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Sex Physiology of Pigs.

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CONTENTS.

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I. INTRODUCTION.

The physiological factors concerned in reproduction and the relationship and interdependence of the various hormones associated with genital physiology, are most complex. The cause of infertility in mammals have been the object of investigation by research workers in many countries. These researches have resulted in a vast amount of accumulated information, especially over the last two decades.

It has been shown that the causal factors concerned in infertility could not always be related to pathological lesions of the genitalia; physiological derangements have suggested themselves. Studies on the sex physiology of domestic animals have resulted in the solution of aetiological questions, relative to fertility, not hitherto understood. The reproductive organs of both sexes are very sensitive to the seasonal, climatological and nutritional influences of the total environment, as has been shown by different studies on sheep, mice and women (Quinlan and Maré, 1931; Roux, 1936; Heape, 1900; Grant, 1934; Mills and Senior, 1930; Mills, 1932; Ogle and Mills, 1933; Ogle, 1934). Pathological conditions, directly affecting fecundity in the pig, would appear to be much less frequent than those of a physiological nature.

Absolute fertility, as measured by the number of viable young delivered at parturition, is, of course, the only aspect which interests the practical husbandman. But the number of viable young produced at birth is dependent on a large number of factors operating prior to parturition. It is therefore a matter of importance that these should be investigated, and, if possible, brought under control.

Reduced fecundity, as distinct from sterility, in uniparous farm animals, such as the mare, the cow and the Merino ewe, is regarded as being of greater importance than in the multiparous species, such as the sow (Hammond, 1914). Fecundity in the sow is, however, of great economic importance and her case has not yet received the necessary attention by the sex physiologists in South Africa.

The pig, unlike the herbivora, cannot be produced and maintained on cheap roughages but subsists for the major part on expensive concentrates; production costs are high and the margin of profit very variable. The payability, or otherwise, of pig production is largely governed by the size of the litter delivered at birth and the number of piglets successfully reared to marketable weight. In practice it is generally considered as uneconomical to rear litters of less than seven to marketable age. In order to rear at least seven pigs from a sow, litter size at birth has to be in excess of that number to provide for unavoidable postpartum losses.

Hammond (1921) has indicated that fertility in mammals is largely controlled by: (1) the number of ova shed; (2) the number of ova fertilized; and (3) the number of embryos which develop normally till birth. To this series Krallinger (1937) proposed a fourth, namely, the regularity of the oestrous cycle. Hammond (1921) mentioned that the factors controlling the number of eggs which develop to reach birth have the greatest influence in domestic animals. Several investigators, especially Corner (1921, 1923) and Hammond (1914, 1921), have shown that atrophy of the embryos in the pig is a matter of common occurrence and may assume considerable proportions. Other workers have demonstrated that the causes underlying embryonic atrophy, and therefore reduced fecundity, in the pig, may be seasonal (Machens, 1915), may be due to poor management after conception (McKenzie, 1928), or to avitaminosis A (Hughes, Aubel and Lienhardt, 1928), or to age (Sinclair and Syrotuck, 1928).

Breeds of animals with prolonged oestrous periods present a special problem under the controlled system of mating, fertility in such cases being largely dependent on the time of mating within the oestrous period. This applies especially to the mare with the longest oestrus of all farm animals, the sow seemingly ranking second in importance, as the duration of oestrus appears to be longer in this species than in both the cow and ewe.

The digestive system of the pig is adapted to the consumption of easily disgestible concentrates, fibrous feeds being only of limited value. Herbivora, on the other hand, subsist entirely or mainly on the natural vegetation or, to a lesser extent, on artificial pastures. The nutritive value of the vegetative parts of plants, especially from the natural herbage, differs enormously in different countries, in different areas of the same country and between seasons (du Toit, Malan and Roets, 1935). Although differences in the chemical composition of the grains and their by-products, grown under different conditions of soil and climate, do exist, even a casual examination of the average analyses of similar grain types, commonly used as feeds, as published by different countries, reveals great similarity in composition. The mature grain is subject to much less variation in composition than the vegetative portions of plants. Consequently, herbivora, transported from their countries of origin to different parts of the globe, are being subjected not only to environmental conditions differing climatologically from those of their natural habitats, but also to different conditions of nutrition. The pig, however, is maintained not only on feeds which vary much less nutrively between countries, but, under all systems of sound management, is fed on rations well balanced from the nutritional aspect. Hence, outspoken differences in the total reaction within the same breed of pig between different countries, should largely be ascribed to climatological differences obtaining between those countries, nutritional differences under standard conditions of management being of less consequence.

Climatic conditions in South Africa differ greatly from those in the Northern Hemisphere, where all our improved breeds of pigs originated and where most of the research work on the sex physiology of the pig has been conducted. So far no systematic investigations on the physiology of sex in the recognised breeds of pigs have been conducted in South Africa. The principal breeds at present are the Large Black and Large White, both of British origin. During 1928 Küpfer carried out some observations on pigs in this country. He described his material as "... a small type of pig, undoubtedly a cross between various breeds". Such a type is not representative of the improved breeds produced commercially in the Union today. A great need, therefore, exists in South Africa for more information on the sexual history of the pig under our climatic conditions, especially with regard to those aspects which are relevant to fecundity in this class of farm animal. Conclusions arrived at by overseas' workers should, furthermore, be verified for South African conditions and breeds of pigs.

The climate of Potchefstroom is representative of the major portion of the South African High Veld, especially of the Western Transvaal and Western Orange Free State provinces.

II. Climatic Conditions under which the Reported Observations were Conducted.

This Institution possesses a well equipped sub-station of the Meteorological Department of the Union of South Africa and records are available, in some instances, for 38 years. For a report on the climatic conditions obtaining the

writer cannot do better than to quote from Science Bulletin No. 14, 1942, being "A Summary of the Investigations conducted during the Period 1903-1940", by Dr. A. R. Saunders, Senior Research Officer. With the kind permission of the author, the following almost verbatim excerpts have been taken from the above publication.

Situation.

The Potchefstroom Experiment Station is situated 26° 44′ S. latitude and 27° 05′ longitude, at an altitude above sea level of approximately 4,430 ft. The surrounding countryside is generally flat with scattered low hills and the vegetation is typically grassveld, dotted here and there with areas of thornbush.

Rainfall.

The mean rainfall over 38 years is 23·63 inches, the range being 13·85 to 34·60 inches. Approximately 20 inches, or 85 per cent. of the average, falls during the six summer months October to March. The average deviation of the yearly rainfall is 16·5 per cent., whereas the lowest for any month is 35·9 per cent. Not only is the rainfall during the winter months much lower than during the summer, but it is at the same time much more uncertain. On an average rain has fallen on 73 days per year during the past 38 years, or on one day in five. The mean evaporation from a free water surface is 64·95 inches. The mean total evaporation per month, or per year, is in all cases far in excess of the mean rainfall. During June, July and August, it is approximately ten times as great and, at its lowest relative level in February, it exceeds the rainfall by very nearly 50 per cent. The average annual evaporation is 2·75 times the rainfall.

Temperature.

The following table shows mean maximum, minimum and grass minimum temperatures in °F. for the 10 years 1930-40.

Mean Maximum, Minimum and Grass Minimum Temperatures.

Month.	Maximum.	Minimum.	Grass Minimum.
July	65·3	32·2	25·9
August	71·2	36·6	30·2
September	77·1	43·7	38·1
October	83·1	53·2	47·0
November	83·6	56·2	51·3
December	83·9	58·2	53·6
January	83·3	58·9	55·2
February	82·3	58·9	55·3
March	80·1	55·2	50·5
April	75·6	47·6	43·1
May	71·2	39·7	34·3
June	65·4	31·9	26·4
Mean	76·8	47·7	42·6

Grass minimum temperatures are taken at 2 inches above the surface of ground covered with short grass. The lowest recorded so far has been 6° F., and the lowest in the standard Stevenson screen 12° F. Maximum temperatures above 90° are not infrequent in summer, but it is seldom

that 100° F. is exceeded. The first frosts usually occur by the middle of April and freezing temperatures may continue until the middle of September or even later.

Relative humidity and atmospheric pressure.

The mean monthly relative humidity and atmospheric pressure, over the 10 years 1930-40, appear in the following table.

Month.	Relative Humidity (Per Cent.)	Atmospheric Pressure. (Inches.)
July	59·1	25·831
August	51·5	25·820
September	45·4	25·751
October	47·5	25·704
November	55.9	25·666
December	60·1	25·646
January	64·9	25·631
February	68·9	25·645
March	70·4	25·686
April	69·3	25·748
May	64·2	25·778
June	61·3	25·856
Mean	59·9	25·730

The moisture content of the atmosphere is lowest in September-October and highest in March-April. Atmospheric pressure declines steadily from July onward until January and thereafter rises to a peak in June.

The Potchefstroom area cannot be classed as windy, for nearly 90 per cent. of the wind has a velocity of less than 14 miles per hour, with a relatively high percentage of calms.

III (*a*). Experimental Animals.

The Large Black and Large White breeds of pigs were used in these studies. The following is a brief review of the histories of the two experimental herds.

Large Blacks.

Six generations of females were bred and reared to provide material for these studies. The foundation sows were all related with the exception of two gilts, which were transferred from the University of Pretoria. Thirteen boars were used. One boar was obtained from the "Benmore" herd belonging to Mr. Montagu Simpson, Johannesburg; five second generation sows being served by him. All the other boars used were either bred by the University of Pretoria or were direct sons of these boars, bred at Potchefstroom. The University herd is well known for its excellence of type. Extensive line-breeding and inbreeding to an outstanding female "Universe Virtue 1161" has been practised in that herd, and all males obtained from that source carried "Virtue" blood to a greater or less degree.

Large Whites.

Five generations of females were bred and reared. All females were bred at this Station, with the exception of three, which were purchased from the "Benmore" herd mentioned above. Seven boars were used. One was obtained from a local farmer; three were bought from the "Benmore" herd and three

were bred at this Institution, the latter being sired by the "Benmore" boars. The locally obtained boar was also derived from the "Benmore" herd, so that the experimental animals in this breed consisted almost exclusively of blood from that particular herd. The owner, Mr. Montagu Simpson, is a regular importer of Large Whites from Great Britain, his animals securing championships at all the leading livestock shows. The animals obtained from that source were unrelated and a minimum of line-breeding was practised in this breed at Potchefstroom.

The type of animals used in these studies can be judged from the various photographs appearing in the text.

III (*b*). Care and Management of Experimental Animals.

Farrowings and testing for oestrus took place in a modern piggery. Farrowing pens were disinfected with strong caustic soda solution before admission of sows. All quarters were cleaned daily. All litters were reared in cement-floored pens. The majority were weaned at 56 days of age, dosed with oil of chenopodium for Ascaris worms, and removed to free-range. Except when under observation for oestrous studies, experimental animals were managed in paddocks on the free-range system. Eucalyptus trees provided ample shade during the warm summer months. Free access was provided to a six acre plot of lucerne, blocked off into paddocks with an electric fence. Abundant grazing was available during the months September to May. Photographs in the text illustrate the general conditions which obtained.

The ingredients of the rations fed varied according to season and feeds available. The following are typical examples of the concentrate mixtures used for the different classes of pigs.

Class of Pig.	Rations.	Pounds.							
		Maize Meal.	Wheat Mid-lings.	Barley Meal.	Fish Meat Meal.	Soybean Meal or Peanut Oil Cake.	Mung-bean Meal.	Lucerne Leaves.	Total.
A.....	1	34	—	50	6	—	—	10	100
	2	—	—	84	6	—	—	10	100
	3	82	—	—	4	4	—	10	100
B.....	1	20	—	65	10	—	—	5	100
	2	—	—	85	10	—	—	5	100
	3	85	—	—	5	5	—	5	100
	4	70	—	—	5	—	20	5	100
C.....	1	24	—	70	6	—	—	—	100
	2	94	—	—	6	—	—	—	100
	3	90	—	—	5	5	—	—	100
	4	75	—	—	5	—	20	—	100
D.....	1	—	15	80	5	—	—	—	100
	2	—	—	95	5	—	—	—	100
	3	80	—	—	10	5	—	5	100
	4	70	—	—	—	5	20	5	100

(2 lb. of bonemeal and 1 lb. of salt were added to each 100 lb. of all rations.)

Class—
A.... Sows with litters and boars in dry lot.
B.... Gilts during oestrous tests in dry lot.
C.... Gilts on lucerne grazing.
D.... Weaner pigs on lucerne grazing (rations I and II) or in dry lot during winter (rations III and IV), up to a live weight of about 80 lb.

Whenever skimmilk was available the fishmeal or meatmeal fraction was adjusted to obtain the necessary balance. The animals were fed twice daily, at 8 to 9 am. and at 4 to 5 pm. Weights were taken on Friday mornings.

Owing to serious droughts and to emergency conditions arising out of the war years, feed was drastically rationed by the Government. As a consequence it was necessary to feed restricted rations, with the inevitable result that optimum growth could not be obtained for the majority of experimental animals. This is to be regretted, but as rations were well balanced in every respect from the nutritional aspect, the only result was subnormal weights-for-age. This condition is discussed under the relevant sections of the text.

PART 1.

IV. Morphological Studies of the Ovary.

This section is to be devoted to the morphological changes of the ovary and it is proposed to limit this study to the following four distinct phases in the sexual life of the sow.

Observation 1 (*a*). The morphological changes of the ovary during dioestrus.

Observation 1 (*b*). The morphological changes of the ovary during oestrus.

Observation 1 (*c*). The morphological changes of the ovary during pregnancy.

Observation 1 (*d*). The morphological changes of the ovary during post-partum oestrus.

Observation 1 (*a*).

The Morphological Changes of the Ovary during Dioestrus.

Object.

The object was to study the morphological changes of the ovary during dioestrus, with special reference to the corpus luteum and the Graafian follicle.

Material and Method.

It was decided to slaughter two females at intervals of three days during dioestrus, reckoning from the onset of oestrus. Intervals were fixed relative to the onset rather than to the cessation of oestrus. Such a method would provide a more exact chronological basis, owing to the great variability obtaining between the durations of different oestrous periods. The hour at which each animal was killed was the same as that of the onset of oestrus, but in those instances in which the onset occurred over night, slaughtering was arranged to take place as close to that hour as was practically possible, that is, either in the late afternoon or early morning. Because of a lack of material it was not possible to use more than one female of each breed for the different intervals.

A full description of the appearance of the ovaries is presented in Appendix 1, and a summary of the data in Appendix 1, Table 1.

Random selection was practised so that where certain group mates have identical ages, the position is due to chance. All the females were gilts with the exception of Large White No. 140, which had one litter and, when killed, had gone through one complete cycle after weaning.

