

**Genetic evaluations for fertility traits in dairy crossbred
under Thailand condition**

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タイの環境下における乳用交雑種の 繁殖形質に関する遺伝評価

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Abbreviations

A	AFC	age at first calving
	AFS	age at first service
	AG	additive genetic
	AI	artificial insemination
	AM	animal model
B	BBLP	Bureau of Biotechnology in Livestock Production
	BCS	body condition scores
	BLUP	Best Linear Unbiased Prediction
C	CI	calving interval
	CR	conception rate
D	DFLS	days between first and last service
	DHHU	Dairy Herd Health Unit
	DIM	days in milk or day after calving
	DLD	Department of Livestock Development
	DO	days open
	DPO	Dairy Promotion Organization
	DTFH	days from calving to first heat
	DTFS	days from calving to first service
E	EBV	estimated breeding value
F	FAO	Food and Agriculture Organization of the United Nations
	FMD	foot and mouth disease
	FSC	conception at first service
G	GOF	goodness of fit

H	HF	Holstein-Friesian
L	LAM	lactation animal model
M	MOAC	Ministry of Agriculture and Cooperative
	MoU	Memoranda of Understanding
	MSE	mean squared error statistic
N	NEB	negative energy balance
	NR _x	non-return rate at x days
	NSPC	number of services per conception
P	PA	predictive ability
	PE	permanent environmental
	PRA	predicted service results of animal
	P90	pregnancy within 90 days after the first service
R	RP-THM	repeatability threshold model
	RRM	random regression model
	RR-TDM	random regression test-day model
	RR-THM	random regression threshold model
	RTD	ready to drink
S	SM	sire model
	SMP	School Milk Program
T	TD-FPR	test-day fat-to-protein ratio
	TD-MY	test-day milk yield
	TH	Tropical-Holstein
	TMR	total mixed ration
V	VWP	voluntary waiting period

Chapter I

General introduction

Demand for dairy products is rapidly growing in Asia, Africa, and Latin America, induced by urbanization and preferences for nutritious foods (Guyomard et al., 2013). Typical dairy system in these regions is based on smallholder farming in tropical environment, poor genetic potential of animals for milk, low quality feeds, high risks of epidemics, lack of technical man power for dairy industry, high environmental stresses, reproductive failure and high udder abnormalities, orthodox management practices, poor extension services and lack of commercial rations. Increase of milk production is expected to supply the demand as well as to raise income of dairy farmers. Genetic improvement of the dairy cattle, along with changing feeding practice, is shown to largely increase milk production (McDermott et al., 2010). Crossbreeding of local breeds with temperate dairy breeds, such as Holstein-Friesian (**HF**), has been recommended to achieve both high productivity and resistance to heat stress (Philipsson, 2000). However, cattle with high proportions of exotic temperate blood tend to be managed intensively. Additionally, these exotic breeds are by definition not well-adapted to the local climate, feed resources and management systems and require some level of environmental modification (such as cooling and ventilation system) to remain reasonably healthy and productive (Herath and Mohammad, 2009). As a matter of fact, the main dairy market in the tropical countries mentioned above including Thailand is ready to drink milk. Therefore, milk yield is a major trait of selection in breeding programs for the dairy cattle in such areas, leading to increasing productivity per animal.

Not different from advanced dairy raising countries, increasing incidences of health and fertility problems in dairy cattle was reported as milk yield increased (De Vries and Veerkamp, 2000; Oikonomou et al., 2008) due to the antagonistic genetic relationship between milk production traits and fertility traits (Roxström et al., 2001; VanRaden et al., 2004; Liu et al., 2008). These concerns have been confirmed by work on reproductive efficiency carried out by several authors (e.g., Bagnato and

Oltenacu, 1993; Hoekstra et al., 1994; Philipsson et al., 1994; Pösö and Mäntysaari, 1996; Pryce et al., 1997; Collard et al., 2000; Lucy, 2001; VanRaden et al., 2004). Current breeding programs tend to combine both productive and functional aspects to select high-producing and robust cows. In support of this global objective, the interest in functional traits such as fertility is increasing because of its relationship with economically important traits that take an increasing weight in modern breeding objectives. It also impacts on herd productivity and the overall profitability in dairy farming.

Fertility is one of the most economically important traits for the dairy cattle industry. It is a complex trait with a low heritability which can be defined as the ability to puberty, the ability to return to cycling after calving within an acceptable period, the ability to conceive following insemination and maintain a pregnancy, and the combination of these abilities (Jorjani, 2007; Abe et al., 2009). It greatly influenced by many factors, which include milk production, heat stress (seasons), management (voluntary waiting period, synchronization, and service protocols), nutrition, cow age, and genetic background as well as others (Huang, 2009). Poorer fertility results in higher inseminations, labor and veterinary cost, decrease of milk production (fewer progeny born), slippage in dairy pattern, less intensive selection and increase replacement rate due to involuntary culling (Hodel et al., 1995; Roche, 2006). In several countries, impaired reproductive performance is the predominant reason for culling of dairy cows.

Even through heritability of fertility traits is low depending on the definition of the trait and the methodology used for analysis, ranging from 1 to 10% as reported in many studies (Weller and Ron, 1992; Muir et al., 2004; Weigel, 2004; González-Recio and Alenda, 2005; Jamrozik et al., 2005; González-Recio et al., 2006a; Kuhn et al., 2006; Estrada-León et al., 2008) which genetic response for these traits is expected to be slow. The additive genetic variation for these traits was deemed to be sufficient such that selection for fertility could be effective. Therefore selection for fertility traits is worth considering (Weller and Ron, 1992; Boichard and Manfredi, 1994; Weigel and Rekaya, 2000; Makgahlela et al., 2007) due to it can be also transmitted through the next generation. Accurate genetic

evaluations are needed to identify the best animals in the population. When better methods are applied to predict breeding values, higher genetic response can be expected.

Genetic evaluation of fertility traits are widely considered in different manners as national genetic evaluation programs across countries (INTERBULL, 2012) (see Table 1-1), but an evaluation for these traits in Thailand is not yet available. Some countries evaluate only one of the traits whereas other countries combine different fertility traits into a selection index (Weigel and Rekaya, 2000; VanRaden et al., 2004). Therefore, including the fertility in the breeding goal other than milk production trait in Thailand is considered to be necessary to optimize the result of genetic improvement of dairy cattle or stopping its downward genetic trend of fertility traits.

Aim of dissertation

The overall objective of this dissertation was to study the genetic evaluation of female fertility traits of Thai dairy cattle by applying appropriate methodology and introduce to a Thailand national genetic evaluation. The more specific objectives were outlined in the following:

1. to estimate genetic parameters for various fertility traits on Thai dairy heifers and cows in a smallholder system under tropical conditions using data sets from the Thailand national recording scheme;
2. to estimate genetic parameters for fertility traits, test-day milk yield (TD-MY) and test-day fat-to-protein ratio (TD-FPR) as well as their relationship during different stages of lactation using random regression models (RRM) on Thai dairy cows in a smallholder system under tropical condition; and
3. to estimate genetic parameters and breeding values for conception rates (CR) of Thai dairy cows using the repeatability threshold model (RP-THM) and random regression threshold models (RR-THM) and compare covariance functions for modeling the additive genetic (AG) and permanent environmental (PE) effects in the RR-THM;

Table 1-1. Descriptions of national evaluation system for fertility traits

Country	Breed(s)¹	Traits definition and units²	Genetic evaluation model³
Australia (AU)	HOL, JER, GUE, RDC	CI, LL, DTFS, NRR25, PR	MT-BLUP-AM
Belgium (BE) (Walloon Region)	HOL	PR, DO	ST- BLUP-AM
Canada (CA)	HOL, AYR, BSW, GUE, JER	NRR56h, DTFS, NRR56c, DFLS,DO	MT-BLUP-AM
Czech Republic (CZ)	HOL	CR	ST-BLUP-AM
Denmark (DK), Finland (FI), Sweden (SE)	HOL, JER, RDC	NRR56h, DTFS, NRR56c, DFLS,DO	MT-RP-BLUP-SM
France (FR)	HOL, BSW, RED	CR, DTFS,	CR: ST-RP-BLUP-AM, MT-BLUP-AM DTFS: ST-RP-BLUP-AM
Germany (DE), Austria (AT), Luxembourg (LU)	HOL, JER, RDC	NRR56h (%), DTFS, DFLSh, NRR56c (%), DFLSc, DO	MT-ML-RP-BLUP-AM
United Kingdom (UK)	HOL, AYR (RDC), BSW, JER, GUE	NRR56c, CI	MT-BLUP-AM includes TD-MY100, DTFS, NSPC,BCS
Ireland (IE)	HOL, JER, RDC	DTFS, NSPC, CI	MT-BLUP-AM
Israel (IL)	HOL	CR	ST-BLUP-AM
Italy (IT)	HOL BSW	CI, DTFS, NRR56 (%), CI, DTFS, DO, CR	MT-BLUP-AM ST-BLUP-AM
Netherlands (NL) Including Belgium (Flemish region)	All breeds	DTFS, NRR56 (binary trait), DFLS, CI, M305, F305, P305, BCS	MT-BLUP-AM
New Zealand (NZ)	HOL, BSW, GUE, JER, RDC	PM21, CR42	MT-ML-BLUP-AM
Norway (NO)	NRF	NRR56h, NRR56c1, NRR56c2-3, DTFSc1, DTFSc2-3, CI	MT-BLUP-AM Trait sets: (NRR56h, NRR56c1, NRR56c2-3); (DTFSc1, DTFSc2-3); CI
Poland (PL)	PHOL	NRR56h, DTFS, NRR56c, DO	MT-BLUP-AM
South Africa (ZA)	HOL, AYR, GUE, JER	CI1, CI2, CI3	MT-ML-BLUP-AM HOL: with Milk yield, Rump height, Angularity and Rear udder height JER: with Milk yield, Rump height, Angularity and Rear udder height GUE: with Milk yield

Table 1-1 (Continued). Descriptions of national evaluation system for fertility traits

Country	Breed(s) ¹	Traits definition and units ²	Genetic evaluation model ³
Spain (ES)	HOL	DO	MT-BLUP-AM with Milk in 120 Angularity and BCS
Switzerland (SZ)	HOL, BSW, RHOL	NRR56c (%), NRR56c (binary), DTFS	MT-BLUP-AM HOL:NRR56 (%), DTFS BSW:NRR56c (binary), DTFS RHOL: NRR56 (%), DTFS
United States of America (US)	HOL (B&W, R&W), AYR (RDC), BSW, GUE, JER, MSH (RDC)	HCR, CFI, CCR, DPR	MT-MB-BLUP-AM

Source: INTERBULL (2012)

¹**Breed:** AYR= Ayrshire; BSW= Brown Swiss; B&W=Black and White; GUE= Guernsey; HOL= Holstein; JER= Jersey; MSH= Dairy Shorthorn; NRF= Norwegian Red; PHOL= Polish Holstein; RDC= Red Dairy Cattle; RED= Pie rouge des Plaines; RHOL= Red Holstein; R&W= Red and White

²**Traits definition:** BCS= Body condition score; CCR: Lactating cow's ability to conceive; CFI: Lactating cow's ability to start cycling; CI =Calving interval; CR = Conception rate; CR42 = Success/failure for re-calving in the first 42 days of the herd's calving period; DFLSc =Days between first insemination and conception, cow; DFLSh =Days between first insemination and conception, heifer; DO=Days open; DPR: Lactating cow's interval calving-conception (percentage of non-pregnant cows that become pregnant during each 21-day period)-DO; DTFS= Days from calving to first service; DTFS1= Days from calving to first service in first parity; DTFS2-3= Days from calving to first service in second to third parity; F305= 305-d fat yield; HCR: Maiden heifer's ability to conceive (percentage of inseminated heifers that become pregnant at each service); LL=Lactation length; M305= 305-d milk yield; NRR25 = Twenty-five-day first service non-return rate; NRR56h= Non return rate at 56 days at first insemination, heifer; NRR56c = Non return rate at 56 days at first insemination, cow; NRR56c1 = Non return rate at 56 days at first insemination in first parity; NRR56c2-3 = Non return rate at 56 days at first insemination in second to third parity; P305= 305-d protein yield; PM21= Success/failure at being presented for mating in the first 21 days of the herd's mating period; PR= Pregnancy rate

³**Genetic evaluation model:** ST- BLUP-AM= Single trait animal model; ST-RP-BLUP-AM= Single trait repeatability animal model; MT-BLUP-AM= Multiple traits animal model; MT-MB-BLUP-AM= Multiple traits multi-breed animal model; MT-ML-BLUP-AM= Multiple traits multiple lactation animal model; MT-RP-BLUP-SM= Multiple traits repeatability sire model

Dissertation organization

The dissertation is comprised of six chapters. The chapter I and II contain a general introduction and review of literature for the whole dissertation, respectively. Chapter III to V are written as a separated papers that each focus on a particular aspect of the estimation of (co)variance components and related parameters of Thai dairy cattle for a selected female fertility traits, milk production trait and energy balance trait. Chapter III provides genetic parameters for various fertility traits on heifers and cows in a smallholder system under a tropical condition. Chapter IV gives genetic parameters for fertility traits, test-day milk yield and test-day fat-to-protein ratio as well as their relationship during different stages of lactation using random regression models in tropical smallholder dairy farms. Chapter V gives genetic parameters and breeding values for conception rate using repeatability and random regression threshold models and provides a comparison different random coefficient functions for modeling the additive genetic and permanent environmental effects in a random regression threshold model. Chapter VI gives the general conclusions and recommendations from the previous three chapters.

Chapter II

Literature reviews

1. Dairy industry in Thailand

Thailand is located between 5° 35' to 20° 30' North latitude and 97° 20' to 105° 40' East longitude and is situated in the middle of mainland Southeast Asia, neighboring with Myanmar (northern and western), Laos (eastern) and Malaysia (southern). There are a rough geographical area of 514,000 sq. km (200,000 sq. miles). This makes Thailand roughly equivalent in size to France or Texas. Annual mean temperatures typically range from 24 to 30 °C (75 to 86 °F), relative humidity ranges from 66 to 81% and annual rainfall ranges from 777 to 5,111 mm. There are three seasons: summer (March-June), rainy season (July-October) and winter (November-February) (Meteorological Department, 2013) and can best be described as tropical and humid for the majority of the country during most of the year. During the summer, the temperature rises dramatically in the second half of March, well over 40 °C in some areas by mid-April.

The Ministry of Agriculture and Cooperative (**MOAC**) is responsible for livestock development. The Department of Livestock Development (**DLD**), government organization and Dairy Promotion organization (**DPO**), semi-government organization are the two of organization under this ministry and they are the main state agency having responsibility for providing technical services for the dairy cattle sector. These services are provided with the assistance of 77 Provincial Livestock Offices through 307 District Livestock Offices. Milk and milk product committee (Milk Board) is under the purview of MOAC and is involved considering strategies of raw milk quality, quantity and the quota of the imported skim milk powder.

The structure of the Thailand dairy milk chain does not deviate to a great extent from any dairy milk chain around the world, with the exception of the large volume of imported dairy ingredients to supplement local milk production. In general, the majority of locally produced milk is collected by milk

collection co-operatives and subsequently sold to processors. Very few milk collection co-operatives also have processing activities. Dairy processors use both local raw milk and imported dairy ingredients as inputs in their manufacturing process. Their products are sold to retail and foodservice customers before they reach the end consumer.

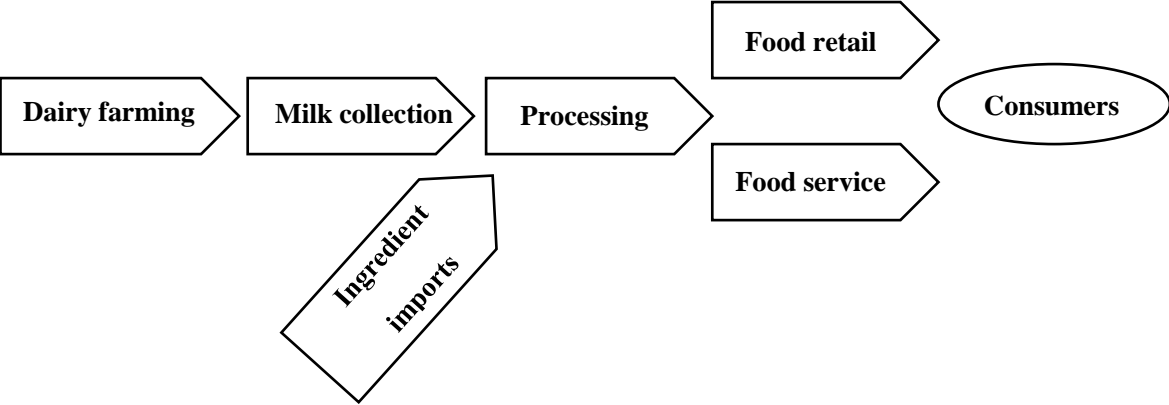


Figure 2-1. Thailand dairy milk chain

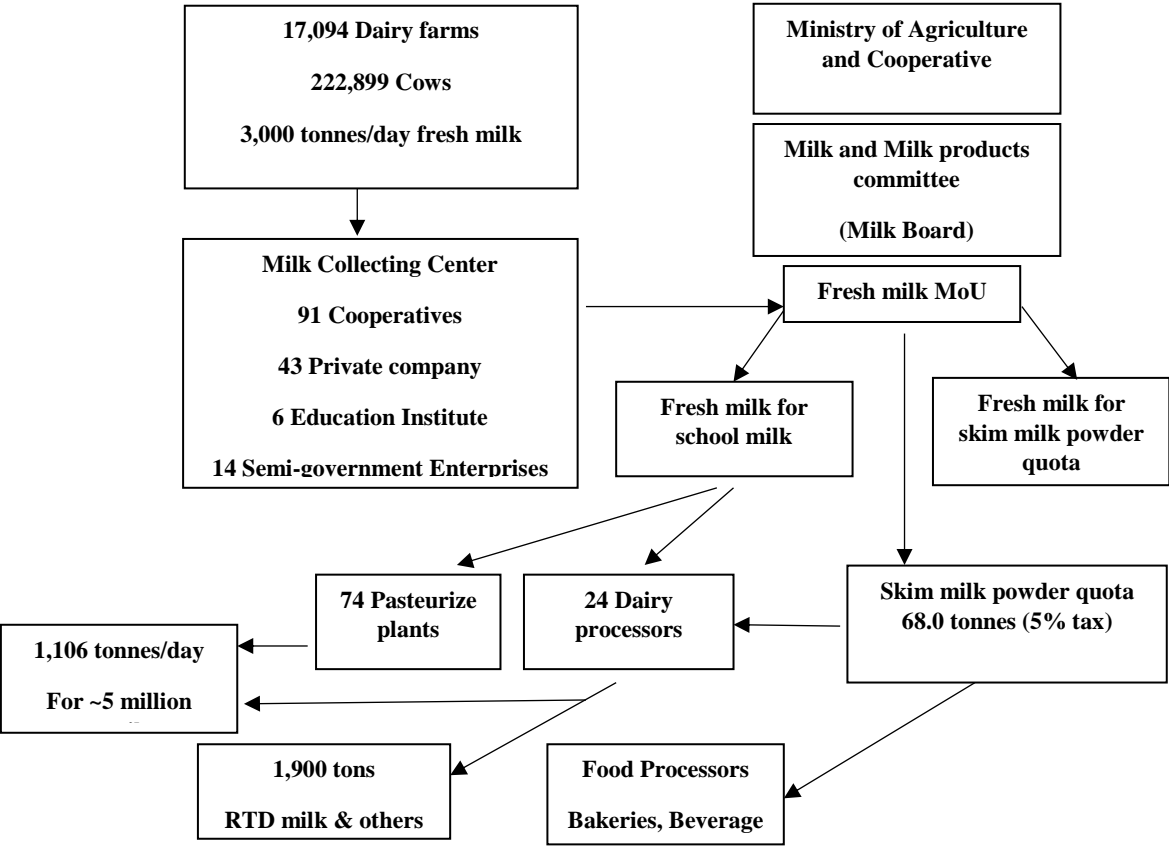


Figure 2-2. Overall Thailand dairy industry

1.1 Dairy farming

Dairy population

The total dairy cattle population in Thailand reported in 2013 were 512,205 animals which concluded of 500,418 female animals with 229,899 milking cows in 17,094 farms (Department of Livestock Development, 2014a) and raw milk production was around 1,067,452 tonnes per year or 3,000 tonnes per day (Office of Agricultural Economics, 2014a). The number of dairy farms decreased about 18% whereas milk production increased about 36% during 2006 to 2013. The majority of dairy farmers (80%) are small holders with the average of 30 animals per farm, including calves, heifers, and cows (Department of Livestock Development, 2014a). The raising area are scattered all over the country, 60% in the central, 20% in the north eastern, 10 % in the eastern, 8% in the northern and 2% in the southern region. Among total dairy cattle, about 356,687 animals (70 %) were registered and about 50,350 animals (10 %) have milk recording that were in database of the Bureau of Biotechnology for Livestock Production (**BBLP**), DLD and some small amount were in DPO database and private farms. The trend of dairy population size has been increasing with locally born animals by AI rather than imported.

Table 2-1. Descriptions of dairy cattle population and milk production in Thailand during 2006-2013

Year	Dairy Farm* (households)	Dairy Cattle* (animals)	Milking Cows* (animals)	Milk Production** (tonnes)
2006	20,907	412,804	310,085	803,250
2007	21,230	489,593	291,965	729,098
2008	19,214	469,937	206,680	786,186
2009	17,837	483,899	204,805	840,691
2010	19,863	529,572	225,390	911,391
2011	20,645	560,659	243,089	982,453
2012	20,624	577,841	258,030	1,022,190
2013	17,094	512,205	229,899	1,095,314

Source: *Department of Livestock Development (2014a)

**Office of Agricultural Economics (2014a)

Dairy breeds and breeding

Most of the dairy cows are crossbred of *Bos indicus*, such as Sahiwal, Brahman, and Thai Native cattle upgraded by HF. Currently, the majority of the dairy population are >75% HF blood (Department of Livestock Development, 2015). The gene fraction of HF varies widely, even within farms. Cow productivity differs around the country. The central region is considered to be more productive than the other region. Average milk yield per cow is 4,000 kg per 305-d lactation (Department of Livestock Development, 2014b), which is relatively low compared to international standards (7,500 kg in the EU; 9,800 kg in Canada; 9,500 kg in the US; 5,900 kg in Australia; 8,100 kg in Japan). To a certain extent this can be explained by the tropical weather, the use of low nutrient local grass, the improper management especially in term of culling. The cows are kept as long as they can still produce milk even the cows that have passed the peak production period of life. On specialised dairy farms with 30 cows or more, average annual milk yield per cow can be up to 5,000 kg or more. These crossbreds are relatively well adapted to local conditions and are well accepted by farmers. Purebred HF could be reared to increase the level of milk production, but the cost of production per kg of milk remains high. Milk yield of some highly selected crossbreds are as high as or higher than the average milk yield of some purebreds.

