

# Mechanisms linking nutrition and reproduction in postpartum cows

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The reproductive physiology of postpartum cows is different from that of heifers because of the combined effects of the past pregnancy and lactation. Neither lactation nor pregnancy has a major effect on postpartum fertility when calving is free from disease and lactation is moderate. Postpartum beef cows in good body condition have conception rates nearly equivalent to those of virgin heifers once their uteri are involuted and they initiate ovarian cycles. However, cows will experience infertility when nutrient requirements for maintenance and lactation exceed nutrient intake (postpartum beef cows) or when nutrients are specifically partitioned toward lactation (postpartum dairy cows). The subsequent loss of body fat that occurs in either case has effects on a variety of reproductive processes and reproduction becomes less efficient. The mechanisms that lead to abnormal reproduction in nutritionally compromised postpartum cattle have been investigated intensively. Much of the effort has focused on the nature of the signal (endocrine or otherwise) that controls pituitary secretion of LH and FSH, the response of the ovary to LH and FSH, and other ovarian effects that are independent of gonadotrophins. Reproductive studies in ruminants have tended toward studies of follicular development and this focus relates back to solving the problem of anoestrus. Less work has been done on the effects of nutrition on the early embryo, the health of which may be predetermined by factors affecting the oocyte within the preovulatory follicle. Few studies have examined the effect of nutrition on uterine function in postpartum cattle. Solutions to postpartum reproduction will probably arise from a variety of approaches that include traditional physiology as well as more modern genomic and proteomic technologies.

## Introduction

The effects of nutrition and lactation on reproduction are well recognized. Ancient societies were well aware of the effects of nutrition and lactation on reproduction. Egyptians in the 15th century BC practised prolonged lactation as a method of birth control in women (Medvei, 1982). Aristotle (384–322 BC) wrote that nutrition was the most important environmental

factor controlling conception (Medvei, 1982). The effects of nutrition on reproduction in the modern era are similar to those reported by ancient societies. Cattle that are in poor condition or losing body weight generally have poor reproductive performance. This relationship is often explained by using the argument of nutrient prioritization. Postpartum cows prioritize their metabolizable energy toward production of milk for the calf and then toward regaining body condition (adipose tissue). It is only after these immediate needs are met that reproductive processes (perhaps viewed as non-essential for the individual but nonetheless essential for the species) are resumed. The mechanisms through which nutrition controls reproduction in postpartum cows are of great interest because calves and milk are the commodities of agriculture in cattle. Beef cattle are maintained on yearly calving intervals so that one calf is produced per year. Dairy cattle are maintained on yearly calving intervals so that maximal milk production is timed with seasonal growth of grasses (seasonal dairy systems) or so that dairy cows are dried off at an optimal time in the lactation curve (year-round calving systems). The energy required to ovulate a follicle, form a corpus luteum and maintain an early pregnancy is very small compared with the other energy demands of lactating cows. Therefore, the aim of bovine reproductive biologists is to establish pregnancy early in lactation when seemingly little energy is required for the pregnancy. In late gestation, the energetic demands for the pregnancy are greater but the energetic demands for lactation are lower or non-existent (dry cow). The problem is that this seemingly easy solution to maintain a yearly calving interval is inconsistent with the evolution of reproduction in cattle. Cattle initiate cyclicity and are fertile after minimum nutrient requirements are met.

### Three phases of the postpartum period

There is a need to think broadly about the relationship between nutrition and reproduction in postpartum cattle and to discuss the process in its basic components. Three phases of the postpartum reproductive cycle have been reviewed (Inskeep, 1995; Jolly *et al.*, 1995; Macmillan *et al.*, 1996). The ruminant placenta produces copious amounts of steroids (progesterone, oestrogens and their derivatives) during late pregnancy and the steroids of late pregnancy have a suppressive effect on the reproductive hormones of the hypothalamus and pituitary gland just as they do in cyclic animals. Thus, the first phase of postpartum reproduction is the recovery of the hypothalamus and pituitary gland from the effects of the previous pregnancy and the resumption of FSH secretion and pulsatile LH release. The LH surge mechanism (positive oestradiol feedback loop) must also be re-established. The first phase is relatively short and cows begin normal LH pulsatility at 1–2 weeks after parturition and recover the LH surge mechanism shortly thereafter. There are a variety of factors that affect the resumption of LH pulsatility (most notably suckling and energy balance) and the relative impact of these depends on their intensity. The primary limitation to LH release is the secretion of GnRH and, thus, the hypothalamus is a key player in the process (see below). Lack of GnRH release leads to a lack of LH release and a breakdown of reproductive processes. FSH is needed for follicular growth in postpartum cows, but is not viewed as limiting for reproduction. In fact, most anoestrous cows have relatively high concentrations of FSH because they have smaller, less-active follicles that are incapable of fully suppressing FSH secretion through the cumulative actions of ovarian oestradiol and inhibin (Bossis *et al.*, 1999).

