Short communication: Genetic lag represents commercial herd genetic merit more accurately than the 4-path selection model

C. D. Dechow*[1] **and G. W. Rogers†**
*Department of Animal Science, Pennsylvania State University, University Park 16802
†Geno Global Ltd., N-2326 Hamar, Norway

ABSTRACT

Expectation of genetic merit in commercial dairy herds is routinely estimated using a 4-path genetic selection model that was derived for a closed population, but commercial herds using artificial insemination sires are not closed. The 4-path model also predicts a higher rate of genetic progress in elite herds that provide artificial insemination sires than in commercial herds that use such sires, which counters other theoretical assumptions and observations of realized genetic responses. The aim of this work is to clarify whether genetic merit in commercial herds is more accurately reflected under the assumptions of the 4-path genetic response formula or by a genetic lag formula. We demonstrate by tracing the transmission of genetic merit from parents to offspring that the rate of genetic progress in commercial dairy farms is expected to be the same as that in the genetic nucleus. The lag in genetic merit between the nucleus and commercial farms is a function of sire and dam generation interval, the rate of genetic progress in elite artificial insemination herds, and genetic merit of sires and dams. To predict how strategies such as the use of young versus daughter-proven sires, culling heifers following genomic testing, or selective use of sexed semen will alter genetic merit in commercial herds, genetic merit expectations for commercial herds should be modeled using genetic lag expectations.
Key words: genetic progress, genetic lag, dairy cattle

Short Communication

Expectations for the rate of genetic progress in dairy cattle selection schemes are generally derived assuming the 4-path selection model where genes are transmitted to the next generation though sires of bulls (**SB**), dams of bulls (**DB**), sires of cows (**SC**), and dams of cows

(**DC**; Rendel and Robertson, 1950). The rate of genetic change (Falconer and Mackay, 1996) is then

$$\Delta G = \frac{\Sigma i r \sigma_A}{\Sigma L},$$

where the product of selection intensity (i), accuracy (r), and the additive genetic standard deviation (σ_A) for SB, DB, SC, and DC are summed and divided by the sum of generation intervals (L). This equation has routinely been applied to determine how changes to the structure of a breeding program will alter the rate of genetic progress (Nicholas and Smith, 1983; Schaeffer, 2006; Garcia-Ruiz et al., 2016).

The derivation of the 4-path model assumed a closed population (Rendel and Robertson, 1950). Whereas the AI breeding population could be considered a closed population dispersed across many herds, commercial farms using AI sires from other herds are not closed. Moreover, Bichard (1971) demonstrated that genetic merit in commercial herds will increase at the same rate as genetic merit in an elite breeding population. This could only be true under the 4-path model assumptions if selection parameters were the same between elite herds generating AI sires (henceforth referred to as the nucleus) and commercial dairy herds, which is not realistic.

Bichard (1971) derived expectations for genetic merit in commercial herds that can be distilled into the following formula for calculating genetic lag on commercial dairy farms:

$$\text{Lag} \cong -\left(L_{\text{SC}} + L_{\text{DC}}\right) \times \Delta G + i_{\text{SC}} r_{\text{SC}} \sigma_A + i_{\text{DC}} r_{\text{DC}} \sigma_A,$$

where Lag = the difference between commercial herds and the nucleus at any given time, the subscript SC refers to sires of commercial cows and the subscript DC refers to dams of commercial cows.

The aim of this work is to clarify whether genetic merit in commercial herds is more accurately reflected under the assumptions of the 4-path genetic response formula or by the genetic lag formula.

Table 1. Four-path[1] model (ΔG) and genetic lag (Lag) predictions in terms of genetic SD (σ) or years assuming an accuracy of 80% and for the given selection intensities (i) and generation intervals (L) for nucleus and commercial herds that use randomly selected nucleus bulls when young ($L_{SD}2$) or old ($L_{SD}6$)

Herd	i			L		ΔG	Lag	
	SB, DB	SC	DC	SB, DB, DC	SC		σ	Years
Nucleus	1.75	1.75	1.75	2	2	0.70	0.0	0
$L_{SD}2$	1.75	0	0	2	2	0.35	−2.8	4
$L_{SD}6$	1.75	0	0	2	6	0.23	−5.6	8

[1]SB = sires of bulls; SC = sires of cows; DB = dams of bulls; DC = dams of cows.