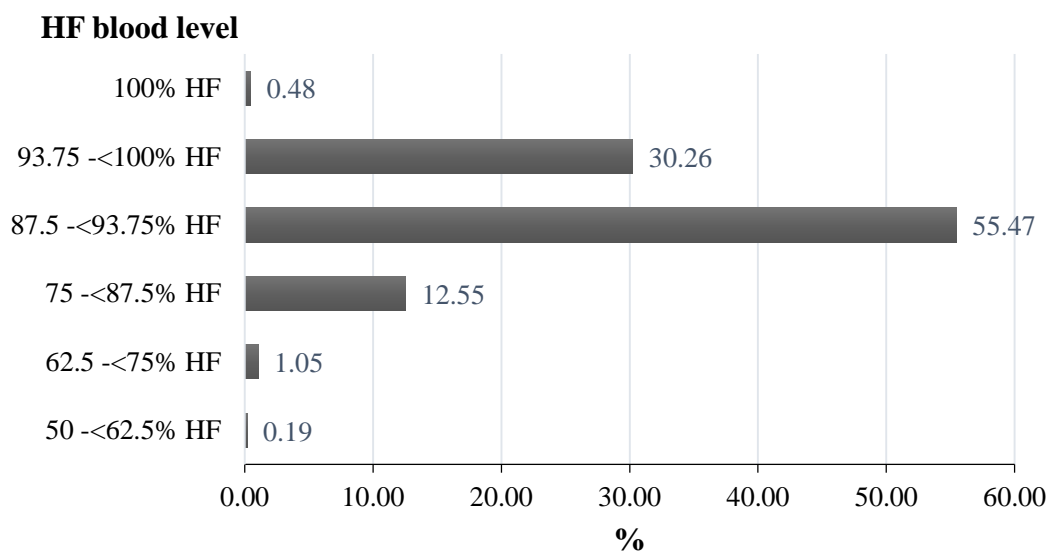


Figure 2-3. Distribution of dairy cattle population by fraction of HF blood level

Source: Department of Livestock Development (2015)

AI services by the government organization, DLD are provided for more than 90% of dairy cattle in the country and the left were serviced by the semi-government organization, DPO and the dairy cooperatives in the areas. Frozen semen used for AI services is both imported and locally produced.

Dairy feed and feeding

Dairy cattle in Thailand are usually raised in a smallholder environment with varying feed and feeding methods from region to region. Generally, the daily feed ration has been based heavily on concentrates which produced by local large private companies and distributed by the cooperative. A few farmers used maize grain meal and rice bran as supplement but its use was not systematic throughout the year. With regard to the quantity of concentrates used, many farmers provide 1 kg concentrate: 2 kg milk production per day as norm of practice. It was obvious that the nutrition required by milking cows in most farms could not be satisfied because the quality of concentrated feed might be low both in energy and protein. Relative volumes of the ingredients in the composition of the concentrate feed depend on local availability and price. In addition there was the problem of poor quality roughage used by many farmers. Poor nutrition meant that many cows took a long period to recover their body weight after calving and some of them had chronic problems of reproductive disorder after calving. Roughages commonly used consist of tropical grass, rice straw and some agro-wastes. However, large-scale dairy farms are using corn silage and/or total mixed ration (TMR) throughout the year. The use of crop residues, such as corn stover, rice straw, soybean stems or pineapple peel is very common. For routine use as cattle feed, hay is too expensive. However, shortages of roughage feeds are serious in dry or summer seasons and farmers have to buy hay or straw, or have to increase their use of commercial mixed rations.

The feeding methods of dairy farmers also vary from region to region. In the South region, where pineapple factories exist, farmers feed 30-40 kg of pineapple waste, 5-10 kg of concentrate and an additional 2-3 kg of rice straw per cow per day. In the Central and Northern region, farmers feed their cows with 5-10 kg concentrate, 20-30 kg of silage from sweet corn and pineapple waste, 3-5 kg of rice straw and 2-3 kg of waste from ethanol factories. In the Northeast region, farmers feed their cows with 5-10 kg concentrate, 20-30 kg of silage from sweet corn and pineapple waste, 4-6 kg of rice straw and 3-5 kg of waste from tapioca factories. Silage of mixed grass varieties from backyards is given in small amounts and is available only in the rainy season (Yeamkong et al., 2010).

Dairy herd health management

An increase in the number of animals would lead to an enlargement in the number of diseases and accidents involving the cattle. Currently, DLD has established a system for dairy health in the dairy dense populated areas called Dairy Herd Health Unit (**DHHU**). Veterinarian officers are assigned to local offices for dairy health services. With regular farm visit by the DHHU, the dairy farmers can get quick services when their cows have problems. The proactive policy for diseases control is done by regular diseases surveillance and vaccinations which are routinely run according to the infectious disease prevention programs such as foot and mouth disease (**FMD**), Brucellosis, Tuberculosis and para-tuberculosis. Deworming programs are also recommended. In addition to the vaccination program, DLD also encouraged farmers to participate in good animal husbandry practice standard. The standard includes bio-security and food safety. At sires' side, as the regulation, all the sires in semen production centers must be certified for infectious diseases and reproductive diseases free by the DLD.

Dairy income and cost

The average total cost of dairy farming is varied depending mainly on the number of animals raised and herd structure. The main cost component is feed (60%) followed by labour (20%), veterinary

services, equipment and other expenses (20%). About 40% to 50% of total revenues can be considered “profit including management returns”. In cost comparison exercises, the factor labour cost is often difficult to assess since the farmers’ own family labour has to be added into the equation. Since this does not take into account the return for management, we consider the 40 to 50% profit inclusive management returns.

It is possible for dairy farming to enjoy cost benefits from economies of scale. Since most of the larger dairy farms in the country are still relatively small or medium-sized by international standards, scaling up definitely offers scope for higher cost efficiency. Size strongly impacts the costs of concentrate feed. The cost of concentrate feed per kilogram of milk ranged from Thai Baht (**THB**) 12.0 on farms with around 10 cows, to THB 10.0 on farms with over 40 cows. Small farms spend much more on concentrate feed compared with the larger farms because they do not own machines for blending their own concentrate feed and so have to buy much more expensive ready-made feed. The same is also true for the relative costs of roughage since their operations are too small for growing their own materials or buying it in bulk.

1.2 Milk collection

Most dairy farms milked the cows twice a day in the morning and afternoon. Generally, no cooling devices are available in the barns except in some large commercial farms. Raw milk will be transported to the milk collection points. Most of the milk collection points are operated by co-operatives, but private companies, education institution and semi-government enterprises, DPO, are active in milk collection as well. In 2013, there are 91 co-operatives, 43 private companies, 6 education institution and 14 semi-government enterprises. Most milk collection co-operatives have other activities besides collecting and selling raw milk for their member farmers. They also provide reliable and competitively priced energy, feed, financial and services i.e. AI and veterinary services. Raw milk from collecting

centres is normally transferred to milk factories for further milk processing. A few co-operatives also have their own processing facilities.

The government guaranteed raw milk price of THB 18 per kg for factory gate price. Moreover, the reward and reduction of the price from guarantee price are applied according to the milk quality standard which is set by the milk Board. The farm gate prices are determined by turnover and business benefit of the cooperatives. As the result, the present farm gate price are around THB 16.5 to THB 17.5 per kg, depending on the quality of the milk but also on the cost level of the co-operative. All the cost of services provided by the co-operative will be included into the cost of the cooperative and used in calculation for farm gate price. However, the co-operatives also pay a dividend to their farmers at the end of business year.

Table 2-2. Description of milk price in Thailand during 2006-2013

Year	Farm Gate Price (THB/kg.)	Factory Gate Price (THB/kg.)
2006	11.50	12.50
2007	12.91	12.50/13.75/14.50
2008	14.56	14.50/18.00
2009	15.60	16.50
2010	15.43	16.50/17.00
2011	15.73	18.00
2012	16.88	18.00
2013	16.92	18.00

Source: Office of Agricultural Economics (2012a, 2013a)

1.3 Processing

In 2013, about 97% of the total milk production were supplied to the processing plants for the producing of ready to drink milk, 2.8 % was used for cheese production and the remainder were sold and distributed in local markets. There are 98 milk processing plants in Thailand, where 24 are large-scale plants and 74 plants are considered small-scale. From these 74 small-scale plants, 21 are operated by co-operatives, 19 plants are owned by educational institutions and the rest 34 plants are run by

private sector. Large-scale plants are mixture of local players like Dutch Mill, Thai Dairy Industry (TDI), Nong Pho Dairy Cooperative, DPO, the joint venture CP Meiji and multinationals like Foremost, Nestlé, and Dumex. Multinationals are driving the industry in terms of product differentiation and innovation. The environment is very competitive and innovation plays a very important role in the fight for dairy market share. Health benefits from the main research area are necessary for processors to look for opportunities to innovate.

1.4 Retail and foodservice

Dairy products reach the consumer either through retail or foodservice, i.e. restaurants and catering. The Thai retail market is currently equally divided between traditional trade and modern trade. Each of the categories accounts for approximately 50% of the overall sales volume. Wet markets and the so-called mom and pop grocery stores are categorised as traditional trade and modern trade comprises supermarkets, convenience stores, cash and carry stores, department stores and specialty stores. Sales through the modern trade category are growing at the expense of the traditional trade category. Still, for certain products like Yakult's cultured drinks, the traditional mom and pop grocery stores are still very important.

Foodservice comprises a category that is very important for dairy consumption in Thailand, the School Milk Programme (SMP) initiated in 1989 by the National Milk Drinking Campaign Board and providing children from kindergarten up to grade 4 with a ration of free milk. The Thai government's budget for 2014 includes THB 15.0 billion for the programme. Currently, 260 days a year over seven million children are allocated 200 ml. of milk daily.

The importance of the SMP is twofold. Firstly, it creates a familiarity with dairy products at a very young age. It is generally considered that the SMP has played a very important role in the increase of per capita dairy consumption in Thailand over the last decade. Secondly, processors supplying the SMP

are only allowed to use local raw milk for the pasteurised and ultra-high-temperature milk they supply to the programme.

A negative side effect of the dependence of the local industry on the SMP is that it tends to create a temporary over supply situation during school breaks when demand for school milk comes to a halt. This has recently caused industry and government representatives to call for a milk powder factory to overcome of these temporary over supply situations. This solution, however, seems like a clear case of dealing with the symptom instead of addressing the cause which is lack of competitive strength of locally produced milk.

1.5 Consumers

The daily per capita consumption of milk in Thailand is extremely lower than that of Western industrialized countries. Thailand per capita consumption is one-tenth of that in Australia and New Zealand and one-fourth of that in Japan. As mentioned earlier, 96% of milk production are used to produce ready to drink milk. Of these, 34% are processed for school milk and 61% are supplied to commercial markets. The consumption of drinking milk, as well as other milk products such as sweetened condensed milk, continuous increase steadily every year. In 2013, per capita availability of milk in Thailand is 14.5 kg (Office of agricultural economics, 2013b). Especially consumption of drinking milk, is confined almost totally to urban or peri-urban populations where marketing facilities and purchasing power exist.

Thailand still has to import milk and other milk products every year to fulfill the ever increasing demands. During year 2012-2013 Thailand expended about 7,381 million THB of valuable foreign exchange to import the milk and milk products i.e. skimmed milk, whole milk, milk for infant and other dairy products from New Zealand (42%), Australia (14%), America (12%), Netherland (8%), France (5%), Belgium (5%), Czech (3%), and others (11%) (Office of agricultural economics, 2015). The increasing demands for dairy products are attributed to high population growth rate and rapid

urbanization. The annual average import growth between 2006 and 2013 was 6.83 % as well as an increase in import values about 10.66% per year.

However, Thailand has also exported assorted types of dairy products to such neighboring countries as Cambodia (31%), Singapore (19%), Philippines (18%), Myanmar (8%), Lao (7%), Malaysia (5%), Hong Kong (4%), Indonesia (3%), Vietnam (2%) and others (3%). In 2013, the export values of dairy products was 19,826 million THB, 5 % higher than that of in 2012. Major dairy products exported are condensed milk, and sweetened condensed milk.

Table 2-3. Description of Thai dairy product trade during 2006-2013

Year	Imported		Exported		Trade Balance
	Quantity	Values	Quantity	Values	Values
2006	114,385	4,130,167	184,642	13,190,083	-9,059,916
2007	110,207	4,505,723	162,621	16,194,910	-11,689,187
2008	99,530	4,501,131	161,949	17,897,522	-13,396,391
2009	100,276	4,357,716	149,521	9,661,702	-5,303,986
2010	115,094	5,309,126	178,873	15,393,101	-10,083,975
2011	127,774	6,322,210	198,019	18,429,881	-12,107,671
2012	131,750	6,069,332	226,907	18,845,664	-12,776,332
2013	178,504	7,381,473	188,897	19,826,454	-12,444,981

Quantity: Tonnes

Values: Thousand THB

Source: Office of Agricultural Economics (2012a, 2012b, 2013b, 2014b)

2. Dairy genetic improvement in Thailand

Originally, dairy cattle are not the local animal of Southeast Asian nations which located under tropical condition (hot and humid). Cattle were raised as a source of draft power for their agricultural businesses and also for meat production. These countries have an increasing demand for dairy products due to prospering in economy and growing up urban or peri-urban populations. One of the first proposals to meet these requirements is to increase the production capacity of the dairy animals. However, the productive potentials of indigenous cattle are low compared to temperate breeds. Hence several efforts are made to increase livestock production through breeding strategies (by selection, cross-breeding or even importation of female stock) and policies that encouraged the introduction and breeding of exotic temperate breeds (Stetshwaelo and Adebambo 1992).

Genetic improvement of dairy cattle in Thailand has a very long history almost 60 years ago when artificial insemination (AI) service was established in 1956 under strategies and policies recommended by Food and Agriculture Organization of the United Nations (**FAO**). The recommendation is to improve native draft cattle by crossing them with dairy breeds would increase milk production significantly. Initially dairy cattle breed from the countries in temperate zone (i.e. Brown Swiss, Jersey, Red Dane and Holstein Friesian breed) and tropical zone (i.e. Red Sindhi and Sahiwal breed) in terms of both live

purebred dairy cattle and frozen semen were imported to cross with Thai native cattle in order to produce dairy crossbreds. Crossbreeding of local breeds with temperate dairy breeds has been recommended to achieve both high productivity and resistance to heat stress (Philipsson, 2000).

However, the upgraded dairy cattle with more than 75 % *Bos taurus* in that time were faced the problem of reproductive efficiency, disease resistance and environment tolerance. The FAO specialist have recommended that Thailand should keep the upgraded dairy cattle not more than 75 % *Bos taurus*. Therefore, in 1969 purebred HF was selected to be the predominant breed for upgrading Thai native cattle in developing and have controlled population within 75 % HF. The HF was selected to be the predominant breed because HF had larger body size and produced more milk, which were preferable characteristic for the local marketing system and socio-economic conditions of Thailand. In 1985, the first sire evaluation for milk production were computed using daughter-dam comparison (Sanpote et al., 1986).

In the meantime, different opinion on continued upgrading percentage of HF in crossbred dairy cattle had been discussed due to improved farm management and nutritional situation. As a consequence, the number of dairy crossbred has increased rapidly with multi-breeds and higher percentage of HF than 75% or close to purebred. Since then many farmers across the country have decided to get into the dairy cattle business (Sukhato and Kengvikkum, 2000).

Many researches concerning this topic have been performed. One of most promising research which was studied from fairly large database of DLD revealed that crossbred dairy cows with higher percentage of exotic blood (more than 87.5%) tended to produce more milk but needed more intensive management to remain reasonably healthy and productive. Otherwise, these animals would exhibited low resistance to diseases which led to low productivity as they could not adapt well to environment, management and feed resources (Tumwasorn, 2014).

Therefore breeding improvement of dairy cattle in Thailand emphasized on individual genetic ability (breeding value) of both male and female with HF blood level between 81.25 and 93.75. As the

consequences, the government, DLD which plays the important role in producing the suitable breed for tropical condition (hot and humid), have supported the crossbreeding policy to continue and initiated dairy cattle genetic improvement program in Thailand. The most important improvement program is the Master Bull Project which launched in 1992. The necessary facility for development such as progeny testing program, milk recording scheme and national AI recording have also been performed. Pedigree, milk and artificial insemination records have been collected in the DLD database system by officers since then.

Master Bull Project, also known as under the name “Tropical Holstein (**TH**) program” was a research and development program conducted by BBLP, DLD Thailand. The main objectives of the project were to develop new synthetic dairy cattle breed through selection and inter se mating, combining dairy production, reproduction, growth and adaptation traits. The new dairy breed is develop to suite the dairy production systems, market system, climate and environment of tropic conditions like Thailand. The breeding program was shown as follow:

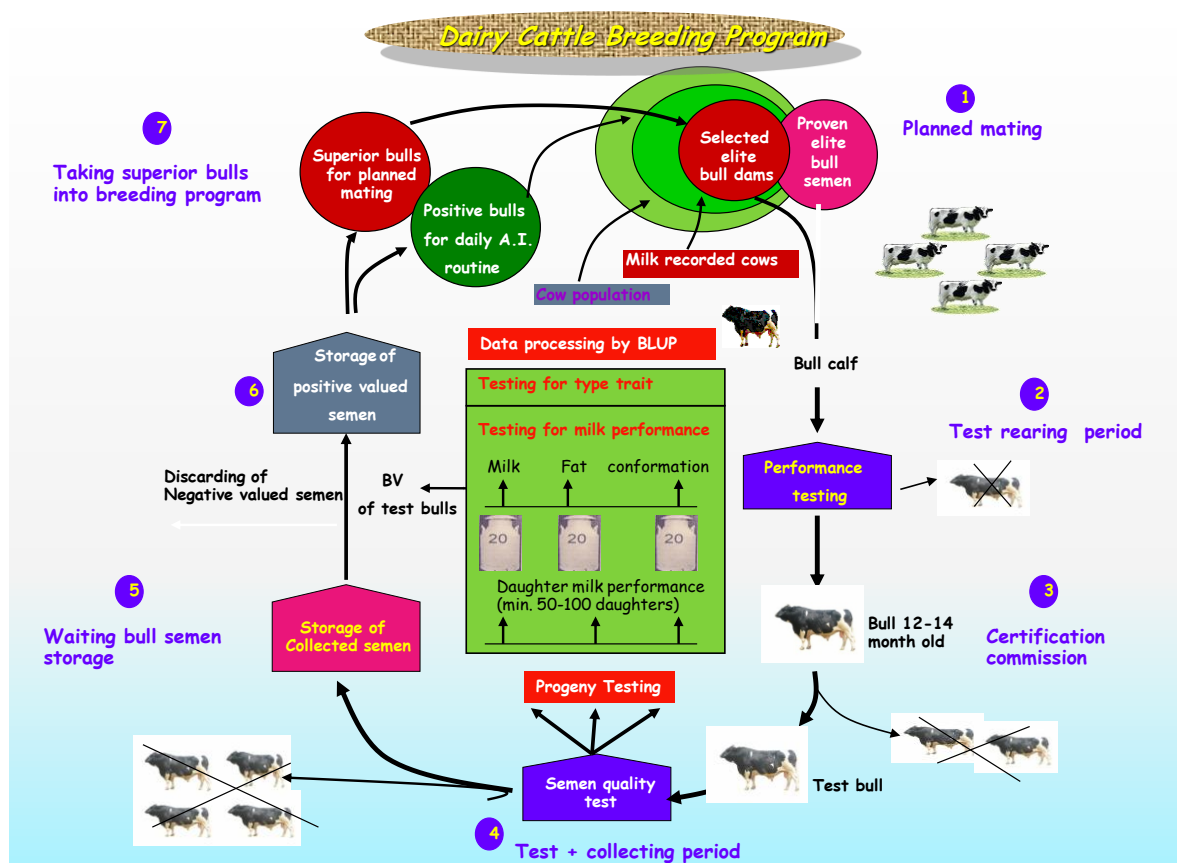


Figure 2-4. Dairy cattle breeding program in Thailand

1. 200 elite cows (bull dams) selected based on their national genetic evaluations. Bull dams selected are also limited by the blood level of HF for not higher than 87.50 % HF in order to reproduce elite crossbred bull calves. About 2/3 of these cows are planned mating to domestic elite sires (bull sires), and the remainder with elite foreign sires. The number of sires selected is around 5-10 heads each year. A large portion of foreign bull sires are USA and Canada. Linear type and udder traits which are used as criteria for herd management are also observed. Milk let-down and temperament are observed for culling poorly adapted animals.
2. About 40 bull calves, sons of elite cows that are collected from farmer by the AI research centers yearly are all move into bull testing center for performance test.
3. Up to 12-14 month old, all young bulls were selected by commissions on the basis of the growth, conformation. The ones that could not pass the criteria will be culled. The left will

be sent to semen production center and go through the semen quality test for semen collection and progeny test program.

4. The test bull's semen is distributed to many different herds nationwide for test mating. About 50-100 milk recorded daughters are produced from each test bull randomly. The daughters of test bull are expected to be milk-recorded in the herds they were born. The herd owners usually keep them in the herds at least until their first lactation is completed. In the milk recording program, milk yield is recorded once a month and a milk sample of each cow is also taken for analysis of fat and protein contents. The data used for sire evaluation and selection is collected by the officer of project.
5. During waiting for result of progeny test, the collected semen of test bull will be stored in semen bank.
6. After genetic evaluation, semen of tested bull with positive value will be selected as proven sire and continue keep in semen bank, and the negative valued semen will be discarded. Official sires and dam's evaluation takes place once a year at the Bureau of Biotechnology in Livestock Production, DLD in September. Method of genetic evaluation is multiple-traits, BLUP with an animal model. The traits for evaluation are milk yield, fat and protein percentage, fat and protein yield, fertility and type traits.
7. The proven sire will be distribute to general service and some semen from top proven sire will be sent to inseminate with elite cows in breeding program for next generation. Recently, semen from crossbred bulls has been used nationwide through artificial insemination (AI) services.

At the beginning of TH dairy cattle improvement have been developed through the national sire selection and mating program focusing on milk production (Department of Livestock Development, 2005). After that we have considered other traits which impact to profit in dairy farming such as milk

quality (fat and protein percentage), 17 type traits (stature, chest width, body depth, dairy form, rump angle, rump width, rear leg rear view, rear leg set, foot angle, rear udder height, udder width, fore udder attachment, fore udder length, udder cleft, udder depth, udder balance, and teat size) and age at first calving. However, other traits such as health and fertility traits will be considered. Currently, the estimated breeding values (**EBV**) of production traits were changed from using Lactation animal model (**LAM**) to test-day animal model with random regression (**RR-TDM**) and the other traits have used the traditional model (Department of Livestock Development, 2014b).

Through genetic selection and improved feeding and management practices, average milk yield per cow of TH is $3,927.38 \pm 1,023.18$ kg per 305-d lactation (13.16 ± 4.44 kg per day) (Department of Livestock Development, 2014b) and some cows achieve to produce over 6,000 kg per lactation. Age at first calving is 31.76 ± 5.40 months. The means (SD) and heritabilities (h^2) of dairy cattle population were shown in Table 2-4.

