Functional Reproductive Physiology

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Introduction

An important aspect of any cow-calf operation involves the reproductive performance of the cow herd. Production losses incurred annually as a result of poor reproductive management have a major economic impact on the U.S. beef industry. Nationally, the percent calf crop is estimated between 75 and 80 percent. However, producers who are also good reproductive managers can realistically achieve an annual percent calf crop approaching 95 percent. On a per cow basis, these managers can realize an increase in profits of $70 to $100.

When considering ways to improve reproductive performance, it is important to first recognize the limitations involved in genetic selection as a tool. Table 1 gives the heritability estimates for traits which cattle breeders commonly use as selection criteria. Performance traits, conformation traits, and carcass traits are generally medium to highly heritable and are useful tools for the improvement of beef cattle.

Reproductive traits, though, are very low in heritability and their use as selection criteria is limited. This is due to the strong effect of environment on these reproductive traits. Infertility is the primary reason for culling beef cows. Indeed, culling can prevent an increase in the detrimental effects of poor reproductive performance. However, the most significant improvement in reproductive performance of beef cattle is through sound management techniques based on an accurate and thorough understanding of bovine reproductive physiology.

Male Reproductive Anatomy

Hypothalamus-Pituitary

The hypothalamus and pituitary glands are located together at the base of the brain. They are responsible for

Table 1. Heritability of Beef Cattle Traits

Trait	Heritability
Calving interval	.10
Conception rate	.10
Days open	.10
Dystocia	.15
Weaning weight	.30
Yearling weight	.40
Rib eye area	.70
Tenderness	.60

the production and secretion of several hormones. Of particular concern to reproduction are a gonadotrophin releasing hormone (GnRH), a luteinizing hormone (LH), and a follicle stimulating hormone (FSH). GnRH is secreted by the hypothalamus and stimulates the release of LH and FSH by the cells of the anterior pituitary. LH and FSH are called gonadotrophins. In the male their target site of action is the testicles. LH is responsible for testosterone production by the leydig cells of the testicles. FSH is responsible for the initiation and maintenance of the early stages of sperm development.

Scrotum (Figure 1)

In addition to supporting and protecting the testicles and epididymis, the scrotum is instrumental in the temperature regulation of the testicles. A constant temperature of 2° to 4° below normal body temperature is necessary for sperm to maintain viability prior to ejaculation. The supporting muscles of the scrotum assist in this task. In cold weather the muscles contract, raising the testicles closer to the body for warmth. In addition, the thickened scrotal wall provides extra insulation. Under hot conditions the muscles relax, lowering the testicles and stretching the scrotal wall.

Testicle (Figure 2)

The testicles, or male gonads, are responsible for a variety of hormones. Of particular interest are the androgens or male steroid hormones. Specifically, testosterone is secreted by the leydig cells of the testes. It acts locally at the testicle and at the epididymis where it promotes sperm maturation and development. Testosterone is responsible for the secondary male sex characteristics that make bulls look and act like bulls. Furthermore, testosterone is an anabolic agent. Its action on muscle cells increases protein deposition. This explains why feedlot cattle that are administered androgen implants develop more muscle.

Figure 2. Testicle and Epididymis
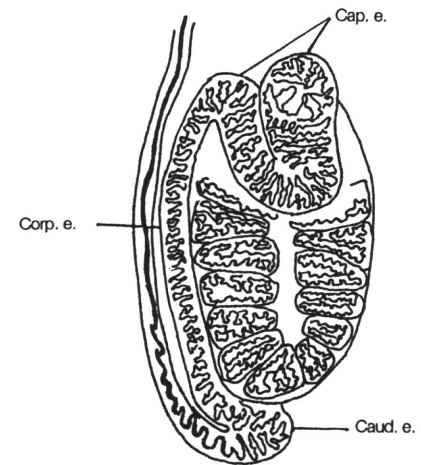

Epididymis (Figure 2)

The epididymis is composed of three distinct segments. The caput epididymis (cap.e.), or head of the epididymis, is attached to the top of the testicle and is directly connected to the seminiferous tubules of the testes. The corpus epididymis (corp.e.), or body of the epididymis, extends from the top to the bottom of the testicle and connects the cap.e. to the cauda epididymis (caud.e.). The caud.e., or tail, of the epididymis is attached to the bottom of the testicle and is easily palpated.

When immature sperm cells are secreted into the seminiferous tubules, they pass first into the cap.e. and then the corp.e., where they complete most of their development.