All animals had gone through several oestrous cycles prior to being slaughtered, except two. Large Black No. 181 (9 days interval) and Large White No. 175 (18 days interval), showed no corpora lutea of the previous ovulation. This was to be expected, as from their pen records there seems to be no doubt that the one recorded oestrus in each case was actually the only ever experienced. Large White No. 140 (6 days interval) farrowed 69 days before being killed, showed postpartum oestrus one day after farrowing and again seven days after weaning. She was killed after this latter oestrus, so that her corpora lutea II were actually corpora lutea of lactation. She was therefore omitted from the discussion on these bodies. Both Large Black No. 234 and No. 233 had experienced at least two oestrous periods, but the actual numbers were unkown. The ovaries of Large White No. 157, (3-day group) had three very large and probably cystic follicles which must have influenced weights abnormally. For the data on ovarian weights during dioestrus she was replaced by Large White No. 188, which was slaughtered 42 hours after the onset of oestrus, with all the follicles already ruptured. Measurements of individual corpora lutea or mature follicles which, macroscopically, were suspected as being cystic, were not included in the data for statistical treatment. Such instances were encountered in the following pigs: Large White No. 157 (3-day group), Large Black No. 176 and Large White No. 140 (both 6-day group), and Large Black No. 233 (12-day group).

The animals were weighed immediately prior to killing. Each individual was carefully post-mortemed for clinical evidence of any pathological conditions. The ovaries were removed immediately after death, placed in small corked specimen bottles suitably marked to ensure the identity of each ovary, and weighed, the whole operation occupying about 30 minutes. The ovaries were then carefully washed under the tap to remove adhering blood. Sufficient clean water was then added to the containers to cover the organs completely so as to prevent drying. Macroscopic examination followed immediately.

The sow's ovary is a most irregular body, so that an average figure for size measurements would be very misleading and difficult to apply. It was therefore decided to record only the greatest measurement in each of the three dimensions taken, namely, from pole to pole, median to lateral face, and from the attached to the free border.

Examination of the Graafian follicles and the corpora lutea was carried out in strong dispersed light or, whenever necessary, in direct sunlight. Whenever any doubt existed as to the presence and nature of any of these bodies the ovary was sectioned so as to reveal information not clearly evident superficially. Detailed descriptions of each organ were made, after which the ovaries were stored in 10 per cent. formalin. Measurements on the sizes of individual corpora lutea and follicles were carried out on the preserved material. Comparisons between preliminary readings on the fresh and the preserved ovaries revealed that no material change in size had taken place as a result of preservation. Readings were made with a transparent celluloid rule, graduated to one-quarter of a millimetre. Observations were conducted through a large lens fixed to a stand and magnifying three diameters, the object being lighted with a "Dakol" microscope lamp, fitted with a blue screen. Measurements were made to the nearest half millimetre.

Because the most important aspects of the various observations under this section are based on the time-relations of the exhibition, duration and disappearance of oestrus, meticulous precautions were taken to ensure the greatest measure of exactness on these phases of the cycle. For a detailed description of the methods employed, reference must be made to Part 3.

Literature.

McKenzie (1924) thought that the ovary with large follicles weighs more than the one containing less advanced follicles. He records maximum weights for those with large corpora lutea, those of the first four days after ovulation weighing least of all. His report also seems to imply that the age and body weight are correlated with the weight of the ovary. This is the only relevant literature of which the writer is aware.

Corner (1921) recorded the initial size of the corpus luteum of oestrus as 4 to 6 mm. and after one week's growth as 8 to 9 mm., retrogressing at 14 to 15 days to 6 mm. The corpus luteum gravitatis only reaches its maximum size of 10 to 11 mm. after two to three weeks development. The corpora lutea of unfertilized ovulation and of pregnancy, he stated, cannot be distinguished during the first two weeks after discharge of the ovum. By the tenth day the corpus luteum is usually solid with fully differentiated cells, though a few in each ovary may remain slightly cystic. The cut surface presents a velvety texture with an initial pink colour which, at 15 days, suddenly transforms to the whitish tone of scar tissue within a period of two to three days, never showing any trace of the yellow or orange pigments so characteristic of the corpora lutea in the bovine or human ovaries. According to Küpfer (1928) involution of the corpus luteum is accompanied by a gradual degeneration of the capillaries and a change in colour from an initial cherry red to yellow. The regression is traceable beyond the inter-ovulation period and at the end of the second cycle the corpora lutea are usually no longer visible externally. McKenzie (1926) found that the corpus luteum has an initial diameter of 5 to 6 mm. and reaches maximum size after seven days, regressing between the 12th and 16th day after ovulation. The corpus luteum of 35 days disappears completely. Rupture points remain visible for some days and the external colour changes from flesh-red when fresh, to pink at 10 days and then to white at 16 days. Hammond (1927) found that, in the cow, the point of rupture persists throughout the life of the corpus luteum as a knoblike protrusion, and only disappears during the late stages of involution. Mumford, Hogan and McKenzie (1926) reported the corpus luteum as being red and 8 mm. in diameter, four days after oestrus, pink and 9·2 mm. in diameter after 10 days, and white and 5·4 mm. in diameter during early oestrus. Robson (1940) mentioned that maximum size of the corpus luteum of oestrus is attained at three days, after which degeneration sets in. Lutein tissue occasionally arises in the unruptured follicle, but such follicles usually undergo atresia.

Corner (1921), McKenzie (1924), Allan, Knoutz and Francis (1924), Mumford *et al* (1926), Robson (1940) and Marshall (1922) described the various phases of the follicle in very similar terms. Normally large-sized follicles are present only immediately prior to and during oestrus. Immediately after ovulation large numbers of only very small follicles of 1 to 2 mm. diameter are to be found, but according to Corner they may be 5 mm. at that stage. A gradual increase in diameter during dioestrus follows till a size of 4 to 5 mm. is attained. Then, a few days prior to oestrus, a sudden maturative increase is witnessed, reaching a final size of 10 to 11 mm. diameter just before ovulation. McKenzie, who worked on eight months old gilts, reported that two days after oestrus ". . . innumerable tiny follicles less than one mm. were observed ... (and) ... as the size of the

follicles increases their number decreases " during the dioestral period. Allan *et al.* (1924) found that 85 per cent. of the follicles were eliminated before ovulation only 15 per cent. reaching maturity. Mumford *et al.* (1926) reported the presence of only six large follicles of 11·7 mm. diameter in early oestrus, while McKenzie (1926) wrote that " ... immediately after ovulation there were found to be quite a few (20 in one sow) small follicles between 1 and 2 mm. in diameter ". Robson (1940) stated that the final growth and maturation of the follicle is accompanied by the " destruction " of all remaining follicles. Corner (1921) mentioned that maximum sizes are only present a few days previous to ovulation and that at all other times " ... there is a reserve stock of small follicles in the ovary, forming a series of all sizes from the microscopic primordial stage to a diameter of about 5 mm.". Also, all active ovaries carry a number of 3·5 to 5 mm. follicles awaiting development for the next ovulation. He furthermore surmised that a rapid enlargement of maturing follicles takes place not more than two or three days before oestrus, bringing them up to 7·8 or even 10 mm. McKenzie (1924, 1926) claimed that during dioestrus a general increase in follicular size takes place, accompanied by a progressive elimination of follicles, that is " . . as the size of the follicles increases, their number decreases ". Allan *et al.* (1924) reported that a vigorous selective elimination of ova in pigs obtains during the two weeks preceding ovulation, claiming that only 6·5 follicles, or 15 per cent, attain maturation, 85 per cent. being eliminated. Mumford *et al.* (1926) supplied similar data. Robson (1940) stated that " ... the ... maturation of a selected group of follicles ... is accompanied by the destruction of all remaining follicles (and that) even during pregnancy the rhythm is continued, though the final maturation stages and ovulation do not occur and that all the follicles undergo degeneration ".

Results.

Detailed descriptions of the morphological appearances of the ovaries are presented in Appendix 1, and a summary of the data appears in Appendix 1, Table I.

Weights of Ovaries.—Appendix 1, Table II, presents the weights of the ovaries in three-day intervals during dioestrus. The data have been subjected to an analysis of variance, the results appearing in Tables 1 (*a*) and 1 (*b*).

TABLE 1.

(*a*)

Analysis of Variance: Weights of Ovaries of Large Black and Large White Pigs at Consecutive Three-day Intervals during Dioestrus.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods.....	5	66·31	13·26	8·28	SS
Breeds.....	1	2·91	2·91	1·82	ns
Interaction.....	5	5·99	1·20	0·75	ns
Error.....	12	19·21	1·60	—	—
Total.....	23	94·42	4·11	—	—

(" SS ", " ss " and " ns " mean significant at the 1 per cent and 5 per cent. levels and not significant respectively, throughout the test).

(*b*)

Summary of Mean Weights, in Grams, of Ovaries at Consecutive Three-day Intervals during Dioestrus.

Period.	Large Blacks.	Large Whites.	Period Means.	Mean Differences.
3 days	3·09	3·73	3·41	—
6 days	4·66	5·19	4·92	+1·51
9 days	5·41	7·46	6·43	+1·51
12 days	9·20	8·04	8·62	+2·19
15 days	6·18	7·70	6·95	—1·67
18 days	6·73	7·32	7·02	+0·07
Breed mean	5·88	6·57	—	0·69

Least significant difference at P=·05 is 1·75.

The analysis shows that breeds do not differ in their mean ovarian weights and that the breeds react similarly at the different intervals. Although differences between consecutive periods are not significant (with the exception as between 9 and 12 days), comparisons between alternate and wider intervals reveal the significant increase in weight of the ovary up to the 12th day after the onset of oestrus. The lowest mean weight is that at the beginning of the cycle (3·41 gm.) after which consistent increases are registered till the maximum weight (8·62 gm.) is attained at the 12th day after the onset of oestrus. Thereafter a tendency to regress to the 18th day is indicated Although the breed mean difference is insignificant, it should be observed that, except for the 12th day interval, the ovaries of Large Whites are consistently heavier than those of Large Blacks.

The Corpora Lutea I.—Sizes of the Corpora lutea I, at the different three-day intervals during dioestrus, are recorded in Appendix 1, Table III. Statistical analysis of the data appear in Tables 2 (*a*) and (*b*).

TABLE 2.

(*a*)

Analysis of Variance: Sizes of Corpora Lutea I, in Large Black and Large White Pigs, at Consecutive Three-day Intervals during Dioestrus.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods	5	142·59	28·52	17·15	SS
Breeds	1	43·51	43·51	26·16	SS
Interaction	5	50·38	10·08	6·06	SS
Error	132	219·49	1·66	—	—
TOTAL	143	455·97	3·19	—	—

(*b*)

Summary of Mean Sizes in Millimetres of Corpora Lutea I, in Large Black and Large White Pigs, at Consecutive Three-day Intervals during Dioestrus.

Period.	Large Blacks.	Large Whites.	Period Means.	Mean differences.	Significance.
3 days.....	7·23	9·37	7·92	—	—
6 days.....	8·17	8·67	8·45	+0·53	ss
9 days.....	10·83	9·42	9·89	+1·42	SS
12 days.....	9·14	11·17	10·20	+0·31	ns
15 days.....	11·00	10·73	10·85	+0·65	ss
18 days.....	8·50	10·75	9·58	—1·27	SS
Breed means.....	8·91	10·01	9·49	1·10	SS

The analysis in Table 2 (*a*) shows highly significant differences in respect of periods, breeds and interaction The data in Table 2 (*b*) show that, except for the 12th day, consistent and significant increases in size of the corpus luteum I occur up to and including the 15th day interval, after which a highly significant decrease to the 18th day is reflected. The non-significant mean increase from the 9th to the 12th day is due to an actual decrease in mean diameter in Large Blacks, which condition is very probably due to normal variation. Involution of the corpus luteum I, 15 days after the onset of oestrus, is clearly shown (vide Fig. 1).

The Corpora Lutea II.—Sizes of the corpora lutea II of the sows slaughtered at the different three-day intervals during dioestrus appear in Appendix 1, Table IV. Owing to an insufficiency of material in the case of Large Whites, a comparative study of the two breeds is not possible. The data for Large Blacks alone were analysed, the results appearing in Table 3.

TABLE 3.

(*a*)

Analysis of Variance: Sizes in Millimetres of Corpora Lutea II in Large Black pigs at Consecutive Three-day Intervals during Dioestrus.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods.....	4	48·074	12·018	17·95	SS
Error.....	73	48·875	0·669	—	—
TOTAL.....	77	96·949	1·259	—	—

(*b*)

Summary of Mean Sizes in Millimetres of Corpora Lutea II, in Large Black Pigs, at Consecutive Three-day Intervals during Dioestrus.

Period.	Mean.	Mean difference.	Significance.
3 days	5·97	—	—
6 days	4·60	—1·37	SS
12 days	3·67	—0·93	SS
15 days	4·23	+0·56	SS
18 days	4·21	—0·02	ns

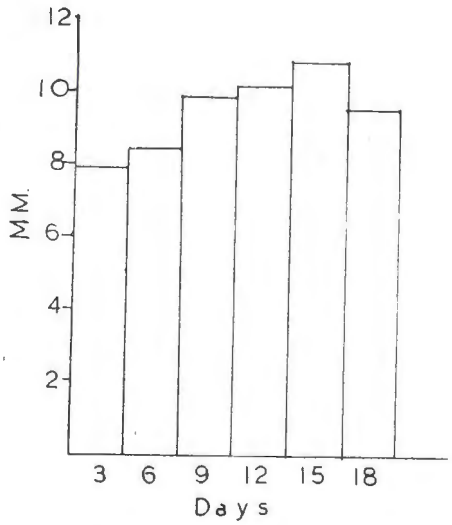

FIG. 1.—Mean size of corpus luteum I during dioestrus.

The analysis [Table 3 (*a*)] shows highly significant differences in mean diameter of the corpus luteum II at the various three-day intervals during dioestrus. Examination of the data in Table 3 (*b*) shows that significant decreases in mean diameter occur only up to and including the 12th day, sizes at the 15th and 18th day intervals being similar to those at the 6th day. As only one animal is represented at each interval, the data for the 12th day will probably have to be considered as exceptional and due to normal variation. Disregarding the 12th day period, it is to be noted that mean diameters at the 6th, 15th and 18th day intervals do not differ significantly between themselves, but all differ highly significantly from the 3rd day. From the limited data available in Large Whites it appears that the condition is very similar to that in Large Blacks. The data would seem to provide full support for the conclusion that the corpus luteum of one oestrus experiences no, or only insignificant, decreases in size during and up to the 18th day of the second inter-ovulatory period.