Table 2-4. Means (SD) and heritabilities (h^2) for milk production and fertility traits in Thai dairy cattle

Traits	Mean (SD)	h^2
305-d milk yield (kg)	3,927.38 (1,023.18)	0.49
305-d fat yield (kg)	131.24 (45.60)	0.44
305-d protein yield (kg)	155.83 (37.23)	0.49
Fat percentage (%)	3.54 (0.73)	0.29
Protein percentage (%)	3.12 (0.44)	0.44
Age at first calving (m)	31.76 (5.40)	0.12
Average milk per day (kg)	13.16 (4.44)	0.45

Source: Department of Livestock Development (2014b)

Table 2-5. Genetic trend for milk production and fertility traits during 1989-2009 in Thai dairy cattle

Year Birth	305 d- milk yield (kg)	305 d- fat yield (kg)	305 d- protein yield (kg)	% Fat	% Protein	Age at first calving (Month)
1989	-51.94	-1.50	-0.52	-0.004	-0.001	0.10
1990	-48.60	-1.59	-0.62	-0.001	-0.003	0.10
1991	-48.61	-1.25	-0.76	-0.006	-0.007	0.10

1992	-49.95	-1.24	-0.69	0.000	-0.004	0.06
1993	-60.67	-1.73	-1.02	0.002	-0.003	0.06
1994	-47.04	-1.19	-0.67	0.003	-0.003	-0.01
1995	-59.05	-1.64	-1.14	0.003	-0.004	0.07
1996	-44.56	-1.39	-1.12	0.003	-0.007	0.08
1997	-33.56	-1.02	-0.82	0.004	-0.009	0.05
1998	-6.24	0.00	-0.14	0.012	-0.005	0.02
1999	-7.36	-0.02	-0.25	0.014	-0.007	-0.06
2000	-20.02	-0.25	-0.71	0.021	-0.007	-0.07
2001	-15.26	-0.28	-0.68	0.020	-0.011	-0.08
2002	-6.05	0.38	-0.35	0.022	-0.008	-0.04
2003	-7.30	0.26	-0.41	0.022	-0.009	0.03
2004	23.54	0.96	0.47	0.022	-0.011	0.04
2005	26.29	0.57	0.57	0.017	-0.006	0.02
2006	28.36	0.73	0.68	0.019	-0.001	-0.05
2007	51.34	1.36	1.11	0.024	-0.003	-0.05
2008	94.88	2.49	2.18	0.018	-0.007	-0.09
2009	92.80	2.04	1.74	0.018	-0.016	-0.10
Average/year	6.89	0.19	0.12	0.002	-0.000	-0.21

Source: Department of Livestock Development (2014b)

Genetic trends for production and secondary traits over the last two decade are given in Table 2-5. Estimated genetic progress in the upgraded Thai dairy population were small (less than 7 kg per year) for 305-d milk yield, and near zero for milk composition traits.

Recently, the first steps have been made to incorporate biotechnological methods into the breeding program. Multiple ovulation and embryo transfers (MOET) are being used to increase the potential number of bull calves from elite dams. In the near future, a genomic evaluation program will be established at the Bureau of Biotechnology for Livestock Production, Department of Livestock Development. This new methodology may be possible to increase the rate of genetic progress by 15 to 25%.

3. Fertility trait definitions

Fertility is a composite and very complex trait. It is difficult to define, record and evaluate all the factors that influence this trait. It is useful to distinguish among traits which are affected by the cow

(female fertility), traits which are affected by the sire mated to the cow (male fertility) and traits which are affected by both. Male fertility may be called the direct effect of the sire, and female fertility the indirect effect of the sire.

For female fertility traits, there are many traits used as indicators. Generally, the traits used in measuring of fertility for genetic evaluations can be expressed in two different categories: interval and success traits (Groen et al., 1997; Weigel, 2004; Andersen-Ranberg et al., 2005). These different traits reflect the ability to puberty, the ability to return to cycling after calving, the ability to conceive following insemination, and the combination of these abilities, as well as, ability to resist reproductive disorders (Jorjani, 2007; Abe et al., 2009; Sun et al., 2009a). All measures are based on insemination records, and in many cases are based on combination with calving records. A brief overview of these traits is reported in Table 2-6.

Table 2-6. Definition of the most common fertility traits

Trait	Acronym	Variable	Definition
<i>Interval traits:</i>			
Age at first service	AFS	Continuous (d, m)	The days from birthday to the first service
Age at first calving	AFC	Continuous (d, m)	The days from birthday to the first calving
Voluntary waiting period	VWP	Continuous (d)	The number of days intentionally left by the farmer before the re-start of breeding
Days from calving to first heat	DTFH	Continuous (d)	The days from calving to the first observed heat
Days from calving to first service	DTFS	Continuous (d)	The days from calving to the first service
Days between first and last service	DFLS	Continuous (d)	The days from the first to the successful service (or the last service if no calving record is available)
Days open	DO	Continuous (d)	The days from calving to the successful service (or the last service if no calving record is available)
Calving interval	CI	Continuous (d)	The number of days between 2 consecutive calving
<i>Success traits:</i>			
Number of services per	NSPC	Count [1,2...n]	The number of services needed to

Trait	Acronym	Variable	Definition
conception			achieve pregnancy
Conception rate	CR	Binary [0/1]	The outcome of an insemination validated by calving data
Conception at first service	FSC	Binary [0/1]	The outcome of an insemination at first service
Non-return rate at x days ($x=56-60-70-90$)	NR _{x}	Binary [0/1]	The outcome of an insemination validated by the occurrence of a second breeding within x days

Interval traits

Interval or continuous traits are most commonly used for fertility evaluation, because of their simplicity and availability at a large scale. They define the distance, usually in days, between two events of relevant importance for reproduction. The traits that represent complete life cycle from heifer to cow can be defined as the following: age at first service (AFS), age at first calving (AFC), days from calving to first heat (DTFH), days from calving to start of breeding (as stated specifically by the farmer, called "*voluntary waiting period*", VWP), days from calving to first service (DTFS), days between first and last service (DFLS), Days from calving to conception (also known as "*days open*", DO), and calving interval (CI). The advantage of the interval traits is that they are fairly continuously distributed and are directly correlated to the economic and breeding goal of dairy producers. Further, their analysis can be accommodated easily using existing standard tools, particularly mixed linear model methodology and had higher heritability than the success measures. The disadvantage of this trait is it is highly dependent upon management (Norman et al., 2002). The wide range of interval traits indicates that there is no unique interval measure that is clearly preferable. However, the traits that widely used and employ in this study are the following:

Age at first service (AFS) is one of traits closely related to age at puberty that are also used as predictors of heifer fertility (Herring and Patterson, 1997). Reproductively efficient heifers reach puberty earlier, and therefore can potentially conceive earlier in the breeding season. This trait is

influenced by a number of factors, including body weight (BW), nutritional status, and, in particular, breed (Martin et al., 1992). Onset of puberty may also be influenced by feed intake parameters, by several metabolites and metabolic hormones indicative of nutritional status, and by various components of reproduction. For example, insulin, triiodothyronine, IGF-I, and leptin have all been shown to be positively correlated phenotypically with age at puberty (Hawkins et al., 2000). A trait associated with age at puberty is BW at first estrus. However, even with extensive knowledge of the physiology of puberty, age at puberty is a difficult trait to observe in field populations.

Age at first calving (AFC) is also defined although it could be argued that this trait may be more a reflection of growth and maturity rather than fertility. This trait is routinely recorded and is highly genetically correlated with age at subsequent calving and the interval between subsequent calving (Gutierrez et al., 2002). Because of these relationships, this measure is often used to evaluate heifer fertility. First calving marks the beginning of a cow's productive life. AFC is closely related to generation interval and, therefore, influences response to selection. In temperate regions, Friesians attain puberty earlier than in the tropics (8-9 months as compared to about 20 months in the tropics) and their AFC is between 17-20 months compared to about 30 months in the tropics (Zaied, 1995). Abuzaid (1999) reported that the average AFC of imported and locally born Friesian in Sudan was 24.5 ± 1.5 and 26.1 ± 3.2 months, respectively. Farm, year, season and breed of sire significantly affected AFC.

Voluntary waiting period (VWP) is the period after calving that a farmer deliberately does not inseminate the cow. The VWP represents the first portion of the calving interval. The duration of this period is partly a management decision, varying from 40 to 70 days on average. Part of its duration is based on the physiological need for the reproductive tract of the cows to undergo an involution. This changes quickly in the weeks following calving as the uterus involutes and returns to normal size and normal estrus activities resume. However, when cows calve down without any complications, this

recovery process requires no more than 40 days (Stevenson, 2001). Any cow that has had some type of reproductive or metabolic incident at calving needs more time to recover.

Days from calving to first service (DTFS) is the number of days from calving to the first insemination of a given lactation, which could be a good assessor of days from calving to first heat (DTFH). It reflects the cow's ability to recover and return to normal reproductive functions after calving, especially the estrus cycle (Pryce et al., 2001) and can be recorded earlier than most interval traits. Therefore, it is regarded as one of the most important practical measures of reproductive performance. However, it is also influenced by the VWP, which depended on the farmer's decision of when to start the service period or estrus might be not observable for many reasons. It may vary between herds and between cows within herds (DeJarnette et al., 2007). Therefore, it needs to be considered in fertility evaluations.

Days between first and last service (DFLS) is an indicator of the time elapsed from the first service to the successful one. It can be derived from the interval from calving to first service, calving interval and an assumed gestation length of 280 days. It reflects the ability of the cow to come into estrus after calving and the ability to conceive following insemination (conception rate). Furthermore, it is influenced by management decisions. The management bias on DFLS can be accounted for if information on culled cows could somehow be included in the analysis. High producing cows tend to have more opportunities for re-insemination in the case of improper management causes the failure of conception.

Days open (DO) also called days from calving to conception, is the days from calving to the successful service (or the last service if calving record is not available), which is a composite trait affected by factors affecting the cow's ability to return to cycling after calving. The DO shows a detectable estrus and the cow's ability to become pregnant. It can be the same measure with DTFS or

VWP in the cows that conceive at first AI service (González-Recio and Alenda, 2005). Additionally, the DO is very high correlated to the CI (CI minus gestation length) and can be obtained earlier than CI. Furthermore, DO is easy to measure from dairy recording data at the farm level and it was a widely used trait for female fertility genetic evaluation in many countries (Dematawewa and Berger, 1998; VanRaden et al., 2004). In some countries such as USA (VanRaden et al., 2004) currently calculate daughter pregnancy rate as $21 / (\text{days open} - \text{voluntary waiting period} + 11)$. However, DO is strongly affected by environmental factors rather than genetic factors. The environmental factors affecting DO are managerial decisions (voluntary waiting period), health, nutrition, welfare and many others management practices (semen quality, the technical ability of the inseminator and the success of estrous detection). For example, a longer VWP before insemination may be preferred to apply for high-yielding cows (Dekkers et al., 1998).

Calving interval (CI), the period of time or the number of days between two consecutive calving is one of the most common traits used as an indicator of female fertility. It covers both the ability to return to cycling after calving and the ability to conceive the following insemination, which is most directly affected by three reproductive outcomes: estrus detection, days to first service, and VWP), with estrus detection be considering the most important (Heuwieser et al., 1997; Nebel and Jobst, 1998). As calving interval increases, days in milk increases and lifetime milk yield decreases (Nebel and Jobst, 1998). Mayne et al. (2002) reported that herds with high estrous detection rates had significantly shorter calving intervals and significantly lower 305-day protein yields, less body condition loss after calving, and significantly smaller negative energy balances. They concluded that calving interval shorter than 380 days is achievable by minimizing negative energy balance in early lactation, good estrous detection, and early insemination of cows after calving. An extended calving interval is generally believed to reduce profit because efficiency of milk production is reduced, fewer calves are born and the rate of genetic gain in the herd is impaired (Weller and Follman, 1990; Westwood et al., 2002). Arbel et al.

(2001) suggested that different results available in the literature on this subject were due to the different criteria and time periods used, yield levels and the seasonality of production patterns. Milk production level and lactation persistency were crucial factors in determining the appropriate calving interval.

CI as a measure of female fertility presents some disadvantage because CI requires that the cow has calved more than once, which implicitly leads to a time delay and to a selected data material, as discussed by Pryce et al. (2000). Therefore, it is restricted only to multiparous cows. Cows which do not survive to the next lactation have not a record for calving interval and will be automatically excluded, likely due to fertility problems (Bascom and Young, 1998). Consequently overestimating of fertility occurred. Evaluations based on this trait alone could be biased as a result of culling of lowly fertile cows. To deal with the culling problem, Roxström and Strandberg (2002) and Olori et al. (2002) both recommended that calving interval should be treated as a censored trait and analyzed jointly with survival scores to consider the non-random scoring of calving interval. Calving interval is also available later than many other measures of fertility, so is not as useful for selection decisions.

Success traits

Success traits are related to the cow's ability to become pregnant that described by proportions of cows pregnant by specified time periods after their calving date. They could be measured on a population or individual basis depending on definition. For a population, success traits are expressed as a ratio from a group of animals and are not suitable for individual genetic selection. Alternatively, success traits measured individually are discontinuous character, binary or category (threshold traits), which require more sophisticated models for analysis and does not follow the patterns of Mendelian inheritance, especially for censored data. Compared to interval traits, such traits are usually measured early during the lactation which will reduce the impact of environmental and management effects and allow for early genetic evaluation (Thaller, 1997). The traits that the most widely used and employ in the literature are number of services per conception (NSPC), conception at first service (FSC),

conception rate (CR), non-return rate (NRx) after a fixed number of days (e.g. 60, 70 or 90 days), and the outcome of insemination (success or failure).

Number of services per conception (NSPC) is the only count or ordinal trait used as a measurement of fertility. It defined as the number of AI services to achieve conceive within each lactation. The NSPC can be considered as a good assessor of fertility, although it does not provide any information about the time elapsed. If inseminations are conducted at regular intervals, it reflects the cow's ability to become pregnant at insemination or a measure of pregnancy rate directly (González-Recio et al., 2004) However, it is seldom the case that inseminations are carried out at regular intervals. Furthermore, censoring is a major problem when analyzing NSPC as too many cows have incomplete records. Additionally, NSPC is not a continuous trait and its analysis requires special methodology (poisson models) and software. The NSPC depends largely on the breeding system used. It is higher under uncontrolled natural breeding and lower where artificial insemination is used. A high NSPC results in prolonged DO and CI, and increased feeding, insemination, and culling costs, decreased the number of calves produced, as well as a delay of onset of subsequent lactation. Therefore, it is considered an economic important trait and a potential selection criterion in fertility. The NSPC was significantly affected by herd, season, placenta expulsion time, lactation length and milk yield.

Conception at first service (FSC) is a binary trait defined as the probability that a female will conceive from the first AI service in each lactation. It is a successful trait with a binomial distribution and also a simple clustering of NSPC in 2 classes, as FSC takes value '1' for NSPC equal to 1, and value '0' for NSPC greater than 1. A female that conceives at the first insemination incurs a lower cost of insemination, lower labor for estrus detection and breeding, and an earlier calving date. Heifers that conceive first AI have higher pregnancy rates in subsequent breeding lactation (Bormann et al., 2006). This trait would only be used on farms with AI service.

Non-return rate at x day after first service (NR x) is the outcome of an insemination validated by the occurrence of a second breeding within a given number of days x days that the cow does not return in heat or is not bred again, and expresses the ability of conception and maintaining pregnancy over the period of early gestation (Miglior, 1999). This trait can be evaluated for both heifers and cows. The number of days considered (x) is generally comprised between 56 (Andersen-Ranberg et al., 2003) and 90 (Fuerst and Egger-Danner, 2002; Gredler et al., 2007). Nonreturn rate at 56 days is also the most widely used trait by Interbull for genetic evaluation of female fertility (Biffani and Canavesi, 2007; Jorjani, 2007). Anyway, considering an x number of days in defining the insemination successful may lead to rely on some false positive records. In the elapsed time after each insemination the VWP plays an important role (Andersen-Ranberg et al., 2005; Sun and Su, 2010), and silent heat, early embryonic death, infertile and non-re-cycling cow. Therefore the use of a higher number of days to be elapsed has been motivated (Rensing et al., 2006), but a more reliable proof of outcome of a given insemination is provided if the x number of elapsed days coincides with pregnancy length. Non-return rate has mostly been used as a measure of female fertility, and it depends on complete recording of all subsequent inseminations. Furthermore, a calving date is not required.

Conception rate (CR) is a measure of a cow's fertility at service. During early years, CR was a fertility measure expressed as a ratio of successful conception to potential breeding; it was not evaluated genetically or used for genetic improvement (Gwazdauskas et al., 1983). Another measure of CR is the inverse of NSPC. For CR, inseminations are validated as successful according to the estimated pregnancy length (Pasman et al., 2006). This allows to avoid the high number of false positives NR x provides, but the necessity of a subsequent calving to validate the insemination leads to a delayed phenotype collection and evaluation. Conception rates are confounded by such factors as the physiologic fertility of the cow, semen quality, and semen handling and insemination techniques.

However, there are alternative CR, which is of individual cows, the most representative definition is the binary outcome (success or failure) for each insemination record and can be considered the previous confound factors in AI day.

4. Genetic evaluation of fertility traits

Female fertility is one of the most economically important traits for the dairy cattle industry. Estimates of genetic parameters for traits of economic importance in dairy cattle are necessary for implementing efficient breeding programs. Accurate heritability and correlation estimates are required to predict expected selection response and to obtain predicted breeding values using the most efficient statistical models. The potential for genetic improvement of a trait largely depends also upon genetic variation existing in the population of interest. Heritability estimate is the assessment of the magnitude of genetic variation for a particular trait in a herd or population under given environmental conditions, whereas the genetic correlations give the information how genes affecting one trait also affect the other traits. If genetic correlation between the two traits is high, the selection for one trait would result in an improvement/deterioration for the other trait as a correlated response.

Compared to many other traits, in tropical area, the study of national genetic evaluations for female fertility traits is very rare. Also, international genetic evaluation of female fertility has started as late as February 2007. Many fertility traits are difficult to handle in parameter estimation and genetic evaluation. Different from production traits, which usually follow a normal Gaussian distribution, the fertility traits cannot be valid considered the same assumptions since the traits are described differently. Interval traits, such as AFS, AFC, DTFS, DFLS, DO, and CI are as the most of time-related measures, generally follow skewed and asymmetric distributions, and success traits such as NSPC, FSC, CR and NR(x) are categorical variables, either dichotomous or ordinal. Different treatments of the variables have been proposed, such as log-transformation of skewed distributions (Pollott and Coffey, 2008) or

threshold models (Gianola, 1982), although the interpretation of results might be not intuitive when these methods are proposed.

Since threshold-liability models have been postulated and developed (Gianola and Foulley, 1983; Harville and Mee, 1984; Gilmour et al., 1985), this methodology has been widely applied to the analysis of non-linear traits, such as calving difficulty and clinical mastitis, besides fertility traits. In calving ease, threshold models have been shown to give higher heritability estimates, rank correlation among the sires close to unity (Guerra et al., 2006), and little advantages in predictions (Varona et al., 1999). In clinical mastitis, Vallimont et al. (2009) and Heringstad et al. (2003) found that threshold models give again higher heritability estimates and similar sire ranks to linear models, and Vazquez et al. (2012) reported that predictions between threshold and linear models are comparable. In fertility, no particular improvement has been found in using threshold compared to linear models (Weller and Ron, 1992; Matos et al., 1997b). However, the recent theoretical and computational developments in the analysis of discrete and binary data have made the use of binary traits for reproductive performance evaluation possible. Although these traits were analyzed for a period of time as continuous responses using existing mixed linear methodology, in clear violation of their distributional assumptions, the threshold liability model is becoming the standard tool for discrete data analysis, especially after the study reported by Sorensen et al. (1995).

More sophisticated models (e.g., proportional hazards model, censored Gaussian model, censored threshold model, and threshold-linear model) have been proposed for genetic evaluation of fertility traits, with the concern on censoring and data distribution (Schneider et al., 2005; González-Recio et al., 2006b; Urioste et al., 2007; Hou et al., 2009). The more sophisticated models require more computational resources and are more complicated to implement. A linear sire model (**SM**) is used for genetic evaluation of fertility traits in most countries. The SM is theoretically inferior to the animal model (**AM**) in the estimation of variances and other genetic parameters (Everett et al., 1979; Schaeffer, 1983; Hudson and Schaeffer, 1984).

Similarly, in the last decades AM have mostly substituted SM, but their application for non-linear variables is not trivial (Tempelman, 1998), due to long computational times and drawbacks in convergence (Ødegard et al., 2010). The superiority and popularity of AM have not been widely supported by strong evidences of improvement in prediction of fertility of dairy cows. Sun et al. (2009b) found that the AM increased stability and accuracy of genetic evaluation for fertility in dairy cattle, whereas Ramirez-Valverde et al. (2001) did not find any significant improvement in prediction. Moreover, scarce data availability and quality may affect the goodness of assessment. For example, the missing of culling reason or pregnancy check records could bias the measure of DO for a given cow. Survival analysis has been proposed to be suitable for female fertility evaluation (Weigel, 2004; González-Recio et al., 2006; Hou et al., 2009). Commonly involved measurement such as parturition, first service and conception are the time elapsed between two reproductive events.

An overview of heritability of fertility traits and genetic correlation between fertility traits and milk yield from across parities data by different authors are summarized in Table 2-7 and 2-8. The reports on heifer fertility and genetic correlation between fertility traits and first lactation yield is reported in Table 2-9 whereas the reports of primiparous showed in Table 2-10 (interval fertility traits) and Table 2-11 (success fertility traits) and that of multiparous are showed in Table 2-12 (interval and success fertility traits).

Heritability of fertility traits

The first step of an investigation at the genetic level is the assessment of the magnitude of genetic variation between individuals. The results from different breeds in different countries were not differ significantly. Results differed mostly according to the model and methodology used. Generally, heritability estimates of fertility traits are low (<0.15) except AFS and AFC, which were low to moderate (0.04-0.38). Traits measured as intervals in time (AFS, AFC, DTFS and DO in particular) have larger heritability estimates than traits of binary or categorical nature. The heritability estimated of

fertility traits of cow are higher than that of corresponding heifer (Jamrozik et al., 2005; Tiezzi et al., 2012; De Haer et al., 2013). Linear models (applied to categorical variables) gave lower heritability estimates than threshold models, and animal models gave higher heritability than sire models. The range of estimates were 0.10-0.23 (AFS), 0.04-0.38 (AFC), 0.02-0.12 (DTFS), 0.01-0.07 (DFLS), 0.02-0.10 (DO), 0.01-0.11 (CI), 0.01-0.09 (NSPC), 0.00-0.12 (FSC), 0.03-0.15 (CR), and 0.01-0.12 (NRx). The heritability estimates of reproductive traits in dairy cattle are low because of a large unexplainable portion of residual variation (Veerkamp and Beerda, 2007) and the considerable influence of management on many of these measures (De Vries and Veerkamp, 2000). In spite of low heritability estimates, the phenotypic and genotypic variation for most fertility traits is relatively large and provides a favorable opportunity for selection.

