EFFECTS OF SELECTION FOR FERTILITY ON LACTATION CURVES

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SUMMARY

Breeding indices have enabled farmers to select for multiple traits simultaneously, including negatively correlated traits such as milk production and fertility. This negative correlation is believed to be either caused by an energy deficit during early lactation or serves a functional purpose in providing optimal birth spacing. A linear regression was carried out between parameters describing a lactation curve and a fertility index (RZR) and milk yield EBVs (mEBVs) to determine the effects of selection on the lactation curve. Breeding values of first lactation milk yield and a RZR were available for 2,405 sires. Additionally, these sires had test-day records of the first lactation of ~2M daughters. There was a negative correlation between mEBVs and RZR ($r=-0.27$, $P<0.0001$). Selection for fertility resulted in higher initial milk yield with an early peak yield. This suggests that an early peak occurs to provide offspring with sufficient milk despite a potential energy deficit. Further, an early peak provides an increased duration over which milk production declines and therefore sufficient time for the cow to recover from the energy deficit prior to a subsequent pregnancy. Finally, current production environments could be optimised to fulfil the genetic potential of high producing dairy cows.

INTRODUCTION

Negative genetic correlations have been reported between milk production and a variety of functional traits (Dekkers *et al.* 1998; Muir *et al.* 2004) including health and fertility (Oltenacu and Broom 2010). Both causal and functional hypotheses have been proposed to account for such negative correlations (Strucken *et al.* 2015). Collard (2000) proposed that the energy deficit experienced during early and peak lactation causes detrimental effects on health and fertility. However, very low correlations have been reported between total milk yield and energy balance (Spurlock *et al.* 2012). Alternatively, the negative impact of lactation on fertility may serve a functional purpose to provide optimal birth spacing for the survival of offspring.

Whilst milk production predominantly remains the most economically important trait for dairy farmers, functional traits such as conformation, udder health and fertility have become more prominent as the importance of animal welfare and longevity has increased (VanRaden, 2004; Miglior *et al.* 2005). Consequently, breeding goals were adjusted to incorporate health and fertility traits into breeding indices (Osteras *et al.* 2007; Boichard and Brochard 2012). These breeding indices allow traits to be weighted according to their economic importance and heritability, and account for phenotypic and genetic correlations between traits (Dekkers 2007). As such, this has enabled dairy farmers to breed for milk production and functional traits without requiring knowledge on how these practices impact upon the dynamics of milk production.

The dynamics of milk production can be described using an appropriate lactation model such as the Wilmink curve (Wilmink 1987). By fitting such a model to milk yield test-day records, a lactation cycle can be summarised using a minimal number of parameter values. These parameter values can subsequently be used to perform a linear regression with estimated breeding values for total milk yield and a fertility index. Understanding the impact of selection for fertility upon the parameter values of a lactation model could aid in determining whether the negative correlation between production and fertility is causal or functional. If the observed impact of production upon

fertility is caused by the energy deficit experienced during early and peak lactation, then a reduced peak milk yield would be expected to occur at a later time point. However, if the negative correlation serves a functional purpose to provide optimal birth spacing for the survival of offspring, then a reduced persistency would be expected.

MATERIALS AND METHODS

Data. Estimated breeding values (EBVs) for 2,405 Holstein Friesian sires, and test-day records for 1,797,852 daughters, were provided by VIT, Verden (Germany). Each bull had an average of 747 daughters (min=50, max=84,387).

Fertility breeding values were pre-corrected for *herd*year*, *month of insemination*, *age at insemination*, *parity*age* at insemination, *status* and *effect of the bull* (c.f. VIT April 2015). Breeding values were available for six measures: *non-return rate* 56 days post-insemination (separated for heifers and cows), *first to successful insemination* (separated for heifers and cows), *calving to first insemination*, and *days open*. The fertility EBVs were summarized in a fertility index (RZR) which was standardized to a mean of 100 and a standard deviation of 12. Further, corrected 305d EBVs for milk yield (mEBV) were available for the first lactation. These breeding values were raw values, representing actual yield deviations from the population mean.

Daughter records comprised the first lactation with an average of 8 test-day records per cow (min=1, max=20). The average lactation length was 259 days (min=5, max=330).

Table 1. Data description for the fertility index (RZR) and 305d milk yield EBVs (mEBV) of the first lactation for sires, and test-day milk yield of daughters

	N	Mean	Min	Max	SD
RZR	2,405	101	62	136	9.90
RZR (top 10 sires)	10	130	128	136	2.37
RZR (worst 10 sires)	10	72	62	75	4.01
mEBV (kg)	2,405	711	-1438	2774	609.43
mEBV (top 10 sires)	10	2583	2408	2774	118.51
mEBV (worst 10 sires)	10	-1119	-1438	-946	157.77
milk yield (kg)	14,862,232	25.57	2	98.8	6.54

Analyses. Pearson's correlation coefficients were calculated between RZR and mEBVs using test-day records. Wilmink curve parameters were estimated per sire with a non-linear model in *R*. The Wilmink curve is given as (Wilmink 1987):

$$y = a + b * exp^{-k*DIM} + c * DIM$$

where *y* is the test-day record; *a* is the potential maximum daily milk yield (kg); *b* determines the y-intercept (y-intercept = *a+b*); *c* is the gradient of the linear decay in milk yield (kg d^{-1}); *k* is the increase in milk yield before the peak production. Parameters *b* and *c* are both negative for a lactation curve. Convergence was achieved for 2,392 sires. Each parameter was subsequently used for a linear regression of the Wilmink curve parameters on RZR and mEBVs.

