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LIVESTOCK IMPROVEMENT CORPORATION LECTURE

Reproductive physiology and management of high-yielding dairy cattle

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ABSTRACT

The future efficiency of the dairy industry will undoubtedly be affected by the decline in fertility and reproductive efficiency in modern dairy cows. The cause of the declining fertility is probably a combination of genetic, physiological and management factors that have an additive effect on reproductive efficiency. Milk production per cow has increased and is one factor that is contributing to the problem. In addition to milk production, however, many other equally important factors may be involved. For example, the reproductive physiology of dairy cattle has changed in response to genetic selection for milk production and these changes may require different management strategies. Compared to traditional dairy cows, modern dairy cows have longer intervals to first ovulation, a higher incidence of anoestrus, abnormal luteal phases, lower blood progesterone concentrations, and greater embryonic loss. Reproductive decline can be reversed in dairy cows but a collective effort that includes more intense reproductive management, genetic selection for improved fertility, and new scientific discoveries will be necessary before the problem can be solved.

Keywords: dairy; reproduction; milk yield; management.

INTRODUCTION

In most modern dairy production systems, dairy cattle are inseminated and pregnancy is established while dairy cows are lactating. Therefore, lactation and the reestablishment of pregnancy must overlap. Unfortunately, recent changes in the genetics and productivity of lactating dairy cows have led to a decline in reproductive efficiency in dairy cattle. Reproductive decline in United States dairy cows began in the mid-1980s and is continuing. An examination of records from 143 dairy herds continuously enrolled in the Dairy Herd Improvement record system clearly shows the trend for worsening reproduction (Figure 1). Milk production (rolling herd average) steadily increased throughout the study period. Calving interval averaged about 13.5 months until the mid-1980s and then subsequently increased to greater than 14.5 months in today's United States dairy herds. The changes in calving interval are correlated with a decrease in fertility in modern dairy cows. Butler (1998) presented data showing a decline in first service conception rate from approximately 65% in 1951 to 40% in 1996 (United States dairy cows from New York State). Declining first service conception rates have also been reported in Ireland (Roche *et al.*, 2000), the United Kingdom (Royal *et al.*, 2000), and Australia (Macmillan *et al.*, 1996). The United States dairy industry consists primarily of continuously calving herds. Thus, reproductive efficiency can be sacrificed for gains in productivity. In countries that depend on seasonal calving, however, the decline in reproductive efficiency of dairy cows represents a tremendous challenge.

MILK PRODUCTION AND REPRODUCTION

Is reproductive decline caused by greater milk production?

Most of the discussion about reproductive decline in dairy cattle has centred on the effects of milk production on reproduction. Indeed, there is a long history of associating greater milk production with reduced

TABLE 1: Effect of milk yield and disease on hazard ratio for conception in 13,307 New York State Holstein cows (Gröhn and Rajala-Schultz, 2000).

Production level or disease	Hazard ratio[1]
First 60-day cumulative milk yield (kg)	
≤ 1582	1.0
1583 to 1891	0.99
1892 to 2195	1.01
2196 to 2641	1.01
> 2541	0.92
Disease	
Retained placenta	0.86**
Metritis	0.85**
Ovarian cysts	0.79**

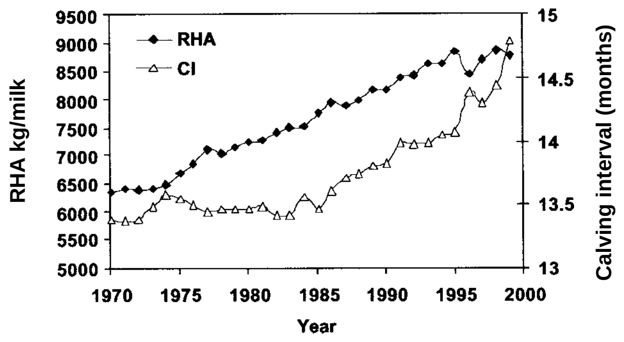
[1]The hazard ratio is the relative risk of conception. A hazard ratio of 1.0 equates to a neutral effect. Hazard ratios less than one indicate reduced likelihood of conception (i.e., cows experiencing a disease with a hazard ratio of 0.86 are 14% less likely to conceive compared to a healthy cow). $^{**}P < 0.01$.

