

Uncovering genetic variation in cow fertility using simulation

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Abstract

Dairy cow fertility is currently measured using two traits: the proportion of cows mated within 21 days of the start of mating (PM21) and the proportion of cows that calve within 42 days of the start of calving (CR42). These traits indirectly measure a cow's genetic propensity to return to a fertile state after calving. Both PM21 and CR42 have low heritability (0.05 and 0.03, respectively) and fertility is suspected to have much stronger genetic drivers than indicated by these lowly heritable components. The purpose of this study was to explore genetic and environmental factors that contribute to dairy cow fertility using a stochastic simulation model. The model traces the reproductive life of cows from birth until their second calving date using environmental and genetic variables to simulate fertility phenotypes. The model demonstrated that even when significant genetic variation was simulated in underlying fertility traits, this variation appears only weakly as genetic effects using the current fertility traits evaluated for genetic selection purposes. Potential alternative traits (e.g. gestation length, heifer puberty trait, strength of oestrus expression or post-partum anoestrous interval) were shown to have potential to add value when identifying sires whose daughters calve earlier in the season.

Keywords: dairy cattle; fertility; simulation

Introduction

Reproductive ability of dairy cows is a major driver of profit in dairy farming, especially in seasonal, pasture-based systems. Poor dairy cow fertility increases reproductive intervention and mating costs, restricts days in milk, and can lead to premature culling restricting the productive life of the cow. Culling for poor reproductive performance limits farmer ability to cull animals on production and thereby reduces the rate of genetic gain for production traits. Maintaining high reproductive efficiency in dairy cattle is a challenge, and its success involves several distinct, but sequential, biological events leading to birth of a healthy calf. Since 2002, fertility has been included in the New Zealand economic selection index, Breeding Worth (BW). The fertility breeding value is expressed as the percentage of cows within a herd expected to calve within 42 days of the planned start of calving (CR42) and includes as a predictor of CR42, the proportion of cows mated in the first 21 days of mating (PM21; Harris *et al.* 2006). These traits indirectly measure a cow's genetic propensity to return to a fertile state after calving and to become pregnant in a time frame that will allow her to maintain a 365-day calving interval. Both PM21 and CR42 have low heritability (0.05 and 0.03, respectively). However, it is suspected that there are much stronger genetic drivers than indicated by the low heritable components of these fertility traits. There are underlying and interacting biological events that contribute to fertility that may not be effectively captured in the PM21 and CR42 traits due to masking by random environmental factors during young stock rearing, the dry period and lactation, reproductive management interventions, and recording errors.

Mathematical modelling can help unravel the effects of multiple factors on reproductive performance, or conversely, integrate these to characterise an animal's

reproductive state more efficiently (Vetharaniam *et al.* 2010). Results from stochastic simulation models that represent the events and effects that apply to practical dairy farm systems can be used to make informed choices such as which reproductive technologies to use (short-term), which management procedures to apply (mid-term), or which strategies for genetic selection to adopt (long-term) (Blanc *et al.* 2001; Beukes *et al.* 2010).

The objective of the research described in this paper was to explore genetic and environmental factors that contribute to dairy fertility by developing and utilising a stochastic simulation model. This will help to quantify key underlying determinants of genetic variation in fertility and to develop strategies to capture extra genetic variation in fertility, which could lead to improved genetic evaluation of dairy cows and their sires.

Methods

Model description

The stochastic fertility model was built in R (R Core Team 2014) and used to simulate 20,000 heifers (progeny of 200 sires and 20,000 dams, parents were assumed to be unrelated and not inbred) per replicate, with 100 replicates. The simulation began by assigning a sire and dam to each heifer. True breeding values (TBVs) for 13 genetic traits (Table 1) were assigned to both sires and dams using genetic parameters summarised in Table 1. The eigendecomposition of the positive definite variance-covariance matrix was used to generate genetically correlated TBVs (Ripley 1987). Genetic parameters used to generate TBVs were derived from the literature and are summarised in Table 1 and Table 2. Heifer TBVs were then simulated using the parental average of TBVs plus simulated Mendelian sampling term.

