Original Article

Genetic parameters and trends for daughters of imported and Thai Holstein sires for age at first calving and milk yield

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A B S T R A C T

Age at first calving (AFC) and accumulated 305 d milk yield (MY) data from first-lactation daughters of imported Holstein (IH) and Thai Holstein (TH; purebred and crossbred Holstein-Other Breeds) sires were used to estimate genetic parameters and to compare genetic changes. The dataset included information from daughters of 3137 IH and 5686 TH sires that calved from 1991 to 2014 on 1012 dairy farms. The 2-trait animal model considered herd-year-season, difference between Other Breeds and Holstein, and heterosis as fixed effects, and animal and residual as random effects. Variance components and genetic parameters were estimated using an average information restricted maximum likelihood procedure. Regressions of mean estimated breeding value (EBV) per calving year were computed to assess genetic trends. The heritability (estimate $\pm$ standard error) was 0.149 ± 0.036 for AFC, and 0.147 ± 0.035 for MY. The genetic correlation between AFC and MY was -0.083 ± 0.174. The genetic trend was -0.008 ± 0.001 mth/yr ($p < .001$) for AFC, and 1.529 ± 0.219 kg/yr ($p < .001$) for MY. The genetic trend for AFC was -0.003 ± 0.002 mth/yr ($p = .084$) for daughters of IH sires, and -0.014 ± 0.002 mth/yr ($p < .001$) for daughters of TH sires. The genetic trend for MY was 0.585 ± 0.326 kg/yr ($p = .072$) for daughters of IH sires, and 4.091 ± 0.294 kg/yr ($p < .001$) for daughters of TH sires. The near zero genetic correlation between AFC and MY indicated that selection to increase MY would not affect AFC. The genetic predictions and trends indicated that daughters of IH sires tended to have higher EBV for MY than daughters of TH sires, but daughters of both IH and TH sires tended to have similar EBV for AFC.

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Introduction

Farmers and associated people in the dairy industry need to be adaptable and competitive under variable economic conditions in Thailand (Koonawootrittriron et al., 2012). Genetic improvement is an important contributor to improve efficiency of dairy production at a farm level (Sarakul et al., 2011). In particular, prediction of the genetic potential of cows for age at first calving (AFC) and accumulated 305 d milk yield (MY) requires knowledge and understanding of their genetic basis to develop appropriate selection and mating strategies (Koonawootrittriron et al., 2006). Selection of cows that have early AFC would help farmers reduce production costs and increase their chance to have cows with a long productive lifespan (Tozer and Heinrichs, 2001; Hare et al., 2006; Do et al.,

2013). Similarly, selection of cows for high MY would increase farm revenues and profitability (Ettema and Santos, 2004).

Many tropical countries import frozen semen from Holstein and other high-production, temperate dairy breeds to inseminate local cows in order to improve milk yield. The genetic ability of imported dairy sires for economically important traits is frequently assessed and compared to locally-produced sires under local conditions using information from their daughters (Koonawootrittriron et al., 2009; Hossein-Zadeh, 2011; Gebreyohannes et al., 2013). This way farmers can choose sires with the highest predicted genetic abilities among imported and local sires for genetic improvement of their dairy herds.

Thailand is a tropical country located in Southeast Asia characterized by high temperatures and high humidity most of the year plus two tropical monsoons each year (Thai Meteorological Department, 2010). Imported Holstein (IH) and Thai Holstein (TH; purebred and crossbred Holstein-Other Breeds) sires have been

used consistently to inseminate Holstein purebred and Holstein-Other Breeds crossbred cows (Ritsawai et al., 2014). Currently, most Thai dairy cattle are 75% Holstein or higher (Department of Livestock Development, 2006). A regular assessment of the genetic variation and trends for AFC and MY in first-lactation daughters of IH and TH sires is necessary to monitor the existing mating and selection program in the Thai dairy population, and to determine needed changes to improve their effectiveness. Thus, the objectives of this research were to estimate the genetic parameters and trends in daughters of imported Holstein and Thai Holstein sires for AFC and MY in the Thai multibreed dairy population.