TABLE 2: Effect of periparturient disorders and milk production on reproduction in herds enrolled in the InCalf Project of the Australian Dairy Research and Development Corporation (Melbourne, Australia; http://www.drdc.com.au).

Condition or Production level	Number of Cows	100-day in-calf rate[1] (%)	200-day not-in-calf rate[2] (%)
Dystocia			
Not affected	27,713	58	10
Affected	1,749	51	14
Twin calving			
Not affected	29,070	58	10
Affected	392	43	10
Retained placenta			
Not affected	28,132	59	10
Affected	1,330	46	15
Vaginal discharge			
Not affected	29,188	58	10
2 weeks or less after calving	105	45	0
2 to 4 weeks after calving	83	50	40
More than 4 weeks after calving	86	34	43
Milk volume (litres)			
4,000 or less	3,102	56	11
4,000 to 6,000	13,781	57	9
6,000 to 8,000	10,019	58	8
More than 8,000	1,888	57	9

[1]Percentage of cows that became pregnant by 100 days after calving.
[2]Percentage of cows that had not become pregnant by 200 days after calving.

FIGURE 1: Rolling herd average (RHA, kg milk per lactation) and calving interval (CI) for 143 United States dairy herds continuously enrolled in the Raleigh DHIA record system from 1970 to 1999 (personal communication, J. S. Clay, Dairy Records Management Systems, Raleigh, NC, USA).



reproductive performance in dairy cattle. Based on the analyses of large data sets, there is clearly an antagonistic relationship between milk production and reproduction in dairy cattle (Dematawewa & Berger, 1998; Hansen, 2000). However, the effects of increased milk production on reproduction are relatively minor compared to the effects of other factors. For example, in their recent paper on the epidemiology of reproductive performance in dairy cows, Gröhn & Rajala-Schultz (2000) reported that the hazard ratio for conception was near 1.0 (i.e., neutral effect) for most levels of milk production in United States Holsteins (Table 1). Thus, milk production was not a major factor for determining whether dairy cows will conceive. The conclusions of an Australian dairy study (the InCalf Study; Australian Dairy Research and Development Corporation, Melbourne, Australia; http://www.drdc.com.au) were similar to the United States studies (Table 2). There were minor effects of milk production on conception. Studies of European cattle have also failed to create a definitive link between milk production and reproduction (Loeffler *et al.*, 1999). The aforementioned epidemiological studies (Tables 1 and 2) suggest that disease in postpartum dairy cattle has a much greater effect on reproduction than level of milk production.

Practical experience in the United States also suggests only minor effects of milk production on reproduction. United States dairy herds with the greatest milk production generally have better reproductive performance (Nebel & McGilliard, 1993; Stevenson, 1999). The improved reproduction in high-producing herds probably reflects a higher level of management that includes better nutrition as well as greater cow comfort and cleanliness. The end result is that high producing herds have healthier cows with fewer reproductive problems. The practical relationship between reproduction and milk production can be seen when summaries of actual herd records are examined (Table 3). Days open and interval to first service decrease for herds stratified from lowest to highest production. Services per conception increase in high producing herds but so does oestrus detection efficiency. Thus, a higher level of reproductive management compensates for a slight decline in reproductive efficiency in high producing cows.

TABLE 3: Summary of reproductive traits for United States dairy herds with different levels of annual milk production per cow (Stevenson, 1999).

Milk yield (kg)	Number of herds	Days open	Interval to first service (days)	Oestrous detection rate (%)	Services per conception
< 6818	909	195	102	19	1.8
6818 to 7727	1,285	170	100	26	1.8
7727 to 8636	1,952	162	98	32	2.0
8636 to 9545	2,425	156	95	36	2.1
9545 to 10454	1,705	152	93	40	2.1

Are the causes of reproductive decline the same in all countries?

Although there is a global decline in fertility, the factors causing reproductive decline in New Zealand, Australia, and Europe may be different from those in the United States. The number of small dairy farms in the United States is decreasing. The most recent USDA National Agricultural Statistics Service survey showed that nearly 30% of all dairy cows in the United States were found on farms with more than 500 cows. The shift in herd size toward larger dairies creates new challenges for reproductive management. Traditional methods of visual oestrus detection followed by artificial insemination may serve poorly the modern dairy industry when cows are managed in large groups. Some of the decrease in reproductive efficiency in the United States may be attributed to "growing pains" as individual dairies increase herd size but attempt to manage reproduction with methods developed for smaller herds.