Ductus deferens (Figure 2)

The ductus deferens (d.d.) comprises the major portion of

Figure 1. Male Reproductive Anatomy
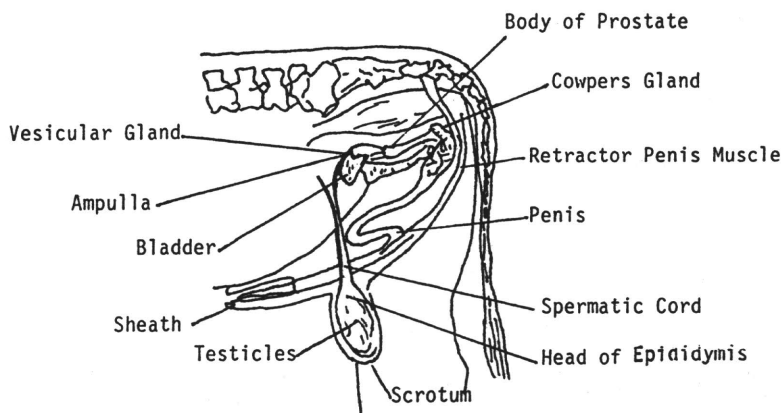
the sperm cord. It delivers the matured sperm and seminal fluid secreted by the testicles and the epididymis to the penis during normal ejaculation. The terminal end of the d.d. contains glandular cells; secretions from these cells contribute to overall seminal composition.

Accessory Organs (Figure 1)

In the bull there are four additional organs located between the d.d. and the penis which make important contributions to the seminal fluids. They are the ampulla, vesicular gland, prostate gland, and bulbourethra gland. These glands can be examined via rectal palpation during a breeding soundness exam (B.S.E.). The exact functions of the accessory gland secretions are not fully understood. In general, they insulate and protect sperm cells in the cow's vagina following ejaculation.

Penis (Figure 1)

The penis is the organ responsible for transfer of semen from the bull to the cow. There are four distinct sections to this organ that warrant discussion. Any injury or genetic abnormality involving the penis can prevent a bull from performing his ultimate function. The retractor muscle and the sigmoid flexure are the anatomical adaptations which permit extension of the penis during copulation. The prepuce or head of the penis is particularly subject to infections and injuries which
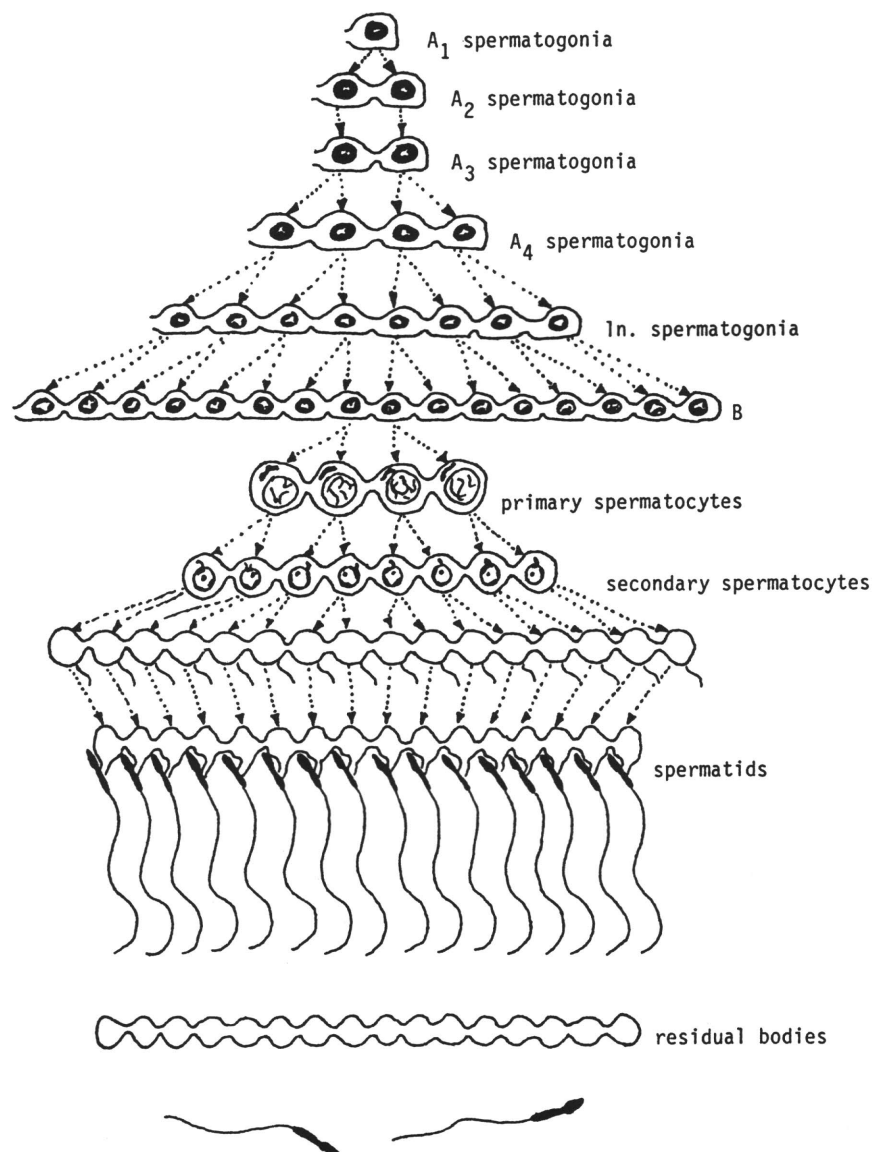
can hinder copulation and infect both the semen and the cow's reproductive tract. These infections can prevent pregnancy, result in early embryonic death, or cause late-term abortions. The integrity and ability of the penis to function properly can be evaluated during a B.S.E.

