associated with age changes on the basis of this classification. Comparison of the oestrous cycles in the first two calving intervals with those in all other calving intervals does not show any significant differences between the standard deviations in the two groups, regardless of the ranges used.

In the swine data no difference in mean or variation associated with age was found.

The records for man, summarized in table 8, show a highly significant inverse correlation between age and cycle length and also a significant decrease in variation with increasing age.

TABLE 8.—*Correlation between length of menstrual cycle, variation of cycle, and age of individual in man* (*11, 17, 18, 19, 21*)

Age (years)	Cycles	Mean length of cycles	Standard deviation
	Number	*Days*	*Days*
17–20	344	28.9±0.42	7.8
21–30	658	28.0± .16	4.0
31–45	408	27.5± .14	2.8
Total or average	1,410	28.1± .13	5.0

SEASON

The restricted breeding season of many animals and the seasonal variation in fertility of others which breed throughout the year testify to the important role that season often plays in reproductive processes.

Ovarian periodicity, insofar as it is marked by oestrus, is one of the functions which is often temporarily suspended at certain times of the year. Less noticeable seasonal effects than complete inhibition also occur. Lee (*22*) has shown that cold tends to lengthen the oestrous cycle of rats. Similarly, in the guinea pig, Stockard and Papanicolaou (*38*) found a slightly longer cycle in winter. Duncan (*8*) states that the menstrual cycle of women in Lapland and Greenland is longer than in hot countries, and Wallace (*42*) gives figures to show that oestrus recurs at shorter intervals in summer than in winter in cows. According to Marshall (*27*) the length of the dioestrous cycle in sheep is reduced when they are taken from highland to lowland. Satô and Hoshi (*35*) point to a gradual shortening of the oestrous cycle in the horse from March to July.

The observations of other authors differ from the above reports of longer cycles in colder weather. Hammond (*13*) reports a longer oestrous cycle in the middle of summer than in winter or spring in cows; Engle and Shelesnyak (*9*) state that long menstrual intervals in puberal girls are most frequently initiated in July, that a low percentage of menarches and a high percentage of temporary amenorrheas occur during the summer months; and Hartman (*15*) records inhibition of ovulation, greater irregularity of menstrual cycles, and increase in amenorrhea in the summer in monkeys.

Analysis of the copulatory and noncopulatory oestrous cycles in the dairy cattle data showed no variation that could be attributed to seasonal changes, regardless of the range considered. Hammond's records, although indicative of longer cycles for the heifers from June to November, do not show a statistically significant effect of season.

In Quinlan and Maré's sheep records (*34*) no evidence of seasonal change is found in the oestrous cycle variation. In Grant's data (*12*), as noted by him, there is, however, a distinct trend to longer oestrous cycles as the breeding season advances. This increase from month to month accounts for 37 percent of the variation in the oestrous cycle length of this group of sheep.

PERIOD FROM PARTURITION TO FIRST SUBSEQUENT OESTRUS

GENERAL VARIATION

Rabbits, rats, guinea pigs, and mice usually come into oestrus a few hours post partum. Rats and mice, however, do not resume the periodicity of oestrus when suckling a normal sized litter. The mare has been reported by Satô and Hoshi (*35*) as coming in heat 3 to 100 days after parturition, but 92 percent of the cases fell between the limits of 5 and 12 days, and shorter intervals occurred in older animals. The sow is reported by Struve (*40*) to come in heat 4 to 9 days post partum. Marshall (*28*), however, believes that 5 weeks is the most frequent interval. Quinlan and Maré's records (*34*) for merino sheep give the time of ovulation as from 10 to 15 days post partum, but they state that heat is expressed at this time only when the ewe is not suckling a lamb. Weber (*43*) gives 3 to 7 weeks for this period in the cow. Hammond (*13*) states the opinion of stockmen to be that 3 to