Materials and methods

Data and animals

The dataset consisted of 9182 AFC and 9158 MY records. These records were from multibreed dairy cows that had calved between 1991 and 2014 on 1012 dairy farms located across five regions (northern, northeastern, western, central, and southern) of Thailand. Imported Holstein (IH; 711 sires) and Thai Holstein (TH; purebred and crossbred Holstein-Other Breeds; 297 sires) sires were used for mating with Holstein purebred and Holstein-Other Breeds crossbred cows (87.71 ± 11.08% Holstein, as mean ± SD). The dataset included daughter records from 3137 IH and 5686 TH sires. The pedigree file contained 18,847 animals (1331 sires and 17,516 cows).

Climate, feed and management

Seasons were defined as summer (March to June; hot and dry), rainy (July to October; hot and humid), and winter (November to February; cool and dry). Feeding was based on fresh grass (direct grazing or cut and carry; 30–40 kg/d) and supplemented with concentrate (12–15 kg/d). Rice straw, crop residues, and agricultural by-products (cassava pulp, brewer grains, soybean meal, corn cobs) were also fed during the dry season because of the limited availability of fresh grasses. A mineral supplement was available throughout the year. Cows were kept in open barns and milked twice a day (0400 h–0600 h, and 1500 h–1700 h). Cows were bred all year round using artificial insemination. Sires were chosen based on semen availability, followed by their genetic ability for high milk yield and early age at first calving. Reproductive and health problems were the most important reasons for culling.

Variance components and genetic parameters

Variance and covariance components were estimated using an average information restricted maximum likelihood procedure. Estimates of variance components were used to estimate heritability for AFC and MY, and to estimate genetic and phenotypic correlations between these traits. The 2-trait mixed animal model used to estimate variance components included the fixed effects of contemporary group (herd-year-season) effects, difference between Other Breeds and Holstein breed effects (as a function of the fraction of Other Breeds), and heterosis (as a function of heterozygosity, that is, the probability of having alleles of different breeds in 1 locus over all loci). Random effects were animal and residual. The model in matrix notation is shown in Equation (1):

$$y = X\boldsymbol{b} + Z\boldsymbol{a} + \boldsymbol{e} \tag{1}$$

where $\boldsymbol{y}$ represents the vector of AFC and MY records, $\boldsymbol{b}$ is the vector of contemporary group (herd-year-season) effects, Other Breeds minus Holstein breed effects, and heterosis effects, $\boldsymbol{a}$ is the vector of random animal additive genetic effects, $\boldsymbol{e}$ is the vector of residuals and the incidence matrices $\boldsymbol{X}$ and $\boldsymbol{Z}$ relate records to environmental and genetic fixed effects in vector $\boldsymbol{b}$ and to random additive genetic effects in vector $\boldsymbol{a}$, respectively.

The variance-covariance matrix among random effects in the 2-trait mixed animal model is shown in Equation (2):

$$var \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G_0 & 0 \\ 0 & I \otimes R_0 \end{bmatrix} \tag{2}$$

where A is the additive genetic relationship matrix among animals, I is the identity matrix, G_0 is the 2×2 matrix of additive genetic variances and covariances between AFC and MY, and R_0 is the matrix of residual variances and covariances between AFC and MY.

Additive genetic predictions were computed for all cows, sires and dams in the population using the 2-trait mixed animal model. The estimated breeding value (EBV) for AFC and MY was computed for each animal as the sum of its genetic group solution and its predicted random additive genetic effect, where the genetic group solution was equal to the product of the fraction of Other Breeds in the animal times the estimate of the difference between Other Breeds and Holstein breed effects.

Phenotypic and genetic trends

Linear regression coefficients of mean EBV and mean phenotypic values for AFC and MY on calving years were computed to assess genetic trends and phenotypic trends, respectively. The REG procedure of SAS (Statistical Analysis System (SAS), 2004) was used to estimate linear regression coefficients of the mean EBV and mean phenotypic values on calving year. Mean EBV of daughters from IH and TH sires were plotted against year to visualize genetic trends over time. In addition, the phenotypic means for AFC and MY for each calving year were plotted to envisage phenotypic trends across calving year.