The Follicle during Dioestrus.—During the entire period of dioestrus the ovary carries large numbers of follicles. At all stages a small number which measures 1 mm. and less in diameter is just visible to the naked eye. From this minimum basis sizes range imperceptibly into each other to maximum diameters of 9 mm. (in Large Whites) two days before oestrus. The majority of follicles belong to the class 1 to 3 mm., a small group is below 1 mm. and a larger class, numbering 15 to 32, have diameters of 4 to 9 mm. This latter condition does, however, not apply to Large Black No. 234 in the three-day group, in which the largest follicles measured only 2 mm.

In order to test out any probable evolution in size of the follicle over the dioestrous period, all the largest follicles appearing on the ovaries of each individual and differing by 2 mm. only were measured and listed in Appendix 1, Table V. The analysis of those data appears in Table 4.

TABLE 4.

(*a*)

Analysis of Variance: the Largest Follicles at Consecutive Three-day Intervals during Dioestrus in Large Black and Large White pigs.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods	5	178·27	35·65	74·77	SS
Breeds	1	32·83	32·83	68·84	SS
Interaction	5	80·37	16·07	33·71	SS
Error	250	119·21	0·48	—	—
TOTAL	261	410·67	—	—	—

(*b*)

Summary of the Largest Follicle Sizes, in mm., in Large Black and Large White Pigs at Consecutive Three-day Intervals during Dioestrus.

Period.	Large Blacks.	Large Whites.	Period Means.	Mean differences.	Significance.
3 days	1·75	4·68	3·98	—	—
6 days	3·90	4·60	4·20	+0·22	ns
9 days	4·85	4·37	4·58	+0·38	SS
12 days	5·00	5·43	5·22	+0·64	SS
15 days	4·18	5·14	4·81	—0·41	SS
18 days	5·68	7·87	6·59	+1·78	SS
Mean	4·62	5·32	—	0·70	SS

The analysis in Table 4 (*a*) shows that the mean diameters, of the largest set of follicles, differ highly significantly over the various three-day intervals during dioestrus. Breeds also differ highly significantly as does also the reaction of

breeds on periods. The particulars in Table 4 (*b*) show that with the exception of a decrease at the 15th day, consistent increases in mean diameters are maintained over the whole of the dioestral period. Although the Large White sow also shows a decrease at 15 days, the significant decrease in mean diameter at this interval is due to the contribution by the Large Black sow in the group. The condition is no doubt due to normal variation. Calculation further shows that, as from three days to 18 days after the onset of oestrus, the mean diameter of the largest group of follicles increases by almost 66 per cent.

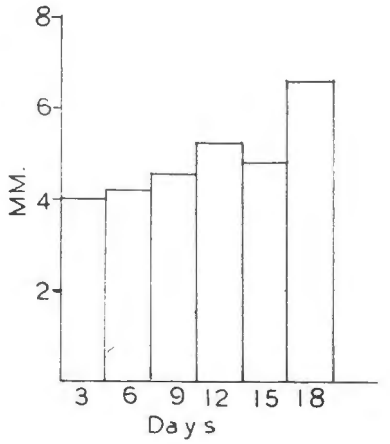

FIG. 2.—Mean sizes of largest group of Graafian follicles during dioestrus.

The total number of follicles at the various time intervals during dioestrus, presented in Appendix 1, Table 1, have been utilised to obtain additional statistical evidence on the extent of the elimination of follicles involved during this sexual phase. The data have been fitted to both a linear and a quadratic regression line, the results appearing in Table 5

TABLE 5.

(*a*)

Total Number of Follicles in Large Black and Large White Sows at Consecutive Three-day Intervals during Dioestrus.

Period.	Large Whites.	Large Blacks.	Total.	Period Mean.
3 days	106	9	115	57·5
6 days	58	55	113	56·5
9 days	117	106	223	111·5
12 days	81	149	230	115·0
15 days	101	84	185	92·5
18 days	101	67	168	84·0

(*b*)

Regression of Mean Follicle Number on Time.

Three-day Intervals.	Number Found.	Number Expected.	
		Linear Regression b—3·49	Quadratic Regression c.—4·137
1	57·5	68·72	48·03
2	56·5	75·70	79·84
3	111·5	82·68	99·23
4	115·0	89·66	106·21
5	92·5	96·64	100·78
6	84·0	103·12	82·93

Analysis of Variance: Linear and Quadratic Regression.

Component.	D.F.	Sum Squares.	Mean. Square.	F.	Significance.
Linear term	1	836·23	838·23	2·65	ns
Quadratic term	1	1,437·61	1,437·61	4·56	ns
Deviations	3	945·99	315·33	—	—

For $P=\cdot05$, $n_1=1$, $n_2=3$, $F=10\cdot13$.

Although the quadratic term gives a reasonable fit, the coefficients are not significant.

During oestrus and immediately thereafter, as discussed below, the majority of follicles are so small as to be practically invisible, making reliable counts difficult. Even though the averages would seem to indicate largest counts for the 9 and 12 day mid-periods, examination of numbers for the breeds suggests that the differences may be entirely due to individual variations. A possible decline in follicle number during the last two periods, in the case of Large Blacks, would seem to be indicated. However, no such reduction in numbers can be claimed for Large Whites, as counts of 101 were obtained for both the 15th and 18th day intervals, practically equal to the maximum of 117 at the 9th day.

Discussion.

Weights of Ovaries.—McKenzie's (1924) finding that maximum ovarian weight and size of corpus luteum are correlated, has been fully borne out by this observation. The lowest mean weight obtains three days after the onset of oestrus, that is one to two days after ovulation, at which period both the corpora lutea and follicles are at their smallest. Maximum mean weight is found at the 12th day after the onset of oestrus, after which an insignificant tendency to lower weights, towards the end of the period of dioestrus, is revealed. Measurements of the corpus luteum, to be discussed below, have shown that maximum diameters occur at the 12th to the 15th day, which period therefore coincides with that for maximum ovarian weight. The insignificant reductions in mean weights beyond

the 12th day can be accounted for from the evidence, to be discussed below, that significant increases in follicle sizes obtain as the cycle advances, thus partly compensating for any tendency to lower weights as a result of regressing corpora lutea.

The corpus luteum I is smallest at the third day of the dioestrous cycle, with a mean diameter of 7·92 mm. Thereafter it goes through a sustained evolutionary phase till a maximum mean diameter of 10·85 mm. is reached at the fifteenth day, beyond which reductional changes are revealed as the next active sexual phase approaches. The greatest increase in size occurs from the sixth to the ninth day after the onset of oestrus. The results of this study therefore disagree with the findings of those authors who claim that the corpus luteum reaches maximum size at the age of 7 to 9 days (Corner, 1921; McKenzie, 1926; Mumford *et al.* 1926). These writers apparently estimated the age of the corpus luteum from the time of ovulation. However, even if one or two days were added to their figures to allow for the pre-ovulatory period during oestrus the disparity between their data and that of this study, relative to the period of maximum diameters, would still persist. This condition should in all probability be ascribed to breed differences or to differences of technique. The results show that the mean diameter of the corpus luteum I, at the eighteenth day of the cycle, is 9·58 mm., and at the third day of the next cycle, about five days later, the mean of the corpus luteum II is only 5·97 mm. It is therefore clear that regression of these bodies is rather rapid as soon as the next oestrus sets in.

McKenzie's (1926) report that, in the pig, only indistinct white remnants are left of the corpus luteum when 35 days old, and Küpfer's (1928) finding that the corpora lutea II are no longer visible externally at the end of the second cycle, are certainly not substantiated by this study and for these two breeds of pigs. The data show that at the 18th day of the second cycle the corpora lutea II, in Large Blacks, still have a mean diameter of 4·21 mm. and are rather conspicuous bodies at this stage. Their age would then be roughly 36 days. The data further show that the corpora lutea of one ovulation experience no or very little reductional changes over the second interoestrous period. Their condition appears to remain almost static over this interval. Their regression, however, is rapid as the next oestrus sets in. Examination of ovaries during oestrus reveals that the corpora lutea II, then about 40 days old, are very inconspicuous bodies, having maximum diameters of 2 mm. and occasionally 3 mm., the majority showing merely as pinhead remnants. Over a brief period of some two to three days, these bodies are thus reduced from a mean size of 4·21 mm. to almost vanishing point.

The colour of the corpus luteum, when fresh or three days after the onset of oestrus, is dark red initially, changing rapidly to a pale purplish vinaceous, which condition remains unchanged up to the fifteenth day of the cycle. Then, between 15 and 18 days after the onset of oestrus, there is a sudden change to yellow or cream yellow, both externally and on section, which change coincides with the general regression of these bodies during the oncoming active phase of the ovary, as noted above. Corpora lutea of over 14 days of age were definitely found to be yellow, but tend to go brownish towards the end of the second cycle as these bodies age and shrink, due probably to a concentration of the luteal pigments. It is rather strange that the finding on the colour of the corpus luteum should disagree so radically from that of the American writers, who describe the change from red or pink to white without any trace of the usual yellow or orange pigments (Corner, 1921; McKenzie, 1926; Mumford *et al.*, 1926). Küpfer (1928), however, also found the ageing corpora to assume a yellow colour.

The points of rupture in the follicle have been found to heal up very rapidly after ovulation and remain visible as small papillae up to the 12th day period. In one case the scars were still showing distinctly on the surface of the corpora lutea eighteen days after the beginning of the oestrous period. This is not in accordance with the finding of McKenzie (1926), who limits the presence of rupture points to a few days only, but closely agreed with Hammond's (1927) conclusions for the cow. The general tendency for the corpus luteum is to assume and retain a spherical shape throughout, though some are inclined to be conical.

From the sixth day period onward a very strong vascularisation of the corpus luteum is plainly evident. This persists up to the 18th day, after which the fine and extensive network of bloodvessels seems to undergo the general involutionary changes already observed in corpora lutea at this period. Only toward the end of the cycle do the corpora change from a soft to a firm consistency.

At the third day stage the central cavity is filled with a dark-red blood clot. In some corpora lutea this has already been absorbed at the sixth day period and the cavity filled with a connective tissue plug, while others now include a colourless or slightly yellowish liquor. These conditions may even coexist on the same ovary, with a large, dark, blood-clot inclusion in some corpora lutea, the clot persisting at times, though reduced in size, up to the 12th day. Those with a fluid inclusion may persist up to the 15th and even 18th day. Hammond (1927) states that, in the cow, the stage with fluid in the cavity must be considered normal in the life of the corpus luteum; this is confirmed by Long and Evans (1922) for the rat. Hammond remarks that the fluid is normally absorbed eight days after the beginning of oestrus, but reabsorption may not occur, giving rise to cysts. Cavities containing fluid as a normal condition therefore appear to persist for a longer period in the sow than in the cow.

Generally speaking, the conclusions reached by the authors quoted, with regard to the size of the Graafian follicle, have been confirmed by the present study. The follicles are smallest immediately following ovulation, averaging about 4 mm. for the largest group. A selected minority, destined for final enlargement and ovulation, experiences a very gradual though significant evolution in size, reaching an average diameter of 6·5 mm. two days before oestrus. At the 18th day some ovaries may already carry follicles of 9 mm. diameter, which closely approximates the maximum size of 10 to 11 mm. during oestrus.

Statistical treatment of the number of visible follicles, counted every three days over the dioestrous period, does not supply confirmation of the generally accepted view by various authors that a progressive elimination of follicles operates during the cycle. They claim that, as a selected group of follicles reaches maturity, those not destined for ovulation are destroyed (McKenzie, 1926; Robson, 1940). The total follicular population does not appear to be reduced at all up to the 18th day of dioestrus or two days before oestrus, and whatever differences that may be registered seem to be due to chance variations. It can reasonably be assumed that selection of a set of follicles for maturation will take place from among the largest group, but even here no evidence is provided in support of an eliminative process, up to two days before oestrus.

Summary and Conclusions.

1. The mean weight of the ovary increases significantly up to the twelfth day of dioestrus, being 3·41 gm. at the third day with a maximum of 8·62 gm. at the twelfth day of the cycle, after which insignificant decreases occur.

2. The mean diameter of the corpus luteum I, at the third day of dioestrus, is 7·92 mm.; the maximum mean is 10·85 mm. at the fifteenth day, after which highly significant decreases up to oestrus occur.

3. The corpus luteum II appears to remain static in size beyond the third day of dioestrus and up to the eighteenth day of the cycle. Involutlon during the hours of oestrus is rapid.

4. The mean diameter of the largest group of Graafian follicles increases by 66 per cent. from the third to the eighteenth day of dioestrus.

5. A reduction in numbers of Graafian follicles does not occur from the third to the eighteenth day of the dioestrous cycle.

Observation 1 (*b*).

The Morphological Changes of the Ovary during Oestrus.

Object.

The main object of this study was to determine the hour of ovulation and, in addition, to make use of the material which thus became available for studies on the sizes, numbers and appearances of mature and immature follicles and of corpora lutea, during oestrus.

Material and Method.

A varying number of females were slaughtered at six-hour intervals, starting at the onset of oestrus and continuing till the 60th hour for Large Blacks and the 48th hour for Large Whites. These end periods were chosen because, as will be shown later, the minimum mean duration of oestrus in gilts is 62·57 hours for Large Blacks and 47·6 hours for Large Whites. The original plan was to kill only two females at each six-hour interval but, as the work progressed, it became increasingly evident that the hour of ovulation varied so much between sows, that larger numbers would be required at the critical phase to establish the time of ovulation with greater certainty. As many females as possible were therefore utilised for slaughter around the probable hour of ovulation. More Large Whites than Large Blacks were killed, simply because larger numbers of that breed were available. Twenty Large Blacks and 27 Large White females were slaughtered. As reliable data on the time of ovulation are dependent on the exactness of the knowledge of the onset of oestrus, great care was exercised to determine that hour as accurately as was practically possible. The methods adopted are discussed in Part 3. Testing for the presence of oestrus was conducted at three-hour intervals. It was therefore assumed that, if a sow exhibited oestrus for the first time at a certain reading, she would then, on an average, already have been in a receptive state for one and a half hours. Her hour of slaughter was fixed accordingly. Selection of animals was random. The majority of animals were below 18 months when killed. Their sexual histories were normal and individuals which showed abnormalities on post mortem were discarded.

The data for the duration of oestrus, as recorded in Appendix 2, Table 1, are for ordinary oestrous periods only. Those at postpartum and post-weaning were not included as they differ significantly from the ordinary oestrus. All females

were allowed to go through a minimum of two oestrous periods before being slaughtered, excepting the following instances: Large Blacks Nos. 12 and 235 and Large White No. 36. Females which had farrowed one or more litters are classed as sows, otherwise as gilts, irrespective of age.