Table 1 Parameters from the literature used in the stochastic fertility model (Banos & Coffey 2010; Berry et al. 2002 & 2003; Coffey et al. 2006; Harris et al. 2006; Heuer et al. 2007; Koeck et al. 2014; Koenen et al. 2001; Lee et al. 1992; Lopez et al. 2004; Macdonald et al. 2005; McDougall 2001; McNaughton et al. 2002 & 2007; Mialon et al. 2000; Pancarci et al. 2002; Pryce & Harris 2006; Pryce et al. 2000; Roche et al. 2007; Roelofs et al. 2005; Roxström et al. 2001; Royal et al. 2000; Veerkamp et al. 2000; Xu et al. 1998)

Trait	h ²	Mean	Phenotypic SD	Genetic SD
Oestrus expression (hours in oestrus)	0.10	9.80	5.12	1.62
Body condition score (BCS) at calving	0.32	4.72	0.64	0.36
Change in BSC from calving to mating	0.19	-0.43	0.68	0.30
Milk yield (litres)	0.33	4406	361	207
Postpartum ovulation (interval from calving to luteal activity)	0.14	26.3	10.2	3.80
Number of services per conception	0.05	1.40	0.24	0.05
Calving difficulty (%)	0.05	7.40	6.80	1.50
Gestation length maternal (days)	0.21	281.5	4.48	2.05
Gestation length direct (days)	0.41	281.5	4.48	2.87
Calf weight at 100 days (% mature weight)	0.40	0.22	0.025	0.016
Post-weaning growth rate (% mature weight gained per day)	0.20	0.0017	0.00024	0.00011
Age at puberty (days)	0.33	342	30	17
Mature live weight (kg)	0.39	480	33	21

Table 2 Genetic correlations used as inputs for the stochastic fertility model. Data taken from (Banos & Coffey 2010; Berry et al. 2002 & 2003; Buttchereit et al. 2011; Cassandro 2014; Coffey et al. 2006; Dechow et al. 2002; Grosshans et al. 1997; Kaps et al. 2000; Knauer et al. 2010; Lee et al. 1992; Lopez et al. 2004; Mäntysaari et al. 2002; Mialon et al. 2000; Morris & Cullen 1994; Olds & Seath 1953; Pryce et al. 2000 & 2001; Pryce & Harris 2006; Roche et al. 2007; Roxström et al. 2001; Royal et al. 2000; Smith et al. 1989; Spicer et al. 1990; Vallimont et al. 2010; Veerkamp et al. 2000 & 2001; Winkelman et al. 2010).

	(1) Oestrus expression	(2) Body condition score (BCS) at calving	(3) Change in BCS from calving to mating	(4) Milk yield	(5) Calving to first postpartum ovulation interval	(6) Number of services per conception	(7) Calving difficulty	(8) Gestation length (maternal)	(9) Gestation length (direct)	(10) Weight at 100 days	(11) Growth rate from weaning to mating	(12) Age at puberty	(13) Mature live weight
2	0												
3	0	-0.74											
4	0	-0.57	-0.45										
5	0	-0.80	-0.30	0.51									
6	0	-0.10	-0.19	0.53	0								
7	0	-0.02	0	0.20	0	0							
8	0	0	0	0	0	-0.02	0.01						
9	0	0	0	0	0	-0.02	0.11	0					
10	0	0	0	0	0	0	0	0	0				
11	0	0	0	0.13	0	0	0	-0.04	0.35	0.66			
12	-0.25	0	0	0	0.45	0.29	0	-0.01	-0.10	-0.04	-0.21		
13	0	0.40	0	0.25	-0.45	0.53	0	0	-0.10	0.48	0.47	-0.20	

Heifers were then assigned a birthdate from a user-defined random distribution. Calf rearing conditions and pre-mating growth rates were simulated using a combination of environmental and genetic factors to influence the timing of puberty onset. User-defined parameters determined the proportion of heifers that were artificially inseminated (AI; here, 21% based on industry average incidence), in which case the model assumes that AI involves the use of oestrus synchrony treatments at the planned start of mating (PSM). First mating date was simulated using puberty onset and synchrony variables as well as environmental factors. A base fertilisation rate of 0.9 was applied for heifers that were inseminated at their second or later oestrus. For heifers bred by AI, a 0.12 reduction in fertilisation rates was assumed, while heifers inseminated at their first oestrus were assumed to have their probability of conception reduced by 0.34 and fertilisation prior to first oestrus was always unsuccessful. After conception, embryo survival was simulated from the heifer's genetic potential for fertility (derived from the number of services per conception trait), and was further influenced by the number of oestrous cycles since puberty, and by how many embryos were present. If an embryo is lost or the heifer fails to conceive on the first mating, further mating events (and subsequent embryo survival) were simulated providing the time of mating was still within the mating season.