Herd sizes are also increasing in other countries besides the United States but the rapid adoption of North American genetics into New Zealand, Australian, and European dairy herds may also play a role in reproductive decline. Through selection for greater milk production we created dairy cattle that undergo a high level of nutrient partitioning and adipose tissue mobilization during early lactation (Bauman & Currie, 1980). Selection in the United States has been practiced on the typical cow whose feed consist primarily of a mixture of corn silage, lucerne hay, and grain concentrate (totally mixed ration; TMR). Grazing plays a small role in the nutrition of most United States cows. When cows with North American parentage are moved to an intensive grazing system, they will initially produce more milk but the increase in milk production may not necessarily be nutritionally supported in a grass-based system. Thus, a situation is created where North American genetics are not matched with local management and feeding practices (Macmillan *et al.*, 1996). Cows with North American genetics have lower herd survival rates when compared to their herdmates with New Zealand parentage because they fail to get pregnant or maintain a 365-day calving interval (Harris & Kolver, 2001). Indeed, the reproductive demands placed on dairy cattle in New Zealand (yearly calving interval) are far greater than those placed on cows in the United States. Thus, the genetics of North American cows may be incompatible with the reproductive needs of a seasonal dairy industry.

Problems of infertility for North American dairy cows in New Zealand grass-based systems have been demonstrated in a variety of studies (Harris & Kolver, 2001).

Thus, there is no question that cows with a high percentage of North American genetics are susceptible to reproductive problems in a New Zealand. The essential question that must be addressed, however, is whether or not North American cows are inherently less fertile. North American cows are larger and produce more milk. Therefore, they have greater nutrient requirements for maintenance and lactation. Their infertility may simply be caused by inadequate energy in a grass-based system. The North American perspective is that infertility in dairy cows in the United States is secondary to negative energy balance caused by high milk production during early lactation. In other words, the reproductive genotype of North American dairy cows is normal and their reproductive phenotype is a function of lactation. Although difficult to prove either way, most investigators would cite the fact that reproduction in virgin heifers has not changed during the period of declining fertility in lactating cows (Butler & Smith, 1989).

Studies in New Zealand have attempted to address the question of whether or not infertility in North American cows is caused by inadequate energy during lactation. In a controlled experiment with a 2 by 2 factorial design, New Zealand Holstein-Friesian and overseas (North American) Holstein-Friesian cows were compared when they were either grazing (grass) or fed a TMR (Kolver *et al.,* 2000; Verkerk *et al.,* 2000). Regardless of feeding systems, the overseas Holstein-Friesians produced more milk and had lower body condition score. The overseas Holstein-Friesians also had higher empty rates indicative of greater infertility. Thus, infertility in North American cows was greater and body condition was lower even when feeding was similar to that used in the United States (TMR). The infertility in cows with North American genetics was not caused by anoestrus because North American cows ovulated earlier postpartum than grass-fed New Zealand cows. It appears that cows with North American genetics will partition energy toward lactation at the expense of reproduction This nutrient partitioning leads to lower body condition score even when a high energy TMR is fed. Thus, feeding more energy will probably not solve infertility problems in cows with a high percentage of North American ancestry.

The focus of reproductive physiologists has been the high producing dairy cow but cows with moderate milk production also have reproductive problems. Therefore, there are general effects of lactation on reproduction in dairy cows. Virgin heifers have high first service conception rates and the assumption is that parturition and subsequent lactation lead to an appreciably lower conception rate. The inherent negative effects of parturition and lactation on reproduction, however, may not be great. Lactating beef cattle in the United States may suffer from anoestrus but once they are cycling their conception rates are approximately 20 percentage points higher than dairy cattle in the United States (Stevenson *et al.,* 2000). There may be a minimum milk production above which reproductive efficiency declines. This minimum may not be reached by beef cattle with low levels of lactation. New Zealand, Australian, Irish, and UK dairy cattle, however, may now have reached the minimum and are now experiencing reproductive decline. United States dairy cattle probably reached the minimum several decades ago.