The genetic relationship with production traits

Most of the estimates show an antagonistic relationship between fertility and production traits, as already stated above. Magnitude of relationship ranges from null to medium-high values. There are some reports that the estimates show a favorable relationship or close to zero such as for AFS (Abe et al., 2009; De Haer et al., 2013); AFC (Montaldo et al., 2010); DFLS (Tiezzi et al., 2012); DO (Lee et al., 2003), CI (Ojango and Pollotte, 2001; Montaldo et al., 2010), NRx (Andersen-Ranberg et al., 2003; Muir et al., 2004; Sun et al., 2010) and FSC (Berry et al., 2013). Heifer fertility is the less correlated to milk yield than cow fertility (Tiezzi et al., 2012). Interval fertility traits are much more related to milk yield than success fertility traits.

The genetic relationship with negative energy balance traits

TD-FPR and fat percentage were TD -FPR and fat percentage were good predictors of fertility; a strong decrease in fat percentage or high TD-FPR had a negative effect on energy balance during early lactation, leading to decreasing fertility performance. The estimates of genetic correlations between

fertility traits and TD-FPR in the literature are very limited. The estimates are reported by Gredler et al. (2006a) in Table 7 and reported by Negussie et al. (2013) in Table 10 and Table 11. Negussie et al. (2013) have found relatively low genetic correlations between TD-FPR and most of fertility traits. However, stronger genetic associations were determined between TD-FPR and DTFS (-0.01-0.28) and DO (0.03-0.24).

Table 2-7. Means, heritabilities, and genetic correlations with milk yield (F/P ratio) for interval fertility traits measured on across parities

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean	h ²	r _g ³ MY (F/P ratio)	Remark
<i>Days from calving to first service (DTFS)</i>							
Kadarmideen et al., 2000	HOL (UK)	63,891	LAM-REML	84.00	0.03	0.36	
Weigel and Rekaya, 2000	HOL (US-CA)	30,000	LAM-REML	70.50	0.06		
Weigel and Rekaya, 2000	HOL(US-MN)	20,000	LAM-REML	91.50	0.06		
Pryce et al., 2001	HOL (UK)	1,211	LAM-REML	77.40	0.06	0.49	
Berry et al., 2003	HOL (IL)	12,262	LAM-REML	72.80	0.02	-0.08	
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	73.00	0.03	0.28	
Kadarmideen, 2004	HOL (CH)	38,930	LAM-REML	79.00	0.12	0.27	
Van Raden et al., 2004	HOL (US)	2,195,643	LAM-REML	90.00	0.07		
Biffani et al., 2005b	HOL (IT)	65,110	LAM-REML	85.70	0.06		
Biffani et al., 2005a	HOL (IT)	2,800,000	LAM-REML	88.00	0.06	0.33	
González-Recio and Alenda, 2005	HOL (ES)	120,713	LAM-GS	81.00	0.05		
Jamrozik et al., 2005	HOL (CA)	35,474	LAM-GS	87.10	0.10		
González-Recio et al., 2006a	HOL (ES)	71,217	LSM-GS	84.00	0.05	0.47	
Jagusiak and Zarnecki, 2006	HOL (PL)	25,013	LAM-REML	79.30	0.06		
López de Maturana et al., 2007	HOL (ES)	33,532	rLSM-GS	83.52	0.09		
König et al., 2008	HOL (DE)	73,344	LSM-GS	93.85	0.07	0.14	
M' Hamdi et al., 2010	HOL (TN)	65,549	LAM-REML	93.20	0.03		
Tiezzi et al., 2011	BSW (IT)	71,556	cLSM-GS	88.20	0.05		
Ghiasi et al., 2011	HOL (IR)	72,124	LSM-REML	72.93	0.06		
Toghiani, 2012	HOL (IR)	7,949	LSM-REML	97.00	0.04	0.02	
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	82.51	0.04	0.49	
Guo et al., 2014	HOL (CN)	42,106	LAM-REML	83.30	0.03		
<i>Days between first and last service (DFLS)</i>							
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	34.00	0.01	0.38	
González-Recio and Alenda, 2005	HOL (ES)	113,373	TAM-GS	36.00	0.03		
Jamrozik et al., 2005	HOL (CA)	16,124	LAM-GS	32.50	0.07		
Tiezzi et al., 2011	BSW (IT)	71,556	cLSM-GS	36.00	0.03		
Ghiasi et al., 2011	HOL (IR)	72,124	LSM-REML	44.76	0.04		
<i>Days open (DO)</i>							
Abdallah and McDaniel, 2000	HOL (US)	23,052	LAM-REML	143.00	0.03	0.62	
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	103.00	0.02	0.27	
Dechow et al., 2004	HOL (US)	157,700	LSM-REML		0.04	0.38	
Van Raden et al., 2004	HOL (US)	2,195,643	LAM-REML	141.00	0.04		
Atagi and Hagiya, 2005	HOL (JP)	483,756	LAM-REML	121.70	0.05		
González-Recio and Alenda, 2005	HOL (ES)	113,375	LAM-GS	117.00	0.04		
González-Recio et al., 2006a	HOL (ES)	71,217	LSM-GS	131.00	0.05	0.63	
Gredler et al., 2006a	SIM (AT-DE)	3,611	LAM-REML	106.60	0.06	0.74 (-0.01)	
Jagusiak and Zarnecki, 2006	HOL (PL)	25,013	LAM-REML	132.10	0.05		
López de Maturana et al., 2007	HOL (ES)	33,532	rLSM-GS	128.64	0.06		
Gutierrez et al., 2008	HOL (US)	1,852	rLAM-GS	148.00	0.08		
Gutierrez et al., 2008	HOL (US)	1,852	rrLAM-GS	148.00	0.07-0.10		

Table 2-7 (Continued). Means, heritabilities, and genetic correlations with milk yield (F/P ratio) for interval fertility traits measured on across parities

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean	h ²	r_g^3 MY (F/P ratio)	Remark
Estrada-León et al., 2008	BSW (MX)	1,235	LAM-REML	172.80	0.05		
Banos and Coffey, 2010	HOL (UK)	1,926	LAM-REML	113.50	0.07	0.68	
M ³ Hamdi et al., 2010	HOL (TN)	65,549	LAM-REML	150.00	0.04		
Tiezzi et al., 2011	BSW (IT)	71,556	cLSM-GS	124.00	0.06		
Ghiasi et al., 2011	HOL (IR)	72,124	LSM-REML	117.67	0.08		
Toghiani, 2012	HOL (IR)	15,895	LSM-REML	124.00	0.06	0.36	
Guo et al., 2014	HOL (CN)	42,106	LAM-REML	118.50	0.05		
Zanbrano and Echeverri, 2014	HOL (CB)	10,156	LAM-REML	127.15	0.08		
Zanbrano and Echeverri, 2014	JER (CB)	715	LAM-REML	125.62	0.09		
Calving interval (CI)							
Kadarmideen et al., 2000	HOL (UK)	63,891	LAM-REML	391.00	0.02	0.54	
Pryce et al., 2001	HOL (UK)	1,211	LAM-REML	396.00	0.01	0.74	
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	383.00	0.03	0.40	
Biffani et al., 2005b	HOL (IT)	40,103	LAM-REML	413.50	0.07		
Biffani et al., 2005a	HOL (IT)	2,800,000	LAM-REML	418.00	0.07	0.37	
González-Recio and Alenda, 2005	HOL (ES)	96,346	LAM-GS	400.00	0.04		
Jagusiak and Zarnecki, 2006	HOL (PL)	25,013	LAM-REML	409.80	0.04		
Estrada-León et al., 2008	BSW (MX)	1,391	LAM-REML	453.90	0.11		
M ³ Hamdi et al., 2010	HOL (TUN)	28,777	LAM-REML	445.00	0.06		
Ghiasi et al., 2011	HOL (IR)	72,124	LSM-REML	393.85	0.07		
Toghiani, 2012	HOL (IR)	11,674	LSM-REML	395.00	0.07	0.59	
Albarran-Portillo and Pollott, 2013	HOL (UK)	176,757	LAM-REML	399.00	0.03	0.62, 0.51*	
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	402.35	0.04	0.48	
Guo et al., 2014	HOL (CN)	41,311	LAM-REML	397.60	0.06		
Zanbrano and Echeverri, 2014	HOL (CB)	10,303	LAM-REML	410.30	0.09		
Zanbrano and Echeverri, 2014	JER (CB)	723	LAM-REML	409.30	0.07		

¹**Breed:** BSW= Brown Swiss; HOL= Holstein; JER= Jersey; SIM= Simmental

²**Model:** LAM = linear animal model; rLAM= repeatability linear animal model; LSM = linear sire model; cLSM = censor linear sire model; rLSM = recursive linear sire model; rrLAM = random regression linear animal model; TAM = threshold animal model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³**r_g*** = daily milk yield

Table 2-8. Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for success fertility traits measured on across parities

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r_g MY (F/P ratio)	Remark
<i>Number of services per conception (NSPC)</i>							
Kadarmideen et al., 2000	HOL (UK)	63,891	LAM-REML	1.56	0.01	0.41	
Berry et al., 2003	HOL (IL)	12,262	LAM-REML	1.80	0.02	0.46	
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	1.94	0.02	0.25	
Van Raden et al., 2004	HOL (US)	2,195,643	LAM-REML	2.10	0.02		
Biffani et al., 2005b	HOL (IT)	64,932	LAM-REML	1.70	0.03		
González-Recio and Alenda, 2005	HOL (ES)	113,375	TAM-GS	1.87	0.02		
Jamrozik et al., 2005	HOL (CA)	37,409	LAM-GS	2.14	0.07		
González-Recio et al., 2006a	HOL (ES)	71,217	TSM-GS	1.90	0.04	0.23	
López de Maturana et al., 2007	HOL (ES)	33,532	rTSM-GS	1.89	0.04		
Estrada-León et al., 2008	BSW (MX)	1,174	LAM-REML	2.41	0.04		
Banos and Coffey, 2010	HOL (UK)	1,926	LAM-REML	2.00	0.05	0.65	
M' Hamdi et al., 2010	HOL (TN)	65,549	LAM-REML	2.55	0.03		
Ghiasi et al., 2011	HOL (IR)	72,124	TSM-GS	2.13	0.05		
Tiezzi et al., 2011	BSW (IT)	71,556	cTSM-GS	1.74	0.06	0.34	
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	2.04	0.02	0.33	
Guo et al., 2014	HOL (CN)	42,106	LAM-REML	1.80	0.04		
Zanbrano and Echeverri, 2014	HOL (CB)	12,883	LAM-REML	1.58	0.04		
Zanbrano and Echeverri, 2014	JER (CB)	879	LAM-REML	1.48	0.09		
<i>Conception at first service (FSC)</i>							
Kadarmideen et al., 2000	HOL (UK)	63,891	LAM-REML	0.64	0.01	-0.42	
Kadarmideen et al., 2000	HOL (UK)	63,891	TSM-REML	0.64	0.01		
Pryce et al., 2001	HOL (UK)	1,211	LAM-REML	0.46	0.00		
Berry et al., 2003	HOL (IL)	12,262	LAM-REML	0.49	0.01	-0.29	
Kadarmideen et al., 2003	HOL (UK)	62,443	LAM-REML	0.47	0.02	-0.16	
López de Maturana et al., 2007	HOL (ES)	33,532	rTSM-GS	0.51	0.12		
Tiezzi et al., 2011	BSW (IT)	71,556	cTSM-GS	0.45	0.06		
Ghiasi et al., 2011	HOL (IR)	72,124	TSM-GS	0.42	0.03		
<i>Conception rate (CR)</i>							
Zanbrano and Echeverri, 2014	HOL (CB)	12,883	LAM-REML	0.80*	0.03		
Zanbrano and Echeverri, 2014	JER (CB)	879	LAM-REML	0.84*	0.15		
<i>Non-return rate at x days (x=56-60-70-90) (NRx)</i>							
Weigel and Rekaya, 2000	HOL (US-CA)	~30,000	LAM-REML	0.35	0.01		x=60
Weigel and Rekaya, 2000	HOL (US-CA)	~30,000	TAM-REML	0.35	0.02		x=60
Weigel and Rekaya, 2000	HOL (US-MI)	~20,000	LAM-REML	0.57	0.04		x=60
Weigel and Rekaya, 2000	HOL (US-MI)	~20,000	TAM-REML	0.57	0.03		x=60
Cassel et al., 2003	HOL (US)	73,017	LAM-REML	0.52	0.01		x=70
Cassel et al., 2003	JER (US)	75,357	LAM-REML	0.56	0.02		x=70
Kadarmideen, 2004	HOL (CH)	38,930	LAM-REML	0.65	0.06	-0.24	x=56
Muir et al., 2004	HOL (CA)	33,312	LAM-GS	0.64	0.04		x=56
Van Raden et al., 2004	HOL (US)	2,195,643	LAM-REML	0.55	0.01		x=70
González-Recio and Alenda, 2005	HOL (ES)	69,833	TAM-GS	0.72	0.05		x=56
Biffani et al., 2005b	HOL (IT)	62,738	LAM-REML	0.63	0.03		x=56

Table 2-8 (Continued). Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for success fertility traits measured on across parities

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r_g MY (F/P ratio)	Remark
Biffani et al., 2005a	HOL (IT)	~2,800,000	LAM-REML	0.65	0.03	-0.21	x=56
Jamrozik et al., 2005	HOL (CA)	41,092	LAM-GS	0.57	0.04		x=56
Jagusiak and Zarnecki, 2006	HOL (PL)	42,283	LAM-REML	0.73	0.12		x=56
König et al., 2008	HOL (DE)	73,344	TSM-GS	0.67	0.03	-0.31	x=56
König et al., 2008	HOL (DE)	73,344	TSM-GS	0.60	0.03	-0.33	x=90
Tiezzi et al., 2011	BSW (IT)	71,556	cTSM-GS	0.71	0.04		x=56
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	0.58	0.01	-0.16	x=56

¹**Breed:** BSW= Brown Swiss; HOL= Holstein; JER= Jersey

²**Model:** LAM = linear animal model; LSM = linear sire model; TAM = threshold animal model; TSM = threshold sire model; cTSM = censor threshold sire model; rTSM= repeatability threshold sire model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³**Mean:*** = [CR = (1/NSPC)*100]

Table 2-9. Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval and success fertility traits measured on heifers

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r_g^4 MY (F/P ratio)	Remark
<i>Age at first service (AFS)</i>							
Muir et al., 2004	HOL (CA)	33,312	LAM-GS	504.06	0.19		
Jamrozik et al., 2005	HOL (CA)	53,158	LAM-GS	499.70	0.13		
Jagusiak and Zarnecki, 2006	HOL (PL)	42,283	LAM-REML	537.60	0.12		
Jagusiak, 2006	HOL (PL)	42,283	LAM-REML	537.60	NA	0.05	
Abe et al., 2009	HOL (JP)	308,238	TAM-GS	518.60	0.13	-0.19	
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	482.40	0.11		
De Haer et al., 2013	HOL (NL)	311,408	LMGSM-REML	488.90	0.23	-0.27	
Guo et al., 2014	HOL (CN)	42,106	LAM-REML	519.80	0.10		
<i>Age at first calving (AFC)</i>							
Ojango and Pollott, 2001	HOL (KE)	3,185	LAM-REML	930.00	0.38	0.54	
König et al., 2005	HOL (TH)	1,623	LAM-REML	858.00	NA		
Abe et al., 2008	HOL (JP)	965,107	LAM-REML	816.00	0.22		
Estrada-León, et al., 2008	BSW (MX)	358	LAM-REML	937.60	0.28		
Jagusiak and Zarnecki, 2006	HOL (PL)	42,283	LAM-REML	835.80	0.30		
Montaldo et al., 2010	HOL (MX)	13,201	LAM-REML	798.00	0.28	-0.01***	
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	777.49	0.04		
Pantelić et al., 2011	SIM (SP)	3,461	LAM-REML	778.73	0.09	0.003	
Berry et al., 2013	HOL (IL)	60,330	LAM-REML	797.00	0.07	0.14	
<i>Days between first and last service (DFLS)</i>							
Jamrozik et al., 2005	HOL (CA)	29,907	LAM-GS	16.30	0.03		
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	17.66	0.03		
Tiezzi et al., 2012	BSW (IT)	37,546	cLSM-GS	35.60	0.02	-0.08	
De Haer et al., 2013	HOL (NL)	311,408	LMGSM-REML	33.00	0.02	0.03	
<i>Number of services per conception (NSPC)</i>							
Jamrozik et al., 2005	HOL (CA)	53,093	LAM-GS	1.64	0.03		
Gredler et al., 2007	SIM (AT, DE)	22,865	LAM-REML	1.52	0.02		
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	1.64	0.01		
Tiezzi et al., 2012	BSW (IT)	37,546	cTSM-GS	1.56	0.03	-0.02	
<i>Conception at first service (FSC)</i>							
Ghiasi, et al., 2011	HOL (IR)	72,124	TAM-GS	0.42	0.03		
Tiezzi et al., 2012	BSW (IT)	37,546	cTSM-GS	0.65	0.02	-0.15	
<i>Conception rate (CR)</i>							
De Haer et al., 2013	HOL (NL)	311,408	LMGSM-REML	0.77	0.01	-0.04	
<i>Non-return rate at x days (x=56-60-70-90) (NRx)</i>							
Andersen-Ranberg et al., 2003	NRF (NO)	1,632,961	LSM-REML	0.75	0.01-0.02	0.04	x=56
Muir et al., 2004	HOL (CA)	33,312	LAM-GS	0.78	0.03	0.12	x=56
Andersen-Ranberg et al., 2005	NRF (NO)	1,524,328	LSM-REML	0.74	0.00		x=56
De Jong, 2005	HOL (NO)	4,795,305	LAM-REML	NA	0.02		x=56
Jamrozik et al., 2005	HOL (CA)	53,158	LAM-GS	0.74	0.03		x=56
Wall et al., 2005	HOL (UK)	27,900	LAM-REML	0.64	0.01		x=56
Jagusiak, 2006	HOL (PL)	42,283	LAM-REML	0.73	NA	-0.12	x=56

Table 2-9 (Continued). Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval and success fertility traits measured on heifers

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r_g^4 MY (F/P ratio)	Remark
Jagusiak, 2006	HOL (PL)	42,283	LAM-REML	0.69	NA	0.05	x=72
Holtmark et al., 2008	NRF (NO)	649,156	TSM-GS	0.75	0.02	-0.07	x=56
Gredler et al., 2007	SIM (AT, DE)	22,865	LAM-REML	0.78	0.01		x=56
Liu et al., 2008	HOL (DE)	215,509	LAM-REML	NA	0.01	-0.11	x=56
Sun, et al., 2010	HOL (DK)	471,742	LSM-REML	0.56	0.01	0.09	x=56
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	0.69	0.00		x=56
Tiezzi et al., 2012	BSW (IT)	37,546	cTSM-GS	0.79	0.02	-0.19	x=56
De Haer et al., 2013	HOL (NL)	311,408	LMGSM-REML	0.74	0.01	-0.08	x=56
Negussie, et al., 2013	NRF (FI)	22,102	rrLAM-REML	0.55	0.02		x=56
Jagusiak et al., 2014	HOL (PL)	4,731-7,379	LAM-GS	0.63	0.12		x=56

¹**Breed:** BSW= Brown Swiss; HOL= Holstein; JER= Jersey; NRF= Norwegian Red; SIM= Simmental

²**Model:** LAM = linear animal model; rrLAM = random regression linear animal model; LMGSM=sire-maternal grandsire model; LSM = linear sire model; cLSM = censor linear sire model; TAM = threshold animal model; TSM = threshold sire model; cTSM = censor threshold sire model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³**Mean:** NA = not available

⁴ **r_g :** *** = 305-d mature equivalent milk production

Table 2-10. Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval fertility traits measured on primiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r _g ⁴ MY(F/P ratio)
<i>Days from calving to first service (DTFS)</i>						
Veerkamp et al., 2001	HOL (NL)	177,220	LSM-REML	89.00	0.07	0.53
Haile-Mariam et al., 2003a	HOL (AU)	~17,000	LSM-REML	77.00	0.13	
Wall et al., 2003	HOL (UK)	~30,000	LSM-REML	81.61	0.04	0.49
Andersen-Ranberg et al., 2005	NRF (NO)	>200,000	LSM-REML	81.00	0.02-0.03	0.47
De Jong, 2005	HOL (NOR)	4,031,330	LAM-REML	NA	0.08	
Wall et al., 2005	HOL (UK)	27,949	LAM-REML	86.90	0.05	
Jagusiak, 2006	HOL (POL)	25,013	LAM-REML	79.30	NA	0.29
Gredler et al., 2007	SIM (AT, DE)	38,498	LAM-REML	70.90	0.06	
Abe et al., 2008	HOL (JP)	832,877	LAM-REML	86.70	0.03	0.53
Estrada- León et al., 2008	BSW (MX)	~1,000	LAM-REML	87.80	0.04	
Holtmark et al., 2008	NRF (NO)	524,268	LSM-GS	NA	0.03	0.48
Liu et al., 2008	HOL (DE)	282,183	LAM-REML	NA	0.04	0.34
Heringstad et al., 2009	NRF (NO)	55,568	rLSM-GS	77.40	0.04	
Hou et al., 2009	HOL (DK)	509,512	LSM-GS	81-198	0.10	
Hou et al., 2009	HOL (DK)	509,512	TLSM-GS	81-198	0.11	
Hou et al., 2009	HOL (DK)	509,512	rcLSM-GS	81-198	0.11	
Hou et al., 2009	HOL (DK)	509,512	SURVw-REML	81-198	0.21	
Hou et al., 2009	HOL (DK)	509,512	SURVc-REML	81-198	0.01	
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	81.30	0.09	0.427
Sewalem et al., 2010	HOL (CA)	15,000	LAM-REML	NA	0.07	0.29**
Buch et al., 2011	SRB (SE)	473,620	LAM-REML	87.00	0.04	
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	74.46	0.14	
Tiezzi et al., 2012	BSW (IT)	24,098	cLSM-GS	90.70	0.14	0.62
Zink et al., 2012	HOL (CZ)	58686	LAM-REML	80.86	0.04	0.30
Berry et al., 2013	HOL (IL)	73695	LAM-REML	82.00	0.07	0.29
De Haer et al., 2013	HOL (NL)	291,053	LMGSM-REML	91.30	0.08	
Haile-Mariam et al., 2013	HOL (AU)	200,635	LSM-REML	86.00	0.01	0.23
Haile-Mariam et al., 2013	JER (AU)	266,795	LSM-REML	82.00	0.02	0.31
Negussie et al., 2013	NRF (FI)	22,422	rrLAM-REML	84.10	0.04	(-0.01-0.28)
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	83.81	0.05	0.39
Zavdilova and Zink, 2013	HOL (CZ)	75,541-103,499	LAM-REML	80.29-83.43	0.04	0.52
Jagusiak, et al., 2014	HOL (PL)	4,731-7,379	LAM-GS	93.80	0.15	
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	51.10	0.04	0.42
Sewalem et al., 2010	HOL (CA)	15,000	LAM-REML		0.05	0.12**
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	50.62	0.00	
Mucha and Strandberg, 2011	HOL (SE)	64,041	LSM-REML	38.14	0.03	
Zink et al., 2011	HOL (CZ)	52,632	LAM-REML	34.30	0.03	
Tiezzi et al., 2012	BSW (IT)	24,098	cLSM-GS	38.30	0.04	0.49
Zink et al., 2012	HOL (CZ)	52,632	LAM-REML	34.20	0.01	0.26
De Haer et al., 2013	HOL (NL)	291,005	LMGSM-REML	50.80	0.03	
Zavdilova and Zink, 2013	HOL (CZ)	75,541-103,499	LAM-REML	43.95-50.13	0.03	0.60