Results and discussion

General performance

The arithmetic mean (SD) was 30.85 mth (5.57 mth) for AFC and 4306.89 kg (1083.47 kg) for MY. The AFC was in the range 17–50 mth, and MY fluctuated between 1500 kg and 8896 kg. Least squares means across herd-year-season subclasses ranged from 17 mth to 51 mth for AFC, and from 1758 kg to 9057 kg for MY. These ranges for AFC and MY were similar to previous ranges reported for the Thai multibreed dairy population (Koonawootrittriron et al., 2006; Jattawa et al., 2012).

The wide range of averages for AFC and MY across herd-year-seasons stressed again the need to account for these effects in the genetic evaluation model to prevent biases associated with diverse environmental conditions and management strategies provided by individual farmers across contemporary groups. Most dairy farms in Thailand and probably other tropical countries (Rhone et al., 2008; Yeamkong et al., 2010; Gebreyohannes et al., 2013) are small (less than 10 milking cows) and generally have limited land area and insufficient resources to provide high quality feeding and management conditions at critical times relative to those of medium (11–20 milking cows) and large size farms (more than 20 milking cows).

Holstein breed effects

The estimate and SE of the difference between Other breeds and Holstein breed effects was 0.836 ± 1.412 mth for AFC,

and −130.4 ± 243.8 kg for MY. These differences between Other breeds and Holstein indicated that under hot and humid tropical conditions, heifers with lower Holstein fractions took longer to calve for the first time and produced less milk than heifers with higher Holstein fractions.

These results confirmed previous differences between Other Breeds and Holstein that had been reported for Thai multibreed dairy populations (Dairy Farming Promotion Organization, 2009; Koonawootrittriron et al., 2009). A slow growth rate and the poor general appearance of heifers with large fractions of Other breeds may have delayed the decision to mate these heifers and contributed to their longer AFC. Holstein is the primary dairy breed that has been used to improve milk yield in Thailand through crossbreeding and upgrading from local breeds to Holstein (Koonawootrittriron et al., 2009). As expected, heifers with larger fractions of Holstein gave more milk than Other Breeds. For every increase in one percentage point Holstein there was, on average, an increase of 1.30 kg in MY. This increase was lower than the 10.02 kg increase per one Holstein percentage increase in a Brazilian dairy population (Martínez et al., 1988), but close to the other Thai multibreed dairy populations per one Holstein percentage point increase reported by Jattawa et al. (2012) of 1.72 kg of MY and by Ritsawai et al. (2014) of 0.39 kg of MY.

Heterosis effects

The estimate of heterosis was −0.001 ± 0.009 mth for AFC, and −0.323 ± 1.574 kg for MY. These estimates indicated that heterosis had virtually no effect on either AFC or MY in this population. A negative and non-significant heterosis estimate for AFC was also reported for a multibreed cattle population in Colombia (−26.0 ± 21.0 d, P = .18, Vergara et al., 2009). The value of heterosis for AFC here was also lower than the heterosis of −60 d obtained in a Brazilian Zebu-Holstein multibreed population (Martínez et al., 1988). Heterosis for MY in the current study was substantially lower than values obtained previously in tropical regions (Koonawootrittriron et al., 2009; Gebreyohannes et al., 2013). Koonawootrittriron et al. (2009) reported an estimate of heterosis for MY of 412.1 ± 481.5 kg (P = .26) in a Holstein-Other breeds multibreed dairy cattle population in Central Thailand, whereas Gebreyohannes et al. (2013) obtained heterosis of 489 ± 44.9 kg in an Ethiopian multibreed population composed of Friesian, Jersey, Simmental, Boran and Horro breeds.

The heterosis effects in the current study were the result of crossbreeding and upgrading between animals of a variety of breed compositions. This occurred because of the multibreed nature of the Thai dairy cattle population where purebred and crossbred males and females were used as parents. An animal in this population could have fractions from two to more than seven distinct breeds (Koonawootrittriron et al., 2002; Ritsawai et al., 2014), and fractions from different breeds could have positive or negative interactions with each other. With the exception of Holstein, all breeds were included into a single Other breeds group because of low numbers of records per specific breed group combination. Consequently, heterosis estimates in the current study accounted for interactions between alleles from any of the breeds included in Other breeds and Holstein alleles at one locus over all loci.