The second phase in the process of postpartum reproduction is uterine involution. Uterine involution is rapid and is completed by days 30–40 post partum. The timing of uterine involution coincides with the recovery of complete fertility in postpartum cows. Thus, most investigators consider uterine involution as the initial block to the re-establishment of normal

fertility. Uterine involution is not considered as a major limitation to postpartum reproduction because most cows are inseminated from day 40 to day 80 post partum when the process of uterine involution is complete.

Perhaps the most intensely studied area of reproduction in postpartum cows is ovarian recovery after calving. Follicular growth continues during pregnancy but the diameters of dominant follicles decrease perhaps because of a decrease in LH pulsatility in late pregnant cattle (associated with high steroid concentrations during late pregnancy; see above). Follicular development begins shortly after calving with a transient increase in FSH, a follicular wave and the development of a dominant follicle. The first dominant follicle post partum undergoes one of three fates (Beam and Butler, 1999): (i) ovulation, (ii) atresia and turnover (followed by new wave emergence) or (iii) cyst formation. The mechanisms that dictate these three events are of keen interest to reproductive biologists. A principal component of the process is the secretion of LH during the early postpartum period. Low LH pulsatility is associated with follicular turnover and anoestrus; moderate LH pulsatility is associated with ovulation; and extreme LH pulsatility and lack of an LH surge is associated with the development of cystic ovaries (Silvia *et al.*, 2002).

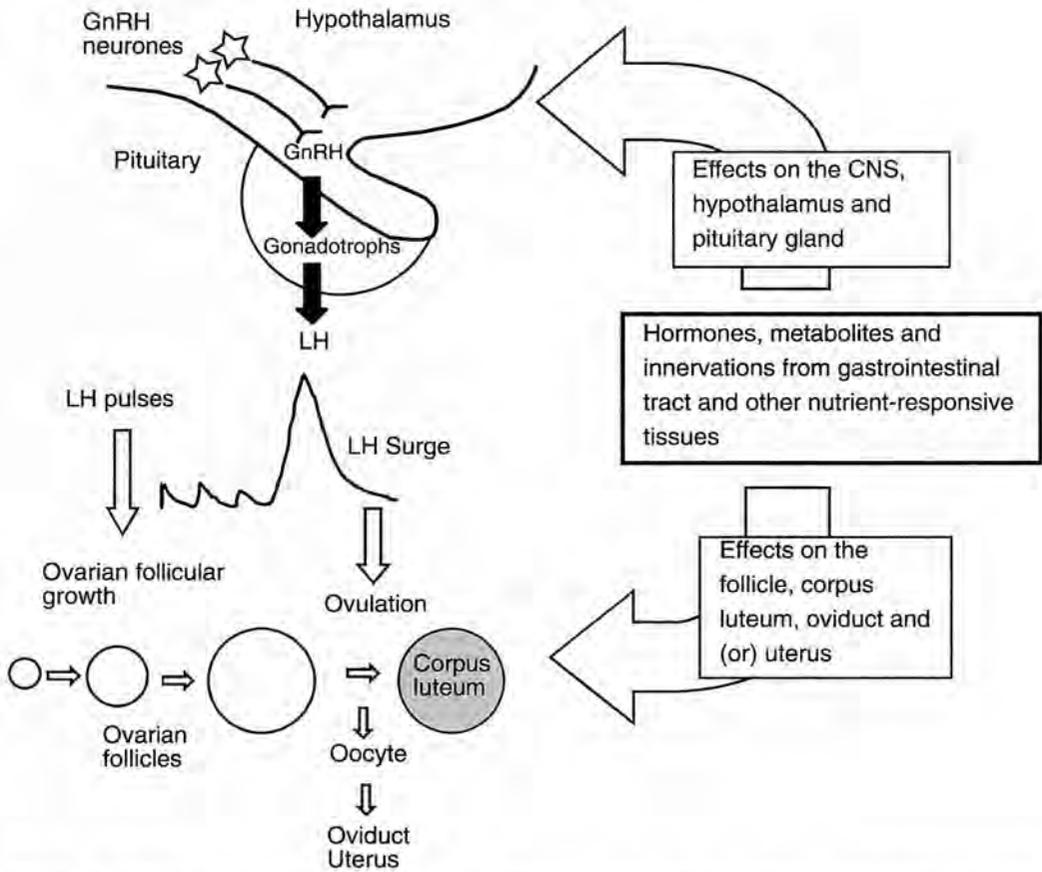
Anoestrus (follicular wave growth without ovulation) can persist for a long time in cattle. The principal causes of anoestrus are different for beef and dairy cows but the essential features are similar. In beef cows, suckling inhibits LH pulsatility and the lack of LH pulsatility leads to anoestrus (Williams and Griffith, 1995). Beef cattle are also susceptible to undernutrition, which dampens LH pulsatility. Anoestrus is traditionally viewed as a problem in beef cattle experiencing the combined effects of undernutrition and suckling. Anoestrus in dairy cattle was viewed as less common (compared with beef cattle) because dairy cattle are not suckled. More recent data indicate greater incidence of anoestrus in dairy cattle that is associated with nutrient partitioning toward milk production in modern dairy cows (Roche *et al.*, 2000).

