

OVULATORY FAILURE IN BOVINES

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Good progress has been made during the past two decades in improving the diagnostic methods for detecting the various types of bovine infertility. Nevertheless, the sterility worker is still frequently confronted with cows and heifers belonging to a category variously designated as "repeat breeders", "problem cows", "slow breeders", "hard-to-settle" cows, etc. Vanderplasse (1957) who refers to the condition as "Symptomlose Unfruchtbarkeit", with some justification states that this "Sterilität *sine materia*" is one about which we know nothing or very little.

Reproductive failure due to physiological or functional derangement of ovarian activity is known to be an important cause of poor breeding performance in bovines, and may be present to such a degree as to constitute a herd problem.

Most forms of this physiological infertility are manifested by objective symptoms, notably cyclic irregularities, which attract attention and render diagnosis of the actual type relatively easy. Ovulatory failure, however, is an exception to this rule since it usually presents no visible evidence suggestive of an ovarian aberration. Even palpation of the ovaries per rectum generally fails to reveal the abnormality unless such an examination is carried out a day or two after the animal was known to have been in oestrus.

This type of infertility frequently presents the most puzzling problems to both the owner and the sterility worker, since the oestrous cycle generally runs a normal course, except when the more advanced stage of cystic degeneration has been reached. Notwithstanding this apparent regularity of the cycle and the absence of evident pathology or infection in any part of the genital tract, the fertility of the affected animal is subnormal.

By virtue of its abstruse nature ovulatory failure has not been subjected to intensive research in the past, and information on its prevalence and significance is scanty. Roberts (1957), for instance, states that delayed ovulation has not been studied sufficiently to ascertain its importance, and that it probably does not occur very frequently.

Successful fertilization of the ovum is conditioned by a close co-ordination between the time of insemination or coitus and the time of ovulation, and by the viability of the sperm in the female genitalia. The cow is unique in that ovulation normally occurs only six to fourteen hours after the cessation of oestrus, and since the fertilizing capacity of sperm is lost after a sojourn of 24 to 48 hours in the female genitalia, any undue delay in ovulation will prevent conception, especially if the cow is bred during the early stages of oestrus.

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OBJECTS

Van Rensburg & van Heerden (1953) showed that ovulatory failure is a common cause of functional infertility in mares. Concurrent field investigations in herds with low breeding efficiency not infrequently revealed cases in which palpation of the ovaries showed that ovulation had not yet taken place although the animals concerned were reported to have been in oestrus a day or two previously.

This finding, following on the observations made in mares, prompted the present investigation which aimed at determining—

1. the frequency of ovulatory failure in both dairy and beef herds maintained under normal South African conditions;
2. the types of ovulatory failure encountered;
3. their influence on conception; and
4. possible aetiological factors.

MATERIAL AND METHODS

The observations were made from 1954 to 1958 on the departmental dairy and beef herds at this institute and on its adjacent farm. The dairy herd consists of Friesians, while Afrikaners and a few Afrikaner × Hereford and Afrikaner × Sussex crosses constitute the beef herd.

All the animals are free from tuberculosis, brucellosis and coital diseases, and have been bred exclusively by artificial insemination since 1954.

At first inseminations were done twice daily, at 9.30 to 10.30 a.m. and 2.30 to 3.30 p.m. but the afternoon inseminations were discontinued in 1956.

At the time of insemination ovaries were palpated rectally, and the size and nature of the graafian follicle were noted. This examination was repeated 24 hours later in order to determine whether ovulation had occurred or not. In those in which the follicle had not ruptured palpation was repeated every 24 hours until ovulation had taken place or it was obvious that the follicle would not rupture.

The animals were not kept under constant observation, but were seen daily four to five hours before insemination and palpation of the ovaries, and oestrous females were then noted. The second examination was therefore made at least 28 hours after the commencement of oestrus. On the assumption that the average duration of oestrus is 16 hours in dairy breeds and eight hours in the beef animals, and that the interval between the end of oestrus and ovulation is on an average $10\frac{1}{2}$ hours as determined by Trimberger (1948), it was considered that all those females that had not ovulated within 24 hours after insemination, were showing ovulatory failure. This criterion receives further justification from Trimberger's finding that cows in which oestrus was first observed before 9 a.m. had usually ovulated by 9 a.m. the next day.

In this investigation every diagnosis of pregnancy was based on rectal examination.

RESULTS

In the period covered by this investigation the ovaries of 279 cows were examined during and subsequent to oestrus, the total number of oestrous periods that were observed in this manner being 536.

The data in Table 1 show that in 98 (35.1 per cent) cows and in 140 (26.1 per cent) of the oestrous periods studied ovulation did not occur normally.

TABLE 1.—*The incidence of ovulatory failure*

	Friesian	Afrikaner	Total
Cows examined.....	118	161	279
Cows with normal ovulation.....	74	107	181
Cows with ovulatory failure.....	44 (37.3%)	54 (33.5%)	98 (35.1%)
Oestrous periods observed.....	262	274	536
Oestrous periods with normal ovulation.....	190	206	396
Oestrous periods with ovulatory failure.....	72 (27.5%)	68 (24.8%)	140 (26.1%)

Although the incidence of defective ovulation was slightly higher in the Friesians than in the Afrikaners, the difference between the two breeds was not significant.

The frequency with which the ovaries of individual cows were examined is shown in Table 2. In 143 animals, which represents just over 50 per cent of the total, only one oestrous period of each was studied, but in the remaining 136 the observations covered from two to seven heat periods.

TABLE 2.—*Frequency of ovarian examination of individual animals*

Frequency of examination	Friesians		Afrikaners		Total	
	Number examined	Number with ovulatory failure	Number examined	Number with ovulatory failure	Number examined	Number with ovulatory failure
Once.....	49	6	94	22	143	28 (19.6%)
Twice.....	30	10	35	13	65	23 (35.4%)
Three times..	17	12	23	11	40	23 (57.5%)
Four times..	15	10	5	4	20	14 (70%)
Five times..	2	1	3	3	5	4 (80%)
Six times...	3	3	1	1	4	4 (100%)
Seven times..	2	2	—	—	2	2 (100%)

Obviously the larger the number of periods that are observed in the same animal the greater is the possibility of detecting ovulatory defects in that individual. Thus while only 19.6 per cent of animals examined once showed such abnormalities, all those in which the observations extended over more than five oestrous periods revealed the defect in one or more of the periods studied. Although the latter group comprised only six animals, the overall results justify the conclusion that every cow probably shows one or other type of ovulatory failure at some or other time during her breeding life.

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The significance of this phenomenon is therefore conditioned by the frequency with which it occurs in individual animals. This is illustrated in Table 3 which shows the number of examinations to which individual cows were subjected and the incidence of ovulatory failure.

TABLE 3.—*Frequency of ovulatory failure in individual animals*

Oestrous periods observed	Number of cows			Number of cows showing ovulatory failure			
	(a) Examined	(b) With normal ovulation	(c) With ovulatory failure	Once	Twice	Three times	Four times
Once.....	143	115	28	28	—	—	—
Twice.....	65	42	23	18	5	—	—
Three times..	40	17	23	14	8	1	—
Four times...	20	6	14	5	7	2	—
Five times...	5	1	4	0	1	2	1
Six times....	4	0	4	1	1	1	1
Seven times..	2	0	2	0	2	—	—

This analysis shows, for instance, that of the 40 cows examined during three oestrous periods ovulation occurred normally in 17, but failed in 23. Fourteen of the latter failed only once, eight twice and one three times. The latter animal therefore did not show one normal ovulation in three examinations.