Variance components, heritabilities, and genetic and phenotypic correlations

Variance components for AFC and MY are shown in Table 1. The additive genetic variance (the estimate ± SE) was 2.98 ± 0.73 mth^2 for AFC, and 93,309 ± 22,982 kg^2 for MY. The residual variance was 16.99 ± 0.72 mth^2 for AFC and 543,638 ± 22,765 kg^2 for MY. These variance component estimates were used to compute heritabilities

Table 1
Variance components for age at first calving (AFC) and accumulated 305 d milk yield (MY).

Trait	Variance component		
	Additive genetic variance	Residual variance	Phenotypic variance
AFC (mth^2)	2.98 ± 0.73[a]	16.99 ± 0.72	19.97 ± 0.42
MY (kg^2)	93,309 ± 22,982	543,638 ± 22,764	636,900 ± 13,290

[a] the estimate ± SE.

for AFC and MY as well as genetic and phenotypic correlations between AFC and MY (Table 2). Heritability estimates were 0.149 ± 0.036 for AFC, and 0.147 ± 0.035 for MY. These low heritability estimates indicated that genetic improvement for these traits would be slow in this population, perhaps due to inaccurate phenotypic and pedigree information and the small dataset available for this research. Thus, accurate phenotypic and pedigree data collection should be emphasized in future years to increase genetic prediction accuracies to improve the identification of superior animals and thus increase the heritabilities and genetic progress for these traits.

The heritability estimate for AFC in the current study was similar to that obtained in previous studies involving multibreed populations in Thailand (0.16 ± 0.10; Koonawootrittriron et al., 2006) and Colombia (0.15 ± 0.13; Vergara et al., 2009), but higher than in US Holstein (0.05 ± 0.03; Seykora and McDaniel, 1983).

Vergara et al. (2009) suggested that AFC was highly influenced by environmental conditions and that nutrition and management would need to be improved for animals to be able to express their genetic potential. This may also be the case in the Thai population in the current study. Perhaps an increase in the level of nutrition, management and health care prior to insemination in the Thai dairy population may help more accurately identify heifers with lower EBV for AFC. Increasing the accuracy of AFC data collection will also be needed to improve the effectiveness of genetic selection (Koonawootrittriron et al., 2006). The heritability estimate for MY here was lower than estimates for Thai Holstein-Other breeds multibreed cattle in Thailand (0.46 ± 0.19, Koonawootrittriron et al., 2003; 0.35 ± 0.03, König et al., 2005; 0.43 ± 0.24, Seangjun et al., 2009; 0.34 ± 0.08, Sarakul et al., 2011; 0.24 ± 0.12, Endris et al., 2013), and for Holstein in temperate countries (Canada: 0.30 ± 0.02, Lee, 1976; 0.22 ± 0.03, Hoque and Hodges, 1980; US: 0.27 ± 0.05, Seykora and McDaniel, 1983). Heritability is specific to the population and depends on the method of estimation. The low heritability estimate for MY found in this population related to the small proportion of trait variance due to additive genetic factors. Milk production of cows in the current study largely responded to Thai tropical environmental conditions that have large variations in temperature and humidity (Thai Meteorological Department, 2010), rather than genetic differences among themselves (Table 1).

Close-to-zero genetic (−0.083 ± 0.175) and phenotypic correlations (0.056 ± 0.015) were estimated between AFC and MY. These correlations indicated that AFC and MY were nearly independent both genetically and phenotypically in this Thai population. The genetic correlation between AFC and MY estimated here was lower than the values obtained in US Holstein (−0.21 ± 0.14, Seykora and McDaniel, 1983; −0.44 ± 0.02, Ruiz-Sánchez et al., 2007), Kenyan

Table 2
Heritabilities (diagonal), genetic correlation (above diagonal), phenotypic correlation (below diagonal) for age at first calving (AFC) and accumulated 305 d milk yield (MY).