Sperm Physiology

Sperm cells must undergo a precisely coordinated sequence of morphological (physical)

and chemical changes before becoming capable of fertilizing an ovum (egg). The morphological changes occur primarily in the seminiferous tubules prior to completion in the epididymis. This process takes approximately 63 days in the bull. The stages of sperm development are outlined in Figure 3. They include acquisition of a haploid number of chromosomes, concentration of the genetic material in the head of the sperm cell, development of a tail for

Figure 3. Stages of Sperm Development

A_1 spermatogonia
A_2 spermatogonia
A_3 spermatogonia
A_4 spermatogonia
In. spermatogonia
B
primary spermatocytes
secondary spermatocytes
spermatids
residual bodies

motility, loss of excess cytoplasm, and development of the acrosome. The acrosome is a cap over the head of the sperm cell that contains enzymes which contribute to penetration of the egg during fertilization. Occasionally excess cytoplasm is retained on the tail of the sperm in the form of a cytoplasmic droplet. This and other morphological abnormalities can be detected during a B.S.E.

Following ejaculation, sperm undergo a process known as capacitation. This process requires 6 to 10 hours and occurs in both uterine and oviductile fluids. Capacitation is necessary for the acrosome reaction, which is in turn a prerequisite for fertilization.

The acrosome reaction occurs in the oviduct. It results in structural changes permitting the release of the enzymes involved in fertilization. Capacitated sperm have a limited life span, which explains in part the need for precise timing of insemination during A.I. and natural mating.

Puberty

Puberty is a period of sexual development during which an individual achieves fertility or becomes capable of reproduction. The age and size or weight at puberty varies both between and within breeds. Most beef bulls reach puberty between 10 and 14 months old. Some calves are fertile as young as 7 months old. Therefore it is a sound management practice to separate male and female calves at weaning. It must also be noted that yearling bulls are only capable of limited breeding. They do not reach their maximum reproductive capacity until three to four years of age. Recommended bull to cow ratios are given in Table 2. These are minimum numbers. Research has shown that some bulls can serve 25% to 50% more females than the minimum. The onset of puberty is influenced by several factors, some of which are under direct control of management.

Genetic Influence

European breeds reach puberty younger than the Brahman influenced breeds. Among European cattle, the dairy and dual-purpose breeds tend to reach puberty earlier than the large, lean, strictly beef-producing Continental breeds. Furthermore, inbreeding and line breeding delay puberty, while crossbreeding hastens puberty.

Nutritional Influence

Nutrition strongly affects the onset of puberty and appears to be more closely related to overall body composition than to size or weight. A decrease in the lean to fat ratio occurs at puberty. It is not clear if the change in body composition is a cause or effect of puberty. There is also evidence that higher than average daily weight gains hasten the onset of puberty. Severe limit feeding of calves can significantly delay the onset of puberty.

Seasonal Influence

There is evidence that long periods of daylight will hasten puberty when compared to short duration (16 hours of light and 8 hours of dark versus 8 hours of light and 16 hours of dark). These effects are limited, however, in cattle.

Endocrine Effects

Ultimately the onset of puberty is mediated through hormonal stimuli. Changes occur not only in the level of hormone production by the hypothalamus, pituitary and testicles but also in the sensitivity of the target cells to the hormones themselves. There has been strong evidence in recent years that pituitary function can be impaired due to poor nutrition.

Table 2. Bull to Cow Ratio

Size or age of bull	Cows per bull[a]
Small yearling bull	0-10
Large yearling bull	10-20
2-year-old	20-30
3-year-old and over	30-40

[a]Reasearch has indicated that these are minimum numbers . Some bulls are capable of serving 25 to 50% more than the number of females in this table.

Breeding Soundness Exam (B.S.E.)