As there was no intention during the early stages of this work to produce a detailed statistical treatment of the sizes, etc., of follicles and corpora lutea, a number of specimens were unfortunately not kept. Material was therefore later lacking for certain periods and a continuous series of this sexual phase cannot be presented. A comparative study for the two breeds, relative to the corpus luteum I and the mature follicle, is impossible and sufficient material is available for a study of these bodies in the Large Black breed only.

Literature.

That the time of rupture of the follicle during oestrus is of great importance in arriving at an optimum service period, has been shown by Hammond (1931) and Andrews and McKenzie (1941) for the mare, Quinlan *et al.* (1932) for the ewe, Kirillov (1937) for the cow and Hammond (1934) for the rabbit.

The findings of various authors with regard to the period elapsing between the onset of oestrus and ovulation in the sow, have been summarised and are presented in Table 6.

TABLE 6.

The Period from the Onset of Oestrus to Ovulation in the Pig as Recorded by Different Authors.

Author.	Period.
Haring, 1937	24 hours, complete after 36 hours.
McKenzie & Terrill, 1934	32 to 37 hours.
Lewis, 1911	Only after 30 hours.
Corner & Amsbaugh, 1937	First or second day.
Dettweiler & Muller, 1924	12 to 18 hours.
Kronacher, 1937	12 to 18 hours.
Mumford et alia, 1926	About 24 hours.
Marshall & Hammond, 1937	30 to 35 hours.
Asdell, 1938	30 to 35 hours.
Kupfer, 1928	First or second day, usually second.

McKenzie (1926) and Corner (1921) for the sow, Grant (1933) for the ewe and Long and Evans (1922) for the rat, think that all follicles rupture at about the same time. Walton and Hammond (1928) found that, in the anaesthetised rabbit, rupture is spread over a period of $9\frac{3}{4}$ to $13\frac{1}{2}$ hours. Marshall (1922) wrote that ovulation takes place during oestrus. Hammond (1914) and Corner and Amsbaugh (1917) have shown that ovulation was independent of copulation. Grant (1933) recorded that the time of ovulation is unrelated to the duration of oestrus in the ewe, whereas Hammond (1927) stated that, in the cow, ovulation occurs some hours after the end of oestrus and is related to the onset and not to the length of the oestrous period. Anderson (1938) reported that, for high

grade Merino and Masai ewes, ovulation only takes place shortly after the end of oestrus and that ovulation is related to the end and not the beginning of oestrus. Quinlan and Maré (1931) found that, in the Merino ewe, the duration of oestrus appears to depend on the time of rupture of the follicle and that delayed rupture may explain the prolonged oestra occasionally observed. Cole and Miller (1932) remarked that it is agreed by the majority of investigators that ovulation occurs spontaneously in the ewe during the second half of the oestrous period. Andrews and McKenzie (1941) reported that, in the mare, ovulation occurs one to two days preceding the end of oestrus, but in some cases not until one to five days after the cessation of oestrus.

Results.

Descriptions of the morphological appearances of the ovaries during oestrus appear in Appendix 2, from which the most important data have been abstracted and tabulated in Appendix 2, Table 1.

The Time of Ovulation—Appendix 2, Table 1, records, in addition to other particulars, the state of the follicles in relation to ovulation at the different six-hour intervals during oestrus. As ovulation was observed to occur for the first time at the 18-hour interval, the data subsequent to the 12-hour period only have been abstracted and presented in Table 7.

TABLE 7.

The Time of Ovulation in Large Black and Large White Pigs at Six-hour Intervals during Oestrus.

Hours after Onset of Oestrus.	LARGE BLACKS.		
	Sow No.	Duration of Previous Oestra, Hours.	Follicular Stage. Ruptured=R. Unruptured=U.
18	171	72, 72, 72, 81, 75, 93	All U.
24	194	57, 69, 54	All U.
	183	54, 54, 54	All U
30	22	51, 60, 63, 63, 66	All U
	17	57, 66	All U.
36	182	63, 81, 63, 69, 60	All U
	19	51, 66, 75	All U
42	218	45, 66, 66	All U
	199	60, 60, 72, 69	All R
	211	54, 63, 66, 54	All U
	180	69, 63, 60, 54, 57	14 R, 2U
48	11	63, 66	All R
	63	75, 78, 78	All U
	171	72, 72, 81, 75, 93	14 R, 1 U
54	186	60, 60, 66, 54, 57	All R
	201	39, 60, 63, 159	All U
60	23	57, 66, 66, 63, 66, 66, 72	All R

TABLE 7 (*continued*).

Hours after Onset of Oestrus.	LARGE WHITES.		
	Sow. No.	Duration of Previous Oestra, Hours.	Follicular Stage. Ruptured=R. Unruptured=U.
18	21	45, 48, 48	2 R, 16 U.
	23	60, 66, 84	All U.
	189	39, 33, 24	13 R, 1 U.
24	438	72, 57, 63, 60, 45	All U.
	57	45, 45, 42	17 R, 1 U.
	56	39, 66, 39	1 R, 19 U.
	67	54, 48, 51, 45, 45, 39, 45	All U.
	165	36, 36, 33	1 R, 19 U.
	191	33, 27, 36, 39	5 R, 10 U.
	190	27, 24, 27, 30	All R.
30	49	54, 42, 36	All R.
	33	42, 39	16 R, 1 U.
	187	48, 51, 60	All U.
	195	33, 24, 36	All R.
	145	30, 48, 39, 30, 36, 39	All R.
36	183	57, 51, 54, 57, 63	3 R, 20 U.
	54	48, 51, 48, 54	17 R, 1 U.
	121	68, 66, 63, 57, 66	All U.
	185	51, 51, 54	All R.
	182	39, 36, 45, 39, 48	All R.
42	188	45, 36, 39, 39	All R.
48	193	45, 24, 36, 39, 36	All R.

A glance at Table 7 at once reveals a surprising breed difference as to the time of rupture of the follicle. Whereas ovulation starts 18 hours after the beginning of oestrus in Large Whites and is apparently over at 36 hours for this breed, in Large Blacks ovulation actually only sets in at the 42-hour interval and is over at 54 hours. The hour at which ovulation can be expected to set in is therefore no less than 24 hours later for Large Blacks than for Large Whites.

Considering the follicular stages for the 18-hour interval for the Large White breed, the data reveal two cases in which ovulation was actually in progress, whereas in the third remaining case the critical stage had not yet been reached. Ovulation for this breed of pig can therefore be assumed to commence at about 18 hours after the onset of oestrus. Furthermore, from the 36-hour period and beyond only one individual out of a total of seven had not yet reached the stage of ovulation. It therefore follows that ovulation can generally be considered to be completed 36 hours after the beginning of oestrus in Large Whites. In Large Blacks, two of the four individuals in the 42-hour group carried ruptured follicles. Of these two No. 180 was in the act of ovulating, whereas the condition of the follicles of No. 199 indicated that rupture had just been completed (vide Appendix 2). In the 54-hour group the condition of the follicles of No. 201 revealed that rupture was imminent, whereas rupture was completed in the remaining group mate, No. 186. Rupture therefore appears to be completed at the 54th hour of oestrus, so that ovulation in Large Blacks occupies about 12 hours.

The question arises as to whether any statistical relationship exists between the mean duration of oestrus and the time of ovulation. The data in Table 7 have been utilised for this purpose. Individuals, actually in the process of

ovulation at certain periods, were classed as falling within that particular ovulatory time-interval. The mean duration of all oestrous periods of each time-group was determined and the regression coefficient of the mean duration of oestrus on time of ovulation calculated, the result appearing in Table 8.

TABLE 8.

Regression of Mean Duration of Oestrus on Time of Ovulation.

Six Hour Intervals.	Duration of Oestrus.	
	Found.	Expected. b=7·80.
3	39·5	33·19
4	40·2	40·99
5	40·5	48·79
6	56·7	56·59
7	60·6	64·39
8	78·6	72·19

Analysis of Variance: Linear Regression.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Regression	1	1,063·92	1,063·92	25·85	SS
Deviations	4	164·63	41·16	—	—
TOTAL	5	1,228·55	—	—	—

For P= ·01, n_1=1, n_2=4, F=21·20.

In this analysis breeds were ignored and it so happens that the periods of ovulation for Large Blacks form a continuous series with those of Large Whites. The data show that a positive regression obtains between the period of ovulation during oestrus and the mean duration of the previous oestrous periods.

The observation on the duration of oestrus (Part 3) reveals a mean duration of oestrus in the gilt of 62·5 hours for Large Blacks and 47·6 hours for Large Whites, a difference of about 15 hours between the two breeds. It will also be observed that ovulation in the Large Black breed can only be expected to commence 42 hours after the onset of oestrus, that is, 24 hours later than for the Large Whites. The time of ovulation therefore appears to be correlated with the duration of oestrus. This matter is again further discussed in Part 3.

The Duration of Ovulation.—According to the authors quoted above, it appears to be generally accepted that multifollicular rupture is either simultaneous or at most spread over a very short period of time. However, the work of Walton and Hammond (1928) shows that, for the rabbit under anaesthesia, rupture takes place over a period of 9·75 to 13·5 hours. Corner (1921) could find only one case in which there were also mature normal follicles present together with the ruptured bodies, in about 200 sows examined by him.

An attempt was made to obtain information on the duration of ovulation in the sow under anaesthesia. A Large Black sow, weighing 420 lb., was put on limited rations for some three weeks to reduce condition somewhat. When in oestrus for 42 hours, being the period when ovulation could reasonably be expected to set in for this breed, she was anaesthetised per rectum by the administration of four ounces of chloral hydrate in nine pints of warm water, given in small doses. She was starved for 22 hours before being operated on. A laparotomy was performed on the right flank, the peritoneum sutured to the skin and some adipose tissue removed. The ovary was very deep-seated and had to be lifted for each observation. The organ was handled with great care and was allowed to withdraw into position after each examination, and covered by the intestines The wound was closed between observations by means of tape sutures passed through the skin. The region of the wound was kept warm with hot moist towels.

On exposing the ovary at 6·30 a.m. one follicle had already ruptured. The body was dark red in colour and collapsed, indicating very recent ovulation. Thereafter observations were made every fifteen minutes, the findings at the various time-intervals being presented in Table 9.

TABLE 9.

Duration of the Rupture of the Follicles of the Right Ovary in the Large Black Sow under Anaesthesia.

Time.																				
?			6 a.m.			7 a.m.				8 a.m.				9 a.m.						
	—	—	30	45	00	15	30	45	00	15	30	45	00	15	30	45				
A		[									B									

Time.																				
10 a.m.					11 a.m.				12 noon.				—							
00	15	30	45	00	15	30	45	00	15	30	45	—								
C				D	E	F		GH]				I and J								

* The letters inside the brackets indicate follicles which ruptured during the observation.

The sow died at 2 p.m., after having been under anaesthesia for eight hours.

The colour of the follicles varied from the usual seashell pink to a very light red. At each examination a decided deepening in the red colour of the follicle about to rupture was noticeable, and none ruptured without first going through the range of hues from light red to dark red. Papillae were not observed as described for the rabbit by Walton & Hammond (1928). Rupture could only be ascertained from the collapsed state of the bodies and the presence of a red liquid over their surfaces. The two last follicles never ruptured, possibly due to the fact that the sow was already *in extremis*, but both had reached the dark-red stage, indicative of imminent rupture. After death the left ovary was removed and all follicles found ruptured. The fresh-formed corpora lutea had

diameters of 5 to 6 mm. and their points of rupture were light red to purplish-coloured. Some were already conically shaped, indicating corpora lutea some hours old, whereas others were still partially collapsed, showing very recent ovulation. The corpora lutea I, from this undisturbed ovary, were smaller and much lighter-coloured than those in the one under observation, which were very congested and dark red. This shows that even with the careful handling practised the technique should have been better.

Unfortunately one follicle had already ruptured when the observation began and two never ruptured, so that the picture remains incomplete. The rupture of seven out of ten follicles was found to occupy a period of three and a half hours. Only in one instance did two ovulate during the same interval of fifteen minutes. The condition of follicle A showed that rupture had occurred just prior to exposure of the ovary at 6.30 a.m. It may, therefore, reasonably be assumed that ovulation occurred at or about 6.00 a.m. Furthermore, on the evidence that five out of the last seven follicles had ruptured in quick succession within one hour, it would appear that the remaining two, which failed to reach the climax, would normally have ruptured within half an hour at the utmost after G and H, that is, at or about 12.30 p.m. On these assumptions it can be taken that ovulation would have occupied a total period of approximately six and a half hours. This observation could unfortunately not be repeated.

The Corpus Luteum I during Oestrus.—Sizes of the corpora lutea I during the ensuing oestrus appear in Appendix 2, Table II. The analysis of variance of this data is presented in Table 10.

TABLE 10.

Analysis of Variance: Sizes of Corpora Lutea I in Large Black Pigs at Consecutive Six-hour Intervals during the ensuing Oestrus.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods	7	183·30	26·19	29·18	SS
Error	105	94·23	0·90	—	—
TOTAL	112	277·53	—	—	—

Summary of Sizes in Millimetres.

Period, Hours.	Mean Sizes.	Mean Differences.	Significance.
0	6·78	—	—
6	7·42	+0·64	SS
18	6·40	—1·02	SS
24	6·55	+0·15	ns
36	6·36	—0·19	ns
42	5·62	—0·74	SS
48	4·33	—1·29	SS
54	3·35	—0·98	SS

The analysis shows that the sizes of the corpora lutea I differ highly significantly at the various six-hour intervals over the ensuing oestrus. The data in Table 2 (b) show that, over the period of oestrus, the corpus luteum I undergoes a highly significant reduction in mean diameter. The significant increases at zero and the 24th hour are undoubtedly due to normal variation in size and cannot be considered as of any moment. Over an interval of $2\frac{1}{4}$ days the corpus luteum I is reduced from a mean diameter of 6.78 mm. to 3.35 mm., showing a regression of 50 per cent. If the mean diameter of 9.58 mm. at the 18th day of the cycle be considered, calculation shows that an involution of 65 per cent. in mean size is registered over a period of $4\frac{1}{4}$ days (vide Fig. 3).

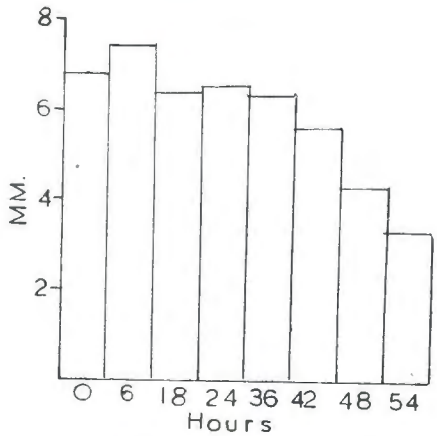

FIG. 3.—Mean sizes of corpora lutea I during the ensuing oestrus.