In the records of some individual animals given below, heifer No. 8076 is a good illustration of an animal showing recurrent ovulatory failure and non-interference thereof with the length of the oestrous cycle.

The ovarian idiosyncrasies of the animals with habitual or recurrent ovulatory failure are illustrated by the following breeding histories of some of the affected cows:—

No. 1892.—Friesian, born 18th November, 1945; very poor breeding record, returning repeatedly to the bull, and had produced only three calves by the time she was nine years old at the commencement of this investigation.

9th Nov., 1954.... Oestrus ending in anovulation.

15th Jan., 1955.... Oestrus, inseminated, ovulated within 24 hours.

21st Oct., 1955.... Calved.

24th Jan., 1956.... Oestrus with anovulation.

22nd Feb., 1956.... Ovulation before the end of oestrus.

26th Apr., 1956.... Oestrus terminating in anovulation.

12th Jun., 1956.... Oestrus terminating in anovulation.

No. 5325.—Friesian.

15th Jun., 1955.... Oestrus, inseminated.

16th Jun., 1955.... Ovulated but no conception.

7th Jul., 1955.... Oestrus, inseminated.

8th Jul., 1955.... No ovulation, but follicle ruptured on palpation; no conception.

27th Jul., 1955....	Oestrus, inseminated.
28th Jul., 1955....	Had ovulated; conceived, and calved in April, 1956.
27th Jul., 1956....	Oestrus with anovulation.
16th Aug., 1956....	Oestrus, inseminated.
17th Aug., 1956....	Had ovulated but no conception.
6th Sep., 1956....	Oestrus with anovulation.

No. 8076.—Friesian, born 4th October, 1955.

2nd Aug., 1957...	Oestrus, but only ovulated on 5th Aug., 1957.
21st Aug., 1957....	Oestrus, but only ovulated two days later.
11th Sept., 1957....	Oestrus, but only ovulated two days later.
29th Nov., 1957....	Oestrus, inseminated.
30th Nov., 1957....	Ovulated and conceived.

No. 3880.—Afrikaner, born 19th November, 1948, had only produced one calf up to December, 1954.

15th Jan., 1955....	Oestrus; inseminated, but ovulation delayed for two days; no conception.
7th Feb., 1955....	Oestrus terminating in anovulation.
24th Mar., 1955....	Ovulation before the end of oestrus.
20th May, 1955....	Oestrus; inseminated.
21st May, 1955....	Had ovulated and conceived.
9th March, 1956..	Calved.
7th Oct., 1956....	Oestrus with anovulation.

No. 6386.—Afrikaner, born 4th December, 1952.

17th Jan., 1955....	Oestrus, with ovulation two days later.
8th Feb., 1955....	Normal oestrus and ovulation.
16th Mar., 1955....	Oestrus with anovulation.
4th Apr., 1955....	Oestrus with anovulation.
21st Apr., 1955....	Oestrus with anovulation.
6th Dec., 1955....	Oestrus with normal ovulation; inseminated and conceived.

The nature of ovulatory failure

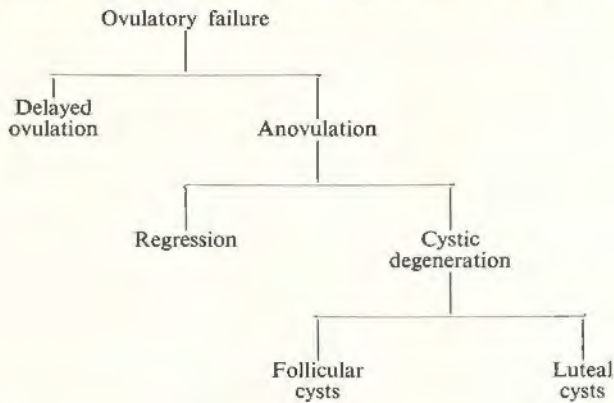
Ovulatory failure may be defined as a condition in which rupture of the graafian follicle and liberation of the ovum either does not occur at all or is postponed for such a period that an otherwise normal female, served or inseminated with normal fertile semen, will fail to conceive, due to non-survival or loss of fertilizing capacity of the sperm in the female genitalia.

The essential feature of this syndrome is failure of the follicle to discharge the ovum within the recognised period post oestrus. This primary and fundamental aberration may then give rise to any one of the following sequelae:—

- (1) Ovulation at an abnormally long period after the termination of oestrus (delayed ovulation).
- (2) Complete failure to ovulate (anovulation). In this case the follicle may either—
 - (i) regress and finally undergo complete atresia, or
 - (ii) develop into a follicular or a luteal cyst.

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The types of ovulatory failure may therefore be classified as follows:—



The classification of the 140 cases of ovulatory failure observed in this investigation and given in Table 4, reveals that in 93 (66 per cent) ovulation was delayed, and that 47 (34 per cent) terminated in anovulation.

TABLE 4.—*Classification of 140 cases of ovulatory failure*

Breed	Delayed ovulation					Anovulation			Total
	Period post oestrus at which follicles ruptured					Re-gression	Cystic degeneration		
	24-48 hr.	48-72 hr.	72-96 hr.	Over 96 hr.	Total		Follicular	Luteal	
Friesian.....	38	6	4	1	49	19	3	1	23
Afrikaner.....	41	1	1	1	44	22	1	1	24
Total.....	79 (85%)	7 (8%)	5 (5%)	2 (2%)	93	41	4	2	47

Delayed ovulation

Very little information is available on the maximum period post oestrus, for which rupture of the relative follicle may be postponed. Hignett (1941) states that liberation of the ovum may be delayed for five to seven days. Hancock (1948) in observing the approximate time of ovulation in 58 cows found that 69 per cent had ovulated the day after heat, and the remaining 31 per cent a day later. He concluded that when ovulation has not taken place 48 hours after oestrus, ovulatory failure is absolute. This deduction, however, is based merely on the evidence of the midcycle corpus luteum. On the other hand, the ovulation time given in Table 4 was derived from daily palpation per rectum of the persisting follicles until their fate was known.

Although in the great majority, namely 79 out of 93 (84.9 per cent), the delay was less than 48 hours, the results are not in complete accordance with Hancock's findings in so far that 14 (15.1 per cent) ovulations occurred more than 48 hours after cessation of oestrus. In 12 of the latter ovulation was retarded for 48 to 96 hours.

The two cases in which ovulation was deferred for more than 96 hours merit individual consideration, as they provide further evidence of the capricious nature of the bovine ovary.

Cow No. 2722, an Afrikaner born 8th November, 1946; had five calves previously, the last having been born on 8th January, 1954. She was in oestrus and was inseminated on 28th March, 1955. The responsible follicle in the left ovary persisted for seven days. No treatment was applied but four further inseminations were made, the last being on the sixth day. Rupture of the follicle took place within the next 24 hours, and conception followed. She calved on 26th January, 1956, showed oestrus with normal ovulation on 9th March, 1956, and conceived again to insemination on this day.

