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Animal Reproduction Science 96 (2006) 323–330

ANIMAL
REPRODUCTION
SCIENCE

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Prospects for improving reproductive performance through genetic selection[☆]

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Available online 3 August 2006

Abstract

Prospects for improving female fertility in dairy cattle using genetic selection are reviewed. Today's high producing cows have shorter estrous cycles, fewer standing events, shorter duration of estrus, and more frequent multiple ovulations. Although high milk production is often implicated as the cause of impaired fertility, the impact of inadequate body condition appears to be greater, as the latter has a significant impact on probability of conception, rate of embryonic loss, and proportion of anestrus animals. Genetic improvement of female fertility can be achieved by indirect selection for longevity or body condition score, or by direct selection for traits such as daughter pregnancy rate. Most leading dairy countries have implemented genetic evaluation systems for female fertility in the past decade, but refinement of these systems to account for hormonal synchronization, differences in the voluntary waiting period, exposure to natural service bulls, and other confounding factors is warranted. Recent work has focused on the development of data collection and genetic evaluation systems that will allow selection of bulls that have daughters that are resistant to common health disorders, including mastitis, lameness, ketosis, displaced abomasum, and metritis. Such systems will allow selection of animals that can remain healthy and fertile while producing large quantities of milk.

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Keywords: Fertility; Dairy; Conception rate; Pregnancy; Body condition; Animal health

1. Introduction

The challenges associated with achieving pregnancy in modern, high producing dairy cows have received considerable attention from scientists, veterinarians, and farmers in recent years. Today's dairy cows tend to have lower conception rate, greater days open, and greater likelihood of

[☆] This paper is part of the special issue entitled Nutrition and Fertility in Dairy Cattle, Guest Edited by A. Evans and F.J. Mulligan.

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culling due to infertility than their counterparts from two or three decades ago. Genetic selection programs have led to rapid gains in milk yield and conformation traits, but performance for traits such as female fertility, longevity, and susceptibility to disease has tended to decline. While it is impossible to completely disentangle the effects of selection from simultaneous changes in nutrition, cow care, and reproductive management, it is clear that geneticists failed to pay adequate attention to health, fertility, and longevity traits until the past decade. The magnitude of genetic variation in such traits is surprising, and we are now poised to take advantage of recent research and development efforts regarding the definition, measurement, and genetic analysis of these traits.

The objective of the present paper is to review some of the biological changes that have occurred in high producing dairy cows and to discuss the opportunities for improving reproductive performance through direct selection of highly fertile animals or through indirect selection of animals that maintain adequate body condition and resist metabolic and infectious diseases during the lactation.

2. Interesting aspects of fertility in high-producing cows

Milk production of dairy cows on modern commercial farms in North America has roughly doubled over the past four decades. First parity cows on large commercial dairy farms in the US typically peak at 40–45 kg/day, while second and later parity cows typically peak at 50–55 kg/day. Furthermore, each group typically sustains daily milk production of 40 kg/day or more during the first 7 months postpartum. Therefore, one might expect differences in the reproductive biology of high producing cows, as compared with low producing cows or yearling heifers.

Lopez et al. (2005) discussed some of the differences between the reproductive biology of lactating Holstein cows and yearling Holstein heifers. In particular, Lopez et al. (2005) noted that lactating cows have shorter duration of estrus (7–8 h versus 11–14 h), longer and more variable estrous cycles (20–29 days versus 20–23 days), larger diameter of ovulatory follicles (16–18 mm versus 14–16 mm), and greater rates of anovulation (20–30% versus 1–2%), multiple ovulation (20–25% versus 1–3%), and pregnancy loss (20–30% versus 3–5%). Lopez et al. (2005) also documented differences in these characteristics between lactating cows according to levels of milk production. They (Lopez et al., 2005) used the HeatWatch system (DDx, Inc., Denver, CO) to monitor the estrous characteristics of 146 high producing Holstein cows (46.4 kg/day for the 10 days preceding estrus) and 177 low producing Holstein cows (33.5 kg/day for the 10 days preceding estrus). High producing cows had shorter duration of estrus (6.2 h versus 10.9 h), fewer standing events (6.3 versus 8.8), and shorter standing time per event (21.7 s versus 28.2 s). Duration of estrus decreased linearly from 14.7 h for cows milking 25–30 kg/day to 2.8 h for cows milking 50–55 kg/day. In addition, the percentage of cows with multiple ovulations increased from 0.0% for cows milking between 25 and 30 kg/day to 51.6% for cows between 50 and 55 kg/day.