The resumption of oestrous cyclicity in cattle is not necessarily synonymous with the resumption of normal fertility. There are of course infertile 'short oestrous cycles' the physiology of which has been studied and reviewed extensively (Inskeep, 1995). Reproductive physiologists have viewed oestrous cycles after the short oestrous cycles as essentially normal with normal fertility. However, it is known now that at least in high producing dairy cattle the resumption of oestrous cyclicity is not synonymous with the resumption of regular oestrous cycles with normal fertility (see below). The factors that control regular oestrous cyclicity with normal fertility represent the biggest challenge to reproductive biologists working with modern cattle.

### **Mechanisms controlling follicular growth in postpartum cattle**

Numerous papers have reviewed specific mechanisms that control reproduction in postpartum cattle (Inskeep, 1995; Jolly *et al.*, 1995; Keisler and Lucy, 1996; Macmillan *et al.*, 1996; Beam and Butler, 1999; Butler, 2000; Lucy, 2000; Roche *et al.*, 2000; Royal *et al.*, 2000; Boland *et al.*, 2001; Lucy, 2001; Monget *et al.*, 2002). Many of these mechanisms are linked directly to the nutrition of the animal. A global visualization of the basic concepts are presented (Fig. 1) and the reviews for more information on specific topics are cited.

Follicular growth in postpartum cattle is controlled by a combination of LH and FSH (Mihm and Austin, 2002). Essential mechanisms that control follicular growth are similar whether or not the cow is undergoing anoestrus or oestrous cycles. Control of follicular development by LH and FSH is dependent on the concentrations of their respective receptors and also the functionality of the second messenger systems that ultimately determine cellular responses.



**Fig. 1.** Conceptual model for the mechanisms through which nutrition affects reproduction in postpartum cows. Hormones, metabolites and innervations from the gastrointestinal tract and nutrient-responsive tissues affect GnRH and LH secretion through their actions on the central nervous system (CNS) and hypothalamus. These hormones and metabolites may have direct effects on ovarian function (both follicles and corpora lutea) as well as on the oocyte, oviduct and uterus. The combined effects of each axis determine postpartum fertility.

Classically described, FSH is viewed as responsible for initiating follicular growth and LH is responsible for final maturation of the dominant-preovulatory follicle. Secretion of LH and FSH is controlled primarily (LH), or in part (FSH), by GnRH from the hypothalamus. The factors that control the release of GnRH from the hypothalamus are major components of a conceptual model for LH secretion (Fig. 1).

Changes in metabolic hormones are dynamic in postpartum cows and reflect the shifting metabolic status of the animal. Blood concentrations of insulin-like growth factor I (IGF-I), insulin and leptin decrease shortly after calving (Butler, 2000; Lucy, 2000; Block *et al.*, 2001). Insulin and IGF-I concentrations gradually increase post partum, whereas leptin concentrations remain low in lactating cows. The blood concentrations of IGF-I, insulin and leptin are higher in cows in positive energy balance. Cows in negative energy balance and cows selected for milk production have lower blood concentrations of insulin and IGF-I (Snijders *et al.*, 2001; Gong, 2002). The aforementioned endocrine hormones that are metabolically controlled can influence GnRH and LH secretion. Their actions may be on GnRH neurones,

on the neuronal pathways that impinge upon GnRH neurones or on the pituitary gonadotroph (Adam *et al.*, 2000; Williams *et al.*, 2002). The hormonal control (endocrine) arises from tissues that respond to the metabolic or nutritional status of the animal (for example insulin from the pancreas; IGF-I from the liver; leptin from adipose tissue). It is logical that these peripheral cues would act upon the hypothalamus to convey information from metabolically important tissues. However, it should also be noted that a number of other mechanisms can communicate nutritional information to the central nervous system. Neuronal control of hypothalamic function by afferent fibres arising from the liver and gastrointestinal tract has been proposed by Keisler and Lucy (1996). A variety of metabolites (for example glucose and fatty acids) and other hormones acting as blood-bourne messengers may also be involved.

