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Addressing the decline in reproductive performance of lactating dairy cows: a researcher's perspective

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In the 1950s and 60s, there was an extraordinary improvement in our ability to determine the genetic merit of dairy bulls for milk production. The implementation of herdmate comparison procedures allowed us to compare accurately the milk production of daughters sired by different bulls, so that finally we were able to determine how well individual sires transmitted the genes for milk production to their offspring. This genetic breakthrough, together with improvements in techniques for artificial insemination, gave dairy farmers widespread access to superior genetics and ushered in a new era of dairy cattle breeding. I believe that this has been the single most important contribution that geneticists and reproductive physiologists have made to dairy farming. In the last 40 years, the genetic potential for milk production in American Holsteins, for example, has increased by over 3000 kg per lactation [1]. The current rate of increase is about 100 kg/year (Figure 1).

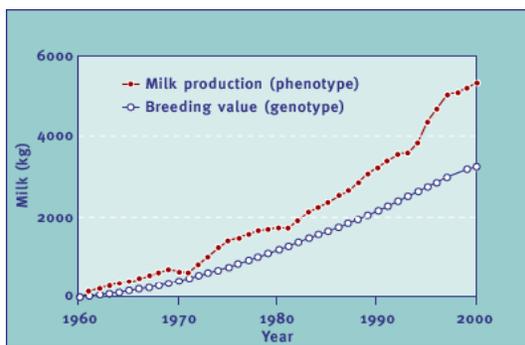


Figure 1. Changes in the genetic merit (breeding value) and actual average milk production of Holstein cows in the United States since 1960. Milk production is expressed relative to the 1960 level (6252 kg). Genetic merit is also expressed relative to the 1960 value.

But this is only part of the story. The genetic

potential for milk production sets the upper limit at which an individual cow can produce milk. How close she comes to reaching that limit is determined by the management conditions under which she is maintained (i.e. her environment), and during the last 40 years these conditions have improved tremendously. There have been improvements in feeding practices, in the control and prevention of disease and in other management practices, which together with improvements in genetics have contributed to an astounding increase in milk production. As a result, the average milk production for Holstein cows in the United States has nearly doubled since 1960, to over 11,000 kg/year (Figure 1).

Clearly, the aggressive genetic selection for higher milk production has been successful.

However, this has not been without costs. Over the same time period, there has been a dramatic decline in the reproductive performance of dairy cows. Both the average number of days open (interval from calving to the next conception) and the number of services per conception have increased substantially (Figure 2). This conclusion has been confirmed independently in the UK [2] and in the US [3, 4, 5]. The results of this alarming decline in fertility are longer lactations and an increase in the number of cows that are culled from herds for reproductive reasons. In a recent survey of dairy farms in the US it was revealed that as many as 27% of cows left the herd because of poor reproductive performance [6]. As Dr. Jos Noordhuizen pointed out in a previous article in *Veterinary Sciences Tomorrow* [7], managing reproduction and treating infertility have become dominant foci of dairy veterinary

practitioners.



Figure 2. Changes in the days open and services per conception in 73 Holstein herds in Kentucky from 1972 to 1996. (Silvia, W.J. (1998) *Journal of Dairy Science* 81, Suppl. 1, p. 244).

An obvious question is 'Why?'. Why has reproductive performance declined so precipitously? This has proven to be a very difficult question to answer due to the complexity of the reproductive process. For cows to reproduce successfully, they must 1) develop healthy follicles containing fertile oocytes; 2) coordinate ovulation and oestrous behaviour; and 3) first maintain a uterine environment that promotes sperm transport and fertilization but then rapidly change that environment to support pregnancy. A deficiency anywhere in this progression of events will result in failure to conceive, but precise points at which fertility has been affected have not yet been identified.

As is the case for milk production, the decline in reproductive performance is probably due to changes in both management and biology. As already mentioned, the last 40 years have seen many major changes in the management of dairy cows. The trend, for instance, towards larger herd sizes has made it difficult for dairy managers to give cows the individual attention that many need, while that towards confinement housing has placed cows on concrete floors that discourage pronounced expression of oestrous behaviour [8]. Furthermore, feeding diets rich in rumen-degradable protein has resulted in a uterine environment that is not conducive to the maintenance of pregnancy [3].