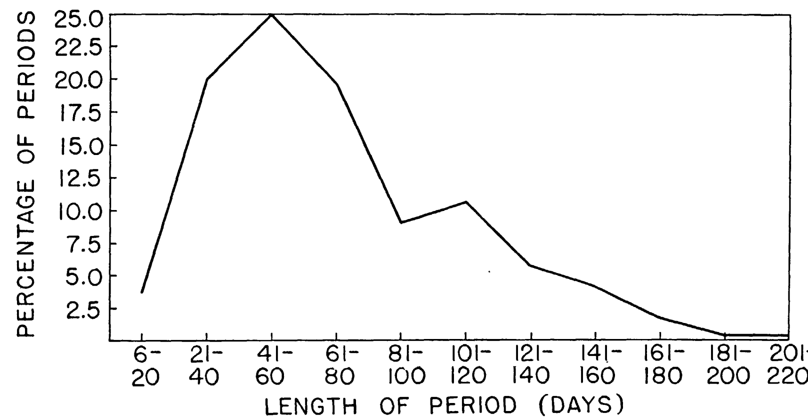

FIGURE 2.—Frequency polygon showing variation in length of period from parturition to first succeeding oestrus in clinically normal cattle

4 weeks is the usual time if the cow is milked, and about 3 months if the calf is suckled. The range given by stockmen was 9 days to 6 months.

The opinion of stockmen, insofar as the range is concerned, is closely paralleled by the records for the clinically normal cattle of the Wisconsin herd, considering only those post-partum intervals preceded by normal gestation periods (nonabortive). The distribution of the different lengths of the period from parturition to the first subsequent oestrus is given in table 9 and figure 2.

The skewness of this distribution needs no explanation further than that already given in connection with the distribution of oestrous cycles. That there is a need for close observation of the oestrous periods following parturition is apparent from the practical standpoint of having cows calve at least every 12 or 13 months. To accomplish this involves fertile service before 115 days following parturition.

CLINICAL ABNORMALITY

In the calving intervals preceding the ones in which cystic follicles or retained corpora lutea were noted, the period from parturition to first oestrus (preceded by normal gestation) was not significantly different from the length of this period in the calving intervals following the ovarian disturbance, and neither of these figures differed significantly from that for the clinically normal animals (table 9). The variations within this period in calving intervals prior to the ensuing abnormality do not, therefore, foretell the subsequent disturbance, nor do the ones following the disturbance show the effects of it.

TABLE 9.—*Frequency distribution of the periods from parturition to first subsequent oestrus in normal and abnormal cattle*

Length of period (days)	Periods of clinically normal cows		Periods of clinically abnormal cows [1]		All periods	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1–20	8	4.5	1	2	9	3.7
21–40	33	18.4	16	25	49	20.1
41–60	50	27.9	11	17	61	25.0
61–80	32	17.9	15	23	47	19.3
81–100	15	8.4	7	11	22	9.0
101–120	20	11.2	6	9	26	10.7
121–140	11	6.1	3	5	14	5.7
141–160	6	3.4	4	6	10	4.1
161–180	2	1.1	2	3	4	1.6
181–200	1	.6	0	0	1	.4
201–220	1	.6	0	0	1	.4
Total	179		65		244	
	Days		*Days*		*Days*	
Mean length of periods	69.3±2.9		71.4±4.9		69.9±2.5	

[1] Preceding and following calving interval of abnormality.

INDIVIDUALITY

The gross variation of the periods from parturition to first subsequent oestrus, in calving intervals preceded by nonabortive gestations and of clinically normal cows, was divided into that between cows and that between calving intervals of the same cow. Within a fairly wide range of variation a cow tends to repeat a similar length of parturition to first subsequent oestrus in different calving intervals.

TABLE 10.—*Analysis of variance in period from parturition to first subsequent oestrus in clinically normal cattle*

Range (days)	Source of variation	Degrees of freedom	Sum of squares	Mean square	*P*	η^2
Entire	Individual	44	102,703	2,334.2	<0.01	0.19
	Remainder	118	146,574	1,242.2		
	Total	162	249,277	1,538.7		
<86	Individual	35	18,874	539.3	≐.04	.16
	Remainder	73	24,563	336.5		
	Total	108	43,437	402.2		
Entire	Season	5	3,829	765.8	>.05	
	Remainder	183	264,141	1,443.4		
	Total	188	267,970	1,425.4		
<86	Season	5	5,903	1,180.6	<.01	.08
	Remainder	129	46,592	361.2		
	Total	134	52,495	391.8		

About the same proportional amount of variation is associated with individuality in the entire range as in the restricted range of less than 86 days (table 10). This repeatability tendency means that the breeding efficiency of a cow is inherently lowered when this period in her reproductive cycle is so long that she cannot conceive in the required time following parturition.