The rate of early embryonic loss in Holstein cows is also a major concern, as noted in several recent studies that have used transvaginal ultrasound for pregnancy detection at 27–31 days after breeding, followed by pregnancy confirmation via rectal palpation at 39–48 days after breeding. Reported rates of embryonic loss during this interval ranged from 0.70% to 1.40% per day (e.g., Cartmill et al., 2001; Cerri et al., 2004; Santos et al., 2004). However, estimates of the rate of embryonic loss (particularly those from commercial farms) may be biased upward by false positive diagnoses at the early ultrasound exam, as most veterinarians tend to use caution when declaring cows as non-pregnant in herds that use hormonal re-synchronization programs.

On large dairy farms in the western US, mean veterinary-confirmed conception rates of Holstein cows at 75 days after breeding were nearly constant over the first five inseminations (0.30, 0.31, 0.31, 0.29, and 0.28, respectively), while means for Jersey cows declined linearly from the first through fifth insemination (0.42, 0.38, 0.34, 0.29, and 0.27, respectively). Mean conception rate at first service tended to decline with age in both breeds (0.35, 0.29, 0.28, 0.26, and 0.25, respectively, for first through fifth parity Holsteins and 0.44, 0.43, 0.41, 0.39, and 0.37, respectively, for first through fifth parity Jerseys), though the rate of decline was less noticeable for repeat inseminations than for first insemination (Weigel, 2006 (unpublished)). Both breeds have been selected for many generations under similar management conditions, and both have made rapid genetic progress over the past three decades (mean mature equivalent 305 days milk yield increased from 6904 to 11,608 kg in Holsteins and from 4461 to 8273 kg in Jerseys from 1970 to 2000). Differences in mean conception rate within the Holstein breed were found among cows at different levels of daily milk yield, but such differences were smaller than one might expect (Weigel, 2005 (unpublished)). Mean conception rates at 75 days after breeding were 0.33, 0.33, and 0.32 for primiparous Holstein cows that averaged <27, 27–36, and >36 kg/day, respectively, during the first 3 months of lactation, whereas corresponding means were 0.28, 0.28, and 0.27 for multiparous Holstein cows that averaged <36, 36–45, and >45 kg/day, respectively. In Wisconsin Holsteins, Lopez et al. (2005) found no relationship between the percentage of cows exhibiting anovulatory condition and level of daily milk yield. The percentage of anovular cows was 27.8% for cows that were milking 25–30 kg/day and 26.3% for cows that were milking 50–55 kg/day (means for 5 kg intervals in between ranged from 21.7% to 35.1%, with no apparent trend). In California Holsteins, Santos et al. (2004) found a weak, non-significant relationship between milk yield and rate of embryonic loss between 31 and 45 days after breeding, with rates of 9.7% for cows that were milking 36 kg/day and 12.7% for cows that were milking 52 kg/day. Thus, it appears that increased milk yield is not solely responsible for the decline in mean reproductive performance.

3. Importance of adequate body condition

High milk production, whether achieved through genetic selection, enhanced nutrition, or improved management, is often implicated as the cause of health, fertility, and culling problems on modern dairy farms. However, a complex relationship exists between milk yield, health, and reproductive performance. High producing cows tend to be more susceptible to metabolic disorders and (to a lesser extent) infectious diseases and these can lead to impaired fertility. On the other hand, healthy cows tend to have higher milk production and greater reproductive performance than unhealthy cows. Conversely, cows that remain non-pregnant for much of the lactation tend to achieve higher levels of total production, because fewer resources are allocated to the developing calf. Thus, one must be cautious when attempting to formulate cause-effect relationships between these traits.