Biological factors that have contributed to the decline in reproductive performance can be divided into two broad categories, genetic and metabolic. While heavy emphasis has

been placed on genetic selection for milk production, reproductive performance has largely been ignored. The heritability of broad-based reproductive traits (e.g. days open or services per conception) is very low. This is probably due to the complexity of the reproductive process, which depends upon the interaction of hundreds of different gene products and thus makes it difficult to improve genetic merit for these traits through selection. It is possible that the genetic potential for reproduction has actually declined in dairy cows. Specific alleles that contribute to high milk production – and, therefore, are positively selected – may inhibit reproductive performance directly. Alternatively, alleles that contribute to high milk production may be non-randomly associated (linked) with alleles that inhibit reproductive performance. Considering our current state of knowledge in this area, it is almost impossible to determine if this is the case. One argument against this possibility, however, is that reproductive performance in heifers has not been affected over this same time period.

The second major factor that may be contributing to the decline in reproductive performance is the alteration in metabolism that occurs in high producing dairy cows. For example, a 600 kg Holstein cow only requires about 10 Mcal of net energy daily for maintenance, but she requires an additional 30 Mcals to produce 45 kg of milk per day. In other words, when lactating, she should consume four times her maintenance needs daily. The activity of the digestive system and liver are elevated to digest, absorb and process this elevated quantity of nutrients. Surprisingly, however, only 20% of the calories consumed by the lactating cow are recovered in milk, the remaining 80% being metabolised to support maintenance and lactation. The cells of the mammary gland use much of this energy to synthesize milk and, by the time a lactation is complete, they are metabolically spent and must be replaced before a new lactation can begin. Furthermore, the lungs, liver and kidneys must process and dispose of an enormous volume of waste material during these periods. To meet this nutrient requirement, there must be a tremendous increase in the caloric intake of lactating cows. However, in dairy cows during peak lactation, the caloric

intake cannot match the metabolic demand. Imagine how much weight you would gain if you increased your caloric intake by four times. Yet, these cows lose weight. Clearly, the enhanced level of metabolism is a severe perturbation of the cow's internal environment.

How, then, does this change in metabolism affect reproduction? One possible explanation is based on the scarcity of available nutrients within the cow. Maintenance, lactation and reproduction all compete for the limited nutrient pool and it is possible that maintenance and lactation take precedence over reproduction. Teleologically, it makes sense to support lactation. It is better to invest limited resources in the survival of the current offspring than to gamble on the fitness and survival of those that are yet to be born. There is no doubt that the limited availability of nutrients, particularly energy, can suppress reproductive performance through effects at the hypothalamic/pituitary and ovarian levels [3].

A second possible explanation is that the changes in levels of critical metabolites and metabolic hormones may suppress reproductive performance. For example, concentrations of GH (growth hormone), IGF-1 (insulin-like growth factor-1), insulin and cortisol undergo striking changes during the first several weeks after calving [9], as do concentrations of metabolites like free fatty acids, glucose and ketones. There is a vast body of literature studying the effects of these metabolites and hormones on gonadotropin secretion and ovarian function [10], although their precise details are beyond the scope of this review. Based on this research, it is clear that these agents can disrupt normal patterns of hormone synthesis and release. Consequently imbalances in one or more could severely impair fertility.

A third possible explanation for a metabolic influence on reproduction is that the adaptations of the viscera to increased intake may alter the metabolism of reproductive hormones. For example, the metabolic clearance of oestradiol and progesterone is greater in lactating than in non-lactating cows [11] and is associated with an increase in blood flow through the

liver. Thus, both the metabolic clearance rate of steroids and the liver blood flow increase when feed intake increases. The authors hypothesize that the increase in blood flow through the liver permits more of the steroid to be metabolized and cleared from the body (Figure 3). Rate of food passage through the gut also increases when intake increases, which diminishes the ability of the gut to reabsorb bile salts and is reflected in an increase in the rate of bile salt secretion. Conjugated steroids, which are normally unconjugated, reabsorbed and reutilized through a similar recycling system, may be lost with the increase in food passage. A reduction in the circulating concentrations of oestradiol could account for the reduction in duration and intensity of oestrous expression observed over the past 30 years [12, 13]. It could also alter the timing of ovulation relative to the onset of oestrous behaviour, as has been demonstrated in sheep [14]. A reduction in circulating concentrations of progesterone, particularly early in the oestrous cycle, may alter the rate of embryonic growth and disrupt the normal progression that is required for effective maternal recognition of pregnancy.