SEASON

In the mare Satô and Hoshi (*35*) noted a tendency to shorter intervals from parturition to first subsequent oestrus as the season advanced from March to June.

The entire range of periods for clinically normal cows does not show any variation which can be attributed to seasonal changes, on the basis of a bimonthly classification, beginning with January. When, however, only those less than 86 days in length are considered, season is found to account for 8 percent of the variation (table 10). In the more typical cases, there is a definite tendency for the period from parturition to the first subsequent oestrus to be longer in the spring (March–April, May–June) than in other seasons of the year.

COMPONENT PHASES OF THE SEXUAL CYCLE

If the variation in length of the component phases of the sexual cycle can be attributed to determinable causes, additional evidence is given as to the type of association between ovarian, pituitary, etc., processes and the external and internal influences studied.

GENERAL VARIATION

The duration of oestrus was not recorded in the cattle upon which the first two sections of this report were largely based. It is therefore necessary to rely on published records for the raw material of this analysis of the component phases of the sexual cycle of the several species, except in the case of swine. Table 11 presents the statistics on the oestrous period, menstrual period, preovulatory (follicular) phase, and postovulatory (luteal) phase, based on the available data.

TABLE 11.—*Statistics of component phases of the sexual cycle*

Species	Reference	Phase	Number	Mean	Standard deviation
				Hours	*Hours*
Cattle	(*13*)	Oestrous period	54	16. 2±0. 7	5. 2
Sheep	(*12*)	do	77	36. 2±2. 0	17. 1
Do	(*34*)	do	59	43. 9±1. 8	14. 5
Do	(*41*)	do	884	30. 4±0. 4	10. 4
Swine	(1)	do	107	51. ±1. 6	16. 2
				Days	*Days*
Horse	(*35*)	do	1, 179	7. 5±. 1	2. 5
Monkey	(*6*)	Menstrual period	132	5. 4±. 2	1. 8
Man	(*17*), (*11*)	do	1, 024	4. 7±. 1	1. 1
Monkey	(*16*)	Preovulatory	53	11. 8±. 3	2. 0
Baboon	(*46*)	do	48	17. 1±. 5	3. 3
Monkey	(*16*)	Postovulatory	53	13. 5±. 5	3. 5
Baboon	(*46*)	do	48	15. 1±. 4	2. 6

1 McKENZIE, F. F. See footnote 5, p. 421.

There is inconsistency in the results of the experimental work on the causation of oestrus. There is, likewise, no complete agreement as to the time relation between oestrus and ovulation, though it would seem from the work of Aitken (*1*) and Seaborn (*36*) on the mare, Lewis (*23*), and Corner and Amsbaugh (*7*) on the sow, Allen (*2*) on the mouse, Long and Evans (*24*) on the rat, Young et al. (*44*) on the guinea pig, Hammond (*13*), Pearl (*32*), Strodthoff (*39*), Murphey et al. (*29*) on the cow, McKenzie and Phillips (*26*), Quinlan and Maré (*34*) and Terrill (*41*) on the sheep, that, if ovulation occurs, it does so toward the end of or shortly after the termination of oestrus. It has, however, been demonstrated that oestrus sometimes occurs without ovulation and that ovulation may occur without observable oestrus.

In addition to the figures on oestrus given in table 11, Aitken (*1*) gives 4 to 11 days; and Hammond (*14*) 3 to 41 days, as the normal variation of oestrus in the mare, the average being approximately 7 days; Weber's figures (*43*) show a variation from 3 to 36 hours for cows; McKenzie (*25*) noted 1 to 3 days, and Struve (*40*) 2 to 4 days as the length of the oestrous period in sows. McKenzie and Phillips (*26*) give the average duration of oestrus in sheep as 26.8 hours, with a range of 5 to 50 hours.

The period of oestrus is poorly defined or is not expressed at all in the primates, whereas the uterine hemorrhage does, as a rule, sharply demarcate a sexual cycle. The general relationship between the ovarian processes and the menstrual flow has been outlined by many investigators, but there is not as yet complete agreement as to the specific causation of menstruation.