Heifer No. 6655, Friesian, born 9th September, 1953, showed oestrus with a well developed follicle in the left ovary and was inseminated on 20th October, 1955. The follicle remained static for seven days, and she was bred again on the seventh day as well as on the eighth. The next day (29th October, 1955), the follicle was found to have ruptured, and conception followed. She calved on 30th July, 1956, and bred normally subsequently.

The significant feature of these cases is that the viability of the ovum is apparently not affected adversely by abnormally long retention in the follicle after the cessation of oestrus.

According to Amoroso (1955) the average threshold dose of oestrogens necessary to bring a cow to heat is very low, about 600 rat units. This is apparently reached early in the development of the graafian follicle, and a refractory period in the brain, which causes sexual desire to cease, sets in before the follicle is sufficiently grown to rupture. There is thus an interval in which heat has ceased before ovulation occurs in cows.

During this lag luteinising hormone is secreted by the pituitary in sufficient amounts to initiate pre-ovulatory swelling of the follicle and an incidental increase in oestrogen, which leads to rupture of the follicle by synergistic action of these two hormones.

In delayed ovulation this quiescent period is unduly prolonged, with no evidence of pre-ovulatory swelling. The follicle remains static, and in exceptional cases, like the two referred to, this may last for seven or eight days.

The follicle that is destined to persist abnormally long is not clearly defined or prominent above the surface of the ovary. It has a thicker wall than normal, shows no fluctuation, and is not easily ruptured by hand. These characteristics enable the experienced examiner to judge with fair accuracy whether ovulation is likely to be retarded or not. In the great majority of cases in which it is only delayed for 24 to 48 hours, the second examination carried out 24 hours after the first often reveals evidence of impending ovulation such as an increase in the size of the follicle, thinning of its walls, decreased turgidity, increased liquor folliculi and greater fluctuation.

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Anovulation with regression

In 41 out of the 47 cases of anovulation recorded in Table 4 the follicles ultimately regressed and terminated in follicular atresia and death of the ovum. That is, in 536 oestrous periods observed regression of the follicle occurred in 41 (7.6 per cent).

As indicated above ovulation very rarely occurs after the fourth day post oestrus. In the great majority of cases the persistent firmwalled follicle decreases in size after the fourth or fifth day and is no longer palpable at mid-cycle. The length of the oestrous cycle is not affected in most of these cases.

While delayed ovulation may be an incidental occurrence in many cows with normal breeding ability, anovulation with follicular regression shows a greater tendency to recur in the same individual, and may therefore be a more potent factor in producing "repeat breeders" than delayed ovulation.

As is evident from the record of some of the cows given above, animals with a predisposition to ovulatory failure tend to initiate this dysfunction with one or two periods of delayed ovulation, followed by several periods of anovulation terminating in regression or cystic degeneration.

Follicular cystic degeneration

The fact that these were grade animals that were not highly bred and fed, probably accounts for the relatively small number of cases of cystic degeneration.

A significant feature of the voluminous literature on ovarian cystic degeneration is that the very extensive study of this important cause of bovine sterility has in the main been confined to the secondary and terminal stages of the condition, and one can find no reference to the incipient forms and early pathogenesis. This is chiefly on account of the fact that the abnormality is usually well advanced by the time it is brought to the notice of the clinician and research worker.

The very nature of the observations made in the present investigation was such that it afforded an opportunity of detecting early aberrations which preceded the development of cystic ovaries.

The most notable feature is that the cysts generally do not appear suddenly as the result of failure of the follicle to ovulate. While there is no definite syndrome which characterizes cystic formation in the early stages, evidence of hormonal imbalance, such as delayed ovulation, anovulation, and in the one case (cow No. 1355) ovulation before the end of oestrus in two successive heat periods, may be shown long before the ovary becomes cystic.

No attempt has as yet been made to define at what stage of ovulatory failure the ovary should be regarded as cystic. The norm that is usually accepted when the result of a histo-pathological examination is available is the successive degeneration of ovum, membrana granulosa and theca interna. In the live animal a very definite syndrome is only shown in the relatively advanced stages, and the clinician frequently makes a mistaken diagnosis of cystic ovaries on finding a thick-walled follicle on the fifth or sixth day post-oestrus, especially when this is accompanied by a reappearance of oestrus at the same time. The latter can be due to a sudden resuscitation of the persistent follicle after it has been dormant for a few days. Another possibility is that this follicle may regress, and another may suddenly appear in the same or in the other ovary as in the mare.

Ovulation eventually occurs in many such cases and may be followed by conception if insemination was performed during the preceding 24 hours. Irregular appearance of oestrus cannot therefore be accepted as reliable evidence of a cystic ovary.

Luteal cysts

In contrast to the follicular type, luteal cysts have thus far received little attention from research workers. McEntee (1958) states that the frequency and significance of cystic corpora lutea in cattle are relatively unknown, and he ascribes this to the fact that they are difficult to detect clinically.

Nevertheless two distinct types of cysts involving the luteal tissue of the ovary can now be recognised, namely:—

- (i) Cystic corpora lutea, in which the normal corpus luteum formed after ovulation has undergone cystic degeneration. In this a definite ovulation scar can be detected, and the apex has the characteristic rosette-like depression of the normal corpus luteum.
- (ii) Luteal cysts, in which no ovulation took place but luteinisation of the persistent follicle occurred. There is accordingly no trace of an ovulation scar, or depression, the free surface of the cyst being smooth and rounded. It would be more appropriate to describe these as luteinised follicles rather than luteal cysts.

Although it is not always possible to distinguish between the two types by clinical examination in the living animal, such differentiation can nevertheless be made, particularly if the animal is examined on a few consecutive days after oestrus. Although the exact nature of the cyst cannot always be determined, its presence in the ovary can be established by rectal palpation when slight pressure on the ovary with the finger tips will reveal the crepitous nature of the luteal tissue and the presence of fluid in the central cavity.

There is a difference of opinion regarding the significance of cystic corpora lutea. Most authorities, however, agree with Hammond (1927) and Asdell, De Alba & Roberts (1949) who hold that fluid in the central cavity of the corpus luteum is a normal phenomenon and that this condition is not of great importance as a cause of sterility. Observations by McEntee (1958) did not support the view that cystic corpora lutea are associated with anoestrus.

There is, however, an important difference in the pathogenesis of the two conditions. It would appear that what is generally regarded as a cystic corpus luteum is a normal corpus luteum formed subsequently to ovulation, but having a central cavity somewhat larger and containing more fluid than normally.

The luteal cyst, or rather luteinised follicle, on the other hand, is a sequel to anovulation.

It can be presumed that in delayed ovulation the level of luteinising hormone secreted by the anterior pituitary is just below the requirements for normal ovulation. In anovulation there is a still greater deficiency of luteinising hormone so that ovulation is completely inhibited and regression takes place. Between these two there occasionally appears to be an intermediate stage in which luteinising hormone is insufficient to cause ovulation but nevertheless adequate to produce luteinisation of the follicle.

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Effect of ovulatory failure on conception

Provided the female genital tract is normal in every respect and fertile semen is used, successful service is conditioned by two main factors, namely—

- (i) the interval between mating or insemination and ovulation; and
- (ii) the survival rate of sperm in the female reproductive tract.