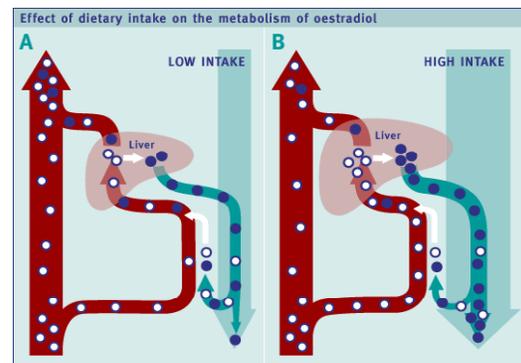


Figure 3. Effect of dietary intake on the metabolism of oestradiol. Metabolism of oestradiol is a complex process that requires the efficient interaction of several tissues. In the liver, oestradiol (open circles) is rendered biologically inactive through hydroxylation and conjugation. Conjugates (filled circles) are secreted into the bile and released into the gut. Once here, some of the conjugates are deconjugated by bacteria, restoring biological activity. Both conjugates and reactivated oestradiol are very efficiently reabsorbed across the gut wall and enter the mesenteric circulation. Active oestradiol can be remetabolized. Conjugates flow through the liver, then are filtered from the circulation by the kidneys and excreted in the urine. When feed intake is low (A), mesenteric blood flow to the gut and then the liver is comparatively low. Consequently, less oestradiol is metabolized in the liver and a greater amount of active oestradiol remains in the circulation. When feed

intake increases (B), mesenteric blood flow increases. The liver increases in size to meet the metabolic demands for nutrient processing. Together, these responses result in an increase in the rate of oestradiol metabolism. More conjugates enter the gut, but the rapid passage of digesta through the gut reduces the reabsorption of oestradiol and its conjugates. The net effect is to increase greatly the elimination of oestradiol and conjugates in the faeces and to reduce the concentration of oestradiol in the peripheral circulation.

In conclusion, many factors have probably contributed to the dramatic decline in reproductive performance of dairy cows that has occurred over the last 40 years. Recent advances in research have revealed numerous new areas that warrant further investigation. Unfortunately, there is no immediate end in sight. Due to the complexity of the reproductive process, it is unlikely that a single 'magic bullet' will be discovered to cure this problem. Scientists will continue to improve on endocrine-based approaches to improve fertility and to develop new ones [2, 15]. Only time will tell if any of these will be successful. I believe that the ultimate solution to the problem must be found at the genetic level. Fortunately, there are some cows that reproduce quite normally while producing more than 15,000 kg of milk per year. These are the cows that will naturally contribute a larger share of the offspring to the total population. Through "natural selection" these cows will help improve the overall genetic potential for reproduction. However,

if we are forced to rely on this selection alone, genetic improvement will be slow and may not be able to keep pace with the consequences of intensive selection for milk production. Although heritability of complex reproductive indexes (days open, services per conception) is low, the heritability of more specific reproductive parameters (e.g. interval to commencement of luteal activity) is reasonably high [16, 17]. Thus, there is hope that some improvement in reproductive performance can be made through selection. We should aggressively apply modern technology to this problem by, for example, conducting a thorough characterization of the genome from these reproductively superior cows so that we can identify the unique combination of alleles that allows a high producing cow to reproduce effectively. These are then the cows that should be cloned. Unless this alarming trend towards low fertility in dairy cows is reversed, we may rapidly reach a point where we are forced to forsake genetic gain in milk production to preserve an acceptable, minimal level of reproductive performance.

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