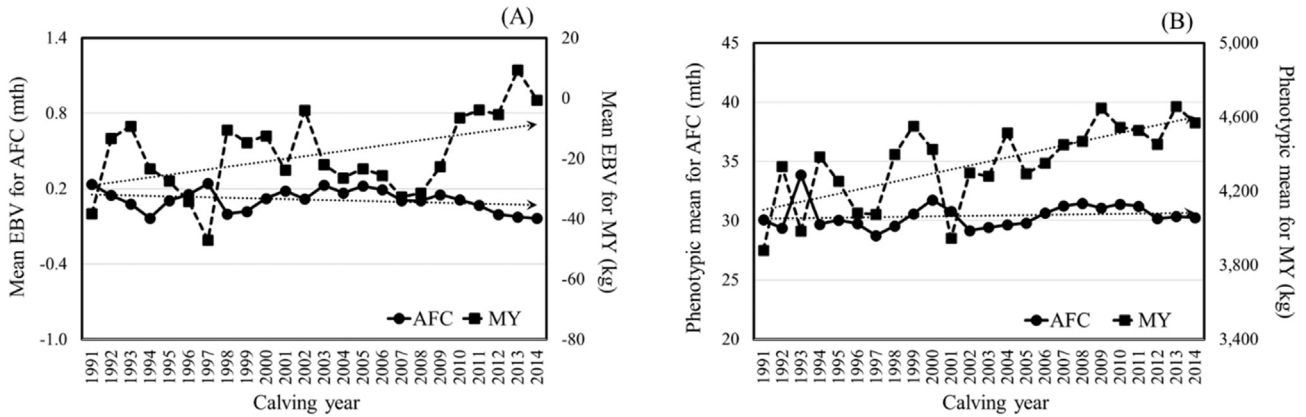| Trait	AFC	MY
AFC	0.149 ± 0.036[a]	−0.083 ± 0.175
MY	0.056 ± 0.015	0.147 ± 0.035

[a] the estimate ± SE.

Fig. 1. (A) Genetic trends and (B) phenotypic trends for age at first calving (AFC) and accumulated 305 d milk yield (MY).

Holstein (0.54 ± 0.12, Ojango and Pollott, 2001) and Iranian Holstein (0.36 ± 0.06, Hossein-Zadeh, 2011). The near zero genetic correlation obtained here suggested that selection to improve MY could be accomplished independently from selection for AFC.

Genetic and phenotypic trends

The yearly EBV and phenotypic means for AFC and MY over calving years are shown in Fig. 1. The EBV means for AFC ranged from −0.04 mth (2014) to 0.24 mth (1997) and those for MY ranged from −47.05 kg (1997) to 9.33 kg (2013). Phenotypic means ranged from 33.87 mth (1993) to 28.75 mth (1997) for AFC, and from 3880.04 kg (1991) to 4658.06 kg (2013) for MY. The regression of yearly EBV means on calving year was near zero and negative for AFC (−0.008 ± 0.001 mth/yr, $p < .001$) and low and positive for MY (1.529 ± 0.219 kg/yr, $p < .001$). However, near zero and positive regression coefficients of phenotypic yearly means on calving year existed for AFC (0.030 ± 0.010 mth/yr, $p = .002$) and it was low and positive for MY (21.334 ± 1.840 kg/yr, $p < .001$).

Vergara et al. (2009) reported a negative genetic trend for AFC (−6.26 ± 1.29 d/yr, $p < .001$) in a Colombian multibreed cattle population. Similarly, a negative genetic trend for AFC was obtained for Holstein cattle in the US (−0.34 ± 0.00 mth/yr, Hare et al., 2006). A decrease in yearly EBV means for AFC might be related to the dairy producers paying more attention to the selection of heifers that are ready to be mated at a younger age, and sires having a low EBV for AFC.

The positive MY genetic trends for cows and dams in previous studies with Thai dairy populations were 6.5 ± 2.1 kg/yr for cows and 17.7 ± 2.0 kg/yr for dams (Koonawootrittriron et al., 2009), and 0.29 ± 1.02 kg/yr for cows and 1.44 ± 0.91 kg/yr for dams (Sarakul et al., 2011). Similarly, the Department of Livestock Development (2004) reported that the genetic trend for MY in another Thai population was 3.3 kg per year. These MY genetic trends were similar to Holstein populations in some temperate countries (Egypt: 2.20 ± 0.93, Abou-Bakr, 2009; Turkey: 3.73 ± 4.07, Katok and Yanar, 2012), but lower than in the US (32 kg, Powell et al., 1980; 42.7 kg, Aguilar et al., 2010).

