

Genetics of Longevity and Productive Life

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■ Take Home Messages

- ▶ Annual herd turnover rates and reported reasons for culling are often misleading, and the timing of culling during the lactation may be a more useful indicator of potential management problems on a given farm.
- ▶ Conformation traits are often used to select for improved cow longevity, but these traits account for only a modest proportion of differences in cow survival.
- ▶ Substantial genetic variation exists between sires in the length of productive life of their daughters, as well as susceptibility to specific health disorders.
- ▶ Genetic improvement of cow survival should focus on direct measures of longevity, fertility, and health if possible.

■ Introduction

Dairy cow survival is influenced by many factors. Non-genetic factors include stall size, bedding type, degree of overcrowding, heat abatement devices, nutrition, veterinary care, herd expansion plans, milk quota restrictions, and availability and affordability of replacement heifers. Genetic improvement of longevity involves breeding animals that can produce a live calf without assistance; cycle normally, show visible heat, and conceive when inseminated; maintain adequate body condition and resist metabolic disorders; avoid udder injuries and fight off infection by mastitis pathogens; walk and stand comfortably without frequent hoof trimming, and efficiently produce milk of desirable composition. Many cows fail to complete these tasks and leave the herd prematurely. In some cases the cow is genetically flawed, while in other cases her environment is lacking. Significant genetic variation exists between sire families for longevity, fertility, calving performance, and disease resistance. Therefore, we can improve longevity

directly, by selecting families that resist culling, or we can improve longevity indirectly, by selecting families that excel for each of its component traits.

■ Annual Herd Turnover Rates

Much negative attention has been given to the annual turnover or replacement rates on commercial dairy farms. However, the overall replacement rate for a given herd doesn't provide enough information to indicate whether or not a problem exists – one needs to know which cows left the herd, as well as the reasons for and timing of their removal. Suppose that 35% of the milking cows in each of two dairies were replaced last year. In one herd, the majority of these were low-producing, older animals that were culled late in lactation and subsequently replaced by younger, genetically superior heifers grown from within the operation. In the other herd, the majority were young, high-producing cows that were culled or died early in lactation due to calving problems, mastitis, lameness, ketosis, and other metabolic disorders, and the owner was forced to buy springing heifers from a cattle dealer at the prevailing market price. Thus, even though the replacement rates on these farms are identical, one's interpretation of each herd's management success is vastly different. Replacement rates can also be misleading in herds that have an excess of replacement heifers. Suppose one herd sells its extra animals as springing heifers prior to first calving, while another herd calves all of its heifers and culls stringently for low production within the milking herd. Both may be successful, in terms of managing the health, fertility, and productivity of their cattle, but the former will have a substantially lower annual replacement rate.

In general, herds with lower replacement or turnover rates tend to be more successful, in terms of cow comfort, health, and productivity. However, replacement rates can be misleading, and more detailed information about the reasons for culling and the timing of culling is needed. Furthermore, herd turnover rates are influenced heavily by external factors, such as expansion plans and replacement heifer prices.

■ Reported Reasons for Culling

Dairy producers routinely report reasons for disposal as part of the national milk recording program. Animals can be recorded as “died”, “sold for dairy”, or “sold for beef”, with the latter category broken down into “low production”, “mastitis”, “infertility”, and so on. These descriptive reasons for disposal can be useful when studying the general demographics of a national dairy herd. For example, one might use such data to conclude that mastitis and infertility are the most common causes of culling on most dairy farms.

However, reported reasons for disposal can be misleading when one attempts to compare the management level of various dairy farms, or when one attempts to draw conclusions about the genetic merit of certain animals or sire families. Many animals are culled for “multiple offenses”. For example, a cow might have a difficult calving, followed by a case of ketosis, and a displaced abomasum. She may then fail to breed back in a timely manner and be culled from the herd when her daily milk production drops below a profitable level. The farmer might code her as “sold for low production”, “sold for infertility”, or “sold due to disease”. Thus, the reported reason for disposal is often a vague indicator of the actual problem. Furthermore, inconsistencies may exist between reported reasons for disposal and the actual health and reproductive history of the culled animals.