These two factors also determine the effect of ovulatory failure on conception.

1. *Effect of delayed ovulation*

When release of the ovum is delayed successful fertilization is dependent on the viability of the sperm.

There is wide divergence of opinion on this latter aspect. Kirillov (1937) found that the longest period at which live sperm were recovered after insemination was 15 hours. Andrew (1957) stated that sperm survived in the female reproductive tract for a relatively short time, namely 24 hours. Beshlevnov (1938) found that satisfactory motility was maintained for 24 hours, and live sperm were observed after 30 hours, but not after 40 hours. Laing (1955) puts the average normal period of survival at 30 hours. Vanderplassche & Paredis (1949) on the other hand inseminated 22 cows from three to 24 hours before oestrus, and 11 conceived, while three inseminated 48 hours before heat did not. From this they concluded that sperm in the uterus and oviducts can retain fertilizing capacity for at least 55 hours. Trimberger (1948) on the contrary bred 14 cows just before the onset of oestrus and none conceived.

La Grange (1958) compared the results obtained from insemination in (a) the first 12 hours of oestrus, and (b) 13 to 30 hours after the commencement of oestrus, in 1,130 first and 380 repeat inseminations. His results are given in Table 5.

TABLE 5.—*Comparison of results obtained from insemination in (a) the first 12 hours of oestrus and (b) 13 to 30 hours after the commencement of oestrus*

	Total	Time of insemination after commencement of oestrus			
		0-12 Hours		13-30 Hours	
		Number	Conception rate	Number	Conception rate
First inseminations.....	1,130	473	58·6	657	60
Repeats.....	380	140	47·1	240	70

These results show that in normal fertile cows there is no noteworthy difference in conception between early and late inseminations. With the repeat breeders, however, there is a very significant difference in that only 47·1 per cent held to insemination in the first 12 hours as against 70 per cent in those bred later in oestrus or even after cessation of heat.

La Grange justifiably concluded that delayed ovulation was mainly responsible for the poor breeding efficiency of the latter group.

In the present investigation 18 cows in which the follicle did not rupture within 24 hours after insemination were bred once only, and none conceived. In 51 others a repeat insemination was given when it was found that ovulation had not occurred 24 hours after the first. Conception resulted in 32 (62.7 per cent). Additional inseminations were given to four others in which ovulation was delayed beyond 48 hours, the last in every case being made during the 24 hours preceding ovulation. Pregnancy followed in all four.

These results establish that under average South African conditions conception will rarely, if ever, follow if ovulation does not take place within 24 hours of insemination. The beneficial effect of repeat inseminations at 24 hour intervals in 55 cases of delayed ovulation supports La Grange's view that this aberration is a common cause of cows repeating.

2. *Effect of anovulation*

In 40 cases of anovulation the animals were bred at least once, and since differentiation between delayed ovulation and anovulation is not always possible in the early stages, many of the affected cows were bred on two or three successive days. Naturally none of them conceived.

In the majority of affected animals delayed ovulation occurred only once, and appeared to be fortuitous resulting from environmental factors rather than an inherent predisposition.

Anovulation, on the other hand, showed a greater tendency to recur in certain individual animals, and was observed particularly in cows with a poor breeding record. The latter abnormality can thus be regarded more as an innate characteristic and therefore as an important aetiological factor in the so-called "problem cows". It was observed too that animals subject to recurrent ovulatory failure did not take readily even when they ovulated normally.

Result of post ovulatory insemination. Autrup & Rasbech (1951) inseminated 293 cows in the post oestrus haemorrhagic period, about 48 hours after the end of oestrus, with the result that 87 (29.69 per cent) conceived. They point out that delayed ovulation may have occurred or that the period during which ova survive in the cow may be longer than is commonly supposed.

In this investigation 17 cows had already ovulated when they were inseminated, although insemination was in no case performed more than five or six hours after the end of oestrus. Only one (5.88 per cent) of the 17 conceived.

It therefore appears that retention of the fertilizing capacity of the ovum after liberation from the graafian follicle is not as long as suggested by Autrup & Rasbech's results. Their presumption that delayed ovulation may have played a role is probably correct.

Result of manual rupture of the follicle. Manipulation of the ovaries during heat always involves the risk of rupturing the graafian follicle. In this investigation too the follicle was broken accidentally in 36 cases. All the cows were inseminated at the time but only one pregnancy resulted.

A noteworthy feature is that the follicles of some individual cows are more liable to be broken in this manner than those of others, and in several animals this happened twice and even three times. These were cows with good breeding records.

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Aetiology

The immediate cause of ovulatory failure is obviously a derangement in the functioning of the hormonal mechanism controlling ovulation.

Reference has been made to the fact that after the threshold of oestrogens necessary to bring a cow into heat has been reached, there occurs a refractory period in the brain which stops sexual desire in the cow before the follicle is sufficiently developed to rupture.

Ovulatory failure results when the requirements and balance of the two synergistic hormones, namely, oestrogen and luteinising hormone, which are responsible for ovulation, fall short of the optimal. This is a direct result of pituitary dysfunction, the activity of which gland again is conditioned by a great variety of intrinsic and extraneous factors.

The data obtained have been analysed to determine the role, if any, played by the following in the causation of ovulatory failure, namely, breed differences, age, length of the parturition-breeding interval, season and hercidity.

In addition the effect of nutrition and neurogenic factors is also discussed.

Breed

According to Table 1, 37·3 per cent of the Friesian cows and 27·5 per cent of the oestrous periods studied in Friesians revealed ovulatory failure. The corresponding percentages for the Afrikaner breed are 33·5 and 24·8. This difference is not significant.

Further, Table 4 shows that there was no noteworthy difference between the two breeds as regards the incidence of the various types of defective ovulation.

The results obtained in this investigation not only reflect the slight difference in the incidence of ovulatory disturbance in the two breeds, Friesian and Afrikaner, but since these are the main dairy and beef breeds in South Africa the data can also be regarded as representative of the dairy breeds on one hand and the beef breeds on the other.

Popular belief is that ovarian dysfunction is more common in dairy animals than in the beef breeds on account of the greater domestication and the strain imposed by high milk production on the former. Marshall & Hammond (1952) for instance state that there is some evidence that, with heavy milkers, ovulation may be postponed until a longer interval than usual after oestrus. This presumption is shown to be fallacious as far as South African conditions are concerned, because ovulatory failure is nearly as prevalent in the beef animal as in the dairy cows. The probable explanation for the surprisingly high incidence of this type of infertility in the Afrikaner is that the nutritional level of beef animals maintained under ranching conditions with no supplementary feeding is frequently sub-normal.

Age

The influence of age on the incidence of ovulatory failure is reflected in Table 6 and in Graph 1.

TABLE 6.—*Effect of Age on Ovulation*

Age in years	Friesians			Afrikaners		
	Number of periods	Ovulation		Number of periods	Ovulation	
		Normal	Failed		Normal	Failed
2.....	26	22	4 (15.4%)	46	35	11 (23.9%)
3.....	44	39	5 (11.4%)	32	18	14 (43.8%)
4.....	28	21	7 (25%)	13	8	5 (38.5%)
5.....	21	18	3 (14.3%)	17	13	4 (23.5%)
6.....	26	19	7 (26.9%)	9	7	2 (22.2%)
7.....	8	7	1 (12.5%)	46	37	9 (19.6%)
8.....	3	1	2 (66.7%)	31	25	6 (19.4%)
9.....	12	6	6 (50%)	22	17	5 (22.7%)
10 and over	34	20	14 (41.2%)	24	20	4 (16.7%)

Owing to the small number of Friesians in the seven and eight year age groups, these two lots are grouped together in the graph.