REPRODUCTIVE PHYSIOLOGY OF HIGH-PRODUCING DAIRY COWS

Interval to first ovulation

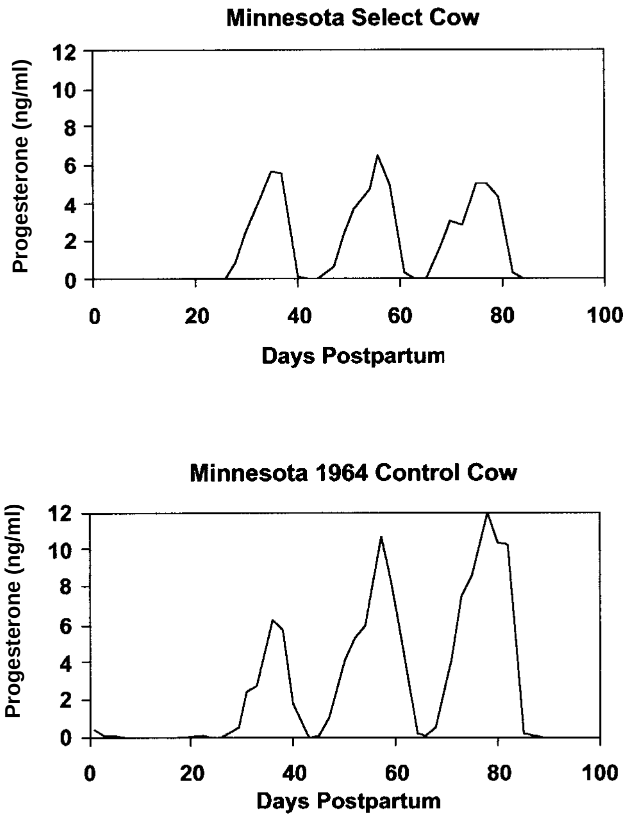
Considerable importance has been placed on interval to first ovulation as a measure of reproductive efficiency because cows must be cyclic before the breeding season. The interval to first ovulation in United States dairy cows has been classically described as occurring before 21 days after calving with 5% of the herd anoestrous at the start of the breeding season (Morrow *et al.,* 1966). In modern dairy cows, the average interval to first ovulation is probably about 10 days longer and the percentage of anoestrous cows at the start of the breeding season may be considerably greater (Stevenson, 2000). We examined interval to first ovulation by studying cows at the University of Minnesota Southern Experiment Station at Waseca. The Waseca Experiment Station has maintained a control and selected line of dairy cattle since 1964. The control line is analogous to dairy cattle of the 1960s before intensive genetic selection was done. Control cattle average approximately 6,000 kg milk/lactation. The select line represents the modern dairy cow and averages approximately 11,000 kg milk/lactation. When we compared interval to first ovulation in the Minnesota cows, we found that the average interval to first ovulation was 29 ± 3 days and 43 ± 5 days for control (i.e., 1964) and select (i.e., modern) dairy cows, respectively. The corresponding percentages for anoestrous cows (> 60 days postpartum) were 0 and 38%, respectively. Recent reports in the scientific literature confirm these trends for significantly longer intervals to first ovulation in postpartum dairy cows (deVries & Veerkamp, 2000). In the deVries & Veerkamp (2000) study, the mean for interval to first ovulation was 29.7 days but the mode was 18 days; an interval similar to that reported in the 1960s (Morrow *et al.,* 1966). Therefore, the increase in the average interval to first ovulation in modern dairy cattle may be caused by a subpopulation of cows with extremely long intervals to first ovulation.

Most investigators would suggest that the reason for the delay in interval to first ovulation is greater negative energy balance in modern dairy cows. Negative energy balance reduces postpartum LH pulsatility and, therefore, delays the resumption of ovarian activity (Butler, 2000). In their studies of 275 first lactation heifers, however, deVries & Veerkamp (2000) found that only 3 to 4% of the variation in interval to first ovulation was explained by total energy deficit or energy balance nadir in early lactation. Furthermore, doubling the mean energy balance nadir for cows on the study lengthened the predicted interval to first ovulation by only 4 days. In addition to negative energy balance, therefore, other factors are probably contributing to the increase in the interval to first ovulation in modern dairy cows.