Many recent studies of the relationships between genetic merit, nutritional status, and reproductive performance have identified a common culprit—inadequate body condition. Modern dairy cows undergo a process of building tissue reserves in late lactation and during the dry period, depleting these reserves after calving and in early lactation, and rebuilding them again in late lactation. Inadequate body condition can lead to numerous problems in the lactating dairy cow, including greater susceptibility to metabolic disorders (e.g., ketosis or displaced abomasum) and impaired fertility. Several authors have noted that cows with poor body condition in early lactation or a significant loss in body condition during the lactation tend to have impaired reproductive per-

formance, including increased time from parturition to onset of ovarian activity, lower conception rate, and increased days open (Pryce et al., 2000; Royal et al., 2002).

Lopez et al. (2005) reported an extremely strong relationship between anovulatory condition and body condition score. Among lactating US Holstein cows that had a body condition score ≤ 2.50 (on a five-point scale), 83% were anovular. Corresponding percentages of anovular animals were 38% for cows with a score of 2.75; 34% for cows with a score of 3.00; 22% for cows with a score of 3.25, and 9% for cows with a score ≥ 3.50 . In a large, well-managed Holstein herd in Wisconsin, Caraviello (2005) reported a conception rate of 31% for cows with a body condition score at breeding of 2.25; 36% for cows with a score of 2.50; 40% for cows with a score of 2.75, and 42% for cows with a score of 3.00 or 3.25.

Caraviello (2005) developed a system for evaluating the percentage of body condition score “faults” on a commercial dairy farm. A single trained evaluator measured the condition score of 8036 cows during single visits to 63 large dairy farms over a 3 months period. Thresholds (i.e., minimum scores) for assigning a fault were 3.00 (on a five-point scale) for cows that were 60 days prepartum to 30 days postpartum; 2.50 for cows that were 30 days postpartum to 180 days postpartum, and 2.75 for cows that were >180 days postpartum (but not yet 60 days prepartum in the subsequent lactation). Fig. 1A and B shows herds with low and high percentages of body condition score faults, respectively. The primary advantage of the fault system is that it provides a snapshot of the body condition status of a dairy herd in a single visit.

Although simple, the aforementioned fault system can be a powerful predictor of dairy cow fertility. Caraviello (2005) evaluated the relationship between the percentage of body condition score faults within a herd and the percentage of cows that became pregnant by 150 postpartum. As the percentage of faults increased from 15% to 45%, the percentage of cows in the herd that were pregnant by 150 days postpartum decreased linearly, from 80% to 52%.

Because of recent concerns about the negative consequences of inadequate body condition in high producing cows, the Holstein Association USA introduced a negative economic weight for dairy form, a measure of angularity that has an estimated genetic correlation of -0.80 with body condition score (Dechow et al., 2004) into its selection index (commonly known as TPI) in 2005. It appears that historical selection pressure for cows that exhibited a high degree of “dairy character” or “angularity” (or perhaps cows that were simply too thin) may have been more harmful than selection for high milk production alone, because antagonistic genetic correlations between fertility and body condition score are greater than those between fertility and milk yield.

4. Genetic selection for female fertility

Genetic selection for health, fertility, and longevity has been practiced for more than two decades in some Scandinavian countries, and this has tended to stabilize (or at least lessen) the decline in mean performance for such traits. However, most other leading dairy countries did not pay serious attention to health, fertility, longevity until the mid 1990s. In the US, the introduction of genetic evaluations for length of productive life in 1994 provided the first opportunity to improve female fertility through genetic selection (VanRaden and Klaaskate, 1993). Although length of productive life is an indirect predictor of fertility, a limit of 10 months of productive life per lactation was applied to ensure that cows with a regular calving interval would be favored. As shown in Fig. 2, the genetic decline in daughter pregnancy rate, the measure of female fertility used for genetic evaluation of US dairy sires, tended to stabilize around the time at which sire evaluations for length of productive life became available.