A major cause of infertility in beef cows is actually the result of infertile bulls. Between 10 percent and 25 percent of the bulls used in the United States and Canada are questionable or unsatisfactory. Many infertile bulls are not identified until the end of the breeding season when an exceptionally high percentage of the cows fail to become pregnant. The B.S.E. provides a reasonably accurate estimation of a bull's breeding potential prior to the start of the breeding season. A qualified veterinarian can accurately evaluate both semen and the overall reproductive health of the bull. Any problems can be identified at this time, and proper therapy (if feasible) can be initiated. Often a simple foot trimming prior to the breeding season can save a producer a substantial amount of income.

The first phase of a B.S.E. includes a physical examination of the bull. This includes a general health examination, careful evaluation of the bull's feet and legs, and a rectal examination of the reproductive tract. Failure of any portion of the physical exam can result in failure of the B.S.E.

The second phase involves semen evaluation for sperm morphology and motility, and measurement of the scrotal circumference (S.C.). Total sperm production and testicle circumference are positively correlated, particularly in the case of young bulls. It must be emphasized that there is a threshold of S.C. after which the correlation is no longer significant. Once the minimum requirements for S.C. and age are met, increased testicular size is of no advantage. Table 3 gives acceptable S.C. and point allotment in a B.S.E. for various ages of bulls.

Table 4 gives the point allotments assigned to morphology in a B.S.E. Sperm morphology is highly correlated to overall fertility. Points are given based on the number of abnormally formed sperm present. The more structural defects, the lower the score.

Table 3. Scrotal Circumference by Age

Age (months)	Size (cm)	Score	Classification
12-14	>34	40	Good
	30-34	24	Fair
	<30	10	Poor
25-20	>36	40	Good
	31-36	24	Fair
	<31	10	Poor
21-30	>38	40	Good
	32-38	24	Fair
	<32	10	Poor
30+	>39	40	Good
	34-39	24	Fair
	<34	10	Poor

Table 4. Morphology - Percentage of Abnormal Sperm

Classification	% Primary abnormalities	% Total abnormalities	Score
Very good	<10	<25	40
Good	10-29	26-39	25
Fair	20-20	40-59	10
Poor	>29	>59	3

Table 5 presents the point allotments assigned to motility. While motility has a strong correlation to overall fertility, there are some restrictions to its use in field situations. Sperm require a very precisely controlled environment in order to survive. Such an environment is often difficult or impossible to maintain in the field. This is why motility only receives a possible 20 points vs. 40 points possible for both S.C. and morphology.

If a bull passes the physical phase of the B.S.E. and receives a total of 60 or more points on phase 2, he is classified as a *satisfactory* potential breeder. A score of 40 to 60 points results in a classification as a *questionable* breeder. Such a bull should be retested in 60 days. If he still fails to achieve 60 or more points, it is recommended that he not be used. A score of less than 40 points indicates that a bull is an unsatisfactory potential breeder and should not be used.

A B.S.E. has certain limitations. It is only valid for the time at which it is performed. Therefore, it should be conducted on each prospective herd sire within 60 days of the start of the breeding season. Furthermore, it does not provide a measure of serving capacity or libido, and should not be used as an absolute measure of fertility. Although a B.S.E. is not a guarantee of fertility, it is a useful and valid tool for identifying serious fertility problems in bulls.

Female Reproductive Anatomy

The functions of the female reproductive organs (Figure 4) are regulated by the physiological state of the cow or heifer. Following puberty, the female experiences regularly timed estrous (heat) cycles. The stage of the estrous cycle regulates the hormone production of a particular organ and the sensitivity of that organ to hormonal stimulus. Even the physical structure of some reproductive organs is altered with changes in the stage of the estrous cycle. Pregnancy induces even more dramatic changes in the cow's reproductive system. Adaptations occur in the cow's metabolism to insure proper growth and development of the fetus, to the exclusion of other bodily priorities. If the cow is already nursing a calf, these are further complicated by the

Table 5. Motility (Degree of Vigor)

Classification	Gross motility	Individual	Score
Very good	Rapid Swirling Movement	Rapid Linear	20
Good	Slower Swirling Movement	Moderately Fast Linear	12
Fair	Shaky Movement	Slow Linear to Erratic	10
Poor	Flickers		3