We assume that generation intervals (2 yr), accuracies (80%), and selection intensities (1.75 = the top 10.1% selected) are equivalent among the 4 pathways within the nucleus (Table 1). Based on current reliability for genomic prediction and recently observed generation intervals for AI bulls, these numbers are reasonable approximations of what can be achieved in the SB and DB pathways under genomic selection. Garcia-Ruiz et al. (2016) reported that generation intervals for SB and DB were <2.5 yr in 2015 and still declining. Generation intervals for SC and DC were reported to be 5.2 and 3.5 yr, respectively; however, those values represented generation intervals for commercial cows and here we are concerned with generation intervals for the elite genetic nucleus. Generation intervals and accuracy for SC and DC are similar to those for SB and DB in the elite breeding population because genomically tested virgin heifers are routinely flushed to generate both AI sires and the next generation of elite heifers.

The median net merit $ for genomic young Holsteins bulls with semen available in the United States is in the 92nd percentile (NAAB, 2017), which yields a similar selection intensity (1.86) to our assumption of 1.75. Additionally, our assumed selection differential of 1.4 genetic standard deviations (0.80 × 1.75) is similar to recent estimates for SB and DB pathways. The genetic standard deviation for milk yield is reported to be 610 kg (VanRaden, 2017), and reported selection differentials for SB (919 kg) and DB (752 kg; Garcia-Ruiz et al., 2016) are equivalent to 1.51 and 1.23 genetic standard deviations, respectively.

In Table 1, we report selection intensities and generation intervals for 2 commercial herd scenarios plus the resultant rates of genetic progress and genetic lag predicted for each scenario. These parameters were selected to easily contrast 4-path model and genetic lag assumptions. Accuracies (80%) are the same across scenarios for all pathways, and generation intervals for SB, DB, and DC are set to 2 yr. Selection intensity for SC and DC pathways are set to 0 for both commercial herd scenarios to simplify comparisons. In the first commercial herd scenario ($\mathbf{L_{SC}2}$), the generation interval for the SC pathway is also 2 yr. The SC generation interval was increased to 6 yr for the second scenario ($\mathbf{L_{SC}6}$).

The expected rate of genetic progress for $L_{SC}2$ is one-half that of the nucleus because of the 0 selection intensity for SC and DC pathways, and is lowest for $L_{SC}6$. The lag between the nucleus and $L_{SC}2$ was −2.8 genetic standards deviations, which is equivalent to 4 yr of genetic progress in the nucleus. The 4-yr lag is equivalent to the sum of the SC and DC generation intervals, as is the 8-yr lag predicted for $L_{SC}6$. The genetic lag in these scenarios is equivalent to the sum of parent generation interval because the selection intensities for SC and DC are 0, and the lags would be lessened in practice because superior sires would be selected from the nucleus.

In Table 2, we contrast genetic standard deviations of change in $L_{SC}2$ and $L_{SC}6$ by considering the genetic merit transmitted to cows in such herds by their sire and dam. As selection intensities in the SC and DC pathways are set to 0, sire transmitting ability (**TA**) is simply half the average breeding value (**BV**) of the nucleus 2 yr prior for $L_{SC}2$ and 6 yr prior for $L_{SC}6$. For instance, genetic merit for $L_{SC}2$ in yr 3 (0.35) was half the genetic merit of the nucleus in yr 1. Likewise, dam TA is half the average BV of the commercial herd 2 yr prior. Genetic merit in yr 5 for $L_{SC}2$ cows is 1.23, which is half of the nucleus BV in yr 3 (2.10/2 = 1.05) plus half of the cow BV from yr 3 (0.35/2 = 0.18). Nucleus and commercial herds are assumed to begin with a genetic merit of zero in yr 0, and genetic improvement in the commercial herds does not begin until calves sired by nucleus bulls are born in yr 3 ($L_{SC}2$) or yr 7 ($L_{SC}6$).

The rate of genetic progress is the same in $L_{SC}2$ and $L_{SC}6$ and the BV of $L_{SC}6$ is identical in yr 10 to that of $L_{SC}2$ in yr 6 when considering parent TA. After 25 yr of selection, the system has stabilized and the genetic merit of $L_{SC}2$ (−2.799 genetic SD) and $L_{SC}6$ (−5.598 genetic SD) lag behind the nucleus by the approximate amount predicted in Table 1 by the genetic lag formula. The genetic lag would be expected to be exact over an infinite number of generations. The results of Table 2 are plotted over a long-term (50 yr) selection horizon along with the predicted rate of genetic progress from