The oestrous cycle

***Corpus luteum and progesterone*.** We measured blood progesterone concentrations in the Minnesota study and found lower plasma concentrations of progesterone in select compared to control cows (Lucy *et al.,* 1998) (Figure 2). Therefore, based on data from the Minnesota selection study, a link between genetic selection for milk production and lower concentrations of blood progesterone was

FIGURE 2: Plasma concentrations of progesterone during the postpartum period in a Minnesota select cow (top panel) and a Minnesota 1964 control cow (bottom panel). These profiles are from individual cows that are representative of select and control cows. Select cows had lower concentrations of progesterone than 1964 control (Lucy *et al.*, 1998),



established. The relationship between genetic selection and progesterone is important because pregnant cows have higher concentrations of blood progesterone within the first week to ten days after insemination (Mann *et al.*, 1999). One possibility is that greater milk production in dairy cattle is negatively affecting blood progesterone concentrations and causing infertility in dairy cows.

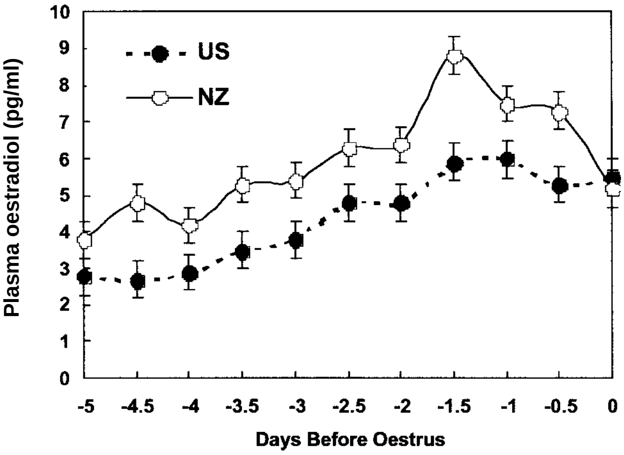
Few studies have compared the corpus luteum (CL) of North American and New Zealand dairy cows. We found that the CL weighed less in North American cows (average CL weight of 3.7 g) compared to New Zealand cows at a similar stage of lactation (average CL weight of 5.1 g) (Bilby *et al.*, 1998). Size of the CL and secretion of progesterone is only part of the equation determining blood progesterone concentrations because progesterone clearance (metabolism) is also important. Rabiee *et al.* (2000) studied progesterone metabolism in dairy cows implanted with progesterone-releasing devices. They found that cows grazing pasture *ad libitum* had lower plasma concentrations of progesterone than cows grazing pasture for a restricted period of time. Likewise, Sangsritavong *et al.* (2000) demonstrated that liver blood flow and progesterone metabolism increased by greater than 50% when feed intake was either acutely or chronically increased. The conclusion from these studies is that modern dairy cows have lower blood concentrations of progesterone because they consume more feed and metabolize progesterone at a higher rate.

It is possible that high-producing dairy cows have lower blood concentrations of progesterone and that the lower blood concentration of progesterone lead to infertility. In addition to lower progesterone, several groups have recently reported that modern dairy cows also have a higher proportion of abnormal luteal phases. Opsomer *et al.* (1998) examined postpartum luteal function in moderate-yielding Friesian dairy cows and high-yielding Holstein dairy cows. Holstein cows were nearly seven-times more likely to have a prolonged luteal phase (high progesterone for greater than 20 days; 3% versus 20%; Friesian versus Holstein, respectively). Lamming & Darwash (1998) found similar patterns of abnormal progesterone in UK cows. We also found that United States Holsteins had longer luteal phases than New Zealand Friesian cows (Bilby *et al.*, 1998). Opsomer *et al.* (2000) concluded that negative energy balance, periparturient disorders, and postpartum diseases were risk factors for delayed cyclicity and prolonged luteal phases. Therefore, common ailments of early postpartum cows caused luteal phase abnormalities in later lactation.

A change in luteal phase length in modern-day dairy cows is an important observation because it changes the approach used for reproductive management in dairy cattle. Cows that are not in controlled breeding programmes will have delayed breeding because their oestrous cycles are longer. Abnormalities in luteal phase length also make it more difficult to predict when cyclic cows will return to oestrus.