Gestation length was simulated from genetic parameters (both the mother's maternal genetic effects and the simulated calf's direct genetic effect) and environmental factors such as calf sex, calf breed and twin pregnancies. First calving date was calculated from successful conception date and gestation length. Milk yield, body condition score (BCS) at calving and change in BCS from calving to mating were also simulated. Change in BCS influences how rapidly a cow returns to a fertile state after calving. The first post-partum ovulation and oestrus date were simulated. High milk yield affects the first post-partum oestrus by decreasing oestrus expression and by increasing subsequent cycle lengths. Low BCS at mating also affects post-partum anoestrus by increasing the likelihood of silent oestrus (ovulations not accompanied by an oestrus). A proportion of cows (70%) were randomly assigned a truncated first cycle.

The proportion of anoestrous dairy cattle identified and treated with CIDR devices was set at 95%. These cows were assumed to be mated at the PSM. Fertilisation rate in cows was simulated in the same manner as in heifers except that cows have a longer AI season and tend to have more variability in the rate of successful oestrus detection. Modelling of embryo survival for cows was similar to the approach for heifers, except that cow fertility was also dependant on the level of calving difficulty observed. Gestation length was simulated as described above to estimate the next calving date.

Derived industry fertility traits

Cow records generated from the simulation were used to assign industry-equivalent phenotypes to each cow.

The three main phenotypes of interest were calving season day (CSD) defined as the number of days between planned start of calving and a cow's calving date, CR42 and PM21 (Harris et al. 2006). The two calving traits CSD and CR42 were considered at the time of second calving, while the mating trait (PM21) was considered following the first calving (as in the current genetic evaluation system).

Additional simulated traits included in the genetic evaluation of fertility merit were age at puberty (measured by an activity meter with simulated errors around the true age at puberty), conception rate to first heifer mating (binary), heifer pregnancy diagnosis after conclusion of the breeding season, gestation length of the cow prior to first calving, heifer calving rate (binary), heifer calving rate in 21 days, heifer calving season day, post-partum anoestrous interval (days from calving to first farmer observed oestrus), post-partum ovulation interval (days from calving until first post-partum ovulation), BCS at mating, and change in BCS from calving to mating (i.e., in peak lactation).

Genetic analysis

The model produced simulated cow phenotypic records (y) for both underlying traits, and also for derived industry fertility traits which were then analysed in ASReml (Gilmour et al. 2009) using the following univariate sire model:

$$y_{ij} = \mu + \text{sire}_i + e_{ij},$$

Where μ was the overall mean, sire_i was the random genetic effect of the sire i of the cow, and e_{ij} was the random residual term. For each trait and replicate the sire genetic variance (V_s) and residual variance (V_e) were estimated. The heritability was calculated as:

$$h^2 = 4V_s / (V_s + V_e).$$

As the univariate analysis was used, genetic correlations between traits were approximated using the correlations between estimated breeding values (EBVs) for those traits weighted by average accuracy of prediction. For this paper, the main focus was on evaluating the genetic correlations between derived industry fertility traits with CSD and CR42. The current fertility breeding value used in the national Breeding Worth index is CR42, although recent research (Bowley et al. 2015) suggests that this might be better replaced with CSD, which is a continuous version of the same trait.

Model outputs were simulated and stored for 100 unique replicates to reduce the sampling error. Genetic analyses were undertaken separately after every iteration and results were averaged over the number of replicates.

Results

The estimated heritabilities of the underlying simulated traits were very similar to those specified in Table 1 and they are not reported. Heritabilities for the derived industry fertility traits are shown in Table 3 along with their correlations with CR42 and CSD. The heritabilities of CR42 and PM21 were 0.01 and 0.05, respectively, which are low and in an alignment with recent estimates (Harris

et al. 2006; Bowley et al. 2015). Many of the other derived industry fertility traits had higher heritabilities, for example, gestation length, age at puberty, post-partum ovulation interval, BCS at calving, and BCS change between calving and mating all had heritabilities higher than 0.15. Both heifer and cow calving season day had higher heritabilities than their binary counterparts.

Genetic correlations of model-derived traits with CR42 and CSD (Table 3) followed similar patterns for

both calving traits, however they are stronger for CSD compared with CR42 for the majority of traits. Exceptions were post-partum intervals, PM21 and BCS traits. The strongest difference between correlations with CR42 and CSD was observed for gestation length and heifer calving traits, both binary and continuous, with CSD having stronger correlations with those traits than CR42. Genetic correlation between CSD and CR42 was -0.93.