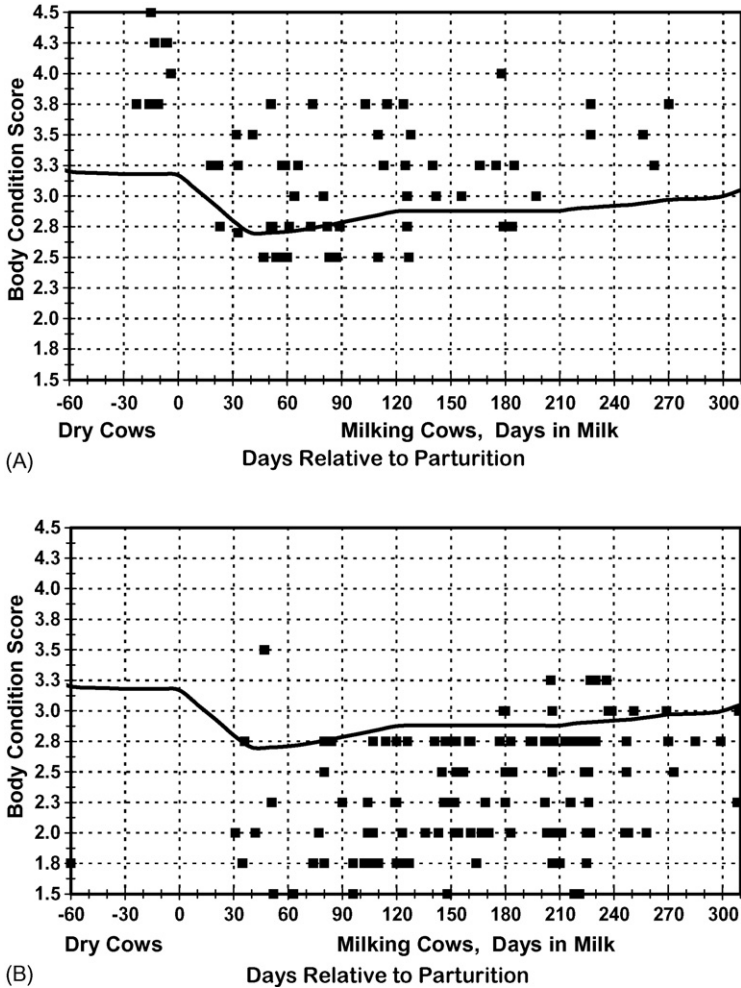


Fig. 1. (A) Example herd with a low percentage of body condition score faults (each dot represents an individual cow, and the solid line represents mean body condition score by stage of lactation for all 63 herds in the study). (B) Example herd with a high percentage of body condition score faults (each dot represents an individual cow, and the solid line represents mean body condition score by stage of lactation for all 63 herds in the study).

Although indirect selection for improved fertility based on genetic evaluations for length of productive life can be helpful, direct selection for improved fertility is more desirable. In the US, genetic evaluations for daughter pregnancy rate were introduced in 2003 (VanRaden et al., 2004). Input data are days open, computed from reported breeding dates for current cows and from calving interval for historical cows, and these are subsequently transformed to 21-day pregnancy rates for the purpose of genetic evaluation. The latter is a common, timely measure of reproductive efficiency on commercial dairy farms in the US, and it is calculated as number of cows that became pregnant during a given 21-day period divided by the number of cows that were eligible for breeding at the beginning of the period. The pool of eligible cows includes those that have passed the voluntary waiting period but are not yet pregnant. Although 21-day pregnancy rate is typically used as a “herd measure” of reproductive performance, sire evaluations for this