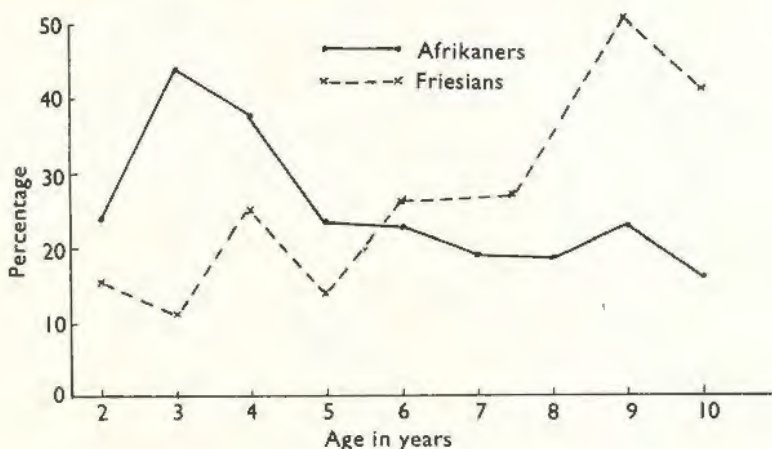
The breeding practice followed in both herds, was to inseminate heifers at the age of two years. The three-year old group therefore represents heifers that have calved once.

Marked ovarian functional abnormalities were shown by the heifers in both groups, sub-oestrus being a very frequent occurrence. In one group of 11 two-year old Friesian heifers kept under very close observation only 15 oestrous periods out of 37 were normal, the remaining 22 showing ten cases of delayed ovulation, nine sub-oestrus and three anovulation. Although Olds, Trautman & Seath (1952) point out that age influence on the fertility of heifers has not yet been adequately studied, several other investigators have reported lower fertility in heifers than in cows. Miller & Graves (1932) found that at the end of three services 67 per cent of the heifers and 73 per cent of the cows had conceived. Morgan & Davis (1938) reported that among 537 heifers and 2,090 cows, the heifers required 2.52 and the cows 2.21 services per conception. Olds (1950) found that the fertility of heifers was 2.3 per cent lower than that of cows. Davis (1951) analysed reproductive efficiency in the University of Nebraska Holstein herd from 1897 to 1950, and found that heifers required 2.94 services per conception as against an average of 2.51 for all calvings in this period.

The same disparity is found with artificial breeding, and analysis of the results of this work suggests that delayed ovulation and suboestrus are important aetiological factors.

Table 6 and Graph 1 reveal that the fluctuations were even more marked in the Afrikaner heifers, in which breed the incidence of ovulatory failure reached its highest point at three years, that is, after the first calving.

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GRAPH 1.—Incidence of ovulatory failure in the different age groups

It appears that despite having reached puberty the hormonal mechanism controlling reproduction in the slow maturing Afrikaner has not yet reached the necessary level of development to undertake that function satisfactorily at the age of two years. Pregnancy and parturition at the relatively early age appear to cause an upset in that system, which is manifested in the high incidence of ovulatory failure in the three and four year old groups.

The aberration, however, is only temporary, and restoration of normal ovarian activity in the Afrikaner is rapid between the fourth and fifth years. From then on the improvement is almost linear up to the age of ten years and over. It is therefore apparent that on a basis of ovarian activity, reproductive efficiency in the Afrikaner increases progressively from the third till the tenth year and over.

The fluctuations shown by the Friesians in the first three breeding seasons are not so marked, the Friesian heifer being basically better adapted for breeding at an early age than the Afrikaner.

The most outstanding feature, however, revealed by the data is that, contrary to what applies in the Afrikaner, the breeding efficiency of Friesians deteriorates rapidly after the age of five years when the incidence in ovulatory disorders increases progressively with age.

This observation is congruent with the findings of Morrison & Erb (1957) from a study of 9,994 reproductive periods of 2,607 Holstein-Friesian cows from 1920 to 1950. Their analysis showed that maximum reproductive efficiency was reached during the third and fourth breeding period, and that decrease in reproductive efficiency with age is linear up to 14 years.

In an attempt to explain this dissimilar trend in ovarian activity in the two breeds concerned one must regard the animals in the experiment as representatives of two distinct types, namely, dairy and beef animals, rather than the two specific breeds. It then appears that in the dairy animal the strain of high milk production is beyond that which the genetic make-up of many cows can cope with successfully

over a number of years. The beef cow, and particularly the Afrikaner, produces only sufficient milk to rear the calf, and is in lactation for no more than six to eight months per year. Being maintained under ranching conditions in a more natural environment, her endocrine system is not subjected to such a variety of different adverse conditions and demands as that of the dairy cow.

Further, domestication and all the attendant handling to which dairy cows are subjected expose them to genital infection to a far greater extent than animals kept under ranching conditions, and it is known that, apart from pathological lesions in the genitalia, infection of the female genital tract also gives rise to derangement of the normal physiology of the ovaries.

Finally, the nutritional defects and imbalances to which animals in South Africa are particularly exposed will manifest their harmful effects on reproduction much earlier in the exotic dairy breeds than in the indigenous Afrikaner which is better adapted to local conditions. Moreover, where intake of a certain mineral is deficient or on the borderline, depletion of the body reserves will be more rapid in the dairy than in the beef breeds.

Length of the parturition to breeding interval.—It is generally accepted that fertility is affected by the length of the interval between parturition and breeding, and that service too soon or too late after calving may give poor conception results.

Confirmation that the optimum period for breeding is between the second and fourth months post partum is provided by the findings of the undermentioned workers who investigated this question very fully, and concluded as follows:—

<i>Authors</i>	<i>Maximum breeding efficiency post partum (Days)</i>
White, G. S. <i>et al.</i> (1925).....	90–120
Hofstad, M. S. (1941).....	90–100
Olds, D. <i>et al.</i> (1949).....	50–75
Vandemark, N. L. (1952).....	81–120
Trimberger, G. W. (1954).....	118·8
Morrison, R. A. & Erb, R. E. (1957).....	75–115

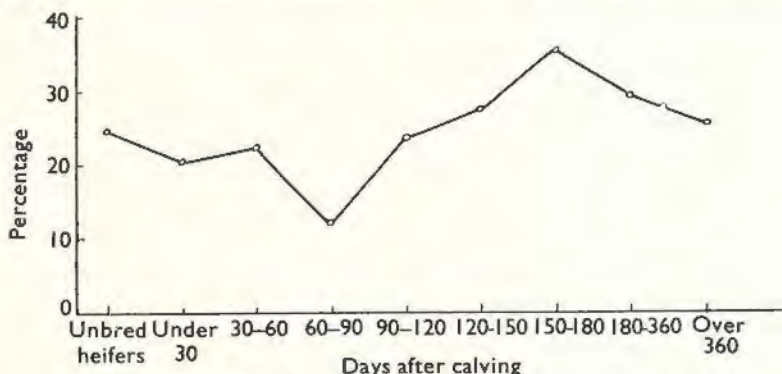
No noteworthy difference in this respect was shown by the two breeds studied in this investigation. Therefore the results are not considered separately but have been combined and are given in Table 7 and Graph 2.