The same metabolites and hormones that influence GnRH secretion and ultimately LH and FSH secretion may act directly on the ovary to influence the sensitivity of the ovary to LH and FSH. Ovarian cells treated with either insulin or IGF-I have greater numbers of gonadotrophin receptors and greater activation of second messenger pathways in response to gonadotrophins (Lucy, 2000). There is also the potential for effects of insulin and IGF-I that are completely independent of LH and FSH. Although the interaction of metabolic hormones with the ovary has been described for insulin and IGF-I (Butler, 2000; Lucy, 2000; Monget *et al.*, 2002), it is likely that a variety of hormones and metabolites act on the ovary and change the ability of the ovarian cells to grow or respond to gonadotrophins. Leptin is unusual in that it is stimulatory to LH secretion (Williams *et al.*, 2002), but inhibitory to steroidogenesis in theca and granulosa cells (Spicer *et al.*, 2000).

The potential for neuronal control of ovarian function in postpartum cows is generally overlooked. The ovary is heavily innervated and adrenergic neurones control blood flow and steroidogenesis within the ovary (Kotwica *et al.*, 2002). Information on the nutritional status of cows may be integrated within the central nervous system and communicated to the ovary via the autonomic nervous system.

It may be impossible to dissect the relative importance of gonadotrophins, locally and peripherally produced growth factors, metabolites and ovarian innervation for controlling reproduction in the postpartum cow. Cows that are nutritionally compromised have low concentrations of metabolites and metabolic hormones in their blood (Snijders *et al.*, 2001; Gong, 2002). The lower metabolic hormone concentrations theoretically reduce ovarian responsiveness to gonadotrophins (see above). At the same time, postpartum cows have low blood concentrations of LH, in part because of the effects of metabolic hormones on GnRH secretion from the hypothalamus. Thus, the effects of nutrition on reproduction are manifested at the ovary and at the pituitary gland and hypothalamus. Overcoming one limitation will not necessarily recover ovarian function. The overriding effects of gonadotrophins may be greater in as much as oestrous cyclicity was induced in anoestrous sheep by the peripheral infusion of LH (Keisler and Lucy, 1996). Treatment of cows with somatotrophin (and hence, increasing IGF-I concentration) may increase follicular growth but probably cannot cause enough follicular growth to bring anoestrous cows out of anoestrus (Lucy, 2000).

The duration of the postpartum anoestrous period depends on the suckling stimulus (beef cows), body condition (beef and dairy cows) and the depth of negative energy balance (primarily a factor in postpartum dairy cows). An intense suckling stimulus will slow down LH pulsatility and delay oestrus (Williams and Griffith, 1995). Poor body condition has a similar effect and the effects of suckling and poor body condition may be accumulative. Dairy cows do not experience the suckling stimulus, but they do experience a period of negative energy balance early post partum. Energy requirements for milk and maintenance exceed energy consumed in the feed. The resulting negative energy balance is associated with a decrease in LH pulsatility (Beam and Butler, 1999). A critical feature of the energy balance curve is the

'nadir' (period of greatest negative energy balance). The LH pulsatility is increased after cows pass the nadir and begin to recover toward a positive energy balance.

Postpartum cows will become cyclic once LH pulsatility reaches a critical level. The increase in LH pulsatility stimulates the maturation of a dominant follicle (Mihm and Austin, 2002). The dominant follicle produces oestradiol that reaches a threshold amount to trigger an LH surge. The cow will then have an LH surge and ovulate as long as the LH surge mechanism (positive feedback of oestradiol) is established (Williams and Griffith, 1995). Hypothetically, mechanisms that increase LH pulsatility through their actions on the hypothalamus and pituitary gland also coordinate an increase in the responsiveness of the ovary to LH. For example, LH pulsatility increases in cows during the postpartum period. Both blood concentrations of insulin and IGF-I increase too (Butler, 2000; Lucy, 2000). Thus, there is a coordinated series of events that act to promote follicular development and eventually ovulation.

### Factors affecting fertility in cyclic cattle

#### *Carry-over effects of anoestrus*

Beef cattle experience extended periods of postpartum anoestrus before the breeding period, but their fertility is normal once they resume oestrous cyclicity. In a study of postpartum beef cattle, cattle diagnosed as anoestrus before the breeding period were found to be less likely to be inseminated successfully during a 31 day breeding season (Table 1; Lucy *et al.*, 2001). Sixty-seven per cent of cows diagnosed as anoestrus before the breeding period became cyclic during the breeding period and were inseminated successfully. Once cyclic, the fertility of the previously anoestrous cows was not different from that of cows diagnosed as cyclic before the breeding period. Thus, carry-over effects of anoestrus were not detected once the cows became cyclic. Similarly, New Zealand dairy cattle (grazing management system) are anoestrus for longer than USA dairy cattle (confinement management system) but have better fertility during the breeding period (Macmillan *et al.*, 1996). Thus, the duration of anoestrus *per se* may not be a major factor contributing to infertility of cattle unless the period of anoestrus extends beyond the breeding period. However, factors that cause extended anoestrus may affect gametes or other reproductive tissues.