Table 3 Estimates of heritability of model-derived traits and their genetic correlations with CR42 and calving season day (CSD); standard errors (SE) in parenthesis

Trait	h ²	Genetic correlation	
		with CR42	with CSD
Age at puberty (activity meter)	0.175 (0.017)	-0.125 (0.004)	0.130 (0.002)
Conception to first heifer mating	0.043 (0.005)	0.097 (0.004)	-0.112 (0.003)
Heifer pregnancy diagnosis	0.035 (0.004)	0.100 (0.004)	-0.111 (0.003)
First gestation length	0.250 (0.024)	-0.466 (0.004)	0.739 (0.002)
Heifer calving rate	0.029 (0.003)	0.146 (0.004)	-0.162 (0.003)
Heifer calving rate in 21 days	0.016 (0.002)	0.452 (0.004)	-0.634 (0.003)
Heifer calving season day	0.044 (0.005)	-0.491 (0.004)	0.727 (0.003)
Post-partum anoestrus interval	0.087 (0.009)	-0.392 (0.004)	0.280 (0.003)
Post-partum ovulation interval	0.180 (0.018)	-0.390 (0.004)	0.277 (0.003)
PM21	0.053 (0.006)	0.663 (0.004)	-0.616 (0.002)
Body condition score (BCS) at calving	0.146 (0.015)	0.388 (0.004)	-0.289 (0.003)
Change in BCS from calving to mating	0.201 (0.020)	0.145 (0.004)	-0.107 (0.003)
CR42	0.011 (0.002)	---	-0.933 (0.002)
CSD	0.042 (0.005)	-0.933 (0.002)	---

Discussion

The results obtained in this study showed that while genetically almost the same as CR42, CSD was demonstrated to be a better trait for evaluation of cow fertility than CR42, due to a higher heritability and stronger genetic correlations with other traits. This confirms our earlier findings based on the industry data that CSD is a superior trait (Stachowicz et al. 2014).

Post-partum interval to rebreeding may be a useful new selection criterion but it is reliant on a farmer heat detection and has lower heritability (compared with post-partum ovulation interval), which may undermine the value of the trait. Automated recording systems that capture first heat of all cows, including those calving early and already cycling by the time conventional pre-mating heat checks start, might be useful, particularly if post-partum ovulation interval has a stronger genetic correlation with other underlying fertility traits than assumed here in this current model.

First gestation length and heifer calving patterns (heifer calving rate in 21 days and heifer CSD) have demonstrated their potential as useful traits. Conversely, age at puberty and heifer calving rate may have limited value, because of their lower genetic correlation with cow calving traits, and practical difficulties in determination of age at puberty.

Post-partum ovulation interval and BCS at calving have promising genetic parameters as candidates for new fertility traits. BCS in heifers at day 60 of lactation is already used as a correlated predictor trait in the national fertility genetic evaluation model and this result supports its continued use. There would be marginal additional value from including the change in BCS between calving and mating, as it has weaker genetic correlations with calving traits compared with BCS at calving.

These results suggest that the low heritability of current fertility phenotypes observed in the industry data is a consequence of many random non-genetic factors that impact the timing of mating and calving in a typical farm system. The alternative hypothesis is that pedigree errors and failure to record reproductive interventions such as induction of early calving and progesterone treatment of non-cycling cows contribute to the low heritability. A recent study using data from the national herd fertility trial indicated that missed recording of reproductive interventions and pedigree errors were contributors to the low heritability, but only by relatively modest amounts (Bowley et al. 2015). In this study we simulated perfect pedigree assignment and recording, and minimal influence of reproduction intervention on the quality of data available.