Yearly EBV means for AFC and MY over calving years for daughters of IH and TH sires are shown in Fig. 2. Genetic trends for AFC were extremely low and negative for daughters of IH sires (−0.003 ± 0.002 mth/yr, $p = .084$) and TH sires (−0.014 ± 0.002 mth/yr, $p < .001$). Conversely, genetic trends for MY were low and positive for daughters of IH sires (0.585 ± 0.326 kg/yr, $p = .073$) and TH sires (4.091 ± 0.294 kg/yr, $p < .001$).

The steeper upward trend in mean yearly EBV values of daughters from TH than of daughters from IH sires indicated that TH sires had a wider range of EBV for MY than IH sires. The mean EBV of daughters of IH sires was higher until 2013, but in 2014 the mean EBV value for MY of daughters surpassed that of daughters of TH sires. This may be an indication that the genetic evaluation program implemented in this population was able to successfully identify sires with the best combination of genes for production under Thai tropical conditions, and most of these sires belonged to the TH population.

The mean AFC yearly EBV for daughters of TH and IH sires showed a small advantage for daughters of TH sires across years. This suggested that TH sires may have an advantage over IH sires in
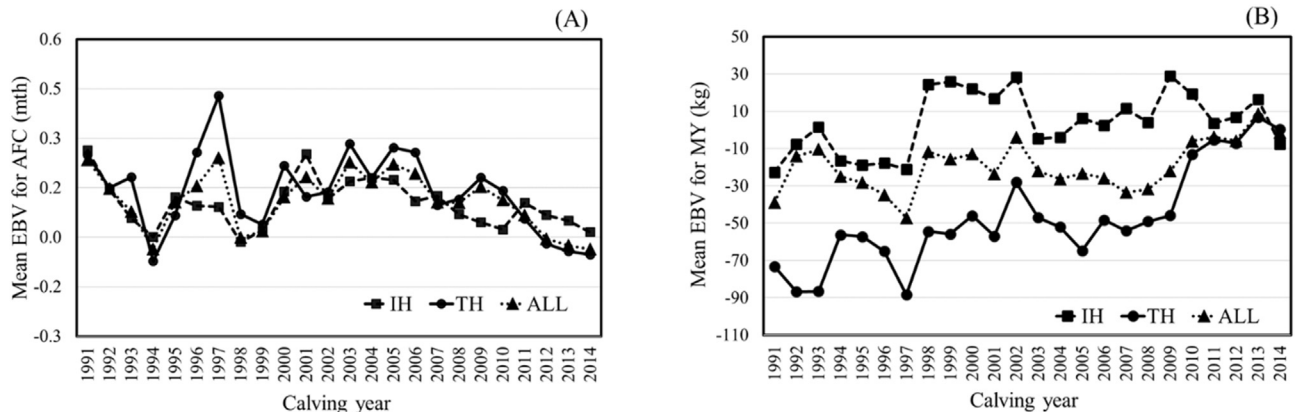

Fig. 2. Genetic trends for cows from imported sires (IH), cows from Thai sires (TH), and all cows (ALL): (A) age at first calving (AFC); (B) accumulated 305 d milk yield (MY).

terms of the ability of their daughters to become pregnant and calve earlier in their first calving. This may also be an indication that daughters of TH sires were better adapted than daughters of IH sires to the tropical climate conditions and the nutritional and management programs in Thai dairy farms, and this superior adaptability allowed them to perform closer to their genetic reproductive potential.

The heritability estimates of AFC and MY were low indicating that genetic progress for these traits would be slow in this population. The near zero genetic correlation between AFC and MY suggested that selection for high milk yield would be largely independent from selection for early age at first calving. The genetic trends for AFC and MY were in the desired direction (decreasing for AFC and increasing for MY with time). Daughters of TH sires showed a small advantage over daughters of IH sires over the duration of the study in terms of their ability to become pregnant and calve earlier in their first calving, suggesting superior adaptability and reproductive ability under the tropical conditions and associated nutrition and management on Thai dairy farms.

Conflict of interest

The authors declare that they do not have any conflicts of interest.

Acknowledgements

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