#### *Abnormal oestrous cycles*

Modern dairy cattle that have been selected intensively for milk production have longer postpartum intervals to first ovulation (Roche *et al.*, 2000; Gong, 2002). The longer interval to first ovulation reflects a compromised state of LH secretion and perhaps compromised local endocrine support within the ovary. Recent studies have examined oestrous cyclicity in modern dairy cattle (Lamming and Darwash, 1998; Roche *et al.*, 2000; Royal *et al.*, 2000) and have identified an increased incidence of anoestrus in modern dairy cattle. An additional observation arising from these studies is that modern dairy cattle have an increased incidence of irregular or abnormal oestrous cycles (Table 2). These abnormalities can be manifested through a variety of oestrous cycle pathologies that include temporary cessation of luteal phases and long luteal phases (> 20 days; Fig. 2). Our most recent study comparing dairy cattle selected for milk production with traditional 1964 dairy cattle (Waseca herd selection project, University of Minnesota, St Paul) has also demonstrated a greater incidence of anoestrus and a greater incidence of long luteal phases in cows selected for milk production (M. C. Lucy, B. A. Crooker and S. J. Kolath, unpublished). Factors known to affect postpartum cows, such as negative energy balance, periparturient disorders and postpartum diseases, are known risk factors for delayed cyclicity and prolonged luteal phases (Opsomer *et al.*, 2000). The

**Table 1.** Reproductive performance for postpartum beef cattle diagnosed as cyclic or anoestrus before the breeding season

Characteristic	Anoestrus	Cyclic
Number of cows <sup>a</sup>	447	404
Number in oestrus within 3 days after treatment (%)	110 (25)	191 (47)
Number in oestrus within 31 days after treatment (%)	300 (67)	353 (87)
Number pregnant to first service (%)	175/294 (60)	227/348 (65)
Number pregnant after 31 day breeding period (%)	199/441 (45)	259/399 (65)

<sup>a</sup>Cows were control, prostaglandin F<sub>2α</sub> (PGF<sub>2α</sub>)-treated or progestogen and PGF<sub>2α</sub>-treated immediately before the breeding season. Blood samples were tested for progesterone to determine status (anoestrus or cyclic) before the breeding season (Data from Lucy *et al.*, 2001).

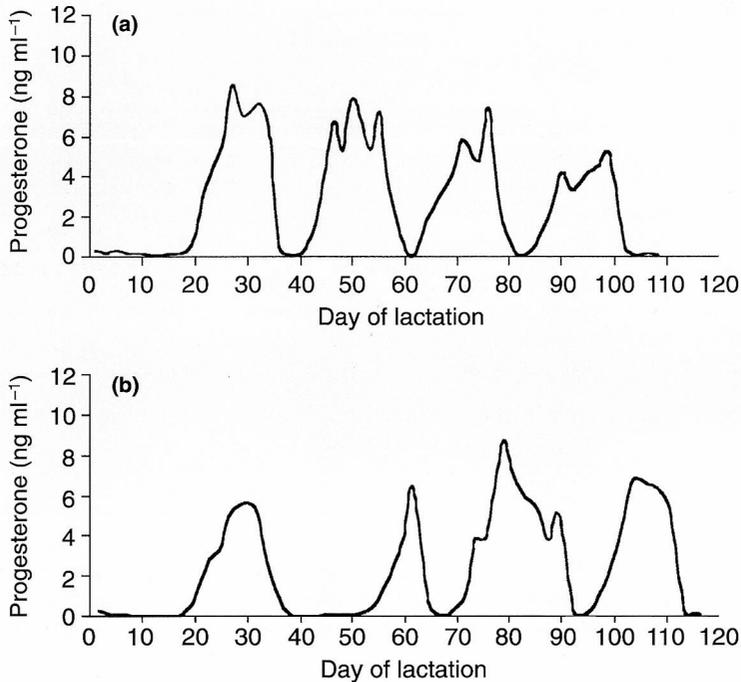
**Table 2.** Summary of oestrous cyclicity based on analyses of progesterone profiles in traditional and modern lactating cows

Characteristic	Traditional	Modern
Number of oestrous cycles	463	448
Normal pattern (%)	78	53
Anoestrus (%)	7	21
Temporary cessation of cycle (%)	3	3
Prolonged luteal phase (%)	3	20
Short cycles (%)	4.0	0.5
Other irregular patterns (%)	4.0	2.5

Data from moderate-yielding Friesian cattle (traditional; Fagan and Roche, 1986) and high-yielding Holsteins (modern; Opsomer *et al.*, 1998) were summarized by Roche *et al.* (2000).

incidence of twinning (presumably caused by double ovulation; Fricke and Wiltbank, 1999) has also increased in modern dairy cattle because there are positive genetic correlations between the incidence of twins and amount of milk production (Kinsel *et al.*, 1998).