Table 2-10 Continued). Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval fertility traits measured on primiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r _g ⁴ MY(F/P ratio)
<i>Days open (DO)</i>						
Veerkamp et al., 2001	HOL (NL)	177,220	LSM-REML	127.00	0.07	0.61
Lee et al., 2003	HOL (KR)	11,472	LAM-REML	113.40	0.02	-0.28
Oseni et al., 2004	HOL (US)	318,078	LAM-REML	108-183	0.03-0.06	0.12-0.60
König et al., 2005	HOL (TH)	1,623	LAM-REML	129.50	0.03	
Chang et al., 2006	NRF (NO)	1,454,916	cLSM-GS	68-200	0.04	
Jagusiak, 2006	HOL (PL)	25,013	LAM-REML	132.10	NA	0.35
Gredler et al., 2007	SIM (AT-DE)	38,498	LAM-REML	105.60	0.04	
Abe et al., 2008	HOL (JP)	763,194	LAM-REML	129.5	0.04	0.54
Estrada- León et al., 2008	BSW (MX)	~1,000	LAM-REML	172.80	0.05	
Liu et al., 2008	HOL (DE)	282,183	LAM-REML	NA	0.03	0.41
Abe et al., 2009	HOL (JP)	400,016	TAM-GS	124.60	0.09	0.43
Hou et al., 2009	HOL (DK)	475,926	LSM- GS	120-208	0.07	
Hou et al., 2009	HOL (DK)	475,926	TLSM-GS	120-208	0.07	
Hou et al., 2009	HOL (DK)	475,926	rcLSM-GS	120-208	0.07	
Hou et al., 2009	HOL (DK)	475,926	SURVw-REML	120-208	0.12	
Hou et al., 2009	HOL (DK)	475,926	SURVc-REML	120-208	0.01	
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	133.30	0.07	0.50
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	125.20	0.07	
Pantelić et al., 2011	SIM (SP)	3,461	LAM-REML	110.79	0.11	0.09
Tiezzi et al., 2012	BSW (IT)	24,098	cLSM-GS	129.00	0.09	0.51
Zink et al., 2012	HOL (CZ)	53,026	LAM-REML	113.93	0.03	0.39
Bastin et al., 2012	HOL (BE)	29,792	rrLAM-GS	147.00	0.05	0.51 ⁺⁺ 0.45-0.54 ⁺⁺⁺ (0.03-0.24)
Negussie et al., 2013	NRF (FI)	22,422	rrLAM-REML	124.70	0.03	
Zavadilova and Zink, 2013	HOL (CZ)	75,541-103,499	LAM-REML	127.40-130.40	0.05	0.65
Jagusiak et al., 2014	HOL (PL)	4,731-7,379	LAM-GS	131.80	0.14	
<i>Calving interval (CI)</i>						
Pryce et al., 2000	HOL (UK)	19,042	LAM-REML	385.00	0.02	
Ojango and Pollott, 2001	HOL (KE)	3,185	LAM-REML	406.00	0.06	-0.64
Veerkamp et al., 2001	HOL (NO)	56,577	LSM-REML	385.00	0.04	
Haile-Mariam et al., 2003a	HOL (AU)	~17,000	LSM-REML	372.00	0.04	
Wall et al., 2003	HOL (UK)	~30,000	LSM-REML	387.64	0.03	0.27
Muir et al., 2004	HOL (CA)	33,312	LAM-GS	395.41	0.07	0.51
De Jong, 2005	HOL (NO)	4,031,330	LAM-REML	NA	0.06	
König et al. 2005	HOL (TH)	1,623	LAM-REML	462.60	0.02	
Wall et al., 2005	HOL (UK)	21,901	LAM-REML	399.60	0.04	
Jagusiak, 2006	HOL (PL)	25,013	LAM-REML	409.80	NA	0.35
Dal Zotto et al., 2007	BSW (IT)	32,359	LAM-REML	421.00	0.05	0.56
Makgahlela et al., 2007	HOL (SAF)	16,183	LAM-REML	396.00	0.03	
Montaldo et al., 2010	HOL (MX)	6,524	LAM-REML	419.00	0.01	-0.45
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	413.10	0.07	0.48
Eghbalsaied, 2011	HOL (IR)	14,707	LAM-REML	403.91	0.07	

Table 2-10 Continued). Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval fertility traits measured on primiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean ³	h ²	r _g ⁴ MY(F/P ratio)
Mucha and Strandberg, 2011	HOL (SE)	59,056	rrLSM-REML	416.09	0.04	
Albarran-Portillo and Pollott, 2013	HOL (UK)	69,319	LAM-REML	399.00	0.03	0.38, 0.34*
Berry et al., 2013	HOL (IL)	112,289	LAM-REML	402.00	0.03	0.44
De Haer et al., 2013	HOL (NL)	287,085	LMGSM-REML	403.70	0.07	
Haile-Mariam, et al., 2013	HOL (AU)	200,635	LSM-REML	405.00	0.03	0.31
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	402.24	0.04	0.49

¹**Breed:** BSW= Brown Swiss; HOL= Holstein; JER= Jersey; NRF= Norwegian Red; SIM= Simmental; SRB= Swedish Red

²**Model:** LAM = linear animal model; rrLAM = random regression linear animal model; LMGSM =linear maternal grand sire model; LSM = linear sire model; cLSM = censor linear sire model; rLSM = recursive linear sire model; rcLSM= right-censored linear gaussian model; rrLSM = random regression linear sire model; TLAM = threshold-linear model; SURVc=cox proportion hazard model; SURVw=weibull proportion hazard model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³**Mean:** NA = not available

⁴**r_g:** ++ = lactation genetic correlations; +++ = daily genetic correlations; * = dairy yield change in early lactation; ** = test-day milk yield closest to 90 DIM

Table 2-11. Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for success fertility traits measured on primiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean	h ²	r_g^3 MY (F/P ratio)	Remark
<i>Number of services per conception (NSPC)</i>							
Veerkamp et al., 2001	HOL (NL)	177,220	LSM-REML	2.00	0.03	0.48	
Haile-Mariam et al., 2003a	HOL (AU)	~17,000	LSM-REML	1.85	0.03		
Wall et al., 2003	HOL (UK)	~30,000	LSM-REML	1.67	0.02	0.06	
König et al., 2005	HOL (TH)	1,623	LAM-REML	2.81	0.01		
Chang et al., 2006	NRF (NO)	1,454,916	cTSM-GS	1.51- 2.05	0.04		
Gredler et al., 2007	SIM (AT, DE)	38,498	LAM-REML	1.84	0.02		
Estrada- León et al., 2008	BSW (MX)	~1,000	LAM-REML	2.41	0.04		
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	2.24	0.03	0.29	
Buch et al., 2011	SRB (SE)	473,620	LAM-REML	1.80	0.02		
Tiezzi et al., 2012	BSW (IT)	29,582	cTSM-GS	1.75	0.05	0.47	
Negussie et al., 2013	NRF (FI)	22,102	rrLAM-REML	1.98	0.01	(-0.21-0.03)	
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	2.01	0.02	0.44	
Berry et al., 2013	HOL (IL)	73,695	LAM-REML	1.68	0.03	0.38	
<i>Conception rate (CR)</i>							
Haile-Mariam et al., 2003a	HOL (AU)	~17,000	LSM-REML	0.47	0.02		
Averill et al., 2004	HOL (US)	297,823	TAM-GS	0.43	0.03		
Mitchell et al., 2005	HOL (US)	~6,000	LAM-REML	0.27	0.01		
Averill et al., 2006	HOL (US)	369,353	rrTAM-GS	NA	0.03-0.11		
Tsuruta et al., 2009	HOL (US)	265,093	rrTAM-GS	0.32	0.03-0.07		
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	0.42	0.02		
Sun et al., 2010	HOL (DK)	471,742	Logit	0.42	0.05		
Sun et al., 2010	HOL (DK)	471,742	Probit	0.42	0.02		
De Haer et al., 2013	HOL (NL)	291,005	LMGSM-REML	0.68	0.03		
<i>Conception at first service (FSC)</i>							
Veerkamp et al., 2001	HOL (NL)	177,220	LSM-REML	0.27	0.02	-0.49	
Abe, et al., 2009	HOL (JP)	400,016	TAM-GS	0.51	0.05	-0.35	
Mucha and Strandberg, 2011	HOL (SE)	64,041	LSM-REML	0.43	0.02		
Tiezzi et al., 2012	BSW (IT)	29,582	cTSM-GS	0.55	0.03	-0.55	
Berry et al., 2013	HOL (IL)	48,279	LAM-REML	0.47	0.01		
<i>Non-return rate at x days (x=56-60-70-90) (NRx)</i>							
Veerkamp et al., 2001	HOL (NL)	177,220	LSM-REML	0.49	0.02	-0.41	x=56
Wall et al., 2003	HOL (UK)	~30,000	LSM-REML	0.65	0.02	-0.25	x=56
Muir et al., 2004	HOL (CA)	33,312	LAM-GS	0.64	0.04	0.02	x=56
Andersen-Ranberg et al., 2005	NRF (NO)	~200,000	TSM-GS	0.67	0.04	-0.18	x=56
Andersen-Ranberg et al., 2005	NRF (NO)	~200,000	LSM-REML	0.67	0.01		x=56
Heringstad et al., 2006	NRF (NO)	475,270	TSM-GS	0.68	0.02		x=56
Gredler et al., 2007	SIM (AT-DE)	38,498	LAM-REML	0.67	0.01		x=56
Holtmark et al., 2008	NRF (NO)	~524,268	TSM-GS	0.67	0.02	-0.24	x=56
Liu et al., 2008	HOL (DE)	282,183	LAM-REML	NA	0.02	-0.2	x=56
Heringstad et al., 2009	NRF (NO)	55,568	rTSM-GS	0.67	0.06		x=56
Sun et al., 2010	HOL (DK)	471,742	LAM-REML	0.56	0.01	0.09	x=56

Table 2-11 (Continued). Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for success fertility traits measured on primiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean	h ²	r_g^3 MY (F/P ratio)	Remark
Sun et al., 2010	HOL (DK)	471,742	Logit	0.56	0.03		x=56
Sun et al., 2010	HOL (DK)	471,742	Probit	0.56	0.01		x=56
Sewalem et al., 2010	HOL (CA)	15,000	LAM-REML	NA	0.02	-0.13**	x=56
Tiezzi et al., 2012	BSW (IT)	29,582	cTSM-GS	0.71	0.02	-0.55	x=56
De Haer et al., 2013	HOL (NL)	291,053	LMGSM-REML	0.63	0.02		x=56
Negussie et al., 2013	NRF (FI)	22,102	rrLAM-REML	0.55	0.02	(0.01-0.12)	x=56
Pritchard et al., 2013	HOL (UK)	124,793	LSM-REML	0.59	0.01	-0.28	x=56

¹**Breed:** BSW= Brown Swiss; HOL= Holstein; NRF= Norwegian Red; SIM= Simmental; SRB= Swedish Red

²**Model:** LAM = linear animal model; rrLAM = random regression linear animal model; LMGSM =linear maternal grand sire model; LSM = linear sire model; TAM = threshold animal model; rrTAM = random regression threshold animal model; cTSM = censor threshold sire model; rTSM= repeatability threshold sire model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³**Mean:** NA = not available

⁴**r_g**** = test-day milk yield closest to 90 DIM

Table 2-12. Means, heritabilities, and genetic correlations with milk yield / (F/P ratio) for interval and success fertility traits measured on multiparous cows

Author(s) and Year	Breed ¹ (Country)	No. records	Model ²	Mean	h ²	r_g^3 MY (F/P ratio)	Remark
<i>Days from calving to first service (DTFS)</i>							
Abe et al., 2008	HOL (JP)	579,122	LAM-REML	86.4	0.03		Lac2
Abe et al., 2008	HOL (JP)	337,455	LAM-REML	87.1	0.03		Lac3
Tiezzi et al., 2012	BSW (IT)	15,653	cLSM-GS	90.30	0.12	0.47	Lac2
Berry et al., 2013	HOL (IL)	58,577	LAM-REML	78.00	0.04	0.38	Lac2
Berry et al., 2013	HOL (IL)	58,577	LAM-REML	75.00	0.03	0.05	Lac3
De Haer et al., 2013	HOL (NL)	248,801	LMGSM-REML	92.20	0.09		Lac2
De Haer et al., 2013	HOL (NL)	176,269	LMGSM-REML	94.40	0.11		Lac3
<i>Days between first and last service (DFLS)</i>							
Tiezzi et al., 2012	BSW (IT)	15,653	cLSM-GS	36.30	0.03	0.49	Lac2
De Haer et al., 2013	HOL (NL)	248,717	LMGSM-REML	53.30	0.04		Lac2
De Haer et al., 2013	HOL (NL)	170,253	LMGSM-REML	56.60	0.04		Lac3
<i>Days open (DO)</i>							
Abe et al., 2008	HOL (JP)	501,369	LAM-REML	130.7	0.04		Lac2
Abe et al., 2008	HOL (JP)	282,601	LAM-REML	131.8	0.03		Lac3
Tiezzi et al., 2012	BSW (IT)	15,653	cLSM-GS	126.00	0.05	0.40	Lac2
<i>Calving interval (CI)</i>							
Montaldo et al., 2010	HOL (MX)	4,501	LAM-REML	416.00	0.02	-0.01	Lac2
Montaldo et al., 2010	HOL (MX)	2,576	LAM-REML	421.00	0.01	-0.17	Lac3
Albarran-Portillo and Pollott, 2013	HOL (UK)	46,439	LAM-REML	399.00	0.03	0.53, 0.34*	>=Lac2
Berry et al., 2013	HOL (IL)	82,909	LAM-REML	398.00	0.04	0.40	Lac2
Berry et al., 2013	HOL (IL)	100,700	LAM-REML	393.00	0.03	0.43	Lac3
De Haer et al., 2013	HOL (NL)	239,289	LMGSM-REML	405.80	0.09		Lac2
De Haer et al., 2013	HOL (NL)	160,985	LMGSM-REML	408.30	0.11		Lac3
<i>Number of service per conception (NSPC)</i>							
Tiezzi et al., 2012	BSW (IT)	15,653	cTSM-GS	1.72	0.05	0.43	Lac2
Berry et al., 2013	HOL (IL)	58,577	LAM-REML	1.70	0.04	0.14	Lac2
Berry et al., 2013	HOL (IL)	43,548	LAM-REML	1.70	0.04	0.40	Lac3
<i>Conception rate (CR)</i>							
De Haer et al., 2013	HOL (NL)	248,717	LMGSM-REML	0.68	0.03		Lac2
De Haer et al., 2013	HOL (NL)	170,253	LMGSM-REML	0.67	0.03		Lac3
<i>Conception at first service (FSC)</i>							
Tiezzi et al., 2012	BSW (IT)	15,653	cTSM-GS	0.56	0.03	-0.51	Lac2
Berry et al., 2013	HOL (IL)	38,792	LAM-REML	0.44	0.01	-0.46	Lac2
Berry et al., 2013	HOL (IL)	29,081	LAM-REML	0.43	0.02	-0.27	Lac3
<i>Non-return rate at x days (x=56-60-70-90) (NRx)</i>							
Tiezzi et al., 2012	BSW (IT)	15,653	cTSM-GS	0.71	0.03	-0.29	Lac2, x=56
De Haer et al., 2013	HOL (NL)	248,797	LMGSM-REML	0.62	0.02		Lac2, x=56
De Haer et al., 2013	HOL (NL)	176,051	LMGSM-REML	0.62	0.02		Lac3, x=56

¹Breed: BSW= Brown Swiss; HOL= Holstein

²Model: LAM = linear animal model; LMGSM =linear maternal grand sire model; cLSM = censor linear sire model; cTSM = censor threshold sire model; REML = restricted maximum likelihood algorithm; GS = Gibbs sampler algorithm

³ r_g : * = dairy yield change in early lactation

Chapter III

Genetic analysis for fertility traits of heifers and cows from smallholder dairy farms in tropical environment

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INTRODUCTION

Demand for dairy products is rapidly growing in Asia, Africa, and Latin America, induced by urbanization and preferences for nutritious foods (Guyomard et al., 2013). Typical dairy system in these regions is based on low-input, smallholder farming in a tropical environment. An increase of milk production is expected to supply the demand as well as to raise the income of dairy farmers. Genetic improvement of the dairy cattle, along with changing feeding practices, is shown to largely increase milk production (McDermott et al., 2010). Crossbreeding of local breeds with temperate dairy breeds, such as Holstein-Friesian (**HF**), has been recommended to achieve both high productivity and resistance to heat stress (Philipsson, 2000). However, cattle with high proportions of exotic temperate blood tend to be managed intensively. Additionally, these exotic breeds are by definition not well adapted to the local climate, feed resources, and management systems and require some level of environmental modification (such as cooling and ventilation system) to remain reasonably healthy and productive (Herath and Mohammad, 2009).

Thailand is one of the country in tropical area. The dairy cattle have been developed through the national sire selection and AI mating program since 1956, focusing on milk production. Continuous increasing milk yield by selection has induced a decrease in reproductive performance (Pryce and Veerkamp, 2001) due to the antagonistic genetic relationship between milk yield and fertility traits (Roxström et al., 2001; Liu et al., 2008). In particular, during early lactation in high yielding cows, dietary intake of cows fails to keep pace with the demand for peak milk production (Bauman and Currie, 1980), leading to negative energy balance, which has serious consequences on other body functions (Banos et al., 2006; Løvendahl et al., 2010). The inclusion of fertility in the breeding goal is necessary to optimize the result of genetic improvement of dairy cattle.

The reproductive performance of dairy cows under smallholder conditions in Thailand from 2001 to 2005 was studied and reported by Leelasiri et al. (2006). The averages of days from calving to first

service (**DTFS**, d), days between first and last service (**DFLS**, d), days open (**DO**, d), number of services per conception (**NSPC**, no.), and calving interval (**CI**, d) were 86.50 ± 0.12 , 23.33 ± 0.02 , 127.99 ± 0.23 , 1.89 ± 0.00 , and 410.14 ± 0.23 , respectively. Research on genetic studies of fertility traits in tropical conditions, including Thailand, is very limited, but data sets are available from a few herds (e.g., Demeke et al., 2004; König et al., 2005; Estrada-León et al., 2008).

The objective of this study was to estimate genetic parameters for various fertility traits on crossbred dairy heifers and cows in a smallholder system under tropical conditions, using AI data from the national recording scheme.

MATERIALS AND METHODS

Environment and management

Thailand, as a tropical country, is located between 5°35' and 20°30' N and 97°20' and 105°40' E. Annual temperatures typically range from 19 to 38°C (66 to 100°F), relative humidity ranges from 66 to 81%, and rainfall ranges from 201 to 2724 mm. Thailand has 3 seasons: summer (March-June), rainy season (July-October), and winter (November-February; Meteorological Department, 2013). The dairy cattle population reported in 2013 consisted of 512,205 animals with 229,899 cows on 17,094 farms (Department of Livestock Development, 2014a), and raw milk production was approximately 1,067,452 tonnes per year (Office of Agricultural Economics, 2014a). The majority of dairy farmers (80%) are smallholders with an average of 30 animals per farm (calves, heifers, and cows). Most of the dairy cows are crossbred from *Bos indicus*, such as Sahiwal, Brahman, and Thai Native cattle upgraded by HF (Boonkum et al., 2011). Currently, the majority of the dairy population has >75% HF blood. Average milk yield per cow is 4,000 kg per lactation (Department of Livestock Development, 2014b) with some elite cows can produce 6,000 kg of milk per lactation. Generally, no cooling devices are available in the barns. More than 90% of dairy cattle are subjected to AI services provided by a government

organization (Department of Livestock Development, Thailand), and the rest are serviced by a semi-government organization (Dairy Promotion Organization, Thailand) and the dairy cooperatives in the areas. Frozen semen used for AI services is both imported and produced locally. The AI records of dairy cattle have been collected in the database system by AI technicians since 1996. Common feeding was practiced as described by Koonawootrittriron et al. (2009). The daily feed ration is based heavily on concentrates. Roughages commonly used consist of tropical grass, rice straw, and some agricultural wastes. The ingredient composition of the concentrate feed depends on local availability and price. However, shortages of roughage are serious in winter and summer, and farmers have to buy hay or rice straw or increase their use of commercial mixed rations.

Data and trait definitions

Data of pedigrees, breeding records, calving information, and lactation information of Thai dairy cattle, calving between 1996 and 2011, were obtained from the dairy cattle database of the Bureau of Biotechnology for Livestock Production, Department of Livestock Development, Thailand. The investigated traits were age at first service (**AFS**, mo), age at first calving (**AFC**, mo), **DTFS**, **DFLS**, **DO**, **CI**, **NSPC**, and conception at first service (**FSC**). The **NSPC** and **FSC** were considered as ordered categorical and binary traits, whereas the **DTFS**, **DFLS**, **DO**, and **CI** were determined as continuous traits (time interval traits). The traits recorded from birth to first calving were considered as heifer traits. Traits measured on first-lactation animals were considered as primiparous cow traits, and the traits measured from second to fifth lactation were considered as multiparous cow traits. Therefore, **AFS** and **AFC** were considered as specific traits for heifers, whereas **DTFS**, **DO**, and **CI** were considered as specific cow traits. The **DFLS**, **FSC**, and **NSPC** were defined for both heifers and cows. A conception for a heifer or a cow in a specific parity was determined with subsequent calving data that got along with the latest insemination data. A subsequent service within 10 d from previous insemination was considered a double insemination, and was discarded. Animals with complete records were included in

the analysis if at least one contemporary mate was present in a herd-year of first service subclass for heifers, and a herd-year of calving subclass for cows. The sires for heifers and cows in the data set were identified.

The final edited data sets for univariate analyses and bivariate analyses within parity included 68,555, 34,401, and 54,004 fertility records for 68,555 heifers, 34,401 primiparous cows, and 34,400 multiparous cows (1.57 records per cow), respectively. The data of primiparous cows were fewer than heifers in this population because some farmers have limited capacities such as land and funds, so they sold the pregnant heifers to other farms that are not under the Department of Livestock Development database system. For bivariate analyses across parity, the data sets consisted of 20,433, 16,986, and 16,107 animals for heifers-primiparous cows, heifers-multiparous cows, and primiparous-multiparous cows, respectively. For univariate and bivariate analyses within parity, the pedigree records were constructed by tracing 3 generations of ancestors, and 131,689, 72,624, and 67,887 heifers, primiparous cows, and multiparous cows, respectively, were found. In addition, the pedigree records of bivariate analyses across parity for heifers-primiparous cows, heifers-multiparous cows, and primiparous-multiparous cows were 47,413, 38,606, and 37,434 animals, respectively.