Follicular growth and oestradiol. Postpartum dairy cows undergo a natural process of nutrient partitioning, negative energy balance, and weight loss during the early postpartum period (Bauman & Currie, 1980). Negative energy balance and weight loss have an inhibitory effect on ovarian follicular growth and development. Several authors have recently reviewed the mechanisms through which negative energy balance inhibits follicular development (Butler, 2000; Lucy, 2000; Roche *et al.*, 2000; Royal *et al.*, 2000). Beam (1995) studied the effects of negative energy balance on follicular growth in early postpartum cows. He observed that the dominant follicle in cows in negative energy balance required more time to develop and reached a larger size before ovulation. The hypothesis is that follicles in negative energy balance cows are less oestrogenic and therefore must grow to a larger size before they are capable of triggering ovulation. Peripheral oestradiol metabolism also may be greater during negative energy balance so that a higher level of oestrogen synthesis may be necessary to achieve equivalent blood oestradiol concentrations. Data from Beam (1995) agree with a recent report that compared the oestrous cycle of lactating cows and heifers (Sartori *et al.*, 2000). Lactating cows had larger preovulatory follicles than heifers but lower preovulatory concentrations of oestradiol in blood. Our studies also suggest differences in oestradiol for New Zealand grass-fed compared to United States TMR-fed dairy cows (Bilby *et al.*, 1998). We found that cows from our United States herd had lower concentrations of oestradiol during the preovulatory period when compared to New Zealand dairy cows (Figure 3). Whether lower blood oestradiol concentrations are a consequence of lower steroidogenic capacity of the follicle or enhanced oestrogen metabolism is not known.

FIGURE 3: Plasma oestradiol concentration from a comparative study of lactating dairy cows in the United States (US) and New Zealand (NZ) (Bilby *et al.*, 1998). Plasma oestradiol concentrations on the days before oestrus were lower in United States compared to New Zealand cows (P < 0.01).



Oestrous expression

Detection of oestrus and the accuracy with which oestrus is detected in United States dairy cows is an area of increasing concern. Dransfield *et al.* (1998) performed an exhaustive analysis of data generated from electronic mount detectors (HeatWatch System, DDx Inc., Denver, CO, USA). In their study of United States cows, the average dairy cow had 8.5 stands per oestrus with an oestrous duration of 7 hours. Nearly one-quarter of the cows had oestruses that were classified as low intensity (< 1.5 stands/h) and short duration (< 7 h). Longer, more frequent observation periods may be necessary to detect oestrus accurately in modern dairy cows. In addition to failure to detect oestrus, the misidentification of oestrus is also a problem. In a recent study of a research herd of 242 Holsteins, Sturman *et al.* (2000) found that 19% of inseminations were performed on cows that could not have been in oestrus based on milk progesterone concentrations.

Few studies have systematically evaluated the causes of poor oestrous expression in dairy cows. However, there may be a link between oestrous expression and concentrations of growth hormone (GH) in the blood. Growth hormone concentrations are greater in high producing dairy cows. In the United States, cows are treated with recombinant bovine somatotropin (rbST) to mimic the effects of GH in early lactation (Bauman, 1999). Services per conception do not change when cows are treated with rbST. At the same time, days open increase and pregnancy rate decreases by 5 to 10%. Cows that become pregnant when treated with rbST do not seem to require additional inseminations but do require additional time to become pregnant. Our current theory is that longer days open in rbST-treated cows may be associated with decreased oestrous expression. Morbeck *et al.* (1991) found that oestrous detection rate decreased from 75% to 48% in lactating cows treated with rbST. In other studies, oestrous detection rate was 100% for control cows and 57% for cows treated with rbST (Kirby *et al.*, 1997). Lefebvre & Block (1992) examined the effect of rbST on oestrous expression of ovariectomized heifers treated with oestradiol. Heifers treated with rbST instigated fewer mounts compared to heifers treated with saline. Changes in intensity of oestrus in ovariectomized heifers may suggest decreased responsiveness of the brain to oestradiol when cattle have high concentrations of GH in the blood. The effects of GH on oestrous expression are not only found in rbST-treated cows because Minnesota select cows have higher blood GH concentrations and lower rates of oestrous expression (Lucy & Crooker, unpublished). Thus, higher concentrations of GH in cows supplemented with rbST and in cows selected for high milk production may be causing a decrease in oestrous expression. Unfortunately, oestrous expression is hard to study because oestrus is a behaviour that depends on individual cows as well as social interactions among cows. Thus, the biological mechanisms causing the decrease in oestrous expression in high producing cows have not been identified.