The recovery of tubal ova by Corner (*5*) in the monkey, and by Allen et al. (*4*) in man, the more recent work of rectal palpation of the monkey by Hartman (*16*), the physiological test of Knaus (*19*), and other observations, all point to the middle of the menstrual cycle as the usual time of ovulation. Hartman (*15*) and Corner (*6*), however, have records of frequent menstruation without ovulation in the monkey. But insofar as the menstrual periods are correlated with the ovarian cycle they are of just as much value as end points in a study of its periodicity as are the oestrous periods.

Analysis of the variation in the oestrous and menstrual cycles as a unit will not explain fully the mode of action of the associated variables. Where these variables localize, their activity can be learned more readily by analysis of the associated variation in restricted phases (follicular and luteal) of the cycle. The luteal phase is given as the time from ovulation to the beginning of menstruation; the follicular phase, from the beginning of menstruation to ovulation. These phases have been carefully recorded by Hartman (*16*) for the monkey, and by Zuckerman and Parkes (*46*) for the baboon. The general variation of the two phases of the sexual cycle for these species is shown in table 11.

Ogino (*30*) and Knaus (*19*) have stressed invariability of the luteal phase of the cycle in women and rabbits. The reports of Hartman, and Zuckerman and Parkes do not corroborate these conclusions for the monkey and baboon. They find both the luteal and follicular phases of the cycle quite variable. Hartman's records show a significantly longer (mean difference$=1.7\pm0.55$), as well as a significantly more variable (σ difference$=1.5\pm0.39$), postovulatory than preovulatory period. Zuckerman and Parkes' data on the baboon show a significantly longer (mean difference$=2.0\pm0.60$) follicular than luteal phase, and a slightly, but not significantly, greater variability (σ difference$=0.7\pm0.42$) for the follicular period.

INDIVIDUALITY

Individuality, as previously defined, is just as evident in the oestrous period of the four species studied as it is in the oestrous cycle (table 12). Likewise, the menstrual period in man and, to a lesser degree, in monkeys is found to be repeatable. On the basis of these data, individuality of the preovulatory phase of the cycle in monkeys and baboons cannot be established; there is, however, a slight indication of repeatability of this phase in the baboon. In the postovulatory period of the monkey, marked individuality is apparent. Forty-nine percent of the variation in this period is attributable to differences between individuals. In the baboon the differences between the intervariance and intravariances are again too small to be taken as more than the fluctuations of random sampling.

TABLE 12.—*Analysis of variance in component phases of sexual cycle*

Species	Reference	Phase	Grouping	Phases	Groups	*P*	η^2
				Number	*Number*		
Cattle [1]	(*13*)	Oestrous period	Individual	43	8	<0.01	0.44
Sheep	(*12*)	do	do	82	17	<.01	.34
Do	(*34*)	do	do	18	9	>.05	.45
Swine [2]	([3])	do	do	63	23	<.01	.50
Horse	(*35*)	do	do	50	11	<.01	.62
Man	(*17*)	Menstrual period	do	201	11	<.01	.63
Monkey	(*15*)	do	do	514	32	<.01	.17
Do	(*6*)	do	do	109	10	≐.05	.07
Do	(*16*)	Preovulatory	do	37	13	>.05	------
Baboon	(*46*)	do	do	47	9	≐.05	.20
Monkey	(*16*)	Postovulatory	do	37	13	<.01	.49
Baboon	(*46*)	do	do	47	9	>.05	.10
Cattle	(*13*)	Oestrous period	Age	54	2	≐.02	.10
Swine	([3])	do	do	107	2	<.01	.58
Cattle [1]	(*13*)	do	Season	41	4	>.05	.09
Sheep	(*12*)	do	do	82	6	>.05	------

[1] Heifers.
[2] Gilts.
[3] McKENZIE, F. F. See footnote 5, p. 421.

AGE

McKenzie and Phillips (*26*) report a significantly longer oestrous period in yearling and in older ewes than in ewe lambs, and this has been confirmed by Terrill (*41*). Grant (*12*), on the other hand, found no correlation between age and duration of oestrus in sheep; neither did Satô and Hoshi (*35*) in horses. Hammond's records (*13*) point to a slightly longer period in cows than in heifers, and analysis of his records shows this to be significant. But there is strong probability of this being due to individuality. The sows had significantly longer and more variable periods than the gilts (table 12).