One hypothesis that needs to be tested is that the increased incidence of anoestrus, abnormal oestrous cycles and twinning share a common LH-mediated mechanism (Fig. 3). Presumably, the increase in anoestrus is caused by a decrease in LH pulsatility that is secondary to negative energy balance in dairy cattle selected for high milk production. Lower metabolic hormone concentrations (for example insulin and IGF-I) may contribute to a decrease in ovarian LH responsiveness and create gonadotrophin insensitivity at the ovary (see above). It is possible that the compromised state of LH secretion and sensitivity continues in the cyclic animal and disrupts functional aspects of the dominant follicle. Lactating cows had larger preovulatory follicles than did heifers, but lower preovulatory concentrations of oestradiol in blood (Sartori *et al.*, 2000). Thus, the dominant follicle must grow to a larger size to achieve equivalent blood oestradiol concentrations. Whether the lower blood oestradiol is caused by poor steroidogenic capacity of the follicle or greater steroid metabolism in lactating cows with high nutrient intake is not known. The additional developmental time needed by the follicle of lactating cows may create a 'persistent follicle' scenario (and hence lower fertility; Diskin *et al.*, 2002) in which the oocyte is exposed to an extended preovulatory period of relatively high LH pulsatility. Lactating cows also have a higher incidence of multiple ovulations when compared with heifers. The greater ovulation rate in lactating cows may be caused by follicles that fail to produce enough oestradiol to suppress FSH fully (Wiltbank *et al.*, 2000).



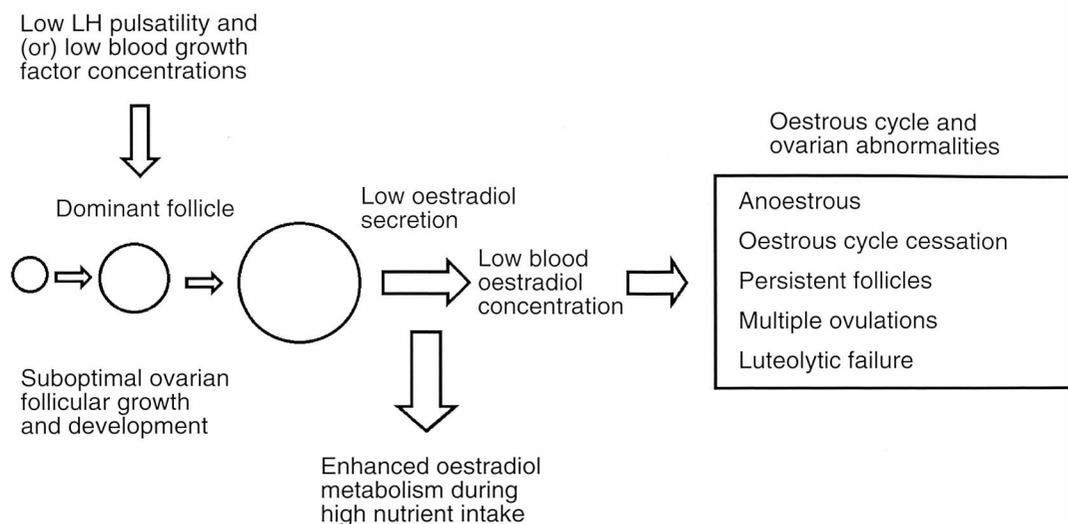
**Fig. 2.** Plasma concentrations of progesterone during the postpartum period for two dairy cows. (a) This cow had four oestrous cycles of approximately normal duration. (b) This dairy cow had a normal oestrous cycle (days 18–38); a temporary cessation of oestrous cycles (days 38–52); a short oestrous cycle (days 52–65); a prolonged luteal phase (days 68–92); and a normal oestrous cycle (days 93–113) (M. C. Lucy and B. A. Crooker, unpublished).