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References

- Banos G, Coffey MP 2010. Genetic association between body energy measured throughout lactation and fertility in dairy cattle. *An International Journal of Animal Bioscience* 4: 189–199.
- Berry DP, Buckley F, Dillon P, Evans RD, Rath M, Veerkamp RF 2002. Genetic parameters for level and change of body condition score and body weight in dairy cows. *Journal of Dairy Science* 85: 2030–2039.
- Berry DP, Buckley F, Dillon P, Evans RD, Rath M, Veerkamp RF 2003. Genetic relationships among body condition score, body weight, milk yield, and fertility in dairy cows. *Journal of Dairy Science* 86: 2193–2204.
- Beukes PC, Burke CR, Levy G, Tiddy RM 2010. Developing a whole farm model to explore the impacts of mating management on the profitability of pasture-based dairy farms. *Animal Reproduction Science* 121: 46–54.
- Blanc F, Martin GB, Bocquier F 2001. Modelling reproduction in farm animals: a review. *Reproduction, Fertility and Development* 13: 337–353.
- Bowley FE, Green RE, Amer PR, Meier S 2015. Novel approaches to genetic analysis of fertility traits in New Zealand dairy cattle. *Journal of Dairy Science* 98: 1–8.
- Buttchereit N, Stamer E, Junge W, Thaller G 2011. Short communication: genetic relationships among daily energy balance, feed intake, body condition score, and fat to protein ratio of milk in dairy cows. *Journal of Dairy Science* 94: 1586–1591.
- Cassandro M 2014. Genetic aspects of fertility traits in dairy cattle—review. *Acta Agraria Kaposváriensis* 18: 11–23.
- Coffey MP, Hickey J, Brotherstone S 2006. Genetic aspects of growth of Holstein-Friesian dairy cows from birth to maturity. *Journal of Dairy Science* 89: 322–329.
- Dechow CD, Rogers GW, Clay JS 2002. Heritability and correlations among body condition score loss, body condition score, production and reproductive performance. *Journal of Dairy Science* 85: 3062–3070.
- Gilmour AR, Gogel BJ, Cullis BR, Thompson R. 2009. ASReml User Guide Release 3.0. VSN International Ltd, Hemel Hempstead, HP1 1ES, UK. www.vsnl.co.uk.
- Grosshans T, Xu ZZ, Burton LJ, Johnson DL, Macmillan KL 1997. Performance and genetic parameters for fertility of seasonal dairy cows in New Zealand. *Livestock Production Science* 51: 41–51.
- Harris BL, Pryce JE, Xu ZZ, Montgomerie WA 2006. Development of new fertility breeding values in the dairy industry. *Proceedings of the New Zealand Society of Animal Production* 66: 107–112.
- Heuer C, Healy A, Zerbini C 2007. Economic effects of exposure to bovine viral diarrhoea virus on dairy herds in New Zealand. *Journal of Dairy Science* 90: 5428–5438.
- Kaps M, Herring WO, Lamberson WR 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationships with weaning weight in Angus cattle. *Journal of Animal Science* 78: 1436–1442.
- Knauer MT, Cassady JP, Newcom DW, See MT 2010. Estimates of variance components for genetic correlations among swine estrus traits. *Journal of Animal Science* 88: 2913–2919.
- Koeck A, Miglior F, Jamrozik J, Kelton DF, Schenkel FS 2014. Genetic relationships of fertility disorders with reproductive traits in Canadian Holsteins. *Proceedings of 10th World Congress on Genetics Applied to Livestock Production*, Vancouver, Canada.
- Koenen EPC, Veerkamp RF, Dobbelaar P, De Jong G 2001. Genetic analysis of body condition score of lactating Dutch Holstein and Red-and-White heifers. *Journal of Dairy Science* 84: 1265–1270.
- Lee AJ, Boichard DA, McAllister AJ, Lin CY, Nadarajah K, Batra TR, Roy GL, Vesely JA 1992. Genetics of growth, feed intake, and milk yield in Holstein cattle. *Journal of Dairy Science* 75: 3145–3154.
- Lopez H, Satter LD, Wiltbank MC 2004. Relationship between level of milk production and estrous behavior of lactating dairy cows. *Animal Reproduction Science* 81: 209–223.
- Macdonald KA, Penno JW, Bryant AM, Roche JR 2005. Effect of feeding level pre- and post-puberty and body weight at first calving on growth, milk production, and fertility in grazing dairy cows. *Journal of Dairy Science* 88: 3363–3375.
- Mäntysaari P, Ojala M, Mäntysaari EA 2002. Measures of before and after breeding daily gains of dairy replacement heifers and their relationship with first lactation milk production traits. *Livestock Production Science* 75: 313–322.
- McDougall S 2001. Effects of periparturient diseases and conditions on the reproductive performance of New Zealand dairy cows. *New Zealand Veterinary Journal* 49: 60–67.
- McNaughton LR, Morgan SR, Gore P, Verkerk GA, Holmes CW, Parkinson TJ 2002. Monitoring onset of puberty in three genetic strains of Holstein-Friesian dairy cattle. *Proceedings of the New Zealand Society of Animal Production* 62: 30–33.