SEASON

Temporary suspension of oestrus occurs in various breeds of sheep during certain seasons of the year. Fluctuations in fertility in swine, cattle, horses, goats, etc., have been noted in correlation with seasonal changes.

Because of the small numbers with which we are dealing, it is not possible to establish whether there is a seasonal influence on duration of oestrus in either the heifers reported by Hammond or the sheep reported by Grant, although Hammond's figures give some indication of a longer period for the summer than for the winter. In the records of Satô and Hoshi on the mare a consistent decrease was noted in the length of the oestrous period from March to July.

CORRELATIONS WITH SEXUAL CYCLE

Hammond found that experimental removal of the corpus luteum in the cow 6 or 7 days following oestrus not only shortened the cycle length, but also resulted in an abbreviated oestrous period. Marshall (*27*) found that in sheep the duration of oestrus and the length of the oestrous cycle are both curtailed when the sheep are brought from the highlands to the lowlands.

Hammond (*13*) noticed a general association between the cycle length and the duration of the immediately subsequent oestrus in his records but did not give an exact measure of it. Calculation of his data gives a highly significant positive correlation coefficient for oestrous cycle and subsequent oestrous period (table 13). The figures for sheep do not show any correlation of significance for a cycle either with its component oestrous period or with its immediately subsequent oestrous period, as pointed out by Grant (*12*). The swine data do not give evidence of any associations between the duration of these periods and cycle lengths.

TABLE 13.—*Correlation of sexual-cycle lengths with various component phases*

Species	Reference	Phase	Correlation calculated	Phases	Individuals	r	P
				Number	*Number*		
Cattle	(*13*)	Subsequent oestrus	Over all cycles of all individuals.	52	11	0.36	<0.01
Sheep	(*12*)	do	do	62	17	−.21	>.05
Swine	([1])	do	do	58	43	.06	>.05
Sheep	(*12*)	Component oestrus	do	65	17	.08	>.05
Swine	([1])	do	do	66	45	.03	>.05
Monkey	(*6*)	Component menstrual period.	Between individuals	109	10	.39	>.05
	(*6*)	do	Within individuals	109	10	.07	>.05
	(*6*)	do	Over all cycles of all individuals.	109	10	.09	>.05
	(*15*)	do	Between individuals	514	32	.49	<.01
	(*15*)	do	Within individuals	514	32	.08	>.05
	(*15*)	do	Over all cycles of all individuals.	514	32	.15	<.01
	(*16*)	Preovulatory	do	53	26	.28	$\doteq$.05
	(*16*)	Postovulatory	do	53	26	.84	<.01
Baboon	(*46*)	Preovulatory	do	48	10	.76	<.01
	(*46*)	Postovulatory	do	48	10	.56	<.01

[1] MCKENZIE, F. F. See footnote 5, p. 421.

Fluhmann (*11*), reporting menstrual cycles in women, divided his subjects on the basis of cycle variation into a "regular" and "irregular" group, and on the basis of cycle length into three subgroups within each of these. The analysis of the variation in duration of the menstrual period within and between the cycle-length classes gives a measure of the degree of correlation between the duration of the menstrual period and menstrual cycle length, at least so far as the average figures of a group of individuals are concerned. The association is found to be highly significant, but to account for only a small amount (7 percent) of the variation. The regular cycle group has a significantly longer menstrual period than the irregular group. The standard deviations of the menstrual periods of the two groups differ significantly, thereby showing that variability in menstrual cycle and menstrual period are correlated. This correlation is positive.

Covariation between menstrual cycle and menstrual period could be more completely studied in Corner's and Hartman's records, because of the detailed protocols given in these papers. The size of the sample in one case (Corner) did not permit of decisive conclusions, but its similarity with the other sample (Hartman) of the monkey population can be seen in table 13.