■ **Timing of Culling within the Lactation**

Stewart (Steve Stewart, Univ. of Minnesota, 2002, unpublished) proposed the idea of using the timing of culling within the lactation as an indirect indicator of the reason for disposal. He constructed a graph showing the proportion of total culled animals that were removed within certain time periods during the lactation. An example of this type of graph is shown in Figure 1, where the percentage of culled cows that left during each 3-week period from calving to 440 d postpartum is shown for 59,390 cows that calved in 2001-2003 and were subsequently culled from 151 herds that participate in the Alta Genetics (Watertown, WI) Advantage Progeny Testing Program. One can hypothesize that cows that were culled between 0 - 62 d postpartum may have left due to calving problems or early lactation metabolic disorders, while cows that were culled between 63 and 293 d postpartum may have left due to mastitis or lameness, and cows that were culled after 294 d postpartum may have left due to infertility. Exceptions to the rule exist, as a cow that is culled today may actually reflect the outcome of a “do not breed” decision that occurred many months earlier. Nonetheless, an analysis of the timing of culling events within a dairy herd may provide a more robust, objective description of management on a given farm than one could obtain by inspecting the overall turnover rate or the reported reasons for disposal. Furthermore, genetic evaluation of dairy sires based on the proportion of daughters that were culled during each period of the lactation may provide a useful indicator of differences in susceptibility to various diseases or disorders. For example, one could compute sire predicted transmitting abilities (PTA) for early lactation survival and this may identify bulls whose daughters avoid calving complications and resist early postpartum metabolic disorders.

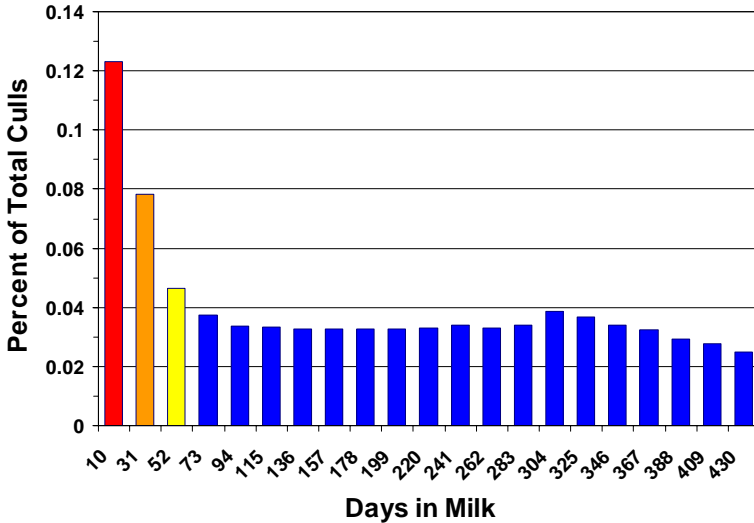


Figure 1. Percentage of total culled cows that left the herd during each three-week period from calving to 440 d postpartum, among cows that calved in 2001-2003 in 151 herds that participate in the Alta Genetics Advantage Progeny Testing Program.

■ Indirect Selection for Conformation Traits

Initial attempts to improve dairy cow longevity through artificial selection began in the 1970's and early 1980's, when breed associations and AI studs first developed linear type appraisal programs. For the next two decades, type and longevity were considered as synonymous. Bulls that sired daughters with high, wide rear udders, strong median suspensory ligaments, well-attached fore udders, and correct teat placement were considered to transmit superior longevity. Likewise, bulls that sired daughters with strong pasterns, a steep foot angle, and correct set to the hock were expected to improve longevity.

Numerous studies have addressed the genetic relationships between linear type traits and longevity (e.g., Caraviello et al., 2004a; Sewalem et al, 2004; Short and Lawlor, 1992). Early studies relied on the estimation of genetic correlations between longevity and linear type traits, and these studies typically invoked a 60-, 72-, or 84-month opportunity period for longevity. However, these studies suffered from two major limitations. First, the use of genetic correlation parameters to assess trait-longevity relationships limited these studies to measurement of linear relationships only. Few traits have a strictly linear relationship with longevity, and the role of traits with intermediate

optima or traits that offer “diminishing returns” as scores increase cannot be evaluated properly using genetic correlations. Second, the use of a long opportunity period, to allow each cow to fully express her genetic potential for longevity, resulted in a tremendous time lag between the birth of animals in the study group and eventual publication of results. For example, the youngest cows in the Short and Lawlor (1992) study were born in 1982, so more than a decade of additional genetic and management improvements occurred prior to publication of results of the study.

The use of survival analysis methodology in more recent studies (e.g., Caraviello et al., 2004b) alleviated several of the aforementioned limitations. In many of these studies, linear type scores were grouped into categories, and no restrictions were placed on the form of the trait-longevity relationship. Furthermore, because survival analysis allows proper modeling of censored records from animals that are still alive (Ducrocq, 1994), these studies used much more timely data than previous studies that invoked a long opportunity period. Results indicated that many type traits, such as rear leg set, rump angle, or dairy form, have intermediate optima, while many others, such as udder support, teat placement, or foot angle, seem to display a pattern of diminishing returns. More importantly, these studies demonstrated that udder depth, fore udder attachment, rear udder attachment, and udder support were of primary importance with respect to longevity, while rear leg set and foot angle were of secondary importance, and stature had no importance.