Figure 4. Reproductive Anatomy of the Cow
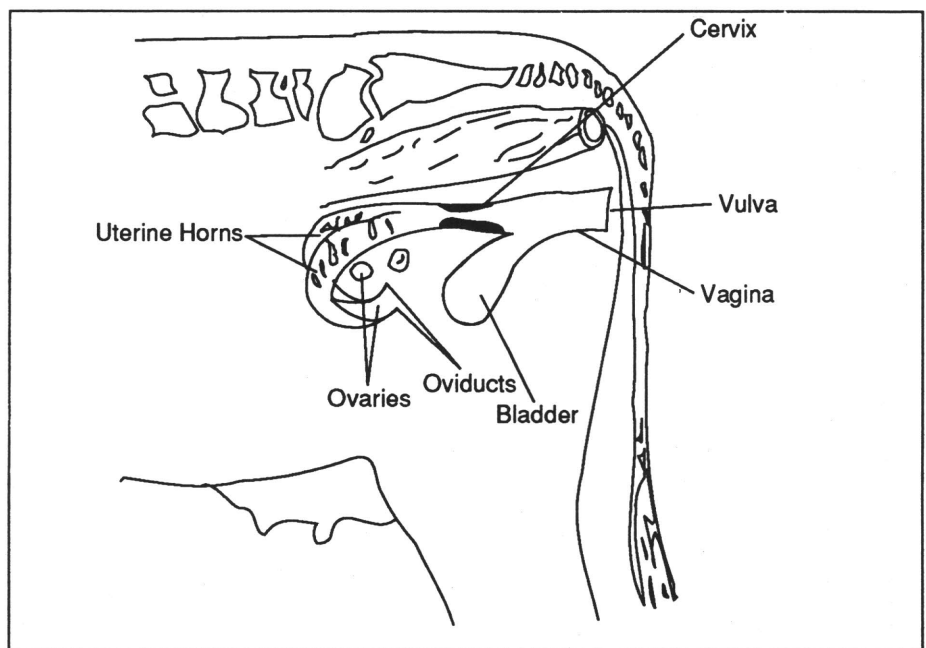
demands of lactation. In the lactating female, reproduction receives secondary priority for metabolism, at best.

Hypothalamus-Pituitary

As in the male, the hypothalamus and the pituitary glands provide a variety of endocrinological stimuli. Of particular importance to reproduction are GnRH and the gonadotrophins LH and FSH. Oxytocin also plays an important role in the female. In addition to its role in milk letdown, oxytocin is instrumental in sperm transport through the uterus and the oviduct (the site of fertilization).

Ovaries

The ovaries are the female counterparts to the male testicles. They are the site of oocyte (egg) development and maturation, through a process known as oogenesis. Oogenesis occurs in a specialized structure called a follicle. Several follicles are present on the ovary at all stages of the estrous cycle. They can be detected by a trained technician via rectal palpation of the ovaries. At estrus (standing heat), one follicle can be palpated which is in a more advanced stage of development than the others. This ovulatory follicle contains a mature oocyte. The process of follicular growth and development is termed folliculogenesis, and is regulated by the hormone FSH from the pituitary gland. Throughout folliculogenesis the follicles produce and secrete estrogen.

Estrogen is a steroid hormone which is responsible for the secondary female sex characteristics. At estrus, when the level of estrogen secretion from the ovulatory follicle reaches a peak, the pituitary gland responds with the release of an ovulatory surge of LH. LH induces the follicle to rupture and release its mature egg into the oviduct where fertilization can occur. Following ovulation, the pituitary continues to secrete constant levels of LH. The LH in turn initiates a transformation of the cells in the follicle. The resulting "luteinized" cells form a new structure on the surface of the ovary known as the corpus luteum (CL), which is primarily responsible for the secretion of the steroid hormone progesterone. Progesterone maintains a uterine environment favorable to the growth and development of the fetus.

Oviduct

The oviduct is the site of fertilization. Structurally it is composed of four sections. The *fimbriae* are fingerlike extensions of the infundibulum which covers the site of ovulation on the ovary. These structural adaptations ensure that the newly ovulated oocyte enters the oviduct rather than being lost in the body cavity. Following ovulation into the infundibulum, the egg is transported via precisely coordinated movements of the oviduct and its fluid secretions through the *ampulla* to the *isthmus* where fertilization can occur. The isthmus of the oviduct is connected to the uterus through the *uterotubular junction*.

Uterus

The uterus in the cow is bipartite, composed of two uterine horns and a uterine body connecting the horns. The sides of the uterus are connected to the pelvic and abdominal walls by the broad ligament. During the later stages of pregnancy, the broad ligament stretches and allows the uterus to descend into the body cavity and provides sufficient room for the developing fetus. The uterus is supplied with blood via the uterine artery. As pregnancy progresses, the uterine artery becomes easily palpated by a trained technician and is useful in pregnancy detection.

If fertilization fails to occur, the uterus secretes a hormone called prostaglandin (PG) which restricts the blood supply to the CL, causing it to regress or become nonfunctional. This in turn allows development of an ovulatory follicle and a subsequent return to estrus.

Lining the inside of the uterus are approximately 110 structures called caruncles, which are specifically adapted to providing nutrients to the developing fetus from the mother's circulatory system. Following implantation of the embryo at about day 33 of gestation, placental structures called cotyledons become

attached to the caruncles. While these structures do not allow mixing of the maternal and fetal blood supplies, the resulting proximity of the blood supply does allow transfer of nutrients by diffusion. When the caruncles are damaged due to either injury incurred during dystocia or to improper removal of retained placenta, they do not regenerate themselves. Occasionally this results in insufficient nutritional support to the fetus in subsequent pregnancies.