The Immature Follicles during Oestrus.—The study of the follicle in Observation 1 terminates at the eighteenth day of the cycle. In this study the thread is again taken up at the onset of the next oestrus, leaving a hiatus of roughly two days, if a 20 day ovarian cycle is assumed.

Descriptions of the immature follicles during oestrus are found in Appendix 2 and a summary of their numbers and size ranges is presented in tabular form in Appendix 2, Table 1.

The immature follicles are so small over the oestrous period that nothing like a reliable count of their total number is possible. By far the largest percentage of these bodies now fall into the 1 mm. and smaller class, and maximum diameters of 2 to 3 mm. have become exceptional. Reference to Appendix 2 will reveal that this group of follicles is repeatedly referred to as: "too small to count", "a few visible of up to 1 mm.", "inconspicuous", etc. Furthermore, in nearly every instance "only a few" were involved in the 2 to 3 mm. size class, and only in rare exceptions did a limited number show diameters of 4 to 5 mm. An approximate count of the total population was possible in only a few instances. The fairly high total number of 110 follicles was encountered in only one case (Large Blacks, 42 hour interval), the remaining five estimates ranging from 22 to 47.

The Mature Follicle during Oestrus.—Sufficient material for statistical treatment was available for Large Blacks only. Sizes of mature follicles during oestrus appear in Appendix 2. Table III and the analysis of the data is presented in Table 11.

TABLE 11.

(*a*)

Analysis of Variance: Sizes of Mature Follicles in Large Black Pigs at Consecutive Six-hour Intervals during Oestrus.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Periods	7	31·30	4·47	4·38	SS
Error	101	103·19	1·02	—	—
TOTAL	108	134·49	1·25	—	—

(*b*)

Summary of Mean Sizes in Millimetres of Mature Follicles.

Period, Hours.	Mean Sizes.	Mean difference.	Significance.
0	8·17	—	—
6	8·86	+0·69	SS
18	9·89	+1·04	SS
24	9·42	—0·47	ns
36	8·86	—0·56	ss
42	9·36	+0·50	ns
48	9·14	—0·22	ns
54	8·50	—0·64	ss
Mean	9·03	—	—

The variance analysis shows that the mean diameter of the mature follicle differs highly significantly at the different six-hour intervals during oestrus. Examination of the data in Table 7 (*b*) shows that the main contribution to this condition is due to an increase in size up to and including the 18-hour interval. Thereafter follicle sizes show a random variation from one period to another, which in two instances may be significant. Small period effects are, however, largely confounded with individuals and, since there appears to be no general tendency, these latter inter-period variations are probably of no moment.

Discussion.

Although a fair amount of work with regard to the time of ovulation in the sow has been undertaken in various countries, in no single instance could the writer, from the literature at his disposal, find any reference to breed differences in respect of the time of ovulation. The records reveal that in many instances material was drawn from abattoirs, apparently of non-descript breeding, or otherwise no mention of breeds is made by authors; only in rare instances are breeds specifically mentioned. Comparative work on breeds could not be traced. From the vast amount of work now accumulating, considerable differences have been revealed in the physiology of sex between the many breeds in the same species of farm animals. It is therefore not surprising to find a significant difference with

regard to the time of ovulation between the two breeds of pigs under discussion. This observation shows that, in the Large White sow, ovulation may be expected at any time from the 18th to 36th hour of oestrus and from the 42nd to the 54th hour in the Large Black sow. The time of rupture of the follicle is related to the mean duration of oestrus, so that ovulation will be later in the individual or breed having a longer oestrous period. Calculation has shown that for every 7·80 hours extensions of the duration of oestrus, ovulation is similarly extended by 6 hours. With the exception of two Large White sows, which ovulated during the 18-hour period and which had an over-all mean duration of oestrus of 39·5 hours, all females ovulated well into the second half of the oestrous period. Ovulation can be said to be completed at the middle of the second day of oestrus in the Large White breed of pig, and at the beginning of the third day in the Large Black breed.

The retarding influences of anaesthesia and handling of ovaries on the ovulation time-spread, cannot easily be gauged. That ovulation is not simultaneous is definitely proved by the finding that 11 out of 28 animals, examined within the ovulation intervals of the two breeds, showed ruptured and unruptured follicles on the same ovary at the same time. In the sow under anaesthesia it was observed that it requires about two hours for the collapsed follicles to become distended and to assume a spherical shape again. Observations on the abovementioned females have revealed instances in which there were present at the same time corpora lutea of recent origin, already conically shaped and protruding prominently from the body of the ovary; others were in a collapsed state, indicating very recent rupture, whereas some follicles were still unruptured. Such conditions, therefore, indicate that the above estimate of a time-spread of ovulation of $6\frac{1}{2}$ hours, can be considered a fairly reliable one. This finding, therefore, disagrees with that of Corner's (1921) and the difference is no doubt due to differences in technique. In this observation the onset of oestrus was known correctly to within three hours, and slaughterings were timed so as to synchronise with the ovulation intervals, two aspects which were apparently not observed by Corner. The conclusions of Walton and Hammond (1928) from their researches on the rabbit, are confirmed for the sow also, excepting that ovulation in the pig apparently occupies considerably less time than in the rabbit.

The results have shown that the corpus luteum I is at its smallest after ovulation. Thereafter it steadily increases in size till an over-all maximum mean diameter of 10·85 mm. is reached at the fifteenth day of dioestrus, after which it regresses to 9·58 mm. at the eighteenth day, or two days before oestrus. In Large Blacks the mean diameter of the corpus luteum I is 8·50 mm. at the eighteenth day and 6·78 at the onset of oestrus (comparative data for Large Whites are lacking). This represents an involution of 20 per cent. over the two days of pro-oestrus. The greatest reduction in size, however, occurs during oestrus when the mean diameter is reduced by 50 per cent. over $2\frac{1}{4}$ days. The most pronounced regression during this phase is reflected between the 42nd and 48th hour of oestrus, which coincides with the period of rupture of the follicles in this breed. There is, apparently, no literature bearing directly on this point relative to the pig. This condition is, however, similar to that in the ewe, as demonstrated by Quinlan and Maré (1931), who found that the corpus luteum I experiences a more rapid atrophy during the time of and immediately subsequent to ovulation.

No support could be found for the assumption that eliminative forces operate on the immature follicles as dioestrus advances (McKenzie, 1924, 1926; Allan *et al.*, 1924; etc.) Observation nevertheless confirms the general consensus of opinion of authors that an appreciable reduction in numbers of this class of

follicles does occur immediately before and during ovulation. This process is, however, only partial. That complete elimination of immature follicles does not take place during oestrus is supported by the finding in this study. In no single instance was an ovary encountered during oestrus without at least a fair number of immature follicles being present. During interoestrus the ovaries carry large numbers of follicles, averaging 86 over the two breeds, the majority being plainly visible and above 1 mm. in diameter. However, a remarkable reduction in mean diameter of these bodies, not destined for immediate ovulation, is revealed over the short interval of from two days before oestrus to oestrus. During this period they are reduced to such small dimensions that any attempt at a macroscopic estimate of the population becomes extremely unreliable or impossible. The vast majority now fall in the 1 mm. and smaller class and are barely visible.

During the pro-oestrous phase the set of follicles, selected to reach maturity, undergoes rapid enlargement and now becomes demarcated from the rest of the population. The maturing group rises from a mean diameter of 5·68 mm. at the eighteenth day of the cycle to a maximum mean of 9·9 at the eighteenth hour of oestrus in Large Blacks.

The general position in the normally functioning ovary therefore seems to be as follows: During oestrus there are present two distinct sets of follicles, namely, a lesser group fully matured and destined for immediate ovulation, with a mean diameter of 9·03 mm,, and a much larger group of immature follicles, usually not measuring above 2 mm., the majority being 1 mm. and less in diameter. Immediately after oestrus and ovulation a gradual increase in size among the immature follicles takes place, so that the majority of visible follicles are between 1 and 3 mm. in diameter during the interoestrous period. As early as the third day of dioestrus a fair mumber of follicles start to grow more rapidly than the rest, enlarging up to an average of 6·59 mm. at the 18th day of the cycle. It is from among this latter group that those follicles intended for maturation and rupture are apparently finally selected. During interoestrus no apparent reduction in the visible numbers of follicles occurs. During oestrus, however, the total number of visible follicles is decreased considerably, but, as the majority have now been reduced to such small dimensions, the observed reduction in total numbers may be more apparent than real.

The general colour of the mature Graafian follicle is seashell pink (Ridgway, 1912), a hue which is already assumed by the larger individuals at the beginning of dioestrus, although the general tone is much less intense during the early stages. A very fine network of bloodvessels is spread over the surface, being generally clearly visible against an almost transparent background. Congestion of the arterial system and the extravasation of blood into the follicle, resulting in haemorrhagic follicles, are of frequent occurrence. Well-advanced follicles are always fully distended. A very transparent nature of the capsule at the apex is an indication of imminent rupture. Large size is not necessarily a corollary of maturity, as follicles much smaller than their mates, showing every indication of rupture, were frequently encountered. Diameters, varying as much as 3 and even 4 mm. among the same group of mature follicles, are not unusual. It is not intended to discuss the mature follicle further in greater detail, as the writer's observations on the pig closely agree with the descriptions given by various authors, especially those of Hammond (1928) for the rabbit, Grant (1933) and Quinlan *et al.* (1931) for the ewe and Corner (1921) for the sow.

Summary and Conclusions.

1. Rupture of the Graafian follicle occurs from the 18th to the 36th hour of oestrus in Large Whites and from the 42nd to the 54th hour in Large Blacks. The time of ovulation is correlated with the duration of oestrus.

2. Rupture of the Graafian follicles in the sow under anaesthesia appears to occupy about 6½ hours.

3. In the Large Black breed the corpus luteum I has a mean diameter of 6·78 mm. at the beginning of the ensuing oestrus and 3·35 mm. at the end thereof; this represents a reduction of 50 per cent. in mean diameter.

4. The majority of immature Graafian follicles during oestrus are 1 mm. and less in diameter, diameters of 3 to 4 mm. being exceptional. The total number of follicles appears to be less during oestrus than during interoestrus.

5. The mean diameter of the mature Graafian follicle during oestrus is 9·03 mm.; maximum size appears to be reached during the first half of the oestrous period.

Observation 1 (*c*).

The Morphological Changes of the Ovary during Pregnancy.

Object.

The object was to study the morphological changes of the ovary during pregnancy, with special reference to the corpus luteum and the Graafian follicle.

Material and Method.

Five Large Black and five Large White sows were settled to the boar. At intervals of three weeks one pregnant sow from each breed was killed, making five periods in all over pregnancy. In order to obtain comparative information on the changes in the ovary immediately following parturition, one female from each breed, killed after completion of her postpartum oestrus, was included in this observation, thus adding a sixth interval. These latter gilts were drawn from the material in Observation 1 (*d*). The animals were all gilts with the exception of Large Black No. 116, which had reared one litter, and Large Black No. 18, which had reared six litters (Appendix 3, Table I). The technique followed in killing the animals and examining the ovaries was similar to that described in Observation 1 (*a*). Owing to unavoidable circumstances it was not always possible to kill all animals at the expiration of the exact time-interval. This applies especially to Large Black No. 116, killed at 25 days instead of 21 days and Large White 148, killed at 16 instead of 15 weeks. It is, however, assumed that the time differences are too small to be of any consequence.

Literature.

Corner (1915, 1921) claimed that, in the pig, the corpus luteum of pregnancy continues to enlarge up to the third week, when a maximum size of 10 to 11 mm. is reached and that the corpus luteum of pregnancy is slightly larger than the corpus luteum of oestrus. The corpus of pregnancy and that of oestrus, he stated,

cannot be distinguished during the first two weeks; the life of the corpus luteum lasts throughout pregnancy. Hammond (1917) wrote that (in the rabbit) "... the further development of the corpus luteum, which takes place during the latter part of pregnancy, is due to the influence of the fetus". Grant (1933) reported that, in the ewe, the corpus luteum of pregnancy seems to undergo slight degeneration at about the 14th day, that is at about the same time that atrophy of the corpus begins in the non-pregnant ewe. The size remains about the same as that of the corpus luteum of oestrus, retrogressing at 2 to 3 weeks before parturition. Quinlan and Maré (1931) working on the Merino ewe reported: "The corpus luteum I changes rapidly in size during the earlier hours of oestrus, and its colour gradually takes on a yellowish tinge. More rapid atrophy still appears to take place towards the time of and immediately subsequent to ovulation, accompanying the progressive stage of the more recent corpus luteum". Marshall (1922) stated that if conception follows ovulation, the corpus luteum continues to increase in size until almost the middle of pregnancy. Long and Evans (1922) found that, in the rat, no difference in size between the corpus luteum of oestrus and that of pregnancy is evident till the middle of pregnancy, but thereafter continued slow growth permits of dimensions never attained by the corpus luteum of oestrus. At the end of gestation marked changes in lipoid globules in the lutein cells are evident, indicative of cessation or diminution of function. Hammond (1927) quotes Marcotty (1914) to the effect that, in women, the corpus luteum of pregnancy only equals in size the maximum stage of the periodic corpus luteum. In the same publication he produced comparative data by himself and other authors to prove that it is generally agreed that, in the cow, the corpus luteum is slightly larger during the latter half of gestation than during the cycle and that this size is maintained throughout pregnancy.

No literature, bearing directly on the history of the follicle in the sow during pregnancy, could be traced. Hammond (1927) wrote that although, in the cow, the presence of an active corpus luteum during pregnancy does prevent the pro-oestrous increase in size of the Graafian follicle and the subsequent ovulation, it does not necessarily prevent a general increase in size of these bodies during this period. He claims that follicular atrophy is greatly increased during pregnancy in the cow. Küpfer (1920), as quoted by Hammond, found that in the cow the number of visible follicles decreases toward the middle and end of pregnancy. Aitken (1926), Cole *et al.* (1931) and Andrews and McKenzie (1941) all agree that, in the pregnant mare, the ovary continues to produce follicles up to the fifth month and that ovulation may even result during this period (Cole *et al.* 1931). After the fifth month till the end of pregnancy the production of follicles apparently ceases completely. Robson (1940) remarked that "... the final growth and ovulation of a selected group of follicles . . . is accompanied by the destruction of all remaining follicles". Waves of follicular maturation, he states, may continue even during pregnancy, though the final maturation stages and ovulation do not occur and all follicles undergo atresia.