Early phases of luteolysis are modulated by oestradiol (Okuda *et al.*, 2002). Therefore, long luteal phases in dairy cattle selected for milk production may be the result of dominant follicles that are developmentally compromised and produce insufficient oestradiol to initiate the luteolytic cascade. Whether long luteal phases in high producing dairy cows are associated with a higher incidence of oestrous cycles with three follicular waves is not known. The lower fertility in cows with two relative to three follicular waves (Townson *et al.*, 2002) would be theoretically exacerbated by longer luteal phases in high producing dairy cows.

Temporary cessation of oestrous cycles could be caused by a similar oestradiol-mediated mechanism in which dominant follicles are incapable of producing sufficient oestradiol to trigger an LH surge for ovulation. We found that 21% of postpartum dairy cows in the luteal phase that were treated with a luteolytic dose of PGF<sub>2α</sub> failed to ovulate the preovulatory follicle (J. M. Borman and M. C. Lucy, unpublished). The phenomenon was completely reversed by oestradiol treatment after an injection of PGF<sub>2α</sub>. Therefore, insufficient blood oestradiol concentrations may be a causative factor leading to ovulation failure after spontaneous luteolysis or luteolysis induced in oestrous synchronization programmes.

### Oocyte quality

Snijders *et al.* (2000) found that the ability of an oocyte to be fertilized and develop to the blastocyst stage *in vitro* was affected by body condition of the donor dairy cow. Oocytes



**Fig. 3.** Mechanisms linking poor LH secretion and suboptimal follicular growth to oestrous cycle and ovarian abnormalities. Low blood oestradiol concentrations may be produced by low follicular oestradiol secretion (secondary to low LH pulsatility and (or) low blood growth factor concentrations) and enhanced oestradiol metabolism during high nutrient intake. A variety of oestrous cycle and ovarian abnormalities may be linked to low blood oestradiol concentrations.

**Table 3.** The percentage of good quality embryos flushed from the uterus on specific days after oestrus for control and repeat-breeder dairy cows\* and for lactating and non-lactating dairy cows<sup>†</sup>

Days after oestrus	Control (%)	Repeat-breeder <sup>a</sup> (%)	Lactating (%)	Non-lactating (%)
2–3	83	71	–	–
4–5	88	80	58	82
6–7	83	42	–	–
17–19	57	43	–	–

<sup>a</sup>Repeat-breeder dairy cows were defined as cows with four or more inseminations and failure to establish pregnancy.

\*Data from Ayalon (1978); <sup>†</sup>Data from Wiltbank *et al.* (2001).

fertilized *in vitro* from dairy cows in low body condition had a lower cleavage rate and a lower developmental rate compared with oocytes from dairy cows in better body condition. The exact period of nutritional imprinting of the oocyte is not known but many have speculated that it occurs during the 2 months that it takes for a follicle to progress from the primordial to preovulatory stage. The possibility that modern dairy cattle have poor oocyte quality and low fertilization capacity *in vivo* has been raised by recent work comparing cleavage stage embryos from lactating and non-lactating dairy cattle (Wiltbank *et al.*, 2001) (Table 3). The percentage of normal embryos 4–5 days after oestrus was low (58%) for lactating cattle and lower than historical values reported by Ayalon *et al.* (1978). The percentage of normal embryos for non-lactating dairy cattle was comparable to historical values for normal lactating cattle (82%). The percentage of early stage embryos in lactating cows approached that expected for 'repeat-breeder' cattle described in the 1970s (cows with four or more inseminations and failing to achieve pregnancy; Table 3). Poor oocyte quality and poor early embryonic development may

reflect a compromised state of follicular development in postpartum cattle. The compromised follicular development may be ultimately tied to factors linking nutrition to reproduction.

### *Size and steroidogenic capacity of the corpus luteum*

Undernutrition may compromise pregnancy through its effects on the corpus luteum. There is a positive association between blood progesterone concentrations and pregnancy (Lamming and Darwash, 1998). Cattle that are underfed have smaller corpora lutea and lower blood progesterone concentrations (Gombe and Hansel, 1973). The effect of nutrition on the size of corpora lutea is probably a consequence of nutritional effects on the follicle before breeding. Cyclic cattle that are underfed have progressively smaller and less oestrogenic dominant follicles before they succumb to anoestrus (Bossis *et al.*, 1999). The smaller dominant follicles give rise to smaller corpora lutea. There is also the potential for direct effects of nutritionally regulated hormones and metabolites on luteal function. Peters *et al.* (1994) blocked LH pulses with an GnRH antagonist and found that the steroidogenic capacity of the corpus luteum was dependent on LH pulsatility during the early luteal phase, a period in which progesterone concentrations may affect embryonic development and pregnancy outcome. The steroidogenic capacity of luteal cells is also dependent on hormones, such as somatotrophin, insulin and IGF-I that are controlled by the nutrition of the cow (Lucy, 2000).