The uterus is responsible for a variety of secretions other than PG. In addition to contributing to sperm capacitation and providing a favorable environment for the developing embryo, uterine secretions contribute to the mucous discharge observed on the vulva during estrus. Furthermore, the breakdown of blood vessels lining the interior of the uterus following estrus contributes to a bloody discharge. This bloody discharge does not indicate a failure of fertilization or conception.

Cervix

The cervix is a two- to four-inch long sphincter-like muscle that serves two related functions. It is primarily a barrier between the contaminated environment existing in the vagina and the precisely controlled, sterile environment of the uterus. In conjunction with this function, the cervix serves as a door which opens only to hormonal stimulus during estrus and parturition.

Vagina

The vagina's chief contribution to reproduction is as a receptacle for semen by the bull during natural mating. It also serves as part of the birth canal during parturition. The environment existing inside the vagina is not only lethal to unprotected sperm cells, but is also conducive to the propagation of many infectious organisms which are detrimental to reproduction. This necessitates strict adherence to a sound reproductive health program, and caution when performing A.I. procedures and when assisting with dystocia cases.

Vulva

The vulva is the external component of the female genitalia and conceals the clitoris. Upon stimulation of the nerves of the clitoris by the bull during copulation, a signal is sent to the pituitary gland, resulting in the release of oxytocin. Oxytocin affects both uterine and oviductal contractions which in turn aid in egg and sperm transport through the female reproductive tract. This ultimately helps insure the proper synchrony of events which allows fertilization to occur. It is a common practice for A.I. technicians to manually stimulate the clitoris following insemination in order to initiate the proper sequence of events.

Puberty

Puberty (sexual maturity) normally occurs at 10 to 14 months of age in heifers. However, well-fed, rapidly growing heifers frequently reach puberty as early as seven months. The onset of puberty is marked by the initiation of regularly occurring estrous cycles, and is influenced by the same factors as in the bull.

Nutritional and genetic factors are particularly important in heifers. Not only is age at puberty affected by such factors as body weight and body condition, but the ability of the heifer to maintain a normal pregnancy and experience a trouble-free parturition are ultimately dependent on breed and level of nutrition. Due to these latter considerations, age at breeding is more important than age at puberty. It is generally recommended that heifers not be bred prior to 14 months of age, particularly if nutrition is a limiting factor.

Estrous Cycle

A pubertal, nonpregnant heifer will experience regularly occurring estrous cycles ranging in length from 18 to 24 days. The average cycle length is 21 days. Figure 5 outlines a normal 21-day estrous cycle with the significant events specified. Also profiled are the regulating hormonal levels. Day 0 represents standing estrus, or heat, and is the time at which the cow is sexually receptive to the bull.

Figure 5. Estrous Cycle of the Cow

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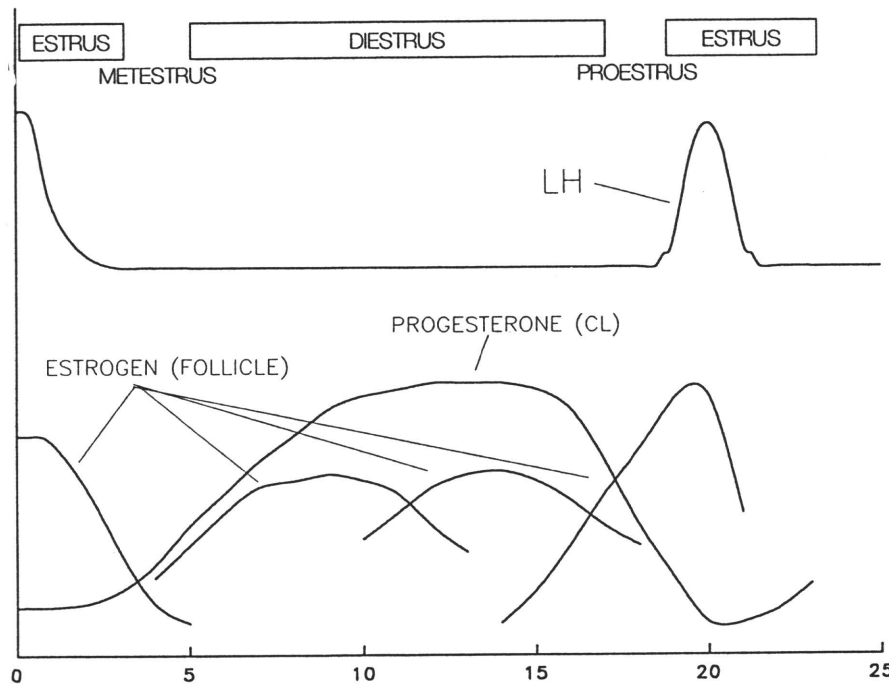
Approximately day 19 through day 3 is termed the estrus period. It is the period during which the female is coming into and going out of heat. It is marked by high estrogen and low progesterone levels. The dominant structure on the ovary is the ovulatory follicle and its development is stimulated by high levels of FSH from the pituitary. Increasing estrogen secretion by the follicle results in the ovulatory surge of LH. This in turn results in rupture of the follicle and the subsequent release of the mature egg into the oviduct. Standing estrus can last from 4 to 30 hours, with an average of 12 to 18 hours. Ovulation occurs 10 to 14 hours following the end of the heat period. An egg is generally capable of fertilization for a period of 6 to 10 hours following ovulation.