Results.

Detailed descriptions of the morphological appearances of the ovaries of the pregnant sow slaughtered for this observation appear in Appendix 3. Numerical data, with regard to corpora lutea, etc., are presented in tables to be referred to in the text.

The Corpus Luteum of Pregnancy.—Sizes of the corpora lutea of pregnancy, appearing in Appendix 3, Table I, have been subjected to an analysis of variance, the results being presented in Table 12

TABLE 12.

(*a*)

Analysis of Variance: Sizes of Corpora Lutea Gravitatis in Large Black and Large White Pigs at Consecutive Three-week Intervals.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Intervals.....	5	307·23	61·45	88·61	SS
Breeds.....	1	46·37	46·37	66·87	SS
Interaction.....	5	8·97	1·79	2·59	ss
Error.....	170	117·89	0·69	—	—
TOTAL.....	181	480·46	2·65	—	—

(*b*)

Summary of Mean Sizes in Millimetres of Corpora Lutea Gravitatis at Consecutive Three-week Intervals.

Intervals, Weeks.	Large Blacks.	Large Whites.	Mean.	Mean difference.	
3.....	9·62	8·50	8·93	—	—
6.....	11·78	9·70	10·68	+1·75	SS
9.....	11.30	9·65	10·20	—0·48	SS
12.....	10·44	10·29	10·35	+0·15	ns
15–16.....	10·79	9·88	10·29	—0·06	ns
Postpartum.....	6·89	6·65	6·73	—3·56	SS
Breed mean (exclusive of postpartum).....	10·68	9·62	10·04	1·06	SS

The analysis shows that both intervals and breeds differ highly significantly and that the reaction of the two breeds over the various intervals differ significantly. Table 12 (*b*) shows that the corpus luteum has the smallest over-all mean diameter (8·93 mm.) at the third week of pregnancy. A highly significant increase in size is revealed as between the third and sixth weeks, at which latter interval the corpus also attains its maximum diameter (10·68 mm.). From the sixth to the ninth week interval a highly significant decrease is reflected, but from this latter interval up to the end of gestation the size of the corpus remains static. The breed difference, in respect of the interval at which maximum diameters are shown, should be considered as tentative in view of the fact that each interval is represented by only one individual from each breed.

Reference to Table 2 (*b*) will show that the maximum mean diameter of the corpus luteum at the fifteenth day of dioestrus is 10·85 mm., which therefore actually exceeds the maximum of 10·68 mm. attained at the sixth week of gestation The general mean diameter (9·49 mm.) over the entire dioestrous period is slightly less than during pregnancy (10·04 mm.). It is further of interest to note that, whereas the mean size of the corpus during dioestrus is significantly larger in Large Whites than in Large Blacks, the position of the two breeds is reversed during pregnancy. It remains to be recorded that one Large

White sow, No. 66 (vide Appendix 3), died while in the act of farrowing, after having delivered eight live piglets and one mummy. She was opened and a further nine undelivered normal piglets and one mummy were found in the uterus. The cause of death could not be diagnosed positively, but she had escaped from her pen on the night previous to farrowing, so that probable injury, coupled with exhaustion in endeavouring to give birth to a litter of 17 piglets, might have been the cause. So that, even though this sow might probably have been abnormal and cannot therefore be considered, it is of interest to note that her corpora lutea resembled the normal type in detail, averaging 10·2 mm. in diameter and ranging from 8 to 11 mm. Vascularisation was distinct and profuse.

The Follicle during Pregnancy.—In order to determine whether any growth of the follicle occurs during pregnancy. all the largest individuals on each ovary were measured to within half a millimetre and listed in Appendix 3, Table II. Selection was confined to the largest follicles falling within a range of roughly 2 mm. Analysis of variance, as applied to this data, is presented in Table 13.

TABLE 13.

(*a*)

Analysis of Variance: Sizes of the Largest Follicles at Three-weekly Intervals during Pregnancy in Large Black and Large White Sows.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Intervals	5	124·97	24·99	43·90	SS
Breeds	1	15·20	15·20	26·70	SS
Interaction	5	11·00	2·20	3·86	ss
Error	271	154·29	0·57	—	—
TOTAL	282	305·46	1·08	—	—

(*b*)

Mean Sizes in Millimetres of the Largest Groups of Follicles in Large Black and Large White Sows at Three-weekly Intervals during Pregnancy.

Interval, Weeks.	Large Blacks.	Large Whites.	Interval	Mean differences.	Significance.
3	4·31	4·63	4·52	—	—
6	4·84	5·80	5·36	+0·84	SS
9	5·05	5·27	5·18	—0·18	ns
12	4·17	4·71	4·39	—0·79	SS
15–16	2·87	3·60	3·24	—1.15	SS
Postpartum	4·92	4·34	4·66	+1·42	SS
Mean (exclusive of post-partum)	4·27	4·88	4·60	0·61	SS

According to this analysis, breeds and intervals differ highly significantly and the two breeds react significantly different at the various intervals.

The data in Table 13 (*b*) show that, from the third to the sixth week of pregnancy, the increase in mean diameter of the follicle over the two breeds is highly significant. After the sixth week consistent decreases in size are registered between succeeding three-weekly intervals, the majority of which are highly significant, up to and including the 15-16th week stage. As from about one week prepartum to four days postpartum a sudden and highly significant increase in mean diameter takes place. The mean size (4·66 mm.) four days after farrowing, does, however, not yet equal to the largest size (5·36 mm.) during pregnancy. Maximum mean size is shown at the sixth week and the degree of regression from this stage to one week before parturition amounts to 39·5 per cent. The two breeds show identical trends, except that maximum size is attained at the sixth week in Large Whites and at the ninth week in Large Blacks. The significantly larger size of the follicle in the Large White sow during dioestrus also obtains during gestation. The general appearance of the follicle during pregnancy and during the cycle is similar.

With reference to the Large White sow No. 66, previously mentioned, which died during parturition, it has to be pointed out that her ovaries carried a total of 10 follicles, distinctly larger and more advanced than the rest. These resembled the mature state during oestrus very closely, the only difference being that their mean diameter was 6·3 mm., instead of the established mean of 9·03 mm. for the mature follicle. Whether or not these follicles would have enlarged with ultimate rupture at postpartum oestrus, or would have regressed is, of course, impossible to predict. This apparent departure from the general finding is recorded even though the sow was probably abnormal.

Follicle Number during Pregnancy.—The total number of follicles in the ovaries, visible to the naked eye, were counted, the mean of at least two counts being recorded. As the smallest groups in many instances were below 1 mm. and were barely visible, the numbers appearing in Table 14 should be considered as approximations only.

TABLE 14.

Approximate Number of Visible Follicles per Sow at Three-weekly Intervals during Pregnancy.

Interval.	Large Blacks.	Large Whites.	Interval Mean.
3 weeks	116	108	112·0
6 weeks	77	73	75·0
9 weeks	181	109	145·0
12 weeks	75	110	92·5
15–16 weeks	135	91	113·0
Postpartum	54	37	45·5
Mean (exclusive of postpartum)	116·8	98·2	107·5

The period means over the two breeds seem to indicate alternating peaks and throughs, strongly suggestive of regular waves of increases and decreases in follicle number during pregnancy. It will be observed that the over-all means at the third and the fifteenth to sixteenth weeks are almost identical, namely, 112 and 113 respectively. This condition, therefore, reveals no eliminative tendency of the follicle as pregnancy advances. The data do, however, show that the population is materially reduced from the 15th to 16th week of pregnancy to about four days postpartum. This reduction amounts to 59 per cent.

Discussion.

By comparing the results obtained in this study with those in Observation 1 (*a*), it is revealed that the maximum mean diameter attained by the corpus luteum of pregnancy (10·68 mm.) is less than that of dioestrus (10·85 mm.). The difference, however, is insignificant. Slightly larger diameters during pregnancy than during the cycle have been recorded only in the case of the Large Black breed. The data over the two breeds do, however, not support those writers who claim that growth continues during the latter half of pregnancy, or that the corpus is necessarily larger during gestation than during the cycle (Corner, 1915, 1921, for the pig; Long and Evans, 1922, for the rat; Hammond, 1917, for the rabbit and Hammond, 1927, for the cow). Generally speaking, however, Corner's findings have been confirmed by this study. The results do show that maximum diameters are reached at an earlier stage during pregnancy than during the cycle. Maximum size is reached the sixth week of pregnancy, if the two breeds be considered jointly. Breed variation in this respect is probably of no moment. It is of importance to note that, although maximum size is reached at the sixth week, regression thereafter is arrested so that the corpora remain large right up to the end of gestation. The general morphological condition of the corpora lutea of pregnancy definitely shows that they remain functional over the whole period but atrophy rapidly immediately after parturition. This contention is further supported by the fact that the corpora of one sow, which died during the act of delivering her litter, still had a mean diameter of 10·2 mm. Within a period of four days from parturition, the dimensions of the corpus luteum is reduced from a mean of 10·29 mm. to 6·73 mm., that is an involution of 34·6 per cent.

The general appearance of the corpus luteum of pregnancy does not differ from that of oestrus, both externally and on section. Small central cavities with fluid inclusions were encountered at the third and sixth week intervals in only two out of ten sows. Four days after parturition the usual light flesh colour of the cut surfaces of these bodies is transformed to a creamy yellow.

The only literature, relative to the follicle during pregnancy, that could be traced, refers to the cow and the mare. In the cow a gradual increase in follicular size during pregnancy may occur, but atrophy is greatly increased during this period (Hammond, 1927). The number of visible follicles decreases beyond mid-term (Küpfer, 1920). It seems to be generally agreed that, in the mare, follicles are being produced during the first five months of pregnancy, after which further production ceases (Aitken, 1926; Cole *et al.*, 1931; Andrews and McKenzie, 1941).

The results of this study show that, in the sow, as in the mare and cow, the follicle experiences a growth phase during approximately the first half of pregnancy, attaining maximum sizes at 9 weeks in the Large Black sow and at 6 weeks in the Large White sow. Beyond these intervals a progressive reduction in size sets in, which continues unchecked down to the threshold of parturition. The data, however, show that four days after farrowing the follicle has again entered into a new trophic phase, but does not at that stage regain the maximum size which obtained during pregnancy. The size of the follicle, three weeks after conception, approaches very closely to that at the 15th day of dioestrus. It may, therefore, be assumed that the growth of the follicle in the pregnant sow, during the first three weeks, follows much the same course as during the first 15 days of the normal cycle. The average size of the follicle during pregnancy, as during dioestrus, continues to be significantly larger in the Large White than in the Large Black breed. Even though reductional changes in follicular dimensions, as pregnancy advances, seem to be indisputable, there is no evidence that in the sow,

as in the mare and cow, new follicles cease to be produced during the latter half of pregnancy. In fact, in the Large Black sow, the count of 135 follicles, one week before parturition, was exceeded only once and that at the 9th week of pregnancy. In the Large White breed the count of 91 follicles, two days before farrowing does not differ materially from the maximum number of 110 at the 12th week. This observation, therefore, clearly shows that eliminative forces do not operate on the follicle during pregnancy, in so far as total number is concerned. However, a reduction in follicle number between parturition and four days post-partum is strongly suggested by the data. The largest follicles nearly always show the same seashell pink colour as the mature ones during oestrus. Faint vascularisation was visible occasionally and then only on the larger follicles. The majority measured below 3 mm., ranging down to 1 mm. and less.

Observation 1 (*d*).

The Morphology of the Ovary Immediately after Postpartum Oestrus.

Object.

The object of this observation was to study the general morphology of the ovary immediately after the cessation of the postpartum oestrus.

Material and Method.

A great dearth in Large Black females at the time of this study prevented the use of an equal number of animals in each breed, hence only two Large Black sows were killed as against six Large White sows. About ten days before the sows were due to farrow they were brought in from free range on lucerne grazing to the farrowing pens. Green feed was provided in abundance and 60 to 70 per cent. of their restricted concentrate allowance consisted of wheaten bran, to guard against constipation so common to pregnant sows at this period. The sows were closely watched as the time of farrowing approached, unbroken attention being provided during the entire event. As soon as the sow began to move about freely in her pen after farrowing, she was tested regularly for the presence of oestrus. The animals were killed the day following the cessation of oestrus, excepting Large Black No. 202 (Appendix 4, Table I), which was slaughtered one hour thereafter. Large White No. 178, and Large Blacks Nos. 202 and 214, conceived during their puberty oestrus, whereas the rest of the females had experienced from three to five oestrous periods previous to conception. They were therefore all first litter sows at the time of slaughter. The duration of the post-partum oestrus was recorded for all females with the exception of Large Black No. 214, whose exact hour of onset and cessation was only approximately known. The corpora lutea were closely examined for evidence of recent ovulation and all ovaries fully described, as recorded in Appendix 4.

Literature.

No reference could be traced in the literature relevant to the appearance of the corpus luteum during or following postpartum oestrus in the pig or any other animal. The only reference is an indirect one by Long and Evans (1922), who found that, in the rat, the corpus luteum of pregnancy brings about the decay and complete resolution of all other corpora occurring in the ovary at the time of conception. Literature on the follicle, during and immediately following post-partum oestrus, does not appear to exist.

Results.

Detailed descriptions of the ovaries of the sows killed for this study appear in Appendix 4, from which certain particulars have been summarised in Appendix 4, Table I. Sizes of the corpora lutea and of the Graafian follicles appear in Appendix 4, Tables II and III.

The Corpus Luteum after Postpartum Oestrus.—The general macroscopic appearance of the corpora lutea at the end of postpartum oestrus and as described in Appendix 4, could be summarised as follows: The mean diameter over the two breeds is 6·5 mm. The shape is spherical and the consistency very firm. There are no central cavities. Faint and indistinct blood vessels were encountered on a few corpora in only two out of the eight pairs of ovaries examined, vascularisation being completely absent otherwise. Externally the corpora are faintly yellow, but on section the colour was almost invariably a deep creamy yellow. In fact the appearance of these bodies at this period agrees almost in detail with that obtaining in the corpora lutea I from the eighteenth day of the ovarian cycle to the end of the cycle.

These results go to prove that the corpora lutea, carried by the ovaries immediately following the cessation of postpartum oestrus, were not of recent origin. They definitely could not be two to three days old, as they would have been had ovulation occurred during that oestrus. The conclusion is unavoidable that these corpora were atrophic and in an advanced state of degeneration and must have originated during an oestrus other than that of portpartum.

No corpora of an older ovulation were encountered other than those from the one under discussion, except that in a few rare instances deep-seated brown-coloured remains only were found on sectioning the ovary. Hence, as in the rat (Long and Evans), all corpora lutea present in the ovary of the sow and not belonging to the ovulation at the time of conception, are completely eliminated during pregnancy.