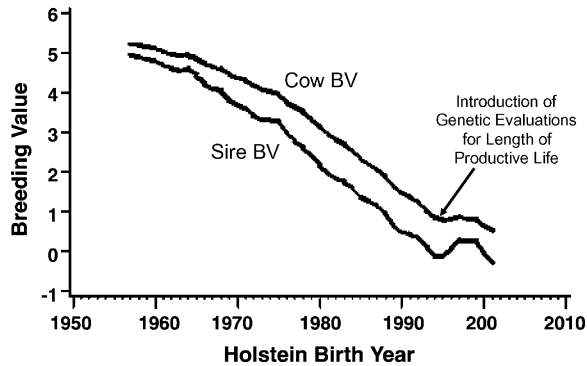


Fig. 2. Genetic trend for daughter pregnancy rate in US Holsteins (Source: USDA-ARS Animal Improvement Programs Laboratory, Beltsville, MD).

trait can be interpreted as the expected difference in 21-day pregnancy rate between the progeny groups of different sires (the 21-day pregnancy rate observation for an individual daughter can also be thought of as the number of 21-day opportunity periods required to achieve pregnancy). Differences between sires are dramatic—the highest and lowest available Holstein sires differ by 7.2% in daughter pregnancy rate. Because a 1% difference in pregnancy rate corresponds to approximately 4 days open (VanRaden et al., 2004), daughters of the highest and lowest sires differ by roughly 29 days open per lactation. Mean daughter pregnancy rate between sires in the top and bottom deciles is 4.9%, which corresponds to a difference of 20 days open per lactation. Breed differences also exist, as mean daughter pregnancy rate for the Jersey breed is 4.6% higher than that of the Holstein or Brown Swiss breed.

Daughter pregnancy rate has been incorporated into all major selection indices used by US dairy farmers, with a relative weight of 5–7% of the total economic value so genetic improvement (or at least stabilization) of female fertility is expected. Furthermore, the estimated genetic correlation of -0.31 between milk yield and female fertility (Weigel, 2003 (unpublished)), although antagonistic, is small enough in magnitude to ensure the availability of some sires with high producing and highly fertile daughters. Additional improvements will be made in genetic evaluations for daughter pregnancy rate in the future, as the USDA Animal Improvement Programs Laboratory (Beltsville, MD) is developing a detailed database of reproductive events, including outcomes of veterinary pregnancy examinations, dates of hormonal synchronization, dates of exposure to natural service sires, and designations of “do not breed” for cows that are destined to be culled at the end of lactation.

5. Genetic selection for male fertility

Declines in female fertility are the primary concern of both scientists and dairy farmers, and genetic improvement programs should focus on measures of female fertility, such as days open or daughter pregnancy rate. However, many dairy farmers have a keen interest in the male fertility evaluations of sires that are available for artificial insemination. In the US, two regional systems exist for the evaluation of male fertility. The first, denoted estimated relative conception rate (Dairy Records Management Systems, Raleigh, NC), encompasses data from small and medium-sized herds in the eastern half of the US and is based on 70-day non-return rate at first insemination. The second, denoted the Western Bull Fertility Analysis (Agri-Tech Analytics,

Visalia, CA), encompasses data from large herds in the western part of the US and is based on 75-day veterinary-confirmed conception rate for up to five inseminations per cow per lactation. The resulting estimates of male fertility are used widely by farmers when purchasing semen. Although differences of 4–5% exist between the highest and lowest deciles of bulls, much of the variation in male fertility is masked by culling of bulls with inadequate fertility and discarding of ejaculates that fail to meet laboratory standards.