Model

The univariate analyses with linear and threshold animal model were performed for Gaussian and categorical traits, according to the following models, which were applied from Abe et al. (2009) and Tiezzi et al. (2012):

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_{hy}\mathbf{h}_y + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_{ss}\mathbf{ss} + \mathbf{e} \quad \text{for heifers and primiparous cows}$$

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_{hy}\mathbf{h}_y + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_p\mathbf{p} + \mathbf{Z}_{ss}\mathbf{ss} + \mathbf{e} \quad \text{for multiparous cows}$$

where \mathbf{y} is a vector of observations for linear traits (AFS, AFC, DTFS, DFLS, DO, and CI) or a vector of unobserved liabilities for categorical traits (NSPC and FSC); $\boldsymbol{\beta}$ is a vector of systematic effects; $\mathbf{hy} \sim N(0, \mathbf{I}\sigma_{hy}^2)$ is a vector of contemporary group (CG) effects, defined as the herd-year of first service effects for heifer traits and herd-year of calving effects for cow traits; $\mathbf{a} \sim N(0, \mathbf{A}\sigma_a^2)$ is a vector of additive genetic effects for all animals in the pedigree $\mathbf{p} \sim N(0, \mathbf{I}\sigma_p^2)$ is a vector of permanent environmental effects for all animals with records (only multiparous cows); $\mathbf{ss} \sim N(0, \mathbf{I}\sigma_{ss}^2)$ is a vector of service sire effects (only for FSC); $\mathbf{e} \sim N(0, \mathbf{I}\sigma_e^2)$ is a vector of residual effects; \mathbf{X} is the incidence matrix for fixed effects; \mathbf{Z}_{hy} , \mathbf{Z}_a , \mathbf{Z}_p , and \mathbf{Z}_{ss} are the incidence matrices for random effects; \mathbf{A} is the additive relationships matrix among animals; \mathbf{I} is the identity matrix; σ_{hy}^2 , σ_a^2 , σ_p^2 , σ_{ss}^2 and σ_e^2 are herd-year, additive genetic, permanent environment, service sire, and residual variances, respectively.

The following systematic effects were considered: breed group (4 classes) and year-month of first service (185 classes) for AFS and AFC in heifers; breed group (4 classes), AFS (5 classes), and year-month of first service (185 classes) for DFLS, FSC, and NSPC in heifers; breed group (4 classes), age at calving (7 classes), and year-month of calving (181 classes) for all traits in primiparous and multiparous cows. Effect of parity (4 classes) was also considered for multiparous cows. The effect of inseminator/AI technician was not considered because only one inseminator/AI technician was assigned to be responsible for one AI unit. Hence, this factor was completely accounted for by the management group effect (only one technician within a herd year or year-month).

Bivariate analyses were used to investigate the genetic relationship among different fertility traits within parity and between the same fertility traits across parity fitting linear-linear, threshold-linear, and threshold-threshold animal models. For within-parity analysis, only animals that had records for both traits were used. For across parity analysis, only animals that had records for both parities were used. The identical model to the univariate approach was assumed for each trait except analyses of AFC and the other heifer traits (NSPC, FSC, and DFLS) where AFS was not included in the model.

Estimation of genetic parameters

Estimates of (co)variance components from both univariate and bivariate analyses were calculated by a Bayesian implementation via Gibbs sampling. Computations were carried out using the program THRGIBBS1F90 (Tsuruta and Misztal, 2006). The total length of the Gibbs chain was 250,000 cycles with the first 50,000 cycles used as the burn-in period, which were determined based on visual inspection of trace plots of selected (co)variance components. Thinning interval was set to 20, and the resulting 10,000 samples were used to calculate posterior means and standard deviations. Posterior means were used as a point estimate of the (co)variance components for calculation heritabilities (h^2), herd contributions (c^2), genetic correlations (r_g) and phenotypic correlations (r_p).

RESULTS AND DISCUSSION

Descriptive statistics

Table 3-1 shows least squares means of various fertility traits in different parities and breed groups. The mean AFS and AFC were 22.9 and 32.9 mo. The FSC of heifers was 16.7 and 15.2% higher than that of primiparous and multiparous cows, respectively, whereas NSPC and DFLS of heifers were 0.57 services and 20.9 d less than primiparous cows and 0.49 services and 17.6 d less than multiparous cows. Moreover, the tendency of all traits in the multiparous cows was better than those in the primiparous cows. Generally, reproductive efficiency in heifers and cows trended to be lower as HF blood increased. The breed group with $\geq 93.75\%$ HF had the lowest reproductive performance.

The mean of AFS was higher than 499.7 ± 53.6 d (16.7 mo) reported in Canadian Holsteins (Jamrozik et al., 2005), 518.6 ± 84.8 d (17.3 mo) in Japanese Holsteins (Abe et al., 2009), 482.4 ± 40.87 d (16.1 mo) in Iranian Holsteins (Eghbalsaied, 2011), and 519.8 ± 51.1 d (17.3 mo) in Chinese

Holsteins (Guo et al., 2014). The longer AFS in Thai dairy cattle could be due to the environmental condition, particularly feeding level. It is generally recognized that dairy heifers in tropical areas have a lower growth rate than those in temperate areas (Vaccaro and Rivero, 1985).

Table 3-1. Least square means (SE) of fertility traits in different parities and breed groups

Item	n	Traits ¹							
		AFS (mo)	AFC (mo)	NSPC (no)	FSC (%)	DFLS (d)	DTFS (d)	DO (d)	CI (d)
Heifers									
<81.25%HF	8,368	23.3 (0.1)	33.3 (0.1)	1.55 (0.03)	67.7 (1.0)	25.5 (1.3)			
81.25-87.49%HF	11,967	22.9 (0.1)	32.9 (0.1)	1.58 (0.03)	67.8 (0.9)	26.6 (1.3)			
87.5-93.74%HF	26,832	22.6 (0.1)	32.7 (0.1)	1.57 (0.02)	67.9 (0.9)	27.4 (1.2)			
>=93.75%HF	21,388	22.6 (0.1)	32.6 (0.1)	1.57 (0.02)	68.0 (1.0)	27.6 (1.2)			
Total	68,555	22.9 (0.1)	32.9 (0.1)	1.57 (0.02)	67.9 (0.9)	26.8 (1.1)			
Primiparous cows									
<81.25%HF	4,911			2.01 (0.03)	54.3 (1.1)	42.0 (1.5)	97.2 (1.0)	134.9 (1.4)	419.9 (1.7)
81.25-87.49%HF	6,394			2.14 (0.03)	51.1 (1.1)	47.8 (1.4)	99.5 (1.0)	141.8 (1.4)	428.2 (1.7)
87.5-93.74%HF	13,039			2.15 (0.03)	50.4 (1.0)	48.3 (1.3)	102.6 (0.9)	145.8 (1.2)	432.3 (1.5)
>=93.75%HF	10,057			2.24 (0.03)	48.9 (1.0)	52.6 (1.3)	104.0 (0.9)	149.6 (1.3)	436.8 (1.6)
Total	34,401			2.14 (0.03)	51.2 (1.0)	47.7 (1.2)	100.8 (0.8)	143.0 (1.2)	429.3 (1.4)
Multiparous cows									
<81.25%HF	9,583			1.95 (0.03)	56.2 (1.1)	38.4 (1.4)	90.2 (0.9)	128.1 (1.2)	411.6 (1.5)
81.25-87.49%HF	11,125			2.02 (0.03)	53.5 (1.1)	42.9 (1.3)	93.2 (0.9)	135.1 (1.2)	419.7 (1.5)
87.5-93.74%HF	19,446			2.11 (0.03)	51.3 (1.0)	46.7 (1.3)	95.2 (0.8)	139.7 (1.1)	425.3 (1.4)
>=93.75%HF	13,850			2.17 (0.03)	49.8 (1.0)	49.7 (1.3)	97.4 (0.8)	143.7 (1.2)	430.2 (1.5)
Total	54,004			2.06 (0.03)	52.7 (1.0)	44.4 (1.2)	94.0 (0.8)	136.7 (1.1)	421.7 (1.3)

¹AFS = age at first service; AFC = age at first calving; NSPC = number of service per conception; FSC = conception at first service; DFLS = days between first and last service; DTFS = days from calving to first service; DO = days from calving to successful conception; CI = calving interval.

The FSC, NSPC, and DFLS in heifers were better than in primiparous and multiparous cows because they were not yet affected by calving and lactation status. The reproductive performance in primiparous cows was inferior compared with multiparous cows. This might be due to the norm of practice of small dairy farmers in Thailand who traditionally raise their female calves, heifers, and pregnant heifers less intensively than cows providing income at the moment. Consequently, these animals are always neglected under improper nutrition management. The results were in agreement with the report of Pongpiachan et al. (2003) and Leelasiri et al. (2006). However, this might be in contrast to results obtained under the normal management protocols in advanced dairy industry countries.

Heritabilities

Table 3-2 shows the posterior means and the 95% high posterior density intervals of heritabilities and herd contributions for various fertility traits in different parities from univariate analyses. Moderate heritabilities were obtained for AFS (0.26) and AFC (0.28). For AFS, the heritability estimate was close to a report of Estrada-León et al. (2008) for Brown Swiss (**BS**) in the tropics of Mexico (0.28) but lower than those reviewed by Lôbo et al. (2000) for tropical dairy cattle (0.60). This value was also higher than the estimates for Canadian Holsteins (Jamrozik et al., 2005), Japanese Holsteins (Abe et al., 2009), Iranian Holsteins (Eghbalsaied, 2011), Dutch Holsteins (De Haer et al., 2013), and Chinese Holsteins (Guo et al., 2014). The result suggested that genetic improvement of AFS could be achieved by selection. The heritabilities for other traits were 0.04 or less, which were lower than previous studies in Canadian Holsteins (Jamrozik et al., 2005) and Japanese Holsteins (Abe et al., 2009) but similar to a report in Thai dairy cattle (König et al., 2005). The heritabilities between 0.01 and 0.04 for cow fertility traits were also found in Cuban Holsteins (Buxadera and Dempfle, 1997), Kenyan Holsteins (Ojango and Pollott, 2001), Ethiopian dairy cows (Demeke et al., 2004), Mexican BS (Estrada-León et al., 2008; Utrera et al., 2010), and Colombian Holsteins (Zanbrano and Echeverri, 2014) under tropical, smallholder conditions. The low heritability in this study suggested that improvement of fertility traits

in heifers and cows could be achieved by improving reproductive managements such as successful detection of heat, timely insemination, and feeding practice for growing and postpartum animals. However, the variability among papers was also due to the methodology used.

Table 3-2. Estimates¹ of heritability and herd contribution for various fertility traits in different parities

Parameter	Traits ²	Heifers		Primiparous cows		Multiparous cows	
		Mean	HPD95	Mean	HPD95	Mean	HPD95
Heritability	AFS	0.26	0.24, 0.28				
	AFC	0.25	0.23, 0.27				
	NSPC	0.02	0.01, 0.03	0.03	0.01, 0.05	0.02	0.01, 0.04
	FSC	0.01	0.01, 0.02	0.02	0.01, 0.03	0.02	0.01, 0.03
	DFLS	0.01	0.00, 0.01	0.02	0.01, 0.03	0.01	0.01, 0.02
	DTFS			0.03	0.02, 0.05	0.03	0.02, 0.04
	DO			0.04	0.03, 0.05	0.03	0.02, 0.05
	CI			0.04	0.03, 0.05	0.03	0.02, 0.05
Herd contribution	AFS	0.38	0.37, 0.38				
	AFC	0.34	0.33, 0.34				
	NSPC	0.09	0.08, 0.11	0.11	0.09, 0.13	0.08	0.06, 0.09
	FSC	0.10	0.08, 0.11	0.10	0.08, 0.11	0.08	0.06, 0.09
	DFLS	0.06	0.05, 0.07	0.07	0.05, 0.08	0.05	0.04, 0.05
	DTFS			0.15	0.13, 0.16	0.11	0.10, 0.11
	DO			0.08	0.07, 0.09	0.05	0.04, 0.06
	CI			0.08	0.07, 0.09	0.05	0.04, 0.06

¹Means and the 95% highest posterior density intervals (HPD95) for the posterior distributions.

²AFS = age at first service; AFC = age at first calving; NSPC = number of service per conception; FSC = conception at first service; DFLS = days between first and last service; DTFS = days from calving to first service; DO = days from calving to successful conception; CI = calving interval.

Herd contributions were always higher than heritabilities in all fertility traits (Table 3-2), ranging from 0.05 for DFLS, DO, and CI in multiparous cows to 0.38 for AFS in heifers. No reference was found to estimate herd contribution for dairy fertility traits in a tropical environment. Jamrozik et al. (2005) and Abe et al. (2009) reported high estimates of herd contribution for AFS in Holsteins (0.48 and 0.50, respectively). The higher estimate in AFS and AFC could be due to different feeding practices and farmer or breeder decisions on breeding age across herds. Another high herd contribution was 0.15 in DTFS for primiparous cows, which is similar to the reports by Jamrozik et al. (2005), Abe et al. (2009), and Tiezzi et al. (2012). The estimates of herd contribution for NSPC, FSC, DFLS, DO, and CI were

low, which implies lower variability of average reproductive efficiency across herd-year class. For FSC, the ratio of variance of service sire to total variance was 0.01 or lower for both heifers and cows (not shown). Very small variance of service sire was reported in an intensive system (Jamrozik et al., 2005; Kuhn and Hutchinson, 2008; Tiezzi et al., 2013). Repeatabilities of fertility traits for multiparous cows (not shown) ranged from 0.10 (DFLS) to 0.17 (DTFS). The estimates were within the range reported for dairy cattle in tropical environment (Ojango and Pollott, 2001; Demeke et al., 2004; Estrada-León et al., 2008).

Genetic correlations among different fertility traits within parity

Table 3-3 shows genetic correlations estimated among different fertility traits within parity. The estimated genetic correlations were close to 1 for AFS and AFC, NSPC and DFLS, and DO and CI, and close to -1 for NSPC and FSC, and DFLS and FSC. The results were in agreement with previous studies (Jamrozik et al., 2005; Abe et al., 2009; Eghbalsaid, 2011; Guo et al., 2014). These results suggested that the traits in this study were essentially the same indicator of fertility and may be originally the same in terms of genetic source. Moreover, the FSC and NSPC in both heifers and cows had very high favorable genetic correlations with DO and CI ranged from -0.96 to 0.89 . However, correlation estimates between DO and CI depended on the definition of DO, which is based on subsequent calving, on non-return to estrus within 90 d after last service or on pregnancy diagnosis. The DO based on non-return in estrus or on pregnancy diagnosis could be more interesting, even if possibly less accurate than those based on subsequent calving because it allows an acceleration of at least 6 mo in genetic evaluation of cows, and especially, of AI bulls at their first proofs.

A slight correlation was found between AFS or AFC and NSPC, FSC, and DFLS. This indicated that selection for lower AFS or AFC had little correlated responses to NSPC, FSC, and DFLS in heifers. This is because AFS and AFC often reflect body growth of the heifer rather than its fertility. Therefore body size of heifers is mainly considered by breeders or farmers when deciding on the right moment for

inseminations. Low genetic correlation of AFC with heifer fertility traits was also reported in intensive dairy systems (Jamrozik et al., 2005; Abe et al., 2009). Eghbalsaid (2011) found low to moderate positive genetic correlations in Iranian Holsteins. The estimated genetic correlations among different fertility traits indicated that selection for cows with high conception rate could lead to shorten DO and CI, as well as DTFS.

Table 3-3. Estimates¹ of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among fertility traits within different parities

Parity		Traits ²					
		AFS	AFC	NSPC	FSC	DFLS	
Heifer	AFS		1.00 (1.00, 1.00)	-0.19 (-0.43, 0.04)	0.15 (-0.15, 0.42)	-0.31 (-0.54, 0.05)	
	AFC	0.94 (0.94, 0.94)		-0.04 (-0.24, 0.22)	0.12 (-0.13, 0.32)	-0.02 (-0.32, 0.31)	
	NSPC	0.26 (0.25, 0.27)	-0.08 (-0.11, -0.05)		-1.00 (-1.00, -1.00)	0.85 (0.70, 0.92)	
	FSC	0.06 (0.03, 0.10)	-0.25 (-0.26, -0.24)	-1.00 (-1.00, -0.99)		-0.99 (-1.00, -0.32)	
	DFLS	-0.08 (-0.11, -0.05)	0.29 (0.29, 0.30)	0.73 (0.72, 0.75)	-0.73 (-0.77, -0.16)		
		NSPC	FSC	DFLS	DTFS	DO	CI
Primiparous cows	NSPC		-1.00 (-1.00, -1.00)	1.00 (0.99, 1.00)	0.58 (0.27, 0.83)	0.87 (0.77, 0.96)	0.89 (0.78, 0.98)
	FSC	-0.99 (-0.99, -0.99)		-1.00 (-1.00, -0.99)	-0.70 (-0.91, -0.41)	-0.95 (-0.99, -0.86)	-0.96 (-1.00, -0.87)
	DFLS	0.81 (0.80, 0.83)	-0.70 (-0.71, -0.69)		0.58 (0.22, 0.81)	0.91 (0.83, 0.97)	0.91 (0.83, 0.96)
	DTFS	-0.09 (-0.11, -0.08)	0.07 (0.05, 0.08)	-0.09 (-0.10, -0.08)		0.87 (0.75, 0.96)	0.86 (0.73, 0.95)
	DO	0.69 (0.68, 0.70)	-0.75 (-0.76, -0.75)	0.83 (0.83, 0.83)	0.48 (0.47, 0.49)		1.00 (1.00, 1.00)
	CI	0.68 (0.67, 0.70)	-0.75 (-0.76, -0.74)	0.83 (0.82, 0.83)	0.48 (0.47, 0.49)	1.00 (1.00, 1.00)	
Multiparous cows	NSPC		-1.00 (-1.00, -1.00)	0.95 (0.88, 0.98)	0.28 (-0.09, 0.63)	0.71 (0.51, 0.86)	0.68 (0.48, 0.84)
	FSC	-1.00 (-1.00, -1.00)		-1.00 (-1.00, -1.00)	-0.28 (-0.72, 0.11)	-0.80 (-0.94, -0.55)	-0.78 (-0.73, -0.72)
	DFLS	0.81 (0.79, 0.82)	-1.00 (-1.00, -1.00)		0.72 (0.42, 0.91)	0.94 (0.86, 0.98)	0.92 (0.81, 0.97)
	DTFS	-0.13 (-0.14, -0.12)	0.12 (0.11, 0.13)	-0.10 (-0.11, -0.10)		0.93 (0.82, 0.98)	0.94 (0.85, 0.98)
	DO	0.67 (0.66, 0.69)	-0.73 (-0.74, -0.72)	0.83 (0.83, 0.83)	0.47 (0.46, 0.48)		1.00 (0.99, 1.00)
	CI	0.67 (0.66, 0.69)	-0.72 (-0.73, -0.72)	0.83 (0.82, 0.83)	0.47 (0.46, 0.48)	1.00 (1.00, 1.00)	

¹Means (and the 95% highest posterior density interval in the parentheses) for the posterior distributions.

²AFS = age at first service; AFC = age at first calving; NSPC = number of service per conception; FSC = conception at first service; DFLS = days between first and last service; DTFS = days from calving to first service; DO = days from calving to successful conception; CI = calving interval.

The FSC and NSPC in both heifers and cows had the highest average of absolute genetic correlations with other traits even though the lowest heritability belonged to this group. Therefore, they could be used as one of the best indicators for heifer/cow fertility and could be complemented by other traits which were genetically considered as different traits such as DTFS and in terms of a fertility index. This would enable efficient selection for better reproductive performance.

Genetic correlation between the same fertility traits across parity

Table 3-4 shows genetic correlations among fertility traits treated as different traits across parities. The highest estimates were obtained between primiparous and multiparous cows, ranging from 0.91 for FSC to 0.99 for DO and CI.

Table 3-4. Estimates¹ of genetic correlations among fertility traits treated as different trait across parities

Traits ²	Heifer-primiparous cows		Heifers-multiparous cows		Primiparous-multiparous cows	
	Mean	HPD95	Mean	HPD95	Mean	HPD95
NSPC	0.83	0.72, 0.93	0.68	0.39, 0.95	0.95	0.90, 0.98
FSC	0.81	0.65, 0.96	0.37	-0.06, 0.87	0.91	0.85, 0.97
DFLS	0.40	-0.04, 0.72	-0.03	-0.80, 0.90	0.98	0.93, 1.00
DTFS					0.98	0.95, 1.00
DO					0.99	0.96, 1.00
CI					0.99	0.96, 1.00

¹Means and the 95% highest posterior density intervals (HPD95) for the posterior distributions.

² NSPC = number of service per conception; FSC = conception at first service; DFLS = days between first and last service; DTFS = days from calving to first service; DO = days from calving to successful conception, calving.

The similar results were found for purebred Holsteins in intensive system (Haile-Mariam et al., 2003b; Abe et al., 2009) and BS in a mountain climate (Tiezzi et al., 2012). No reports of the genetic correlations in tropical dairy cattle were found. The genetic correlations suggested that fertility measured in subsequent parity can be regarded as the same trait as the first parity. Genetic correlation between heifers and primiparous cows was high for NSPC (0.83) and FSC (0.81) but not significantly

different from zero for DFLS (0.40). For NSPC, the estimated genetic correlation between heifers and primiparous cows was higher than the result for Canadian Holsteins (Jamrozik et al., 2005), German and Austrian Simmental (Gredler et al., 2007), and Italian BS (Tiezzi et al., 2012). For FSC, Abe et al. (2009) reported a genetic correlation of 0.74 between heifers and primiparous cows, whereas the value assessed by Tiezzi et al. (2012) on BS was lower (0.35). For DFLS, a moderate to high genetic correlation between heifers and primiparous cows was reported in Swiss Simmental (0.40, Hodel et al., 1995), Canadian Holsteins (0.72, Jamrozik et al., 2005), German dairy cattle (0.48, Liu et al., 2008), and Italian BS (0.55, Tiezzi et al., 2012). Genetic correlation between heifers and multiparous cows was 0.68 for NSPC but not significantly different from zero for FSC and DFLS (0.37 and -0.03). The estimates were lowest compared with the estimates for heifers and primiparous cows, and estimates for primiparous and multiparous cows (0.91 and 0.98). These results were different from the study of Tiezzi et al. (2012), which reported that the genetic correlations of the mentioned traits between heifers and multiparous cows were intermediate and positive between estimates for heifers and primiparous cows and primiparous and multiparous cows. However, the estimated genetic correlation between heifers and primiparous cows, as well as primiparous and multiparous cows in the current study showed the same trend as in studies of Roxström et al. (2001) and Tiezzi et al. (2012).

Overall, the genetic correlations between heifers and cows fertility were far from 1. The results suggested that fertility traits in heifers were genetically different from the traits in cows because the animal was not subjected to the same metabolic load during the heifer period as during the lactation period. Therefore in selection for improvement of heifer and cow fertility efficiency, it should be analyzed as separate traits in a multiple-trait model for fertility index development.

CONCLUSION

In conclusion, reproductive efficiency in heifers and cows showed a trend to be lower as HF blood increased. Estimated heritabilities of reproductive traits in heifer and cow were 0.04 or less, only the heritabilities for AFS and AFC were slightly higher, which were similar to the results in the literature. Selection for cows with high conception rate could lead to shortened DO, CI, and DTFS. The FSC and NSPC could be used as the best indicators for heifer/cow fertility and could be complemented by other traits that were genetically considered as different traits such as DTFS and DFLS in terms of a fertility index. This would enable efficient selection for better fertility. Heifer and cow fertility should be considered as different traits in evaluation for genetic improvement. However, virgin heifer traits are measured relatively early in life, and therefore they should be included in tropical dairy cattle breeding program to improve the efficiency of fertility.