TABLE 7.—*Effect of length of parturition to breeding interval on ovulation*

Days after calving	Number of oestrous periods		
	(a) Examined	(b) With normal ovulation	(c) With ovulatory failure
Unbred heifers.....	166	125	41 (24·7%)
Under 30 days.....	5	4	1 (20%)
30–60 days.....	18	14	4 (22·2%)
60–90 days.....	25	22	3 (12%)
90–120 days.....	17	13	4 (23·5%)
120–150 days.....	22	16	6 (26·7%)
150–180 days.....	28	18	10 (35·7%)
180–360 days.....	78	55	23 (29·5%)
over 360 days.....	108	80	28 (25·9%)

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The data indicate that after due allowance is made for other causal factors of poor breeding efficiency after calving, such as incomplete involution of the uterus and infection, ovarian dysfunction characterized mainly by ovulatory disturbance plays an important role in determining the fertility level at different stages post partum.



GRAPH 2.—Effect of post-partum period on ovulatory failure

The most significant feature revealed by the table and graph is that the period at which the incidence of ovulatory failure was at its lowest (i.e. 60 to 90 days post partum) coincides with the period of maximum breeding efficiency as determined by the workers cited above.

Season

The fertility level of the bovine shows seasonal variations, the general tendency being to decline or even become completely arrested during winter.

Mercier & Salisbury (1947) studied fertility in cattle bred by natural service on three large Canadian farms, and found a significant difference in fertility in the different months. February was the poorest and July the best. Erb & Waldo (1952) came to the same conclusion in respect of insemination results in Washington.

Stegenga (1958) states that the conception rate drops in Holland in autumn, and continues dropping till February, when it is 10 per cent lower than in June.

From the results of a large number of inseminations Rajakoski (1960) in Sweden concluded that fertility is about 5 per cent lower during the six months December to May than during the rest of the year.

A comparison for the three years 1949 to 1952 of conception rates according to month of insemination, given in Report No. 3 (1952) of the Production Division of the Milk Marketing Board shows that fertility of cows in Britain reaches its peak in autumn (October and November), and its lowest point in winter and early spring.

According to Rajakoski (1960) depression of fertility during winter and spring is generally ascribed to poor ovarian function manifest according to the degree of the disturbance as silent heat, suppressed ovulation and oestrus, and ovarian atrophy.

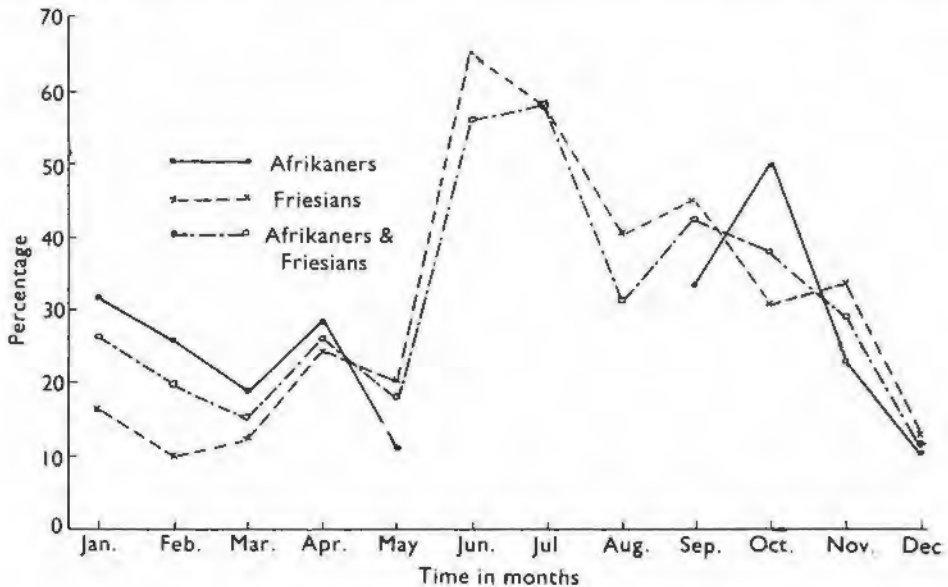
This too is the pattern usually encountered in cows maintained under ranching conditions in South Africa when no supplementary feeding is provided during winter. Anoestrus is the reason for so few oestrous periods in the Afrikaners being observed

during the three midwinter months (June to August) as shown in Table 8 and Graph 3. The data reveal that ovulatory aberration is an important characteristic of midwinter ovarian dysfunction, and that it reaches its peak in the two coldest months of the year (June and July), which incidentally is also the period with the smallest number of daylight hours.

TABLE 8.—*Effect of season on ovulation*

Month	Friesians			Afrikaners			Total		
	Oestrous periods	Normal	Failed	Oestrous periods	Normal	Failed	Oestrous periods	Normal	Failed
Jan.....	30	25	5	52	35	17	82	60	22 (26.8%)
Feb.....	30	27	3	45	33	12	75	60	15 (20%)
March...	34	30	4	66	54	12	100	84	16 (16%)
April....	29	22	7	21	15	6	50	37	13 (26%)
May.....	25	20	5	9	8	1	34	28	6 (17.6%)
June.....	20	7	13	5	4	1	25	11	14 (56%)
July.....	7	3	4	—	—	—	7	3	4 (57.1%)
Aug.....	18	11	7	4	4	0	22	15	7 (30.8%)
Sept....	20	11	9	6	4	2	26	15	11 (42.2%)
Oct.....	23	16	7	14	7	7	37	23	14 (37.8%)
Nov.....	18	12	6	21	16	5	39	28	11 (28.2%)
Dec.....	8	7	1	31	28	3	39	35	4 (10.3%)

Malnutrition is generally considered to be the main cause of lowered fertility in winter, but in the light of the trend shown in Graph 3 this cannot be held solely responsible for the many ovulatory failures in winter, since nutritional conditions are even worse in August to October, and in that period the incidence of defective ovulation dropped notably. The further marked decline in November and December can be ascribed to the green grazing which follows the onset of the summer rains in October.

GRAPH 3.—*Effect of season on ovulation*

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It thus appears probable that in the bovine the decrease in the incidence of ovulatory failure in spring and summer can be ascribed to three factors, namely, the higher environmental temperature, the increase in daylight hours and the availability of green grass.

Heredity

In a review of the literature on the inheritance of functional causes of reproductive inefficiency Gilmore (1949) states: "That fertility is affected by the genotype of mates is borne out by observation, the opinion of popular writers in dairy cattle breeding, and by research investigators."

Largely due to the constantly increasing application of artificial breeding with the attendant recording and closer observation over the progeny of sires and dams, many reports have since appeared, which confirm Gilmore's assertion of the heritability of functional infertility.

The genetic basis for the development of cystic ovaries has received particular attention. Ericksson (1939) first proved that the tendency to develop cystic ovaries is transmitted by dam to daughters. Garm (1949) declares that in Scandinavian countries many veterinarians seem to agree that cystic ovarian degeneration is a symptom of an endocrine disorder related to a hereditary predisposition.