Pregnancy

Oocyte health. Factors affecting the health of the oocyte may ultimately determine the developmental competence of the embryo. Britt (1994) proposed that the developmental competence of the oocyte is determined when the oocyte is growing within the follicle. Therefore, the long period of follicular growth that precedes ovulation has an effect on oocyte health and fertility. Diseases and disorders may negatively affect oocytes within follicles that begin their development during the early postpartum period. Gwazdauskas *et al.* (2000) collected oocytes throughout lactation by twice weekly follicular aspiration and concluded that stage of lactation and dietary energy influenced oocyte quality. They also reported lower success rates for lactating compared to non-lactating cows. Snijders *et al.* (2000) found that the ability of an oocyte to be fertilized and develop to the blastocyst stage in vitro was not affected by the milk production of the donor cow. Body condition, however, influenced oocyte competence because in vitro fertilized oocytes from cows in low body condition had a lower cleavage rate and a lower developmental rate when compared to oocytes from cows in better body condition (Table 4). One speculation arising from these data is that the lower body condition of cows with North American parentage may be negatively affecting oocyte health and causing infertility. Snijders *et al.* (2000) also noted reduced developmental competence of oocytes collected from cows with high genetic merit; again suggesting that reproductive efficiency is compromised by genetic selection.

TABLE 4: Effect of genetic merit for milk yield, milk yield, body condition score, and parity on the in vitro formation of blastocysts from fertilized oocytes (Snijders *et al.*, 2000).

Classification of oocyte donor cow	Percent blastocyst formation (n)
Genetic merit for milk yield*	
High	6.8 (23/338)
Low	11.4 (41/359)
120-day milk yield (kg)	
3162 to 3972	9.9 (18/181)
4559 to 5114	10.1 (13/129)
Body condition score*	
1.5 to 2.5	3.0 (4/134)
3.3 to 4.0	9.9 (15/152)
Parity*	
First lactation	3.9 (5/130)
Third lactation	10.4 (59/567)

*$P < 0.05$.

Early embryonic development. Infertility in dairy cattle is not a new phenomenon but the current trends in reproduction are different because reproductive problems affect a large percentage of dairy cows. Perhaps the most surprising component of reproductive loss in dairy cattle is the large number of seemingly normal embryos that undergo early embryonic death. To my knowledge, there is no inherent biological requirement for a high rate of embryonic loss in dairy cows with genetically normal embryos. There are high rates of embryonic loss between the period of conception and maternal recognition of pregnancy (about 17 to 19 days after insemination) (Mann *et al.,* 1999). Losses after this early period are considerably less but nevertheless influence pregnancy rates. Classical studies of embryonic mortality in dairy cows estimated that approximately 10% of embryos were lost between 28 and 75 days of pregnancy (Ayalon, 1978). More recent studies that employed ultrasonographic pregnancy detection suggest that the rate of embryonic loss between 28 and 60 days is at least 20% (Vasconselos *et al.,* 1997). When reciprocal embryo transfer was done between repeat breeder and normal cattle, the repeat breeder cattle failed to achieve normal pregnancy rates even though an embryo from a "normal" cow was implanted (Gustafsson & Larsson, 1985). Conversely, normal cattle had normal rates of pregnancy when implanted with an embryo from a repeat breeder cow. These data suggest that repeat breeders and perhaps modern dairy cows fail to establish pregnancy because of a suboptimal uterine environment.

The reason that embryos fail to develop within the uterus of otherwise normal cows is not known. The uterus may fail to synthesize adequate amounts of an embryotrophic growth factor that is required by filamentous embryos. Secretion of embryotrophic growth factors into the uterine lumen may be controlled by nutritional status because embryo transfer pregnancy rates are less in recipients with low body condition score (Mapletoft *et al.,* 1986).

MANAGING REPRODUCTION IN HIGH PRODUCING DAIRY COWS

Intense reproductive management at the farm level

Reproduction is a complex process. Successful herd reproduction requires meticulous attention to detail. Periparturient health, uterine and ovarian health, oestrous detection, time of insemination relative to oestrus, semen handling, AI technique, and pregnancy diagnosis are as important today as they were 50 years ago. Minor mistakes in these procedures have cumulative effects on herd reproduction.