Chapter IV

Genetic relationships of fertility traits with test-day milk yield and fat-to-protein ratio in tropical smallholder dairy farms

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INTRODUCTION

In most of tropical regions in Asia including Thailand, dairy farm systems are smallholder, and crossbreeding programs of local breeds with temperate dairy breeds are the most important strategy in increasing milk production (Buaban et al., 2015). Therefore, milk yield is a major trait of selection in breeding programs for the dairy cattle. The condition, that the main dairy market in such areas is ready-to-drink milk, has been a crucial drive to the aforesaid selection criteria.

Not different from advanced dairy raising countries, increasing incidences of fertility problems in dairy cattle related with milk yield increased (De Vries and Veerkamp, 2000; Oikonomou et al., 2008) since the genetic relationship between milk yield and fertility traits is antagonistic (Liu et al., 2008). It is therefore necessary that apart from the milk production, the fertility is also to be included in the breeding goal in order to optimize the result of genetic improvement of dairy cattle.

Negative energy balance (**NEB**) was declared as one of the most important biological pathway and physiological process behind fertility problems, which often occurred during early lactation (Veerkamp et al., 2000; Wathes et al., 2007). However, energy balance is difficult to measure in large populations, leading to increased interest in other traits, which may be the indicators of energy balance (Coffey et al., 2001) and may subsequently be related to health and fertility status of the animals. Milk composition data in term of test-day milk fat-to-protein ratio (**TD-FPR**) could be used as an alternative indicator of a cow's tissue energy status (Heuer et al., 1999) and can serve as predictor for estimating breeding values for fertility traits (Berry et al., 2003). Moreover, TD-FPR data is available in almost every dairy herds recording scheme. Hence, fertility efficiency might be improved as a whole by genetic selection of TD-FPR if it was found heritable and could be incorporated in the breeding objectives together with production traits in term of selection index.

Nevertheless, researches on genetic analyses of fertility traits and energy balance in dairy cattle under tropical condition are very few with limited small data set from a few numbers of herds or within

a breeding station. Most of them have been reported at the phenotypic level or general genetic variation of fat, protein and TD-FPR (König et al., 2005; Estrada-León et al., 2008; Rukkwamsuk, 2010; Puangdee et al., 2012).

Therefore, the objectives of this study were to estimate genetic parameters for fertility traits, test-day milk yield (**TD-MY**) and TD-FPR as well as their relationship during different stages of lactation using random regression models (**RRM**) on Thai dairy crossbred cows in a smallholder system under tropical condition. The data on fertility traits, milk yields and milk components from AI and milk records database under the national recording scheme of Thai dairy cattle were verified and analyzed.

MATERIALS AND METHODS

Data and trait definitions

Data on fertility traits and monthly test-day record of milk production and milk compositions of the primiparous Thai dairy crossbred cows, calving between 1996 and 2011, were obtained from the national dairy database of the Bureau of Biotechnology for Livestock Production, Department of Livestock Development, Thailand.

Fertility traits selected for this study were days from calving to first service (**DTFS**), days between first and last service (**DFLS**), days open (**DO**), calving interval (**CI**), number of inseminations per conception (**NSPC**), conception at first service (**FSC**) and pregnancy within 90 days after the first service (**P90**). DO was defined as the days between the calving and the conception date in the current parity. NSPC was defined as ordered categorical whereas the last two traits, FSC and P90 were considered as binary traits. FSC was defined as '1' if the cow was confirmed pregnant after first insemination or '0' otherwise. P90 were defined as '1' if the successful insemination date was within 90 days after the first insemination otherwise P90 was defined as '0'. The DTFS, DFLS, DO and CI were determined as interval traits. Conception date was determined using subsequent calving date that got

along with the last insemination date before the consecutive calving. A conception record was discarded if the consecutive calving date was unknown or if days between the conception and the consecutive calving were less than 265 or more than 295 (the range of ± 3 standard deviation units from the overall mean of the day between last insemination date and consecutive calving date).

A test-day record comprised of observations on test-day milk, fat and protein yield with approximate 30 days interval from 5 to 365 DIM. Milk compositions were analyzed using CombifossTM, milk composition analyzer machine. The TD-FPR was calculated for each test-day.

To obtain consistent data sets, the data of individual cow was matched between pedigree, lactation, and calving performance information. The data of the cows including in the analysis must have sire identified with age at first calving between 18 and 48 months. Moreover, their records must be under the herd-year of calving subclass with at least one complete fertility contemporary record. The records of fertility traits within the following range were considered allowed: DFLS less than 370 days, NSPC between 1 and 10, DTFS between 20 and 250 days, DO between 20 and 400 days, and CI between 290 and 690 days. Cows with complete records according to the mentioned criteria were included in the analysis.

The final datasets in univariate analyses included 10,055 records (10,055 heads) for fertility traits and 223,449 (25,968 heads) records for milk traits. In bivariate analyses, the datasets consisted of 88,482 records (10,055 heads) for analyses among fertility traits with TD-MY and TD-FPR, and 223,449 records (25,968 heads) for analyses between TD-MY and TD-FPR. The pedigree records were constructed by tracing back 3 generations of ancestors. There were 23,111 animals in univariate analyses of fertility traits and bivariate analyses among fertility with TD-MY and TD-FPR, and 49,403 animals for univariate analyses of TD-MY and TD-FPR and bivariate analyses between TD-MY and TD-FPR. Breed groups of cows were classified into 4 classes considering percentage of HF blood: <81.25%, 81.25 to 87.49%, 87.50 to 93.74%, and $\geq 93.75\%$. Age at first calving was classed to 7 classes by three months interval with <25 month being the first class and >39 months being the last

class. Season of calving was classed to summer (March - June), rainy season (July - October) and winter (November - February). Descriptive statistic of the studied traits is shown in Table 4-1.

Statistical analysis

Preliminary univariate RRM analyses for test-day traits (TD-MY and TD-FPR) were performed to determine the appropriate order of Legendre polynomials for modeling random regression effects in test-day model. A model used for analysis was

$$y_{ijklmpt} = ym_i + age_j + bg_k + \sum_{r=0}^n \beta_{lr} \pi_r(DIM_t) + htm_m + \sum_{r=0}^{n_a} a_{pr} \phi_r(DIM_t) + \sum_{r=0}^{n_p} p_{pr} \phi_r(DIM_t) + e_{ijklmpt} ,$$

where $y_{ijklmpt}$ is test-day observation (TD-MY or TD-FPR), recorded in calving year \times month i , in herd \times test-month m , on a cow p belonging to the calving age class j , breed class k , calving-year \times calving-season class l , and measured on DIM t ($t = 5, \dots, 365$); ym_i is fixed effect of i^{th} calving year \times month ($i = 1, \dots, 234$); age_j is fixed effect of j^{th} age at calving class ($j = 1, \dots, 7$); bg_k is fixed effect of k^{th} breed class ($k = 1, \dots, 4$); htm_m is random effect of m^{th} herd test-month ($m = 1, \dots, 113,739$); $\pi_r(DIM_t)$ is the r^{th} covariate from the third-order orthogonal Legendre polynomial and the exponential term of Wilmink function (Wilmink, 1987) at days in milk t ; $\phi_r(DIM_t)$ is the r^{th} coefficient of Legendre polynomials evaluated at DIM t ; n is the order of fit for fixed regression coefficients ($n=4$); n_a is the order of fit for additive genetic (**AG**) random regression coefficients; n_p is the order of fit for permanent environmental (**PE**) random; β_{lr} is fixed regressions coefficients to describe the shape of the lactation curve within year \times season of calving class l ; a_{pr} is the r^{th} random regression coefficient of **AG** value of p^{th} animal; p_{pr} is the r^{th} random regression coefficient of PE effect of p^{th} animal; and $e_{ijklmpt}$ is the random residual.

The covariables for coefficients β_r were

$$\boldsymbol{\pi}_r(DIM_t) = [c_0 \ c_1 \ c_2 \ c_3 \ \exp(wt)]^T \quad [1]$$

where $c_0 \ c_1 \ c_2 \ c_3$ represent coefficients of the third-order orthogonal Legendre polynomial at DIM t , and w is coefficient of the exponential term of the Wilmink function (Wilmink, 1987). The most appropriate w that fitted the current data for modeling the fixed lactation curves of TD-MY and TD-FPR were estimated to be -0.06 .

The RRM for AG and PE effects, with different orders of fit, were compared by the log-likelihoods, Akaike's information criteria (Burnham and Anderson, 2002). Residual variances and eigenvalues of the AG covariance matrices were analyzed to assess the importance of adding further parameters. The model with the highest log-likelihoods, lowest AIC and residual variance was considered to be the most appropriate and be selected. As a result of the study, Legendre polynomials of the second- and third-order were used to describe regression curves for TD-FPR and TD-MY, respectively. Bivariate analysis were then used to estimate the genetic and phenotypic relationship between the different fertility traits and TD-MY and TD-FPR, as well as, between TD-MY and TD-FPR. Only the intercept term was fitted for the different lactation-wise fertility traits.

The covariables for coefficients of random effects (a_r and p_r) were

$$\boldsymbol{\phi}_r(DIM_t) = [c_0 \ c_1 \ c_2]^T \quad \text{for TD-FPR} \quad [2]$$

$$\boldsymbol{\phi}_r(DIM_t) = [c_0 \ c_1 \ c_2 \ c_3]^T \quad \text{for TD-MY} \quad [3]$$

A model used for a univariate fertility trait analysis was

$$y_{ijkmp} = ym_i + age_j + bg_k + hy_m + a_p + e_{ijkmp} ,$$

where y_{ijkmp} are observations on fertility, recorded in calving year \times month i , herd-year of calving m , on an animal p belonging to the calving age class j , breed class k ; ym_i is fixed effect of calving year \times month i ; age_j is fixed effect of age at calving j ; bg_k is fixed effect of breed group k ; hy_m is random effect of herd-year of calving m ; a_p is AG effect of animal p ; and e_{ijkmp} is the random residual.

The description of the bivariate RRM for TD-MY and TD-FPR (model I) was

$$\begin{bmatrix} \mathbf{y}_m \\ \mathbf{y}_r \end{bmatrix} = \begin{bmatrix} \mathbf{X}_m & 0 \\ 0 & \mathbf{X}_r \end{bmatrix} \begin{bmatrix} \mathbf{b}_m \\ \mathbf{b}_r \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{htm_m} & 0 \\ 0 & \mathbf{Z}_{htm_r} \end{bmatrix} \begin{bmatrix} \mathbf{htm}_m \\ \mathbf{htm}_r \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a_m} & 0 \\ 0 & \mathbf{Z}_{a_r} \end{bmatrix} \begin{bmatrix} \mathbf{a}_m \\ \mathbf{a}_r \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{p_m} & 0 \\ 0 & \mathbf{Z}_{p_r} \end{bmatrix} \begin{bmatrix} \mathbf{p}_m \\ \mathbf{p}_r \end{bmatrix} + \begin{bmatrix} \mathbf{e}_m \\ \mathbf{e}_r \end{bmatrix}$$

where \mathbf{y}_m and \mathbf{y}_r are a vector of observations of TD-MY and TD-FPR, respectively; \mathbf{b}_m and \mathbf{b}_r are vectors of systematic effects; \mathbf{htm}_m and \mathbf{htm}_r are vectors of contemporary group (CG) random effects; \mathbf{a}_m and \mathbf{a}_r are vectors of random regression coefficients of AG effects for all animals in the pedigree; \mathbf{p}_m and \mathbf{p}_r are vectors of random regression coefficients of PE effect for all animals with records; \mathbf{e}_m and \mathbf{e}_r are vectors of random residual effects and $\mathbf{X}_m, \mathbf{X}_r, \mathbf{Z}_{htm_m}, \mathbf{Z}_{htm_r}, \mathbf{Z}_{a_m}, \mathbf{Z}_{a_r}, \mathbf{Z}_{p_m}$ and \mathbf{Z}_{p_r} are the corresponding incidence matrices.

The vector \mathbf{b}_m and \mathbf{b}_r included systematic effects of breed group, age at first calving and year-month of calving, as well as, fixed regression describing the shape of lactation curve within year-season of calving class.

The covariance structure for models was defined as

$$\text{Var} \begin{bmatrix} \mathbf{htm} \\ \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{H} \otimes \mathbf{I} & 0 & 0 & 0 \\ 0 & \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & 0 & \mathbf{P} \otimes \mathbf{I} & 0 \\ 0 & 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{H} is a diagonal matrix having variances of the random htm effects for TD-MY and TD-FPR, \mathbf{A} is the matrix of AG relationships among animals, \otimes is the Kronecker product, \mathbf{G} and \mathbf{P} are 7 x 7

matrices of (co)variances for the AG and PE random regression coefficients, respectively, and \mathbf{R} is 2 x 2 residual covariance matrix.

$$\text{where } \mathbf{H} = \begin{bmatrix} \sigma_{htm_m}^2 & \sigma_{htm_r htm_m} \\ \sigma_{htm_m htm_r} & \sigma_{htm_r}^2 \end{bmatrix},$$

$$\mathbf{G} = \begin{bmatrix} \sigma_{a_{m1}}^2 & \sigma_{a_{m2}a_{m1}} & \sigma_{a_{m3}a_{m1}} & \sigma_{a_{m4}a_{m1}} & \sigma_{a_{r1}a_{m1}} & \sigma_{a_{r2}a_{m1}} & \sigma_{a_{r3}a_{m1}} \\ \sigma_{a_{m1}a_{m2}} & \sigma_{a_{m2}}^2 & \sigma_{a_{m3}a_{m2}} & \sigma_{a_{m4}a_{m2}} & \sigma_{a_{r1}a_{m2}} & \sigma_{a_{r2}a_{m2}} & \sigma_{a_{r3}a_{m2}} \\ \sigma_{a_{m1}a_{m3}} & \sigma_{a_{m2}a_{m3}} & \sigma_{a_{m3}}^2 & \sigma_{a_{m4}a_{m3}} & \sigma_{a_{r1}a_{m3}} & \sigma_{a_{r2}a_{m3}} & \sigma_{a_{r3}a_{m3}} \\ \sigma_{a_{m1}a_{m4}} & \sigma_{a_{m2}a_{m4}} & \sigma_{a_{m3}a_{m4}} & \sigma_{a_{m4}}^2 & \sigma_{a_{r1}a_{m4}} & \sigma_{a_{r2}a_{m4}} & \sigma_{a_{r3}a_{m4}} \\ \sigma_{a_{m1}a_{r1}} & \sigma_{a_{m2}a_{r1}} & \sigma_{a_{m3}a_{r1}} & \sigma_{a_{m4}a_{r1}} & \sigma_{a_{r1}}^2 & \sigma_{a_{r2}a_{r1}} & \sigma_{a_{r3}a_{r1}} \\ \sigma_{a_{m1}a_{r2}} & \sigma_{a_{m2}a_{r2}} & \sigma_{a_{m3}a_{r2}} & \sigma_{a_{m4}a_{r2}} & \sigma_{a_{r1}a_{r2}} & \sigma_{a_{r2}}^2 & \sigma_{a_{r3}a_{r2}} \\ \sigma_{a_{m1}a_{r3}} & \sigma_{a_{m2}a_{r3}} & \sigma_{a_{m3}a_{r3}} & \sigma_{a_{m4}a_{r3}} & \sigma_{a_{r1}a_{r3}} & \sigma_{a_{r2}a_{r3}} & \sigma_{a_{r3}}^2 \end{bmatrix},$$

$$\mathbf{P} = \begin{bmatrix} \sigma_{p_{m1}}^2 & \sigma_{p_{m2}p_{m1}} & \sigma_{p_{m3}p_{m1}} & \sigma_{p_{m4}p_{m1}} & \sigma_{p_{r1}p_{m1}} & \sigma_{p_{r2}p_{m1}} & \sigma_{p_{r3}p_{m1}} \\ \sigma_{p_{m1}p_{m2}} & \sigma_{p_{m2}}^2 & \sigma_{p_{m3}p_{m2}} & \sigma_{p_{m4}p_{m2}} & \sigma_{p_{r1}p_{m2}} & \sigma_{p_{r2}p_{m2}} & \sigma_{p_{r3}p_{m2}} \\ \sigma_{p_{m1}p_{m3}} & \sigma_{p_{m2}p_{m3}} & \sigma_{p_{m3}}^2 & \sigma_{p_{m4}p_{m3}} & \sigma_{p_{r1}p_{m3}} & \sigma_{p_{r2}p_{m3}} & \sigma_{p_{r3}p_{m3}} \\ \sigma_{p_{m1}p_{m4}} & \sigma_{p_{m2}p_{m4}} & \sigma_{p_{m3}p_{m4}} & \sigma_{p_{m4}}^2 & \sigma_{p_{r1}p_{m4}} & \sigma_{p_{r2}p_{m4}} & \sigma_{p_{r3}p_{m4}} \\ \sigma_{p_{m1}p_{r1}} & \sigma_{p_{m2}p_{r1}} & \sigma_{p_{m3}p_{r1}} & \sigma_{p_{m4}p_{r1}} & \sigma_{p_{r1}}^2 & \sigma_{p_{r2}p_{r1}} & \sigma_{p_{r3}p_{r1}} \\ \sigma_{p_{m1}p_{r2}} & \sigma_{p_{m2}p_{r2}} & \sigma_{p_{m3}p_{r2}} & \sigma_{p_{m4}p_{r2}} & \sigma_{p_{r1}p_{r2}} & \sigma_{p_{r2}}^2 & \sigma_{p_{r3}p_{r2}} \\ \sigma_{p_{m1}p_{r3}} & \sigma_{p_{m2}p_{r3}} & \sigma_{p_{m3}p_{r3}} & \sigma_{p_{m4}p_{r3}} & \sigma_{p_{r1}p_{r3}} & \sigma_{p_{r2}p_{r3}} & \sigma_{p_{r3}}^2 \end{bmatrix},$$

$$\text{and } \mathbf{R} = \begin{bmatrix} \sigma_{e_m}^2 & \sigma_{e_{mr}} \\ \sigma_{e_{mr}} & \sigma_{e_r}^2 \end{bmatrix}$$

The description of the bivariate RRM for TD-MY or TD-FPR and a fertility trait (model II) was

$$\begin{bmatrix} \mathbf{y}_m \\ \mathbf{y}_f \end{bmatrix} = \begin{bmatrix} \mathbf{X}_m & 0 \\ 0 & \mathbf{X}_f \end{bmatrix} \begin{bmatrix} \mathbf{b}_m \\ \mathbf{b}_f \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{htm_m} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \mathbf{htm}_m \\ 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{Z}_{hy_f} \end{bmatrix} \begin{bmatrix} 0 \\ \mathbf{hy}_f \end{bmatrix} +$$

$$\begin{bmatrix} \mathbf{Z}_{a_m} & 0 \\ 0 & \mathbf{Z}_{a_f} \end{bmatrix} \begin{bmatrix} \mathbf{a}_m \\ \mathbf{a}_f \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{p_m} & 0 \\ 0 & \mathbf{Z}_{p_f} \end{bmatrix} \begin{bmatrix} \mathbf{p}_m \\ \mathbf{p}_f \end{bmatrix} + \begin{bmatrix} \mathbf{e}_m \\ \mathbf{e}_f \end{bmatrix},$$

where \mathbf{y}_m and \mathbf{y}_f are a vector of observations of TD-MY or TD-FPR and lactation-wise fertility traits divided as score and interval traits, respectively; \mathbf{b}_m and \mathbf{b}_f are vectors of systematic effects;

htm_m is a vector of contemporary group random effects for TD-MY; hy_f is a vector of contemporary group random effects for lactation-wise fertility; a_m and a_f are vectors of random regression coefficients of AG effects for all animals in the pedigree; p_m and p_f are vectors of random regression coefficients of PE effect for all animals with records; e_m and e_f are vectors of random residual effects and $X_m, X_f, Z_{htm_m}, Z_{hy_f}, Z_{a_m}, Z_{a_f}, Z_{p_m}$ and Z_{p_f} are the corresponding incidence matrices. The same model was used for the bivariate analysis of TD-FPR and fertility traits.

The covariance structure for models was defined as

$$\text{Var} \begin{bmatrix} htm \\ hy \\ a \\ p \\ e \end{bmatrix} = \begin{bmatrix} H_{htm} \otimes I & 0 & 0 & 0 & 0 \\ 0 & H_{hy} \otimes I & 0 & 0 & 0 \\ 0 & 0 & G \otimes A & 0 & 0 \\ 0 & 0 & 0 & P \otimes I & 0 \\ 0 & 0 & 0 & 0 & R \otimes I \end{bmatrix}$$

where H_{htm} and H_{hy} are a diagonal matrix having variances of the htm effects for TD-MY or TD-FPR of the form σ_{htm}^2 and the hy effects for fertility traits of the form σ_{hy}^2 , respectively, A is the matrix of AG relationships among animals, \otimes is the Kronecker product, G and P are matrices of (co)variances for the AG and PE random regression coefficients, respectively, and R is 2 x 2 residual covariance matrix. For the bivariate analysis of TD-MY and fertility traits, G and P are 5 x 5 matrices of (co)variances for the AG and PE regression coefficients, respectively, whereas the bivariate analysis of TD-FPR and fertility traits are 4 x 4 matrices.

where $H_{htm} = \begin{bmatrix} \sigma_{htm_m}^2 & 0 \\ 0 & 0 \end{bmatrix}$, $H_{hy} = \begin{bmatrix} 0 & 0 \\ 0 & \sigma_{hy_f}^2 \end{bmatrix}$,

$$G = \begin{bmatrix} \sigma_{a_{m1}}^2 & \sigma_{a_{m2}a_{m1}} & \sigma_{a_{m3}a_{m1}} & \sigma_{a_{m4}a_{m1}} & \sigma_{a_{f1}a_{m1}} \\ \sigma_{a_{m1}a_{m2}} & \sigma_{a_{m2}}^2 & \sigma_{a_{m3}a_{m2}} & \sigma_{a_{m4}a_{m2}} & \sigma_{a_{f1}a_{m2}} \\ \sigma_{a_{m1}a_{m3}} & \sigma_{a_{m2}a_{m3}} & \sigma_{a_{m3}}^2 & \sigma_{a_{m4}a_{m3}} & \sigma_{a_{f1}a_{m3}} \\ \sigma_{a_{m1}a_{m4}} & \sigma_{a_{m2}a_{m4}} & \sigma_{a_{m3}a_{m4}} & \sigma_{a_{m4}}^2 & \sigma_{a_{f1}a_{m4}} \\ \sigma_{a_{m1}a_{f1}} & \sigma_{a_{m2}a_{f1}} & \sigma_{a_{m3}a_{f1}} & \sigma_{a_{m4}a_{f1}} & \sigma_{a_{f1}}^2 \end{bmatrix},$$

$$\mathbf{P} = \begin{bmatrix} \sigma_{p_{m1}}^2 & \sigma_{p_{m2}p_{m1}} & \sigma_{p_{m3}p_{m1}} & \sigma_{p_{m4}p_{m1}} & \sigma_{p_{f1}p_{m1}} \\ \sigma_{p_{m1}p_{m2}} & \sigma_{p_{m2}}^2 & \sigma_{p_{m3}p_{m2}} & \sigma_{p_{m4}p_{m2}} & \sigma_{p_{f1}p_{m2}} \\ \sigma_{p_{m1}p_{m3}} & \sigma_{p_{m2}p_{m3}} & \sigma_{p_{m3}}^2 & \sigma_{p_{m4}p_{m3}} & \sigma_{p_{f1}p_{m3}} \\ \sigma_{p_{m1}p_{m4}} & \sigma_{p_{m2}p_{m4}} & \sigma_{p_{m3}p_{m4}} & \sigma_{p_{m4}}^2 & \sigma_{p_{f1}p_{m4}} \\ \sigma_{p_{m1}p_{f1}} & \sigma_{p_{m2}p_{f1}} & \sigma_{p_{m3}p_{f1}} & \sigma_{p_{m4}p_{f1}} & \sigma_{p_{f1}}^2 \end{bmatrix},$$

$$\text{and } \mathbf{R} = \begin{bmatrix} \sigma_{e_m}^2 & 0 \\ 0 & \sigma_{e_f}^2 \end{bmatrix}$$

For bivariate analyses among TD-MY and TD-FPR with fertility traits, $\sigma_{hy_{mf}}$ was set to zero. For NSPC, FSC and P90, residual variance was set to 1 on the liability scale. The management group and AG effects were assumed to be independent.