The second stage of the estrous cycle is known as the luteal phase and lasts from about day 5 until day 16 or 17. The CL is the dominant structure on the ovary at this time and progesterone is the dominant hormone. If fertilization fails to occur, the uterus begins secreting PG on about day 16 to 17, which results in regression of the CL and a normal return to estrus. If fertilization does occur, the developing embryo is a signal to the uterus to stop PG secretion, allowing pregnancy to continue.

Gestation

Gestation (pregnancy) can range from about 270 days to more than 300 days. Average length of gestation is 285 days and is dependent upon both genotype of the sire and the dam and upon the sex of the calf. Additionally, females carrying twins tend to have shorter gestation lengths.

Following implantation of the embryo, which occurs on about day 33 of gestation, the cow's metabolism is greatly influenced by the hormones produced by the placenta. The placenta is of fetal origin, not maternal origin, and assures the developing fetus of a means of survival, often at the expense of the mother's own well-being.

Parturition

Parturition is initiated by the fetus. Prior to calving, a cow goes through several physical and behavioral changes which are under hormonal control. Particularly noticeable in a cow approaching parturition is an edematous swelling of the vulva and the outward signs of relaxation of the pelvic ligaments. These latter signs include increased prominence of the hook and pin bones, the appearance of a noticeable dip

Table 6. Stages and Duration of Parturition

Stage of Parturition	Heifers (hours)	Cows (hours)
Contraction of uterus and dilation of cervix	6-12	4-8
Passage through birth canal	1-4	.5-1
Expulsion of placenta	1-8	1-8

in the loin, and the general impression of muscle degeneration in the rump of the cow. Caution must be used regarding these signs as an absolute predictor of calving times. They differ among individuals, and may begin to appear as early as 30 days prior to calving in some females.

Parturition itself is marked by three distinct stages of labor and can last from 5 to as much as 24 hours. Heifers will in general take more time to calve than cows, and assistance must frequently be provided. Time ranges for the stages of labor are listed in Table 6 for both cows and heifers. Stage 1 involves beginning uterine contractions and dilation of the cervix. Its initial stages are often accompanied by exhibition of nesting behavior of the cow during which she attempts to isolate herself from the rest of the herd. The end of Stage 1 is marked by the appearance of the water sac. Stage 2 involves entry of the fetus into the birth canal and subsequent birth. Stage 3 involves expulsion of the placental membranes and should be complete within 8 hours.

Postpartum Period

Following calving, the primary physiological changes a cow experiences are the initiation of lactation, the involution of the uterus, and the preparation of the reproductive tract to resume normal

cyclicity. The ability of the cow to accomplish these tasks is correlated to both her body condition (B.C.) at calving and to the level of nutrition she receives after calving. Figures 6 and 7 illustrate the relationship of body condition to the length of the postpartum anestrus period. This is the period of time required by a cow before she is able to

undergo normal estrus periods following parturition. Table 7 further demonstrates the relationship between postpartum body condition loss and infertility. As can be seen, severe feed deprivation resulting in severe body condition loss can be detrimental to overall fertility.