- McNaughton LR, Sanders KM, Pryce JE, Bracefield GE, Harcourt SJ, Spelman RJ 2007. Phenotypic relationships between the interval from calving to first luteal activity and fertility in a seasonal dairy production system. *Animal Reproduction Science* 102: 98–110.
- Mialon M-M, Renand G, Krauss D, Ménéssier F 2000. Genetic variability of the length of postpartum anoestrus in Charolais cows and its relationship with age at puberty. *Genetics Selection Evolution* 32: 1–12.
- Morris CA, Cullen NG 1994. A note on genetic correlations between pubertal traits of males or females and lifetime pregnancy rate in beef cattle. *Livestock Production Science* 39: 291–297.
- Olds D, Seath DM 1953. Repeatability, heritability and the effect of level of milk production on the occurrence of first estrus after calving in dairy cattle. *Journal of Animal Science* 12: 10–14.
- Pancarci SM, Jordan ER, Risco CA, Schouten MJ, Lopes FL, Moreira F, Thatcher WW 2002. Use of estradiol cypionate in a presynchronized timed artificial insemination program for lactating dairy cattle. *Journal of Dairy Science* 85: 122–131.
- Pryce JE, Coffey MP, Brotherstone S 2000. The genetic relationship between calving interval, body condition score and linear type and management traits in registered Holsteins. *Journal of Dairy Science* 83: 2664–2671.
- Pryce JE, Coffey MP, Simm G 2001. The relationship between body condition score and reproductive performance. *Journal of Dairy Science* 84: 1508–1515.
- Pryce JE, Harris BL 2006. Genetics of body condition score in New Zealand dairy cows. *Journal of Dairy Science* 89: 4424–4432.
- R Core Team 2014: R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL <http://www.R-project.org/> [accessed 24 May 2014].
- Ripley BD 1987. *Stochastic simulation*, vol. 2009, no. Nc. Wiley, p. 237.
- Roche JR, Macdonald KA, Burke CR, Lee JM, Berry DP 2007. Associations among body condition score, body weight, and reproductive performance in seasonal-calving dairy cattle. *Journal of Dairy Science* 90: 376–391.
- Roelofs JB, van Eerdenburg FJCM, Soede NM, Kemp B 2005. Various behavioral signs of estrous and their relationship with time of ovulation in dairy cattle. *Theriogenology* 63: 1366–1377.
- Roxström A, Strandberg E, Berglund B, Emanuelson U, Philipsson J 2001. Genetic and environmental correlations among female fertility traits, and between the ability to show oestrus and milk production in dairy cattle. *Acta Agriculturae Scandinavica, Section A - Animal Science* 51: 192–199.
- Royal M, Mann GE, Flint APF 2000. Strategies for reversing the trend towards subfertility in dairy cattle. *The Veterinary Journal* 160: 53–60.
- Smith BA, Brinks JS, Richardson GV 1989. Estimation of genetic parameters among reproductive and growth traits in yearling heifers. *Journal of Animal Science* 67: 2886–2891.
- Spicer LJ, Tucker WB, Adams GD 1990. Insulin-like growth factor-I in dairy cows: relationships among energy balance, body condition, ovarian activity, and estrous behavior. *Journal of Dairy Science* 73: 929–937.
- Stachowicz K, Jenkins GM, Amer PR, Meier S 2014. New approaches to fertility evaluation in a seasonal calving system. *Interbull Bulletin* 48: 89-93.
- Vallimont JE, Dechow CD, Daubert JM, Dekleva MW, Blum JW, Barlieb CM, Liu W, Varga GA, Heinrichs AJ, Baumrucker CR 2010. Genetic parameters of feed intake, production, body weight, body condition score, and selected type traits of Holstein cows in commercial tie-stall barns. *Journal of Dairy Science* 93: 4892–4901.
- Veerkamp RF, Koenen EPC, De Jong G 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *Journal of Dairy Science* 84: 2327–2335.
- Veerkamp RF, Oldenbroek JK, Van Der Gaast HJ, van der Werf JHJ 2000. Genetic correlation between days until start of luteal activity and milk yield, energy balance, and live weights. *Journal of Dairy Science* 83: 577–583.
- Vetharaniam I, Peterson AJ, MacNatty KP, Soboleva TK 2010. Modelling female reproductive function in farmed animals. *Animal Reproduction Science* 122: 164-173.
- Winkelman AM, Wood RM, Harris BL 2010. Enhancement of calving difficulty breeding values in New Zealand. *Interbull Bulletin* 42: 91-94.
- Xu ZZ, McKnight DJ, Vishwanath R, Pitt CJ, Burton LJ 1998. Estrus detection using radiotelemetry or visual observation and tail painting for dairy cows on pasture. *Journal of Dairy Science* 81: 2890–2896.