Despite the importance of physical conformation, a significant proportion of the genetic variation in longevity remained unexplained by existing type or production traits well into the 1990's. Numerous examples were noted of bulls that transmitted outstanding production and type to their daughters, but whose daughters nonetheless tended to leave the herd prematurely. Thus, type traits can be used as an indirect, albeit incomplete, indicator of the expected longevity of a bull's daughters, and actual culling and fertility data are needed to explain the rest of the story.

■ Direct Selection for Length of Productive Life

In 1994, the USDA Animal Improvement Programs Laboratory (Beltsville, MD) introduced national genetic evaluations for length of productive life (PL), which was measured as the total number of months in milk from first calving until 84 mo of age, with a limit of 10 mo per lactation (VanRaden and Klaaskate, 1993). Because the vast majority of cows are culled by 84 mo of age, this seems to provide a reasonable opportunity period. In fact, the additional gain in accuracy that could be achieved by waiting for a few, highly selected daughters to complete 8, 10, or 12 yr of PL would be negligible. Because the starting point of the opportunity period (date of first calving) can vary, it is possible that this definition of PL may favor animals that calve at a

young age. However, the phenotypic variation in age at first calving on most commercial dairies is rather limited.

The limit of 10 mo of PL per lactation was applied for two reasons: because it seemed desirable to penalize cows that have a long dry period and an extended calving interval, and because test-day production data beyond 305 d postpartum were unavailable historically. However, this restriction may have some unintended consequences in terms of the genetic relationships between PL and other traits in the breeding goal. Tsuruta et al. (2005) showed that the genetic correlation between milk yield and PL changed from -0.11 with a 305 d limit, to +0.08 with a 500 d limit, and to +0.14 with a 999 d limit. Corresponding genetic correlations between days open and PL were -0.62, -0.36, and -0.27 for per lactation PL limits of 305 d, 500 d, and 999 d, respectively, while genetic correlations with dairy form were -0.25, -0.12, and -0.08, respectively. An extension of the current 305 d limit to a value that is more closely aligned with the management of modern commercial dairies, such as 365 d or 400 d, has been discussed. An additional argument for extending, or even removing, a limit on PL credits per lactation is that national dairy sire evaluations for daughter pregnancy rate (DPR) are now routinely available, and indirect selection for fertility using PL information is no longer necessary.

An important aspect of current national genetic evaluations for PL is that records of cows that are still alive can be extended or projected to obtain an estimate of the total months in milk that such animals will accumulate by culling or 84 mo of age (VanRaden and Klaaskate, 1993). Thus, the 84-mo opportunity period does not cause a major delay or time lag in computing sire PTA for PL. On the other hand, the accuracy of such projections is low; much lower than the accuracy of projected 305 d milk production records based on the first two or three test day yields.

■ Incorporating Data from Correlated Traits

The primary concern with regard to genetic evaluation of PL is the substantial period of time required to obtain complete culling data for daughters of a given bull. Because a short generation interval is desirable in genetic selection programs, AI studs and pedigree breeders like to make sire selection decisions as quickly as possible. However, when a recently tested sire is being considered as a sire of sons or as an embryo transfer sire, most of his daughters are still alive. Therefore, reliability (REL) of PL evaluations is often low at the most critical points in life. This can lead to errors in selection decisions, particularly for bulls whose daughters fail to follow a typical maturity pattern. If a particular bull's daughters mature more or less gracefully than daughters of an average bull, his PTA can change significantly over time.

Weigel et al. (1998) developed a procedure by which correlated traits, such as type, production, and somatic cell score, can be used to compute an indirect prediction of a bull's PTA for PL. The indirect prediction for a given bull can then be combined with his direct prediction, which is based on actual culling data, using weights that depend on the REL of direct and indirect predictions. The combined PTA will have higher REL than either the direct or indirect prediction, especially early in life. Although the combined PL predictions tend to be more accurate than direct predictions for the majority of sires, there are exceptions. The most disturbing cases are bulls whose daughters appear promising in first lactation but mature less gracefully than daughters of an average bull. These bulls tend to have a high indirect prediction early in life, but their combined PTA tends to decrease over time, as daughters mature and are culled from the herd more rapidly than anticipated.