Figure 6. Effects of Prepartum and Postpartum Body Condition Change on the Number of Days to First Postpartum Estrus (Whitman, 1973)
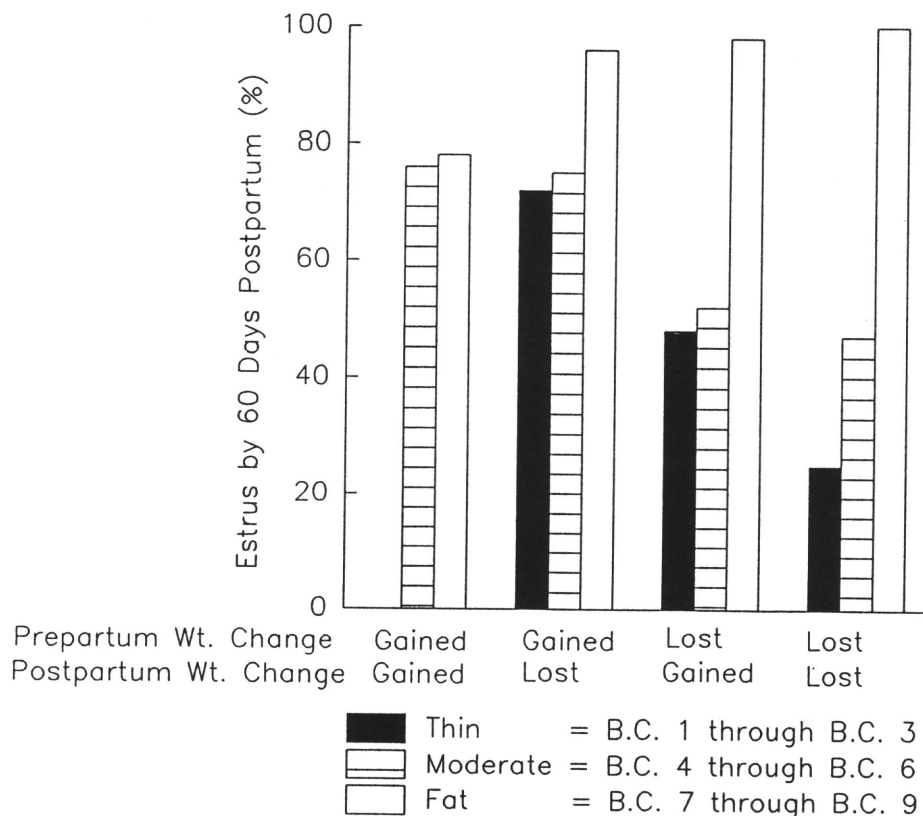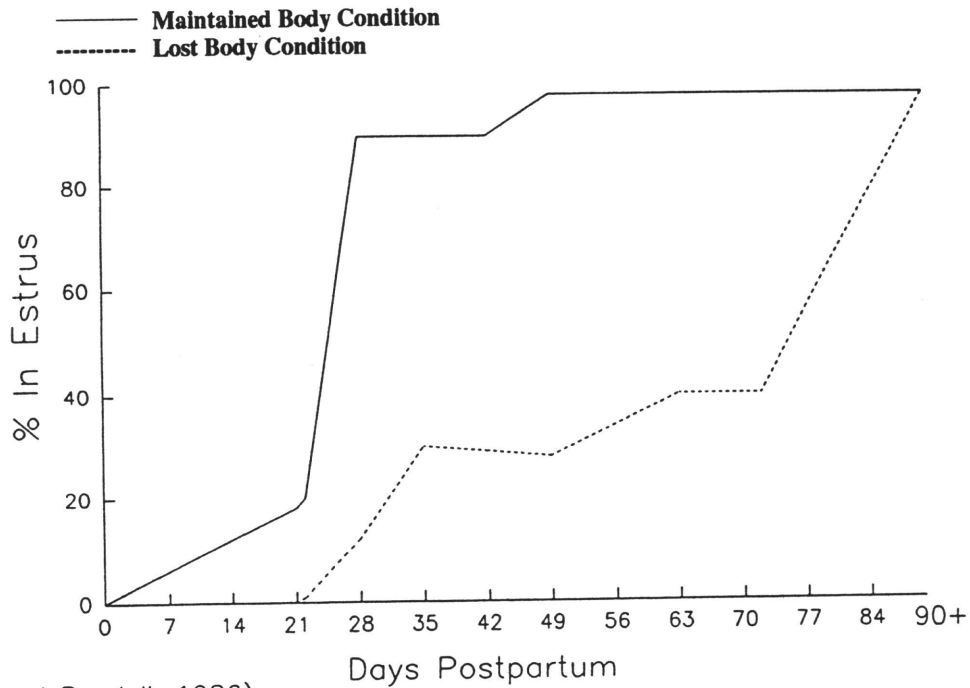
Figure 7. Effects of Loss of Body Condition Score on the Postpartum Interval to First Estrus (Rutter and Randall, 1986)

(Rutter and Randell, 1986)

Table 7. Relationship Between Postpartum Body Condition Loss and Reproductive Performance

Body condition loss	No. of cows	Days to 1st ovulation	Days to 1st estrus	Services - conception	Days open
Minor[a]	23	24	40	1.7	92
Moderate[b]	16	34	35	1.8	88
Severe[c]	15	35	53	1.9	104

[a]Minor B.C. Loss   : Less than 0.5 units

[b]Moderate B.C. Loss : Between 0.5 and 1.0 units

[c]Severe B.C. Loss   : Greater than 1.0 units

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