Environmental factors such as season or age are known to impact upon milk production. To determine the effect of environmental factors, we estimated the Wilmink curve parameters in a linear mixed model including the fixed effects of *age at calving*, *year season*, and *milk recording system* nested within *farm*. Sire was included as a random effect. These calculations were carried out across the top 10 and worst 10 sires for RZR and mEBVs, to provide the greatest contrast between the production curves of high and low ranked sires (**Table 1**). In order to fit a linear

model, Wilmink parameter k was fixed at 0.063 (top 10 RZR), 0.059 (worst 10 RZR), 0.053 (top 10 mEBVs), and 0.073 (worst 10 mEBVs) based on preliminary calculations (**Table 3**).

RESULTS

The pseudo-genetic correlation between mEBVs and RZR was significantly negative (r=-0.27, $P<0.0001$), confirming previous reports (Oltenacu and Broom 2010). As expected, this negative correlation resulted in a negative association between Wilmink curve parameter a (potential maximum) and RZR, and a positive association with mEBVs (**Table 2**). Further, increases in both RZR and mEBV resulted in a less negative value for parameter b, and hence a higher y-intercept.

Table 2. Effects of fertility index (RZR) and mEBVs on lactation curve parameters

	RZR ±se	R^2 (adj)	mEBV ±se	R^2 (adj)
a	-0.042 ±0.005***	0.03	0.0023 ±0.00***	0.36
b	0.031 ±0.008***	0.005	0.0009 ±0.00***	0.02
c	0.000006 ±0.00	0.0003	-0.0000003 ±0.00	0.0008
k	0.0002 ±0.00**	0.003	-0.00001 ±0.00***	0.06

*** $P<0.0001$ **$P<0.001$
a: potential maximum daily milk yield; b: determines y-intercept; c: gradient of the linear decay in milk yield; k: growth rate

Effects of RZR and mEBVs on curve parameter c (determining the gradient of the linear decay in milk yield) were not significant. However, a less negative parameter c is indicated for increasing RZR (i.e. decreased decay rate), whilst increasing mEBV caused a more negative parameter c (i.e. increased decay rate, **Table 2**). Parameter k (increase towards peak) increased for better RZR, and decreased for better mEBVs (**Table 2**).

Correction for environmental effects had an impact upon estimates of lactation curve parameters (**Table 3**). The largest impact was observed for parameter a where correction for environmental effects increased the potential maximum daily milk yield for the best mEBV sires, and decreased for the worst RZR and mEBVs. Further, correction for environmental effects reduced parameter b for the best mEBVs, causing a higher y-intercept (**Table 3**).

Table 3. Corrected and uncorrected Wilmink parameters based on best and worst sires

	RZR		mEBVs	
	10 best	10 worst	10 best	10 worst
	corrected parameters			
a	30.93	30.82	54.14	23.77
b	-10.74	-13.70	-1.3E-07	-9.66
c	-0.038	-0.036	-0.020	-0.036
k	0.063	0.059	0.053	0.073
	uncorrected parameters			
a	30.82	33.07	34.81	28.80
b	-10.80	-13.85	-13.70	-9.61
c	-0.038	-0.037	-0.036	-0.036

DISCUSSION

The functional and causal hypotheses previously proposed to account for the negative correlation between production and fertility may be expected to impact upon the shape of the lactation curve in different manners. Reductions in fertility caused by an energy deficit experienced during early and peak lactation would be expected to impact upon early lactation. Whereas, if the observed reduction in fertility serves a functional purpose to provide optimal birth spacing, then an increased rate of decay (decreased parameter c) would be expected.

All significant impacts of the fertility index occurred for parameters determining early and peak lactation (a, b, and k), whilst no significant effect was found on rate of decay (parameter c).

This is consistent with previous studies which reported genetic loci affecting early and peak lactation (Strucken *et al.* 2011; Strucken *et al.* 2012). These results appear to support a causal hypothesis where the negative correlation between production and fertility is due to an energy deficit in early lactation. The expectation was that the fertility index would cause a decreased potential maximum milk yield and a slower growth rate. However, the results showed an increased initial milk yield (y-intercept) and an increased growth rate causing an early production peak. The increased initial milk yield and growth rate during early lactation occurs to provide offspring with sufficient milk despite a potential energy deficit. Peak lactation occurs earlier when a fertility index is implemented in the breeding program, allowing for a longer decline in milk yield and hence increasing optimal birth spacing (despite no apparent impact upon the gradient of decay in milk yield).

Correction for environmental effects revealed that high producing dairy cows have a higher genetic potential than is currently supported by the production environment. In contrast, cows with a low fertility and milk yield showed a maximised genetic potential where production was biased upwards by a favourable production environment.

CONCLUSION

Selecting for increased fertility increases initial milk yield and growth rate in amount of daily milk production causing an early production peak. Early peak lactation occurs to provide offspring with sufficient milk despite a potential energy deficit, and provides an increased duration over which milk production declines. This provides sufficient time for the cow to recover from the energy deficit during early lactation prior to a subsequent pregnancy. Further, current production environments could be optimised to fulfil the genetic potential of high producing dairy cows.

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