6. Genetic selection for animal health

Although genetic evaluation systems are now available for female fertility and longevity, additional improvements are possible. A topic of increasing interest in the US and Canada is genetic selection for resistance to specific metabolic disorders and infectious diseases. Selection for improved animal health can lead to lower veterinary bills and reduced involuntary culling, as well as enhanced animal welfare. Genetic improvement of animal health will lead to simultaneous improvement of reproductive performance. Using methodology for failure-time analysis, Weigel (2004) showed that the relative risk of achieving pregnancy, which was constrained to 1.00 for a healthy, lactating Holstein cow, was reduced by dystocia (0.74), metritis (0.80), retained placenta (0.82), mastitis (0.93), ketosis (0.92), displaced abomasum (0.89), and lameness (0.90) if these events occurred between calving and 75 days postpartum.

At present, only the Scandinavian countries have national data recording and genetic evaluation systems for traits such as clinical mastitis and digestive, locomotive, and reproductive disorders. However, recent research by Zwald et al. (2004a,b) indicated that health data collected from on-farm herd management software programs could be used effectively for genetic selection purposes. Using data from large, commercial farms that used the Dairy Comp 305 (Valley Agriculture Software, Tulare, CA), PCDART (Dairy Records Management Systems, Raleigh, NC), or DHI-Plus[®] (DHI-Provo, Provo, UT) management software programs, Zwald et al. (2004a,b) grouped farmer-recorded health events into six categories: displaced abomasum, ketosis, mastitis, lameness, cystic ovaries, and metritis/retained placenta. Lactation incidence rates for these disorders ranged from 3% for displaced abomasum to 21% for metritis/retained placenta, and the vast majority of disorders occurred during the first 60 days postpartum. Heritability estimates were 0.14 for displaced abomasum, 0.06 for ketosis, 0.09 for mastitis, 0.04 for lameness, 0.04 for cystic ovaries, and 0.06 for metritis/retained placenta. Predicted probabilities of disease (per lactation) for daughters of individual sires ranged from 1.7% to 6.1% for displaced abomasum, 6.3% to 13.2% for ketosis, 12.9% to 25.9% for mastitis, 7.7% to 13.1% for lameness, 5.9% to 9.1% for cystic ovaries, and 15.1% to 27.1% for metritis/retained placenta. Genetic correlations between disorders were moderate and positive, typically between +0.10 and +0.40, as were correlations between sires' predicted transmitting abilities for resistance to specific health disorders and their predicted transmitting abilities for daughter pregnancy rate. This indicates that genetic selection for improved overall health is possible, as is genetic selection for resistance to specific diseases and disorders.

It is important to note that heterogeneity may exist between farms in the diagnosis, treatment, and recording of specific diseases and disorders. Such heterogeneity can hamper attempts to compare the health status of different herds or to evaluate time trends within specific herds. Because genetic evaluations of dairy sires are based on deviations between the performance of their daughters and the performance of other cows in the same herds at the same time, and because daughters of progeny test sires are distributed across hundreds of herds, small errors or biases that occur within a few herds tend to have a relatively minor impact on estimates of sires' genetic merit.

Nonetheless, validation of the quality and completeness of data from individual farms is important. Overall, the future appears bright for implementation of selection programs for improved animal health, and corresponding gains in fertility should be expected.

7. Conclusions

In summary, it is clear that the reproductive biology of today's high producing dairy cows differs from that of their ancestors and from that of yearling heifers. High producing cows tend to have shorter estrous cycles, fewer standing events (of shorter duration), and a higher rate of multiple ovulation. Direct genetic selection for improved female fertility is possible using traits such as daughter pregnancy rate, and indirect selection using traits such as longevity or body condition score can provide additional gains. Nearly all leading dairy countries now have systems in place to rank dairy sires based on the reproductive performance of their daughters, but improvements in data collection systems are needed to ensure that information regarding pregnancy examinations, hormonal synchronizations, natural service matings, and do not breed designations (of cows to be culled) are routinely reported. Lastly, development of data capture and genetic evaluation systems that can rank dairy sires according to their daughters' susceptibility to common health disorders, including mastitis, lameness, ketosis, displaced abomasum, and metritis/retained placenta, will enable selection for healthy, long-lasting cows that can achieve pregnancy in a timely manner without excessive management interventions.

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