### *Uterine function*

Seemingly normal embryos may fail to develop within the uterus because cattle in poor body condition may not synthesize adequate amounts of embryotrophic growth factors that are required by filamentous embryos. Mapletoft *et al.* (1986) examined pregnancy rates after embryo transfer and found that recipients with low body condition score had lower conception rates when compared with recipients with high body condition score. Embryonic loss after day 28 of pregnancy was highest in cows losing the greatest amount of body condition (Silke *et al.*, 2002). The IGF system is nutritionally regulated and is clearly resident within the uterus and embryo (Watson *et al.*, 1999). Pregnant cows have higher concentrations of uterine IGF-I mRNA than do non-pregnant cows (Kirby *et al.*, 1996) and treating cows with somatotrophin after insemination increased conception rates perhaps through an embryotrophic mechanism involving IGF-I (Bilby *et al.*, 1999; Moreira *et al.*, 2000). Therefore, the IGFs may be tied to a nutritional (body condition) effect on the embryo. Leptin, also known to be nutritionally regulated, was expressed in the uterus and stimulated early embryonic development in mice (Kawamura *et al.*, 2002). Thus, a variety of nutritional factors may affect the uterus and early embryonic development.

## **Controlling reproductive loss in postpartum cows**

Reproduction is a complex process. Progress toward improving reproduction can be made only after basic reproductive management practices are implemented correctly. Dairy cows consume feed *ad libitum*, but nevertheless use all available nutrients for milk production at the expense of body condition. Supplying more energy will probably not solve reproductive problems in dairy cows selected for milk production because dairy cows partition additional nutrients toward milk production and not toward adipose or reproductive tissues. In the short-term, aggressive reproductive management (treatment of anoestrus with progestogens, oestrous synchronization, early pregnancy detection, and re-synchronization of non-pregnant cows; Diskin *et al.*, 2002) should maintain current reproductive rates.

However, the routine use of pharmacological intervention as a method to solve cattle infertility is becoming a public policy concern. Thus, in the future, many of our current reproductive management practices may be viewed as unacceptable for food animals. Basic research that identifies the mechanisms through which nutritional status controls reproduction should elucidate control points that can be manipulated or circumvented to improve reproduction. For example, on the basis of the known effects of insulin and IGF-I on the ovary, a diet was formulated that increased blood insulin concentrations and improved postpartum reproductive performance in dairy cows (Gong, 2002). The techniques of the post-genome era (genomics and proteomics) should increase the amount of available information, but will only increase knowledge if computers can be trained to think like physiologists (Thompson, 2002).

A long-term solution may be found through genetic selection for improved reproductive efficiency. Reproductive traits have low heritabilities, but the coefficient of variation for reproductive traits is very large. Therefore, it should be possible to identify sires of daughters that have poor fertility and avoid using these sires in breeding programmes (Weigel and Rekaya, 2000). There are negative genetic and phenotypic relationships between body condition and milk production, but the relationships are modest. High genetic merit cows lose more body condition but their reproductive performance is more dependent on their body condition than on their level of production (Pryce *et al.*, 2001). There are strong positive genetic trends between body condition and reproductive performance (Dechow *et al.*, 2001; Veerkamp *et al.*, 2001). Selection programmes based on postpartum body condition score should lead to superior reproductive performance in postpartum cattle. Scandinavian breeding programmes already include functional non-production traits (for example fertility and mastitis resistance) in addition to production traits in their selection indices for total merit (Philipsson *et al.*, 1994). Although progress toward greater milk production may be less, their models indicate better economic efficiency when functional non-production traits are included in selection programmes.

## Conclusions

The reproductive physiology of postpartum cows is complex because of the combined effects of the past pregnancy and lactation. Fertility of postpartum cows is high when they are disease-free and producing modest amounts of milk. Infertility occurs when cows are thin or lose too much weight during the postpartum period. Genetic selection programmes for dairy cattle have capitalized on nutrient partitioning and loss of body weight. Thus, reproduction in postpartum dairy cows is problematic because genetic selection indices have not incorporated reproductive traits. Beef cattle are not selected for early postpartum milk production and suffer reproductive problems only when pasture conditions are inadequate. Understanding the signals through which postpartum nutrition regulates gonadotrophin secretion and action is essential so that progress can be made in this area. Few studies have examined the effect of nutrition on uterine function and early embryonic development but the same factors affecting ovarian function may also affect the uterus and embryo. In the long term, a genetic approach that incorporates reproductive and health traits in selection indices will improve reproduction. It is also likely that continued studies in the area of postpartum reproduction will reveal critical control points that can be manipulated to improve reproductive efficiency in cattle.

This research was, in part, supported by the Missouri Agricultural Experiment Station project number ASFC0503.

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