The Follicle After Postpartum Oestrus.—Appendix 4, Table III, presents the sizes of the largest groups of follicles in the ovaries of the eight sows killed within two days subsequent to the end of their postpartum oestrus. In each ovary all follicles falling within a size range of roughly 2 mm. were measured. Owing to the fact that a fair percentage of the follicles were barely visible, being only 1 mm. and less in diameter, exact counts were impossible. The numbers in Appendix 4, Table I, must therefore be considered as approximations of the actual populations.

Calculation shows that the mean size of the largest group of follicles is 3·75 mm. and 3·77 mm. in Large Whites and Large Blacks respectively. The general mean is 3·76 mm. The largest recorded diameter is 7·0 mm. and that only for one follicle, the greatest majority falling into the 3 to 4 mm. class. The approximate total number of follicles range from 37 to 88 per sow with a mean 60·6. Both in respect of size and number the follicles, after postpartum oestrus, resemble those at the third day of dioestrus very closely.

Discussion.

In a separate observation, discussed below, abortive attempts were made to settle sows to the boar during postpartum oestrus. A study of the ovary during this sexual phase suggested itself.

The literature on the physiology of sex contains frequent references to " silent " oestrus, in which ovulation is not associated with the exhibition of oestrus. On

the other hand, oestrus is invariably regarded as the concomitant of at least a mature state of the follicle, even though ovulation may not result. This has been confirmed for the pig from the evidence of scores of cows, killed during or shortly after the end of normal recurring oestrous periods. However, the corpora lutea on the ovaries of the eight sows slaughtered for this observation, are small, firm, solid bodies, creamy yellow in colour with no blood vessels on their surfaces. This condition is in strong contrast with the large, plump, active corpus with its invariably conspicuous vascularised condition, and light flesh colour on section. The corpora lutea in the ovaries of the abovementioned sows are therefore corpora in an advanced state of atrophy and cannot be classed otherwise than as corpora lutea of pregnancy. It must therefore be concluded that, in the Large Black and Large White breeds of pigs, the sow normally exhibits oestrus shortly after parturition, but that this oestrus is sterile in that it is not associated with the rupture of mature, normal Graafian follicles and the liberation of fertilizable ova.

This finding reveals a unique condition among mammals. An exact parallel in other species does not appear to have been established as yet. In all other mammals, oestrus reappears sooner or later after parturition and, normally conception follows coition. The absence of mature follicles during postpartum oestrus raises the very pertinent question as to the source of the estrogenic hormone responsible for the elicitation of sexual desire. However, as this study is not concerned with the source of the sex hormones, the matter is left to the specialist for his attention and explanation.

Summary and Conclusions.

1. Two Large Black and six Large White sows were killed within 24 hours after cessation of postpartum oestrus, the main object being to determine whether ovulation occurs during this oestrus.

2. At postpartum oestrus the mean diameter of the largest group of Graafian follicles over the two breeds is 3·76 mm. The general condition of the follicle during this sexual phase is similar to that found at the third day of dioestrus.

3. The mean diameter, over the two breeds, of the corpus luteum, 1 to 19 hours after the cessation of postpartum oestrus, is 6·5 mm. The general appearance of the corpus luteum during this oestrus is discussed and classed as the corpus luteum gravitatis.

4. The conclusion arrived at is that, in the Large Black and Large White sows used in these observations and under the climatic conditions of the Western Transvaal, postpartum oestrus is not associated with ovulation and that this oestrus is therefore sterile.

PART 2.

V. Sexual Maturity.

Observation 2.

The Age and Weight of the Gilt at Sexual Maturity.

Objects.

The objects of this observation were to determine the age and weight of the gilt at sexual maturity.

Material and Method.

All the animals used in this test were reared on the "free-range" system, being allowed continuous access to well-established lucerne pasture. As the gilts reached the age of 160 to 170 days they were brought in to the pens, where they were under continuous observation and tested every three hours for the appearance of oestrus by active vasectomised or fertile boars. A three-hourly record was kept of the external condition of the vulva of each gilt as well as her reactions in the presence of the boar. As the sow has a long pro-oestrous period in which she exhibits an increasing interest in the male, and as this condition is associated with a gradual increase in the size of the vulva, the method followed enabled the observer to determine the exact time of the onset of oestrus with great accuracy. All animals were weighed regularly on Friday mornings on empty stomachs. Weights at puberty were estimated from these records. As the date of birth of each animal was recorded, the exact age at puberty was known. The total number of gilts recorded in this observation was 202, comprising 103 Large Blacks and 99 Large Whites. The animals used were those that later had to serve as material for various other studies. With the exception of two gilts (U. 44 and U. 45, Appendix 5), which were purchased from the University of Pretoria when a few months of age, all the females were bred on the Potchefstroom Station. They were reared from 76 litters, so that in the majority of cases variously-sized groups of full sisters were available for observation. The number of gilts from one litter varied from one to nine.

Literature.

The literature is not rich with regard to the exact age of puberty in the pig. Reference to this phase in the sexual life of the pig is usually rather vague, as the following quotations will indicate.

Marshall (1922) made the statement that: "Sows will receive the boar when six months old and sometimes two months earlier". Corner (1921) wrote: "Sexual maturity is attained before the age of one year, sometimes as early as four months, often before the uterus has attained its full adult dimensions. Maturity is characterised by the occurrence of periods of sexual activity . . .". Marshall and Hammond (1937) claimed that: "The sow may attain sexual maturity at as early as four months, but she is not usually mated until six to nine months old". Asdell (1938) advised that puberty is reached at from three to five months, but mating should not take place until six to nine months of age. Kronacher (1927) reported that early maturing breeds indicate their awakening sexual urge at $2\frac{1}{2}$ to 3 months of age by mounting their pen mates, and that gilts very often show oestrus for the first time at four to five months. Long and Evans (1922), from their extensive work on rats, reported that: "... it appears that a superior nutrition need not hasten the establishment of ovarian function". Sutton (1941) claimed that under-nutrition delays sexual maturity in both sexes, and that a deficiency in energy alone results in delayed sexual maturity and irregularity, or cessation, of the oestrous cycle; similar results follow on a protein deficiency. These conditions result from a decreased output of the gonad-stimulating hormone by the pituitary. That an invigorating climate is more conducive to the earlier onset of sexual maturity than a less stimulating one, has been shown by Mills and Senior (1930) and Mills (1932) for women, and by Ogle and Mills (1933) and Ogle (1934) for albino mice. Ogle (1936) has demonstrated experimentally that moist heat suppresses fertility in the male mouse to a marked degree. Mills (1937) wrote that "... there must first be discarded the idea, world-wide and centuries old in its acceptance, that girls mature earlier in the tropics

than in temperate regions. Careful analysis of statistics provides no support for this universally held belief. In fact quite the reverse has been found true, for in those regions of tropical moist heat, where body growth lags most, the menses are found to start distinctly later than in the invigorating temperate zones". Extreme cold has the same influence as tropical conditions. He continues: "We may say with a fair degree of certainty that in both animals and man growth and body development proceed most rapidly in regions of greatest climatic stimulation and that in regions of depressing moist heat there is evident a progressive lag proportional to the depressing effects of the stagnating heat. Sexual maturity (in women) in tropical countries comes fully two years later than in the most stimulating temperate regions". The rate at which heat is lost from the body must be regarded as the chief factor determining body development generally, the role of nutrition being only secondary. There appears to be no relevant data bearing directly on the pig.

Results.

Individual ages and weights at puberty are presented in Appendix 5, Table I. The data have been analysed and the results appear in Tables 15 (*a*) and 15 (*b*).

TABLE 15.

(*a*)

Analysis of Variance: Ages of Large Black and Large White Gilts at Puberty.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Breeds	1	282·55	282·55	0·41	ns
Families	75	89,802·16	1,197·36	1·72	SS
Error	125	86,898·05	695·184	—	—
TOTAL	201	176,982·76	880·51	—	—

(*b*)

Analysis of Variance: Weights of Large Black and Large White Gilts at Puberty.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Breeds	1	15·83	15·83	0·13	ns
Families	75	82,654·30	1,102·06	0·91	ns
Error	125	150,668·77	1,205·35	—	—
TOTAL	201	233,338·90	1,160·89	—	—

The results in Table 15 (*a*) show that breeds do not differ with regard to the age at sexual maturity, but that highly significant family differences exist. Genetic differences between families are therefore responsible for a much greater variability than obtains between breeds. Litter mates do, however, occasionally vary

greatly in ages at puberty, differing by as much as 103 days. It is surprising to observe how often litter mates attain sexual maturity either on the same day or within a period of a few days. Such instances are, among others, to be noted in the following litter groups: Large Blacks Nos. 20-23, 177-179, 206-207; Large Whites Nos. 64-70, 72-76, 188-198 (Appendix 5, Table I).

In view of the results in Table 15 (*a*), family bias has been eliminated in the calculations with regard to age at sexual maturity, as presented in Table 16.

TABLE 16.

The Age at Sexual Maturity.

	Large Blacks.	Large Whites.
Number of observations	103	99
Mean age in days	219·19	216·83
Standard deviation	17·04	21·01
Coefficient of variation	7·8	9·7

As the two breeds do not differ significantly in respect of the age at sexual maturity, the data for both breeds were combined to prepare the frequency distributions presented in histogrammatic form in Figure 4. The mode is 210 and the range 161 to 346 days. The over-all mean age is 218·03 days.

The percentage of gilts attaining sexual maturity in different age-groups is shown in Table 17.

TABLE 17.

Percentage of Large Black and Large White Gilts which Attained Sexual Maturity at the Age of:—

	Per Cent.
6 months and less	14·4
6 to 7 months	42·1
7 to 8 months	24·7
8 to 9 months	14·9
Above 9 months	4·0

The percentages in Table 17 have been calculated from a total of 202 observations, including both breeds. The result shows that 56·5 per cent. of the gilts attained sexual maturity at the age of 7 months and less. Examination of the data in Appendix 5, Table I, shows that there were 56 family groups in which the number of sisters numbered two and more per group, the total number of such sisters being 185. Out of this number 99, or 53·5 per cent., reached the age of puberty either on the same day or within a period of five days.

As the analysis [Table 15 (*b*)] has shown that neither breeds nor families differ significantly with regard to weight at the age of sexual maturity, all observations in each breed were used to prepare the further particulars presented in Table 18. All the data over the two breeds were combined in the preparation of the frequency distribution, as presented in Figure 5.

TABLE 18.

Weight at the Age of Sexual Maturity.

	Large Blacks.	Large Whites.
Number of observations	103	99
Mean weight in pounds	177·64	177·06
Standard deviation	32·54	35·76
Coefficient of variation	18·32	20·19

The means for the two breeds are almost identical, namely, 177·64 lb. for Large Blacks and 177·08 lb. for Large Whites; the mode over the two breeds is 170 lb. and the range 110 to 310 lb. The over-all mean weight is 177·36 lb.

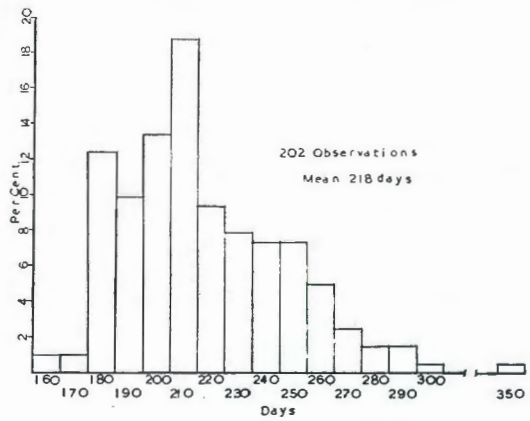

FIG. 4.—Frequency distribution of the age at sexual maturity in Large Black and Large White gilts.

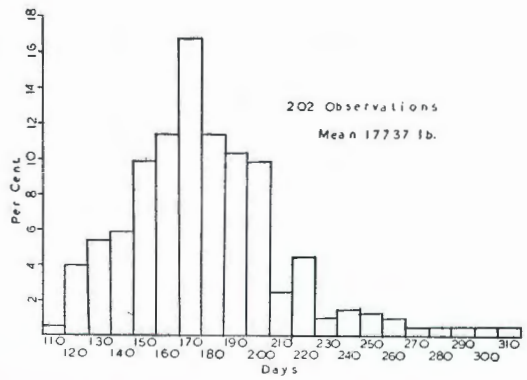

FIG. 5.—Frequency distribution of the weight at sexual maturity in Large Black and Large White gilts.

Under reasonably favourable conditions of feeding and management, an increase in weight of 1 lb. per day on pigs weighing 170 lb. and over could be considered as rather conservative, so that a gilt weighing say, 170 lb. at the age of 180 days, can reasonably be expected to weigh 200 lb. at 210 days, or 7 months of age. Acting on this basis, all gilts listed in Appendix 5, Table I, which had reached puberty at or before 210 days and which weighed 200 lb. or more, or which would ordinarily have weighed 200 lb. at 7 months, were classified in 10 day frequency classes in respect of both age and weight, the result appearing in Table 19.

TABLE 19.

Frequency Distribution of the Weights of 30 *Sexually Mature Gilts Weighing* 200 *lb. or more at* 7 *Months, or Which Would Probably Have Weighed* 200 *lb. at* 7 *months.*

Interclasses (lb.).	AGE INTERCLASSES (DAYS).						
	160	170	180	190	200	210	TOTAL.
170	—	—	2	—	—	—	2
180	1	—	2	—	—	—	3
190	—	—	—	2	5	—	7
200	—	—	1	2	—	6	9
210	—	—	—	—	—	1	1
220	—	1	—	1	1	1	4
230	—	—	—	—	—	—	—
240	—	—	—	—	—	1	1
250	—	1	—	—	—	—	1
260	—	—	—	1	—	—	1
270	—	—	—	—	—	—	—
280	—	—	—	—	—	1	1
TOTAL	1	2	5	6	6	10	30

Under the prevailing conditions of these investigations, feeding was not conducted at optimum levels and no selection was practised. The results in Table 19 nevertheless show that 30 out of 202 sexually mature gilts, or 14·85 per cent. of the population, either actually reached the 200 lb. live-weight level at 7 months of age, or would have attained that weight at 7 months. The number that reached or exceeded the 200 lb. level constituted 8·91 per cent. of the population.

Discussion.