■ Genetic Trends in Productive Life

Figure 2 from the USDA Animal Improvement Programs Laboratory (<http://www.aipl.arsusda.gov>) shows the genetic trend for PL in US Holsteins. Similar trends have been documented by Sewalem et al. (2005) for Canadian Holsteins. Given apparent genetic improvement of 6 mo over the past 40 yr, it is remarkable that a perceived “culling problem” exists. Even more disturbing is the fact that phenotypic trends in these populations show a decline in mean longevity over time.

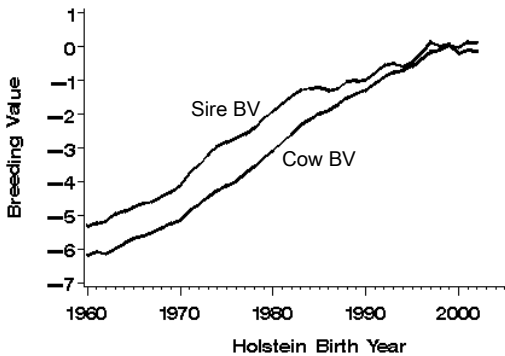


Figure 2. Genetic trend for productive life in US Holstein cattle (from the USDA Animal Improvement Programs Laboratory (<http://www.aipl.arsusda.gov>)).

One explanation, albeit not a palatable explanation in most disciplines of dairy science, is that today's cow is genetically superior for PL, but that management and nutrition conditions have deteriorated. In fact, it does seem that the dairy cow has improved genetically, because if one placed a 2005

model Holstein on a 1960's era dairy farm, she would likely be the prized animal in the herd. One thing has changed even more than the genetic make-up of the dairy cow – our expectations of her performance. A cow of 40 yr ago led a remarkably stress-free life, milking 20-25 kg/d in a herd of 40 cows somewhere in the hills of Wisconsin or Pennsylvania. Today's dairy cow produces more than twice that amount, and she receives much less individual attention and care than her great-great granddam once enjoyed. Management has also improved dramatically, as the typical cow of the 1960's did not enjoy such perks as a total mixed ration or sand free-stalls. Genetics and management must function in concert to produce optimal results, and it's impossible to assign credit or blame to either party.

■ Recording of Health Traits

Internationally, only the Scandinavian countries have national databases for the incidence of specific diseases and disorders among dairy cattle on commercial farms. However, recent studies by Zwald et al. (2004a, 2004b) have demonstrated the potential for compiling health data from on-farm herd management software programs for the purpose of genetic evaluation of dairy sires in the US. Using data from herds in the Alta Genetics (Watertown, WI) Advantage Progeny Test Program and herds that utilize the Dairy Records Management Systems (Raleigh, NC) PCDART software program, Zwald et al. (2004a, 2004b) created data sets of 50,611 - 105,029 cows in 212 - 429 herds for displaced abomasum, ketosis, mastitis, lameness, cystic ovaries, and metritis/retained placenta. Lactation incidence rates were 3% for displaced abomasum, 10% for ketosis, 20% for mastitis, 10% for lameness, 8% for cystic ovaries, and 21% for metritis/retained placenta. Incidence rates reported by producers may be lower than those reported by veterinarians or other evaluators, and tremendous differences in recording practices exist between farms. Different farms may diagnose certain diseases differently, and their thresholds for treating specific diseases may also differ. In addition, different farms may record the same disease with different codes (in customized software installations). Most problematic is “temporary recording”, in which a farm experiences an outbreak of a specific disease or disorder, records it during a diagnostic and problem-solving period, and stops recording it when the problem is solved.

Such heterogeneity in recording practices can render between-farm comparisons of herd management practices useless. However, the structure of AI progeny testing programs makes between-sire comparisons relatively robust to inconsistencies, errors, or biases in data recording. Each young AI sire has semen distributed to hundreds of herds simultaneously, and the resulting PTA are based on 70-120 daughters in 50-80 herds. Daughters of bull X compete with daughters of bull Y on the same farm at the same point in time, so factors such as management changes, disease outbreaks, poor

weather, or herd expansion affect daughters of both bulls equally. This process is repeated across hundreds of herds, and in this manner it is possible to obtain genetic evaluations that are remarkably accurate and stable.