Hignett (1950) records having encountered certain cow families in which there is a very high incidence of cystic ovaries, and points out that adverse hereditary influences often open the way to the full expression of nutritional disturbances. Roberts (1956) cites the reports of a number of authors, and concludes that there is every reason to assume the existence of a hereditary predisposition to cystic ovaries and nymphomania.

On the strength of the evidence furnished by the workers quoted by him Dawson (1957) states that the circumstances strongly suggest that the gene appeared during the present century as a mutation.

The data on the frequency of ovulatory aberrations in individual animals (Table 3) and the cases quoted indicate that in this respect two different types of ovulatory failure may be recognised, namely, (i) that in which the abnormality appears to be fortuitous and conditioned by extrinsic factors, and (ii) the other and more serious form which seems to be due to an inherent weakness or predisposition of the individual animal. In the latter type there is a great tendency for the abnormality to recur in the same cow. Most of the cases of anovulation terminating in follicular regression or cystic degeneration fall within the latter class, while the majority of delayed ovulations belong to the first group.

The breeding performance of the ancestors and of the relations of some of the animals in this investigation are available for the past 20 years. A study of the relevant records reveals that many of the cows and heifers that tend to show habitual or recurrent ovulatory failure belong to families with notoriously low reproductive ability.

TABLE 9.—*Reproductive efficiency of eight cow families*

Ancestral dam	Total progeny produced in four generations		Progeny in this investigation	Oestrous periods observed	Normal ovulation	Delayed ovulation	Anovulation
	Number	Breeding years					
No. 7909 (Friesian).....	53	50	8	16	14	2	—
No. 7910 (Friesian).....	84	85	6	17	15	1	1
No. 8271 (Afrikaner).....	33	38	2	3	3	—	—
No. 9059 (Afrikaner).....	39	39	4	5	4	1	—
No. 8428 (Friesian).....	8	16	2	9	5	3	1
No. 8924 (Friesian).....	11	20	1	6	2	—	4
No. 1229 (Afrikaner).....	10	19	1	4	2	—	2
No. 8973 (Afrikaner).....	10	16	1	2	—	1	1

An analysis of the breeding achievement through four generations of eight cow families, consisting of four Friesians and four Afrikaners is given in Table 9. This reveals that two of each breed (No. 7909, 7910, 8271 and 9059) and their progeny possessed high reproductive ability, which resulted in the birth of 209 calves in the 20 years under review. The 209 progeny of these four great-grand-dams were produced in a total of 212 breeding years which is equivalent to an average inter-calving period of 369 days. In the 41 oestrous periods of the members of these families that were studied, ovulation was normal in 36 (87·8 per cent), delayed in four and ended in anovulation in only one. The latter was a cow that developed a cystic ovary after her sixth calving. This responded to treatment; and she conceived again subsequently.

On the contrary the other four families (No. 8428, 8924, 1229 and 8973) proved to have a very low breeding potential, and they only yielded a total of 39 descendants in the same 20 year period. These were produced in a total of 71 breeding years representing an average inter-calving interval of 664 days. Owing to the very low fertility level of these four families, only a small number of them were available for this investigation, and only 21 of their oestrous periods were observed. Only nine (42·8 per cent) of these ovulated normally, four showing delayed ovulation and eight anovulation.

The breeding records of the eight families considered in conjunction with the results of this investigation establish that, with possible rare exceptions, the reproductive capacity of the progeny is very largely conditioned by that of the ancestral dam, that defective ovulation is an important causal factor of low breeding efficiency and the creation of "repeat breeders" or "problem cows", and that this defect, particularly in the form of anovulation, probably has a genetic basis.

Nutrition

Although the scope of this work did not embrace a special study of the effects of faulty nutrition, this is a factor of such great aetiological significance that no treatise on any aspect of ovarian dysfunction would be complete without some consideration being given to the possible role of nutritional defects.

Gross malnutrition is an undisputably common cause of poor fertility, and is manifested in a disturbance in the normal physiology of the reproductive organs of the female, being characterized mainly by suppression of follicular development and maturation with resultant static ovaries and anoestrus.

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Beyond this generalization information is scanty, and few have attempted to correlate specific forms of functional infertility with definite types of dietetic errors. There is still a lot of contradictory evidence on the specific effect of excess or deficiency of the various constituent elements of the food normally taken in by bovines, and not much is known of the influence of imbalance of the individual constituents on the different facets of ovarian activity, such as follicular growth and maturation, ovulation, and development and regression of the corpus luteum.

Most of the information which is available in this connexion emanates from the researches of Hignett and co-workers. He (1941) was probably the first to associate a mineral deficiency with ovulatory disturbance when he stated that in certain herds in Britain one meets with a high incidence of sterility due to delayed ovulation, the ovum not being liberated until perhaps five to seven days after oestrus. The evidence suggested that this is due to a manganese deficiency.

Hignett (1959) also shows the importance of the inter-relationship between the calcium, phosphorus and manganese consumption for fertility. He further indicates that apart from a direct effect on breeding performance, nutrition may also influence the importance of hereditary defects or infective agents, and expresses the belief that a great deal of infertility in cattle is associated with enzyme dysfunction resulting from trace mineral deficiency or excess.

Bently & Phillips (1951) found that heifers raised on low manganese rations were slow to exhibit oestrus and slow to conceive upon breeding.

Tesink (1960) compared the results obtained with artificial breeding during the 1958-59 winter in 19 herds in Holland, which received trace mineral cakes, with that of 20 control herds, and found the conception rate to be 16 per cent higher in the former. The most marked improvement was seen in those herds in which the copper and manganese content of both the ration and the hair of the animals was low originally.

In view of the marked depressing effect of phosphorus deficiency on fertility of cattle in South Africa, reported by du Toit & Bisschop (1929) measures were taken to obviate this in the current investigation by supplying bonemeal-salt licks.

Although the nutritional aspect did not receive special consideration in this work, data have been obtained in subsequent investigations, which indicate that faulty nutrition may play a very important role in the causation of the surprisingly high incidence of ovulatory failure.

An experiment during the 1958 breeding season to determine the effect of manganese supplementation on ovarian activity of ranching cattle on this farm yielded negative results, and provided no reason to suspect a deficiency of this mineral in the soil or vegetation.

Further investigations, however, suggest the possibility of copper being closely connected with several types of ovarian dysfunction in South Africa. Van Rensburg (1961) reports a high incidence of static ovaries and other types of functional abnormalities in a herd in a copper deficient area, with remarkably rapid restoration of normal ovarian activity and high fertility following the administration of copper per os.

Subsequent research work which entailed liver biopsies and hair analyses has revealed that the copper content of the liver and hair of animals at this institute is below normal. The observations do, however, indicate that the depressing effect of a copper deficiency on ovarian activity may not be absolute, but conditional and determined to some extent by other dietetic errors and adverse conditions which produce stress.

Neurogenic factors

Cognisance must be taken of the fact that the commencement of this study was congruent with the change over from natural to artificial breeding. The possibility of an adverse neurogenic or psychogenic influence on ovulation cannot therefore be disregarded, particularly in view of the widely-held belief that the stimulus for ovulation is provided largely by coitus. This theory is supported by the indisputable fact that cows which fail to hold to repeated inseminations in spite of no obvious abnormality of the genitalia, may conceive to service by a bull.