The mean age at puberty over the two breeds of pigs is 218 days or 7 months, 43·6 per cent. of the population attaining sexual maturity at over 7 months of age. Only 14·4 per cent. of gilts reached puberty at 6 months and less, the minimum age being 161 days, or almost $5\frac{1}{2}$ months. The results of this observation therefore disagree appreciably from the findings of authors in Europe and the United States of America (Marshall, 1922; Corner, 1921; Marshall and Hammond, 1937; Asdell, 1938; Kronacher, 1927). Everyone of the five authors quoted refer to the age at puberty as also occurring at 4 months, whereas the extreme minimum recorded in this study was 161 days ($5\frac{1}{2}$ months), and that for only 2 out of 202 individuals.

Obviously, therefore, sexual maturity in the Large Black and Large White breeds of pigs under Western Transvaal conditions, is delayed till a much higher age than under those obtaining in Europe and North America. Although experimental evidence has not been produced by any of the authors quoted with regard to the age at sexual maturity as laid down by them, there are no grounds for doubting their generalised statements. The assumption would therefore seem to be justified that the female pig is much more precocious in the more temperate and stimulating climates of the Northern latitudes than in that of the Western Transvaal, where higher average temperatures and a lower humidity prevail. This finding would therefore seem to support the conclusions reached by other workers in respect of the effect of climate on the age of puberty in women and albino mice (Mills and Senior, 1930; Mills, 1932; Ogle and Mills, 1933; Ogle, 1934; Mills 1937).

The genetic relationship within litters was strong enough to establish significant family differences at the 1 per cent. level with regard to age at puberty. No such family relationship existed in respect of weight at sexual maturity. This finding very strongly suggests that, in the pig, the genetic factors associated with age at sexual maturity are of a rather simple nature.

The pig subsists mainly on expensive concentrate feeds. It is generally recommended at present that gilts should not be bred before the age of eight to nine months. Production costs would therefore be considerably reduced if the age of breeding could be appreciably lowered. The overhead cost associated with maintenance in slow-maturing gilts is a matter of no small importance to the pig breeder. Precociousness in respect of both age and weight at puberty is therefore of practical significance to the bacon producer. Relevant to this argument the present observation has revealed certain interesting points. It was shown that in an unselected herd, such as that used in these studies, 18·9 per cent. of gilts attain breeding age only after eight months, yet 56·5 per cent. of the population becomes sexually mature at or below the age of seven months. Furthermore, there exists a very strong tendency for litter mates to reach sexual maturity within a very brief space of time, the results showing that 53·5 per cent. of sisters attained puberty either on the same day or within a period of five days. The apparently simple genetic constitution of this character should make it a comparatively easy task to eliminate late-maturing and establish early-maturing family-lines by selective breeding. Ample genetic variability certainly does exist on which the breeder could exercise his powers of selective breeding for the production of blood-lines that should mature sexually at the age of six months.

On the other hand, it is generally accepted that in any system of sound pig husbandry, the gilt should not be bred till she has reached a weight of about 200 lb. Early sexual maturity should therefore not be divorced from the propensity to a high rate of growth in the young female. The results have shown that, even though optimal growth-increases in the experimental animals could not be maintained through unavoidable circumstances, it was still possible for 14·85 per cent. of the gilts to weigh 200 lb. and more at or before they were seven months old. Surprising individual exceptions have been recorded: 256 lb. at 187 days, 184 lb. at 165 days, 249 lb. at 171 days, and 316 lb. at 174 days. The ages are those at puberty. Under present-day conditions of high-quality rations and without undue forcing, weights of 200 lb. and more at six months of age are by no means uncommon. This statement is supported by two observations conducted at this Institution. Under the results obtained under Observation 3, reported on below, it has been shown that, in a group of six gilts under optimum feeding conditions, a mean bacon weight of 194·3 lb. was obtained at the mean

age of 188·5 days. In a second observation (not yet published) the writer planned to determine the average amount of feed required to rear a bacon pig from birth to about 200 lb. live weight. Five litters, involving 36 baconers, were used for this purpose. Creep feeding was practised and, after weaning at 8 weeks, they were fed according to appetite. They attained a mean weight of 201·75 lb. at a mean age of 157·36 days.

The opinion is advanced that, by the application of a sound system of inbreeding, coupled with systematic selection for precocity in respect of both sexual maturity and weight-for-age, gilts could be produced which should be capable of being bred at the age of six months instead of the usual eight to nine months. An appreciable reduction in the cost of production to the farmer would be achieved thereby.

Summary and Conclusions.

1. The mean age at sexual maturity is 219·19 days, S.D. 17·04, in Large Blacks and 216·83 days, S.D. 21·01, in Large Whites; the mean difference is non-significant. The over-all mean age is 218·03 days. Families differ highly significantly. The over-all mode is 210 days and the range 161 to 346 days. Between six and eight months 66·8 per cent. of the population attains sexual maturity. Litter mates show a strong tendency to reach puberty at similar ages, 53·5 per cent. of sisters becoming sexually mature either on the same day or within 5 days. Puberty under Western Transvaal conditions occurs at a much later age than in the colder European climates.

2. The mean weight at puberty, under the conditions of this study, is: 177·64 lb., S.D. 32·54 for Large Blacks and 177·06 lb., S.D. 35·76 for Large Whites. Neither breed nor families differ significantly. The overall mean weight is 177·36 lb., the mode is 170 lb. and the range 110 to 310 lb. It is suggested that blood-lines, capable of being bred at 6 months of age, should be established through selective breeding.

Observation 3.

The Influence of Retarded Growth on the Age at Sexual Maturity.

Object.

The object was to determine the influence of retarded growth on the age at sexual maturity in the gilt.

Material and Method.

The observation was planned to include 14 weaner gilts. Seven of these were to be fed *ad lib.* on a balanced ration; the other seven were to receive limited quantities of the same ration. As it has already been shown under the previous observation that breeds do not differ in respect of the age at puberty, breeds were ignored in this study. The age at puberty has been shown to be just about seven months (218·03 days). Under South African conditions a live weight of 200 lb. at seven months of age is easily obtained. It was therefore decided to restrict the feed intake for the controlled group so as to attain a mean weight of 100 lb. at seven months or 28 weeks. That is, growth was to be retarded to about half the rate of the group on unrestricted feeding. A growth curve was used for all gilts and the feed intake of those on restricted rations controlled so as to obtain

weight increases at the predetermined rate. Pigs were weighed on Tuesday mornings on an empty stomach. The animals were treated for Ascaris worms with oil of chenopodium.

Full sisters were paired off under the two levels of feeding. Each gilt was housed separately and fed individually. In addition to their concentrate allowances all gilts received 5 lb. of skimmilk per day. Fresh lucerne or barley, according to season, was fed to the *ad lib.* group as much as they could clean up, once a day; those on restricted feeding received 2 lb. of green feed per day. The ration employed throughout is given in Table 20. The data on the digestible nutrients are according to the Morrison (1936) tables.

TABLE 20.

Concentrate Ration Fed to all Gilts in the Observation on the Influence of Retarded Growth on the Age at Sexual Maturity.

Ingredient.	Weight. lb.	Digestible Protein. lb.	Total Digestible Nutrients. lb.
Yellow maize meal	80	5·92	67·28
Fishmeal (65 per cent. protein)	5	2·70	3·56
Peanut oil cake meal (45 per cent. protein)	5	2·06	4·17
Lucerne meal	5	0·54	2·19
Bonemeal	3	—	—
Lime	1	—	—
Salt	1	—	—
TOTAL	100	11·22	77·20

The ration has a nutritive ratio of 1:5·9. With the addition of 5 lb. of skimmilk for each pig the nutritive ratio, in the case of an individual receiving 5 lb. of concentrates, for instance, would be 1 : 4·8.

Systematic testing for the presence of oestrus was started only after the age of five months had been reached. Prior to that the condition of the vulvas was noted daily as an indication of the probable appearance of oestrus. The systematic testing was carried out daily at 9 am., active young boars being used as " teasers ".

Results.

Particulars with regard to each gilt are presented in Table 21.

Litters Nos. 1, 2 and 4 were bred at this Station. Litter No. 3 was transferred from the Glen College of Agriculture, Orange Free State, when 68 days old. Litter No. 5 was bred by the Potchefstroom Institute for the Feeble Minded. As gilt No. 1 in litter No. 5 failed to show oestrus up to the age of 330 days, she was considered abnormal and the group discarded. The particular gilt ultimately developed a large abscess on the left hock and had to be destroyed. Her ovaries carried a number of Graafian follicles, measuring about 4 mm. in diameter. One ovary carried three and the other one corpora lutea, all 3 mm. in diameter and of a creamy yellow colour. These corpora probably resulted from a " silent " oestrus some weeks prior to slaughter.

TABLE 21.

Particulars of Gilts in the Observation on the Effect of Retarded Growth on the Age of Sexual Maturity.

Breed.	Litter No.	Date of Birth.	Gilt No.	Weaning.		Puberty.				
				Age Days.	Wght. lb.	Date.	Unrestricted Feeding.		Restricted Feeding.	
							Age Days.	Wght. lb.	Age Days.	Wght. lb.
Large White...	1	11·8·44	1	56	36	23·4·45	—	—	255	129
			3	56	32	2.3.45	203	209	—	—
			4	56	30	28.4.45	—	—	260	131
			5	56	31	24.2.45	197	192	—	—
Large White...	2	7.9.44	7	56	26	23.3.45	197	211	—	—
			8	56	28	3·3·45	177	200	—	—
			9	56	29	1·5·45	—	—	236	118
			10	56	39	27·4·45	—	—	232	116
Large White...	3	20.8.44	75	?	?	19.3.45	—	—	211	107
			76	?	?	2·3·45	194	188	—	—
Large Black....	4	20.9.44	2	62	41	23.4.45	—	—	215	108
			4	62	36	2.3.45	163	166	—	—
Large Black...	5	3.9.44	1	55	40		—	—	—	—
			3	55	38	2.3.45	180	205	—	—
Mean (litters 1 to 4 only)...							188·5	194·3	234·8	118·2

Variance analysis, as applied to the data on ages, is presented in Table 22. Family bias has been eliminated in the calculations.

TABLE 22.

Variance Analysis: the Ages at Puberty of Gilts under Optimum and Retarded Growth.

Component.	D.F.	Sum Squares.	Mean Square.	F.	Significance.
Families.....	3	2,368.4	789·5	6·82	ss
Treatment.....	1	6,440·4	6,440·4	55·66	SS
Error.....	7	809·9	115·7	—	—
TOTAL.....	11	9,618·7	—	—	—

Least significant difference for ages is 14·69 days.

The analysis shows that the difference of 46·3 days between the mean age at puberty of 188·5 days for the optimum growth group, and 234·8 days for the retarded growth group, is highly significant.

Table 21 shows that the group of gilts under unrestricted feeding attained sexual maturity at the mean age of 188·5 days, or roughly 6 months, with an average weight of 194·3 lb., the age range being 163 to 203 days and the weight range 166 tot 209 lb. In the group under restricted feeding the mean age at puberty is 234·8 days, or roughly 8 months, with an average weight of 118·2 lb., the age range being 211 to 260 days and the weight range 107 to 131 lb. The oldest gilt in the optimum growth group is therefore 8 days younger than the youngest gilt in the retarded growth group.

PHOTO NO. 1.—Sows on lucerne pasture.

Discussion.

No reference could be traced from the literature relative to the influence of retarded growth on the age at sexual maturity in the gilt. The only relevant literature would appear to be that contained in a general survey by Sutton (1941), who claims that under-nutrition in animals delays sexual maturity in both sexes.

The results of this study have shown that if growth in the gilt be limited to about half that for ordinary standards, sexual maturity will be significantly delayed. The age of puberty under such conditions will be postponed, on the average, by 46·3 days. According to the rations fed, it is probable that the controlled-fed gilts never suffered from a deficiency of vitamins A, D and G. Deficiencies, however, undoubtedly obtained in respect of all other requirements, especially of protein and total energy. This finding therefore supports Sutton's (1941) claim that under-nutrition delays sexual maturity.

Attention is invited to the fact that the very favourable mean weight of 194·3 lb. was obtained at the mean age of 188·5 days, or just over 6 months, in the *ad lib.* fed group of gilts.

The mean age at puberty of the gilt under optimum conditions of growth, as revealed by this observation, is relevant to the study on the age of sexual maturity, already reported. The results under Observation 2 have shown that, under the conditions obtaining, puberty is reached at the mean age of 218·03 days with a mean weight of 177·36 lb. Under the very optimum conditions of feeding

accorded the one group of gilts in this observation, the mean age at puberty is 29·5 days less and the mean weight 16·9 lb. higher, than that obtained in Observation 2. It would, therefore, appear that the mean age of 218·03 days is not truly representative of the age at puberty under optimum conditions of growth. The mean age at puberty would in all probability have been a few days less than the established mean of 218·03 days, had the general level of feeding been high enough, so that a mean weight of 200 lb. could have been obtained at 7 months. It can, however, be stated with a fair amount of confidence that, on the average South African farm, bacon pigs are well over seven months by the time they reach a 200 lb. live weight. Numerous farmers have informed the writer that they cannot get their baconers to weigh 200 lb. before the age of 8 months. Inefficient rations, and Ascaris worm infection, were almost invariably found to be responsible for such a condition. The mean age of 218·05 days at puberty, coupled with a mean weight of 177·36 lb. could, therefore, be considered as being fairly representative of conditions obtaining in this country.

Summary and Conclusions.

1. One group of six gilts was fed *ad lib.* and one group of six gilts was fed restricted rations, to determine the influence of growth on the age at sexual maturity.

2. Gilts fed at an optimum level attain sexual maturity at a mean age of 188·5 days with a mean weight of 194·3 lb.; whereas, if growth is retarded through restricted feeding so that the gilt reaches a weight of 100 lb. at seven months, sexual maturity is attained at a mean age of 234·8 days with a mean weight of 118·2 lb.

PART 3.

VI. Oestrus and Associated Phenomena.

Observation 4.

Literature.

McKenzie and Miller (1930) measured the width and height of the vulvas of 25 spotted Poland-China gilts, 21 of which were again measured after farrowing and weaning their litters. They found that the vulva begins to swell the ninth to the tenth day before the onset of oestrus and to subside for some 8 or 9 days immediately after oestrus. This is the only available reference in which conclusions were drawn from actual measurements. McKenzie (1926) reported that " . . . about 2 days (0 to 3½ days) before oestrus the vulva had swollen till at the onset of heat . . . the labia had reached a much greater size". With the passing of oestrus the swelling had subsided, the contraction, frequently, being very marked the day immediately following oestrus. McKenzie and Marshall (1912) briefly referred to the pro-oestrous period by stating that it ". . . . lasts for perhaps 2 or 3 days ".

The duration of the oestrous period and the length of the oestrous cycle, as recorded by different authors, are summarized in Table 23.