The correlation coefficient ($r=0.15$) worked out for the 514 cycles and their component menstrual periods proves to be highly significant. Further analysis establishes the fact that this positive association is due to a correlation between the averages of these two variables per individual and not to any association between cycle length and its component period within each individual's lifetime. In other words, on an average, each individual has a typical cycle length which varies within small limits; similarly, each individual has a typical period duration which varies within small limits. These "cycle-length" and "period-duration" variations are not correlated within each individual's records; but the typical (or average) period of an individual and the average cycle tend to vary together. The degree of association is given by the regression coefficient (0.96) of cycle on its component period. In this case there is, on an average, approximately 1 day's increase in cycle length for every day's increase in period duration when applied to the means of the individuals' records.

The correlation between the length of the follicular (preovulatory) phase and the entire cycle for the monkey is small, but on the margin of statistical significance, while the correlation between the luteal phase and the cycle is large, very highly significant, and differs significantly from the other correlation. In the baboon the correlations are both significant, but not significantly different from each other. These correlations seem to be quite in accord with the other results found for the cycle and these two phases, that is, the high repeatability of both the cycle and postovulatory period, the lack of repetition of the preovulatory in the monkey, and the indications of repetition in the cycle and the luteal and follicular phases of the baboon.

SUMMARY

An attempt has been made to analyze the variations in the different phases of the reproductive cycle in such a way that their association with other recorded variables may be recognized.

Extreme variations in the lengths of the oestrous cycle of cattle not only indicate disturbances such as the presence of cystic follicles and retained corpora lutea but also serve as a warning of their occurrence in later calving intervals in those animals which are not known to be clinically abnormal at the time of these extreme cycle-length variations.

Potentially fertile matings are, on an average, followed by longer oestrous cycles in cattle, swine, and sheep than are services with a vasectomized male or no mating at all.

The differences between individuals in cattle, sheep, swine, and horses in the length of oestrous cycles, and in man, monkeys, and baboons in length of menstrual cycles, are the source of significantly

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more variation than the differences between the cycles of each individual except in immature monkeys, in which the variations of the cycle lengths of each individual are more marked than the variations in cycle lengths between individuals.

Slight increase in mean cycle length, but not in variation, is found with increasing age in cattle. No average cycle-length trends are apparent with increasing age in sheep, swine, horses, or monkeys. In man, however, there is a definite decrease in average cycle length and variation as menstrual life increases. The latter association, between variability of menstrual cycle and age, is also noted in monkeys.

No seasonal effects are evident in the cycle lengths of cattle or man. In one group of sheep, however, the length of the cycle increased as the breeding season advanced.

Clinical abnormality is not expressed in the variations of the period from parturition to first subsequent oestrus in calving intervals before and after the one in which abnormality has been recorded on the basis of manual rectal palpation of the ovaries. Individuals tend to repeat a similar length of parturition to first subsequent oestrus within fairly wide limits of variation. The length of this period does not show the effect of seasonal changes unless the range is restricted to include only those periods less than 86 days in length; on an average the longer periods were then found to occur in the spring.

Analysis of the published records on the length of the component phases shows that there is a very marked individuality in most of these in the different species studied. This was evident in the oestrous period of the cattle, sheep, swine, and horse, the menstrual period of man and monkey, and the postovulatory phase of the monkey. The preovulatory phase in the baboon showed no significant individual repeatability.

Average increase in the duration of oestrus in cattle and sheep with increasing age is strongly indicated; in swine a highly significant duration increase with age is noted.

No definite seasonal effect is evident in the duration of the oestrous periods of cattle and sheep.

There is a highly significant correlation between the length of the oestrous cycle and the duration of the subsequent oestrous period in cattle, but none was shown in sheep or swine.

A general correlation exists between duration of menstrual period and length of the cycle in man, and between these two (cycle and component period), for the means of individuals in the monkey, but none between these variables within individuals.

The postovulatory (luteal) phase is significantly more variable than the preovulatory (follicular) in the monkey, whereas both are equally variable in the baboon. The length of the luteal phase is highly correlated with cycle length in the monkey, and this correlation differs significantly from the low correlation between the length of the follicular phase and the cycle length. The lengths of both of these phases are correlated (to about the same degree) with cycle length in the baboon.

It is suggested that the factors found to be associated with the variation of the sexual cycle and its component phases be taken into account in analyses and interpretations made of these phenomena, with particular reference to (1) estimation of breeding efficiency and (2) planning and analyses of physiological experiments.

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