The best way to reverse current declines in reproduction is to intensively manage the reproductive biology of the dairy cow. The options available for reproductive management in the United States and New Zealand, however, are different. In the United States, most cows are either untreated (inseminated at spontaneous oestrus) or treated with biweekly injections of prostaglandin $F_2\alpha$ ($PGF_2\alpha$) followed by oestrous detection. Insemination at spontaneous oestrus and the use of $PGF_2\alpha$ and oestrous detection are good but suffer from the age-old problem of detecting cows in oestrus. Combining regular $PGF_2\alpha$ injections with some type of oestrous detection aid (tail paint, patches, electronic devices, etc.) improves the overall response but requires additional management and attention to details.

Anoestrus is very difficult to manage in the United States because anoestrous cows will not respond to $PGF_2\alpha$ and progestagens are not approved for use in lactating dairy cattle. This represents a severe limitation to reproductive management especially considering the high incidence of anoestrus in the United States dairy cows. Most producers in the United States would welcome the approval of a progestagen for lactating dairy cows. The use of progestagens for treatment of anoestrus in New Zealand dairy cows is an obvious management strategy that should be employed.

Timed AI for insemination of dairy cattle is also popular in the United States and represents an important change in reproductive management because cows are inseminated without oestrous detection. Most producers use the standard "Ovsynch" protocol of GnRH (wait 7 days), $PGF_2\alpha$ (wait 2 days), GnRH (wait 1 day), and then insemination. Inseminating cows at a predetermined time is not a new concept because it was tried in the 1970s and 1980s (Roche, 1977; Lucy *et al.,* 1986). The discovery that a follicular wave could be synchronized to improve the consistency of the follicular development around $PGF_2\alpha$ injection, however, was an important step forward because it improved the responses to timed AI and enabled the widespread implementation of the method (Twagiramungu *et al.,* 1995). Timed AI is a good approach but rates of embryonic loss after timed AI are high and calving rates for dairy cows after timed AI are approximately 35%. Therefore, there is still a need to optimize methods for timed insemination of dairy cattle.

Timed insemination and regular $PGF_2\alpha$ injections are good ways to control the time of first insemination. Only 30 to 50% of dairy cows, however, will be pregnant after first insemination. The fate of the 50 to 70% of dairy cows that are open after first insemination usually depends on detecting the return to oestrus after the pregnancy fails. The timing of second oestrus after insemination is variable because many cows have an embryo that dies around the time of maternal recognition of pregnancy and the normal luteolytic mechanisms are delayed (Van Cleeff *et al.,* 1996). The fact that inseminated cows represent a mixture of pregnant and nonpregnant cows and that nonpregnant cows have a variable return to oestrus complicates methods that can be used to synchronize second service. Unfortunately, very few reliable methods are available for resynchronizing second service in United States dairy cattle.

Genetic selection for improved reproduction

Selection of cows for improved reproductive efficiency is a possible solution to reproductive decline. Careful genetic selection may allow dairy producers to use the genetics of high milk production from North American cattle and still maintain acceptable reproductive rates. Reproductive traits have low heritabilities but the coefficient of variation of reproductive traits is very large (Philipsson, 1981). Therefore, genetic selection for improved daughter fertility is possible in dairy cattle. The problem is that there are negative genetic correlations between daughter fertility and milk yield. Scandinavian breeding programs include functional non-production traits (fertility, mastitis resistance, etc.) 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 suggest better economic efficiency when functional non-production traits are included in selection programmes (Philipsson *et al.,* 1994).

CONCLUSIONS

There are no magical solutions to reproductive decline in high-producing dairy cattle. Cows selected for high milk production partition nutrients toward lactation. The partitioning of nutrients leads to cows with less adipose tissue mass (lower body condition) and greater infertility Feeding more energy will probably not solve reproductive problems in cows with a high percentage of North American genetics because they will partition the additional nutrients toward milk production. For the immediate future, the best approach will be to intensively manage the reproductive biology of the cow. This management should include treatment of anoestrus with progestagens, synchronization of first service, and resynchronization of second and third services. In the longer term, a genetic approach that incorporates reproductive and health traits in selection indices will correct some of the reproductive decline. It is also likely, that continued research in the area of postpartum reproduction of dairy cattle will reveal critical control points that can be manipulated to improve reproductive efficiency in dairy cattle.

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