■ Incorporation of Health Traits into Selection Programs

Zwald et al. (2004a) reported heritability estimates of 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. Although these estimates are low, it is interesting to note that they are in the same range as heritability estimates for diseases recorded by veterinarians in government-sponsored national programs in Norway, Sweden, Denmark, and Finland (<http://www-interbull.slu.se>). Furthermore, estimated heritabilities of these disease traits are as high as those of several traits currently evaluated by the USDA Animal Improvement Programs Laboratory (Beltsville, MD), such as DPR and PL (<http://www.aipl.arsusda.gov>).

Zwald et al. (2004a, 2004b) offered several suggestions regarding the analysis, publication, and use of information for specific health disorders. Because these traits are typically recorded in a binary manner, a threshold model is the logical choice for statistical analysis. Results can then be expressed as the expected probability of disease in a given lactation, for a specific (or average) set of management conditions. Zwald et al. (2004a) noted that the range in average PTA for disease probability in first parity between the 10 lowest-ranking sires and the 10 highest-ranking sires was 0.017 - 0.061 for displaced abomasum, 0.063 - 0.132 for ketosis, 0.129 - 0.259 for mastitis, 0.077 - 0.131 for lameness, 0.052 - 0.091 for cystic ovaries, and 0.151 - 0.271 for metritis/retained placenta.

If a multivariate threshold model is employed (Zwald et al., 2004b) results can be grouped into categories, such as probability of an early lactation disorder, probability of a reproductive disorder, and so on. An intriguing option is to compute the joint probability of obtaining any of the six aforementioned diseases during first lactation, as shown in the histogram of sire PTA in Figure 3 (Zwald et al., 2004b). As additional data become available regarding specific diseases and metabolic disorders, these traits should augment direct selection for PL.

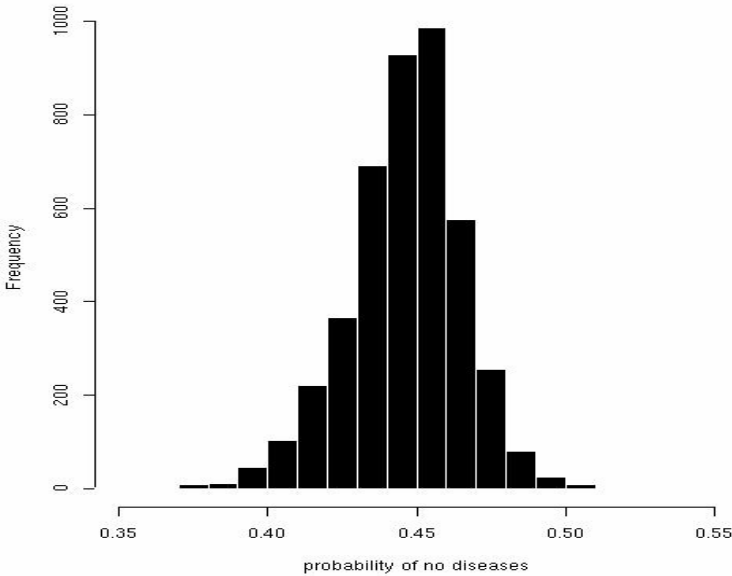


Figure 3. Histogram of sire predicted transmitting abilities for probability of no disease, including displaced abomasum, ketosis, mastitis, lameness, cystic ovaries, or metritis/retained placenta, during first lactation (from Zwald et al., 2004b).

■ Implications for Dairy Cattle Selection Programs

Despite the low heritability of PL and its component traits, such as DPR, somatic cell score, maternal calving ease, and the incidence of specific diseases and metabolic disorders, substantial genetic variation exists between breeds and between sire families. These traits have become increasingly important in the past decade, and most countries have incorporated longevity, udder health, and calving performance into their national breeding goals. In the next decade, development of routine genetic evaluations for specific diseases and disorders, such as mastitis, ketosis, displaced abomasum, lameness, and metritis is likely. Data for these traits can be captured electronically from on-farm computer systems, although trait definitions and recording schemes are not yet standardized across software programs. Nonetheless, the robust structure of AI progeny testing programs seems to allow effective genetic selection, even in the presence of imperfect data recording.

The potential impact of selection for PL and its components on dairy cattle improvement programs should not be underestimated. The structure of the

dairy cattle breeding industry, with superovulation of elite cows, progeny testing of young bulls, and widespread AI usage of proven sires, allows rapid genetic change within the cattle population. Since routine genetic evaluations for PL were introduced in 1994, several sires that rank extremely well for PL have achieved elite status, and these sires have produced hundreds of sons, along with tens of thousands of daughters and granddaughters. Such changes would not have occurred if genetic data regarding PL had not been available, and we can only hope that the recent introduction of genetic rankings for traits such as DPR and maternal calving ease will achieve a similar impact.

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