The only available published data on the effect of copulation on ovulation is that by Marion *et al.* (1950). They observed the effect of sterile copulation on the time of ovulation in 25 dairy heifers, and noted that heifers ovulated on an average at 7.7 hours after the end of oestrus when serviced by a vasectomised bull as compared to 9.9 hours when not serviced. It cannot, however, be inferred from these results that the extension of ovulation time by 2.2 hours is applicable to artificial breeding. No evidence has yet been produced to prove that the manipulation of the genitalia during insemination does not furnish the necessary stimulation for the secretory function of the pituitary as effectively as that derived from natural service. It is, for instance, quite a common phenomenon for lactating cows to "let down" milk while being inseminated, and in some milk can be seen streaming from the four teats during this operation.

A more feasible explanation for the fact that some of the problem cows that fail to hold repeated insemination will conceive readily to natural service, is that the semen in the latter case without doubt has greater viability than that used for insemination, and will therefore be able to fertilize cows in which ovulation may be delayed a few hours, while artificial insemination may fail in such cases.

Mention has already been made of the fact that some of the cows with recurrent delayed ovulation and most of those with a tendency to anovulation were poor breeders even when bred by natural service. An example is cow No. 1892, a Friesian born 18th November, 1945. With natural service prior to 1954 she had only produced three calves by the time she was nine years old, and it required up to six services by the bull to get her pregnant. Her ovaries were observed during six oestrous periods. Four of these were anovulatory; in one the follicle ruptured before the end of oestrus, and only one ovulated normally. She conceived to one insemination during the latter period. Her only sister (No. 689), which was not included in this study, has an equally bad record to natural service, and only calved twice in six breeding years. It would therefore appear that an inherent weakness or predisposition is a greater factor in the causation of ovulatory failure than a lack of stimulus.

Finally it must be noted that the bovine belongs to the so-called "spontaneously ovulating" species in contrast to the "reflex ovulators" like the rabbit and cat which usually ovulate only after coitus. In the normal bovine, therefore, ovulation is not conditioned by or dependent on sexual or external stimuli but occurs spontaneously within the prescribed period. There is thus no evidence to show that neurogenic factors play an important role in causing ovulatory failure.

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SUMMARY AND CONCLUSIONS.

1. An investigation was undertaken to determine—
 - (i) the incidence of ovulatory failure in dairy and beef cattle maintained under normal South African conditions;
 - (ii) the types of ovulatory failure;
 - (iii) their influence on conception; and
 - (iv) possible aetiological factors.

2. The ovaries of 118 Friesian and 161 Afrikaner cows and heifers were examined at various times between 1954 and 1958. Of a total of 536 oestrous periods observed ovulation was normal in 396 and failed in 140.

3. Many of the affected animals revealed a tendency to show recurrent ovulatory failures.

4. Ovulatory failure is of two main types, namely—
 - (i) delayed ovulation, and
 - (ii) anovulation.

The latter may terminate in follicular regression and atresia, or in cystic degeneration, which may be either follicular or luteal.

5. In the 140 cases of defective ovulation it was delayed in 93 (66 per cent), and terminated in anovulation in 47 (34 per cent). Of the latter, 41 regressed, four ended in follicular and two in luteal cystic formation.

6. In 85 per cent of the cases of delayed ovulation the delay was under 48 hours. In two cases, however, the ovum was only liberated seven and nine days respectively after the cessation of oestrus. Both conceived to inseminations done a day before ovulation.

7. Anovulation shows a great tendency to recur in the same animal, and may be a more potent factor in producing problem cows than delayed ovulation.

8. The results show that follicular cystic degeneration may be preceded by other evidence of hormonal imbalance such as delayed ovulation, anovulation and ovulation before the end of oestrus.

9. Luteal cysts are of two types, namely—
 - (i) those resulting from cystic degeneration of the normal corpus luteum, and
 - (ii) those in which no ovulation occurred, but luteinisation of the follicle took place.

It is suggested that the latter be designated luteinised follicles rather than luteal cysts.

10. Of 18 cows in which the ovum was not liberated within 24 hours of insemination none conceived, but of 51 others, which were given a second insemination when the follicle had not ruptured 24 hours after the first, 32 conceived. Under South African conditions pregnancy will rarely follow if ovulation does not occur within 24 hours after insemination.

11. None of 40 cows inseminated in an anovulatory oestrous period conceived.

12. Only one of 17 cows inseminated after ovulation conceived, and of 36 in which the follicle was ruptured manually at the time of insemination also only one became pregnant.

13. The following aetiological factors were considered:—

- (i) *Breed*.—There was no significant difference in the incidence of ovulatory failure between the two breeds (Friesians and Afrikaners).
- (ii) *Age*.—Heifers of both breeds, but particularly Afrikaners, showed a high incidence of ovarian dysfunction. This is in agreement with the findings of other workers who report that the fertility of heifers is lower than that of cows. After the age of four years the Afrikaners showed a gradual decline in the incidence of ovulatory failure, which reached its lowest level in the ten year and over group.

In Friesians on the contrary ovulatory failure reached its lowest level in the three year olds, and from then on it increased with advancing age. Inability of the endocrine system of the dairy cow to meet all the demands for high milk production and reproduction over a long period is postulated as the reason for the increase in ovulatory disturbance with age in dairy animals.

- (iii) *Post partum interval*.—The data show that for both breeds the lowest incidence of ovulatory failure was noted 60 to 90 days post partum, which corresponds with the period of highest fertility noted by other workers.
- (iv) *Season*.—The incidence of ovulatory failure reached its peak in mid-winter. The rapid decline observed in spring and summer is attributed to the rise in environmental temperature, lengthening daylight hours and the availability of green feed.
- (v) *Heredity*.—The breeding performance of four generations of eight cow families over 20 years revealed that the four families with good breeding efficiency produced 209 calves during that period in a total of 212 breeding years, which is equivalent to an average intercalving period of 368 days. In the 41 oestrous periods of members of this group that were studied, 36 (87·8 per cent) ovulated normally. Delayed ovulation was noted in only four, and anovulation in one.

The other four families on the contrary showed poor reproductive ability throughout the four generations, producing only 39 descendants in the 20 year period, and in 71 breeding years, thus averaging an intercalving interval of 664 days. In 21 oestrous periods observed in these families ovulation was normal in only nine, delayed in four, and ended in anovulation in eight.

14. The data derived from this study indicate that in respect of all the different aspects investigated the incidence of ovulatory failure showed a negative correlation with the level of fertility as determined by various investigators. Conditions favouring a high degree of ovulatory failure appear to be congruent with low breeding efficiency, and vice versa. Similarly cow families with poor breeding ability show a high rate of ovulatory disturbance, with a tendency for the defect to recur in individual animals. It is therefore concluded that this type of functional or physiological infertility is the most common causal factor in the production of the "repeat breeder" or "problem cow."

While various conditions such as age, the post partum interval and season play a role in the aetiology, the two main causes under South African conditions appear to be nutritional defects, in which mineral deficiencies and imbalances play an important part, and a hereditary predisposition whereby ovulatory failure, especially anovulation, appears to be a characteristic of cow families with poor breeding ability.

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