Computation of (co) variance components

Estimates of (co)variance components from both univariate and bivariate analysis were calculated by a Bayesian implementation via Gibbs sampling. Computations were carried out using the program THRGIBBS1F90 (Tsuruta and Misztal, 2006). Uniform prior distribution was assumed for each location parameter and variance component. The number of iterations was set to 300,000. The first 50,000 samples were discarded as burn-in, and every 50th sample was kept thereafter. Post-Gibbs analysis by the POSTGIBBSF90 (Tsuruta and Misztal, 2006) program was conducted to obtain posterior distribution statistics for verification of the parameter estimates. Estimated covariance components of the random regression coefficients for AG and PE effects were used to derive the daily heritabilities and genetic and phenotypic associations among the traits. Estimates of heritabilities for the different traits were calculated from univariate analyses, whereas estimates of correlations between traits were calculated from bivariate analyses.

Estimation of heritabilities and correlations

Daily AG variance of the test-day trait (TD-MY or TD-FPR) at time DIM_t can be written as

$$\hat{\sigma}_a^2(DIM_t) = \boldsymbol{\phi}_r(DIM_t) \mathbf{G} \boldsymbol{\phi}_r(DIM_t)$$

where \mathbf{G} is the (co)variances matrices of AG random regression coefficients for TD-MY or TD-FPR. Heritability of a trait at any time DIM_t along the lactation trajectory was estimated as

$$\hat{h}^2(DIM_t) = \hat{\sigma}_a^2(DIM_t) / [\hat{\sigma}_a^2(DIM_t) + \hat{\sigma}_{hlm}^2 + \hat{\sigma}_p^2(DIM_t) + \hat{\sigma}_e^2],$$

where $\hat{\sigma}_p^2(DIM_t)$ is the variance of PE effects given as $\boldsymbol{\phi}_r(DIM_t) \mathbf{P} \boldsymbol{\phi}_r(DIM_t)$. Genetic correlation between a test-day and fertility trait at times DIM_t was estimated as:

$$\hat{r}_g(DIM_t) = \frac{\boldsymbol{\phi}_r(DIM_t) \mathbf{G}_{m,f} \mathbf{1}}{\sqrt{\hat{\sigma}_{am}^2(DIM_t) \hat{\sigma}_{af}^2}},$$

where $\mathbf{1}$ is a vector of ones, $\mathbf{G}_{m,f}$ are random regression coefficients of the AG covariance between the test-day trait and fertility trait, and $\hat{\sigma}_{af}^2$ is the AG variance of the fertility trait.

RESULTS AND DISSCUSION

Descriptive statistic

Mean and standard deviation of test-day milk production and component and reproductive performance of the primiparous Thai dairy crossbred cows in different breed groups were shown in Table 4-1. Mean of DTFS, DFLS, DO, CI, NSPC, FSC and P90 were 100.96 ± 46.65 days, 55.34 ± 74.03 days, 156.30 ± 83.37 days, 434.67 ± 83.44 days, 2.29 ± 1.72 , 0.46 ± 0.50 and 0.75 ± 0.43 , respectively, whereas mean of TD-FPR, TD-MY, %F and %P were 1.15 ± 0.30 , 12.60 ± 4.51 kg, 3.64 ± 0.87 , and 3.20 ± 0.43 , respectively. The average of fertility traits were higher than reported in purebred dairy cattle raising under intensive system i.e. Purebred Holsteins (Abe et al., 2009; Berry et al., 2013; Zavadilová and Zink, 2013), Brown Swiss (Tiezzi et al., 2012), Jersey (Haile-Mariam et al., 2013); Swedish Red (Buch et al., 2011), Iranian Holsteins (Eghbalsaied, 2011), and Nordic Red cattle (Negussie et al., 2013), but are lower than Northern Thai dairy crossbred (König et al., 2005). The mean TD-FPR and TD-MY of first-lactation cows in this study were lower than the results reported by Negussie et al. (2013), which were 1.29 ± 0.21 for TD-FPR and 21.3 ± 4.85 kg for TD-MY. The result of descriptive statistics of the studied traits by breed group showed the tendency of lower reproductive efficiency and milk component, whereas the tendency of TD-MY averages were higher as the HF blood increased. However, the TD-FPR averages were found constant (1.15-1.18) in every breed group. Traditionally, the optimum TD-FPR is 1.2-1.4. The lower TD-FPR (<1.2) are likely to lead to subclinical rumen acidosis which enhance a possible development of mineral metabolism disorders and endanger reproductive performance of the cows. The TD-FPR which is higher than 1.4 signals energy deficit and subclinical ketosis if ketone bodies are present (Haas and Hofreik, 2004). Richardt (2004) confirms that the TD-FPR higher than 1.5 indicates subclinical ketosis whereas rumen acidosis is suspected when the TD-FPR is lower than 1.1. However, FPR in this study is a little bit lower than the range showed in the literatures which infer that Thai dairy crossbred cows may be subjected to subclinical rumen acidosis

due to daily feed ration is based heavily on concentrates, especially in winter and summer. The time that roughage shortage happened every year and most of the farmers tried to solve the problem by using higher proportion of commercial mixed ration instead.

Table 4-1. Means (SD) of fertility and test-day traits of primiparous Thai dairy crossbred cows in different breed groups

Traits ¹	Breed group ²				Total
	<81.25% HF	81.25-87.49% HF	87.5-93.74% HF	>=93.75% HF	
Fertility traits	n=1,339	n=1,607	n=3,940	n=3,169	n=10,055
DTFS (d)	95.62 (43.52)	99.17 (46.32)	100.44 (46.67)	104.78 (47.78)	100.96 (46.65)
DFLS (d)	49.70 (69.46)	51.74 (72.31)	54.82 (74.17)	60.19 (76.47)	55.34 (74.09)
DO (d)	145.33 (77.67)	150.91 (82.63)	155.26 (83.24)	164.97 (85.42)	156.30 (83.37)
CI (d)	424.07 (77.63)	429.31 (82.42)	433.59 (83.46)	443.19 (85.50)	434.67 (83.44)
NSPC (no.)	2.19 (1.66)	2.23 (1.66)	2.28 (1.72)	2.38 (1.77)	2.29 (1.72)
FSC (x100%)	0.48 (0.50)	0.47 (0.50)	0.46 (0.50)	0.43 (0.50)	0.46 (0.50)
P90 (x100%)	0.78 (0.41)	0.77 (0.42)	0.75 (0.43)	0.72 (0.45)	0.75 (0.43)
Test-day traits	n=70,007	n=85,821	n=31,825	n=35,796	n=223,449
TD_MY (kg)	11.61 (4.29)	12.30 (4.41)	12.78 (4.51)	13.01 (4.58)	12.60 (4.51)
%F	3.77 (0.83)	3.65 (0.82)	3.62 (0.89)	3.58 (0.88)	3.64 (0.87)
%P	3.25 (0.45)	3.20 (0.43)	3.19 (0.43)	3.17 (0.44)	3.20 (0.43)
TD-FPR	1.18 (0.29)	1.15 (0.28)	1.15 (0.31)	1.15 (0.31)	1.15 (0.30)

¹DTFS = days from calving to first service; DFLS = days between first and last service; DO = days from calving to successful conception; CI = calving interval; NSPC = number of service per conception; FSC = conception at first service; P90 = pregnancy with 90 days after the first service; TD-MY = test-day milk yield; %F = percentage of fat; %P = percentage of protein; TD-FPR = test-day fat-to-protein ratio.

²The dairy crossbred cows of *Bos indicus*, such as Sahiwal, Brahman, and Thai Native cattle upgraded by HF

Lactation curves

According to TD-MY curve of primiparous Thai dairy crossbred cows, lactation curve for milk yield was of similar shape of TD-FPR, which peak yield was shown at the beginning of lactation around DIM 35 and steady decline afterwards to the end of lactation (see Figure 4-1). The TD-MY curve in this study showed the same pattern as reported by Jamrozik and Schaeffer (2012), and Negussie et al. (2013). The TD-FPR curve was found different from that reported by Buttchereit et al. (2010) which found highest TD-FPR at the beginning of lactation and became stable afterwards. Jamrozik and Schaeffer (2012) also reported highest values of TD-FPR immediately after calving and decrease as

lactation proceeded towards the peak of lactation, after that become steady and slowly increase as lactation progressed. A study in Nordic Red cattle also found highest TD-FPR at early lactation, stable in the mid lactation (from 100 to 200 DIM) and slightly increase toward the end of the lactation (Negussie et al., 2013). Although the average TD-FPR obtained in this study show no different in each stage of lactation but the standard deviations were in wide range. This indicated that some of the cows might have ability to cope with the negative energy balance in early stage of first lactation.

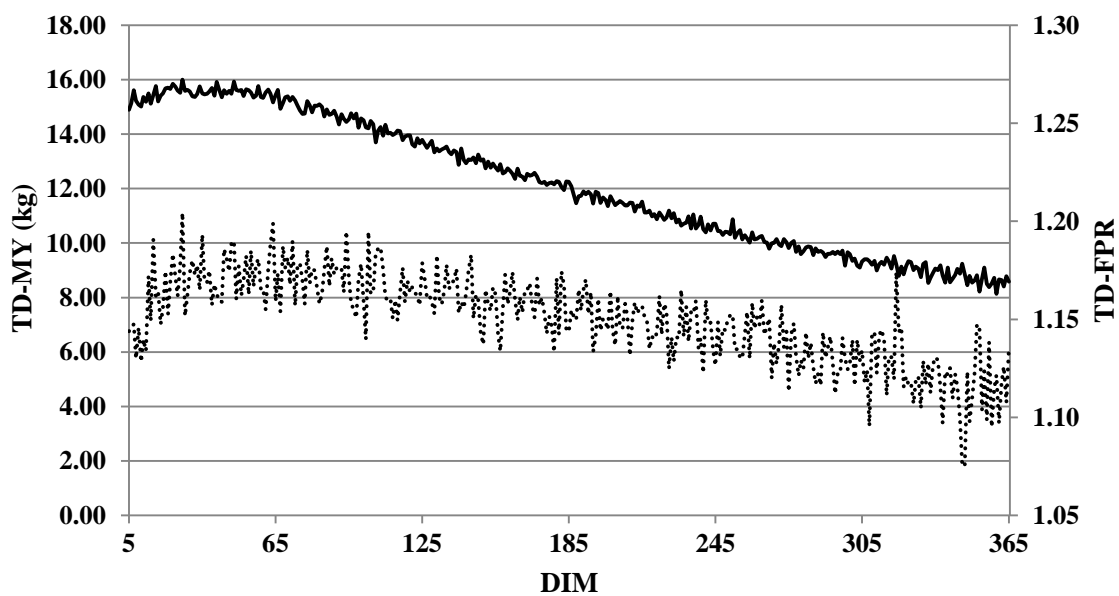


Figure 4-1. Average lactation curve for TD-MY (bold line) and TD-FPR (dash line) of primiparous Thai dairy crossbred cows

Heritabilities

The heritabilities of TD-MY and TD-FPR for particular days in milk are given in Table 4-2. The averages of estimated daily heritability were 0.52 and 0.18 for TD-MY and TD-FPR (not shown in the table), whereas heritabilities estimate of fertility traits are shown in Table 4-3. Each unique DIM heritabilities for TD-MY and TD-FPR are shown in Figure 4-2. Throughout the lactation, heritabilities of TD-MY ranged between 0.31 and 0.58, whereas the heritabilities of TD-FPR ranged from 0.17 to 0.19. Although the heritability of TD-FPR were generally lower than that of TD-MY, the same trend was

observed with slightly lower values at both end of the lactation trajectory and high values around mid-lactation. The heritability estimates of TD-MY in this study were slightly higher than others reports (Lidauer et al., 2003; Negussie et al., 2013) but the same trend was observed.

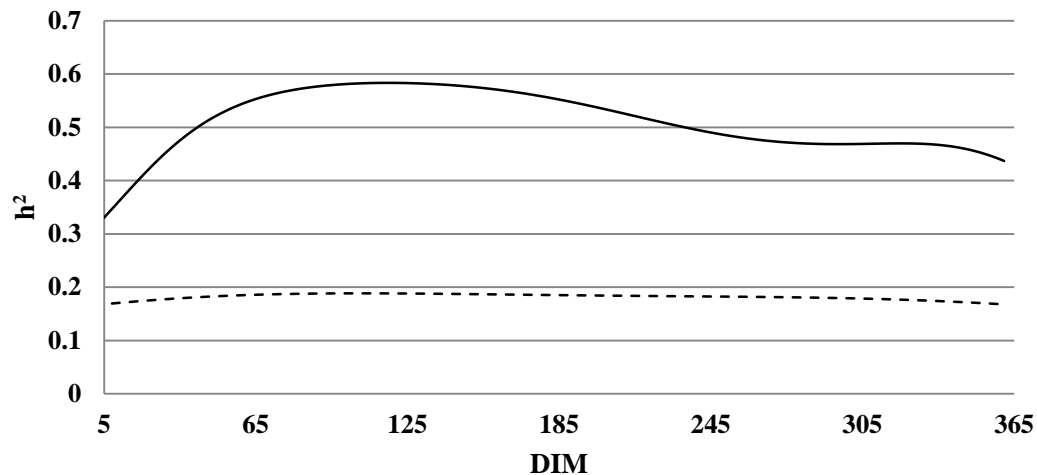


Figure 4-2. Daily estimated heritabilities for TD-MY (bold line) and TD-FPR (dash line) of primiparous Thai dairy crossbred cows

For TD-FPR, the estimated heritability was close to the TD-FPR heritability studied in Austrian Simmental (0.14), Spanish Holstein (0.14 to 0.19) and Thai dairy crossbred (0.15 to 0.19) reported by Gredler et al. (2006b), Pena (2006) and Puangdee et al. (2012), respectively, but lower than the estimates in Dutch Holstein Black and White cattle (0.79), German Holstein (0.20 to 0.54), Canadian Holstein (0.14 to 0.40) and Finish cattle (0.14 to 0.25) reported by Vos and Groen (1998), Buttchereit et al. (2011), Jamrozik and Schaeffer (2012) and Negussie et al. (2013), respectively. In this study, including previously mentioned studies, a large variation of genetic effect for TD-FPR was found. The large differences of the heritability estimates for TD-FPR among the studies might due to the breed differences and the different types of models and effects included in the estimation models.

The heritability of fertility traits (DTFS, DFLS, DO, CI, NSPC, FSC and P90) were very low and ranged from 0.02 to 0.05 as same as the ones found in the report of Kadarmideen et al. (2003) and Wall et al. (2003).

Table 4-2. Heritabilities¹ (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between TD-FPR and TD-MY for selected DIM; posterior standard deviations are in parentheses

Traits ²	TD-MY at DIM							TD-FPR at DIM						
	5	65	125	185	245	305	365	5	65	125	185	245	305	365
TD-MY at DIM														
5	0.31 (0.03)	0.86 (0.02)	0.78 (0.03)	0.78 (0.03)	0.77 (0.03)	0.72 (0.03)	0.68 (0.03)	0.05 (0.07)	0.02 (0.08)	-0.01 (0.08)	-0.02 (0.08)	-0.02 (0.08)	-0.01 (0.08)	0.02 (0.07)
65	0.66 (0.01)	0.55 (0.02)	0.99 (0.00)	0.95 (0.00)	0.86 (0.00)	0.73 (0.01)	0.73 (0.01)	-0.21 (0.05)	-0.29 (0.05)	-0.33 (0.05)	-0.35 (0.05)	-0.35 (0.05)	-0.33 (0.05)	-0.26 (0.04)
125	0.46 (0.01)	0.83 (0.00)	0.58 (0.02)	0.98 (0.00)	0.89 (0.00)	0.77 (0.00)	0.76 (0.01)	-0.30 (0.04)	-0.38 (0.04)	-0.42 (0.04)	-0.43 (0.04)	-0.44 (0.04)	-0.42 (0.04)	-0.34 (0.04)
185	0.39 (0.01)	0.73 (0.00)	0.83 (0.00)	0.56 (0.02)	0.96 (0.00)	0.87 (0.00)	0.84 (0.01)	-0.33 (0.04)	-0.40 (0.04)	-0.42 (0.04)	-0.44 (0.04)	-0.44 (0.04)	-0.42 (0.04)	-0.36 (0.04)
245	0.37 (0.01)	0.57 (0.00)	0.68 (0.00)	0.80 (0.00)	0.49 (0.02)	0.97 (0.00)	0.91 (0.00)	-0.32 (0.04)	-0.36 (0.04)	-0.37 (0.04)	-0.38 (0.04)	-0.38 (0.04)	-0.37 (0.04)	-0.33 (0.04)
305	0.35 (0.01)	0.44 (0.00)	0.53 (0.00)	0.67 (0.00)	0.79 (0.00)	0.47 (0.02)	0.96 (0.00)	-0.30 (0.04)	-0.32 (0.05)	-0.32 (0.05)	-0.31 (0.05)	-0.32 (0.04)	-0.32 (0.04)	-0.29 (0.04)
365	0.27 (0.01)	0.43 (0.00)	0.48 (0.00)	0.53 (0.00)	0.60 (0.00)	0.71 (0.00)	0.44 (0.02)	-0.34 (0.05)	-0.37 (0.05)	-0.37 (0.05)	-0.37 (0.05)	-0.37 (0.05)	-0.36 (0.04)	-0.32 (0.04)
TD FPR at DIM														
5	0.01 (0.01)	-0.04 (0.01)	-0.05 (0.01)	-0.05 (0.01)	-0.04 (0.01)	-0.04 (0.01)	-0.05 (0.01)	0.17 (0.02)	0.98 (0.00)	0.95 (0.01)	0.93 (0.01)	0.91 (0.01)	0.88 (0.02)	0.78 (0.03)
65	0.00 (0.01)	-0.06 (0.01)	-0.08 (0.01)	-0.08 (0.01)	-0.07 (0.01)	-0.06 (0.01)	-0.06 (0.01)	0.33 (0.01)	0.19 (0.01)	0.99 (0.00)	0.98 (0.00)	0.96 (0.01)	0.91 (0.01)	0.79 (0.01)
125	-0.01 (0.01)	-0.07 (0.01)	-0.09 (0.01)	-0.09 (0.01)	-0.08 (0.01)	-0.07 (0.01)	-0.07 (0.01)	0.24 (0.01)	0.32 (0.00)	0.19 (0.01)	0.99 (0.00)	0.98 (0.00)	0.93 (0.00)	0.78 (0.01)
185	-0.01 (0.01)	-0.07 (0.01)	-0.10 (0.01)	-0.10 (0.01)	-0.09 (0.01)	-0.07 (0.01)	-0.06 (0.01)	0.18 (0.01)	0.28 (0.00)	0.34 (0.00)	0.19 (0.01)	0.99 (0.00)	0.95 (0.00)	0.83 (0.00)
245	0.00 (0.01)	-0.07 (0.01)	-0.09 (0.01)	-0.10 (0.01)	-0.08 (0.01)	-0.07 (0.01)	-0.06 (0.01)	0.14 (0.01)	0.25 (0.00)	0.31 (0.00)	0.34 (0.00)	0.18 (0.01)	0.98 (0.00)	0.63 (0.00)
305	0.01 (0.01)	-0.06 (0.01)	-0.08 (0.01)	-0.08 (0.01)	-0.07 (0.01)	-0.06 (0.01)	-0.05 (0.01)	0.13 (0.01)	0.19 (0.00)	0.24 (0.00)	0.28 (0.00)	0.32 (0.00)	0.18 (0.01)	0.76 (0.00)
365	0.02 (0.01)	-0.03 (0.01)	-0.05 (0.01)	-0.06 (0.01)	-0.05 (0.01)	-0.04 (0.01)	-0.03 (0.01)	0.13 (0.01)	0.12 (0.00)	0.14 (0.00)	0.17 (0.00)	0.24 (0.00)	0.34 (0.00)	0.17 (0.01)

¹Estimates of heritabilities are from univariate analyses.

²TD-MY = test-day milk yield; TD-FPR = test-day milk fat-to-protein ratio.

Genetic correlations between TD-FPR and TD-MY

Genetic and phenotypic correlations between TD-FPR and TD-MY for a specific DIM are shown in Table 4-2. Genetic correlations between TD-MY during the different stages of lactation were all positive, ranged from 0.68 to 0.99. The correlations of milk yield between consecutive days of recording were higher when compared with those for the days that were far apart. The genetic correlation of TD-FPR ranged from 0.63 to 0.99 with the trend similar to TD-MY correlations.

Daily genetic correlations among TD-MY and TD-FPR during early lactation were small but positive (0.05) after that decrease to zero and negative estimates to the end of lactation ranged from -0.44 to -0.29. Trend of the correlations in this study are similar to the results studied in Nordic Red cattle (Negussie et al., 2013) and Canadian Holstein (Jamrozik and Schaeffer, 2012), which reported higher positive genetic correlation between TD-MY and TD-FPR until 60 DIM and 40 DIM, respectively. In addition, phenotypic correlations between two traits were the same trend as the genetic correlations with lower values. The low positive genetic correlations between the two traits and decreased to zero in early lactation indicated that this period is associated with an energy deficit in a high-producing dairy cows, which have the tendency to mobilize body energy reserved to cope with the high energy demand and hence leads to a relatively higher fat-to-protein ratio. However, most of Thai dairy crossbred cows, raised in smallholders produced low milk production especially in peak lactation together with proper management at farm level. These kind of cows may not face with NEB condition, which confirmed by the nearly zero or negative genetic correlation between TD-MY and TD-FPR even in early lactation. In the cows with excessive body tissue mobilization, coming out of NEB, may take up to 20 weeks to regaining a positive energy balance status (Taylor et al., 2003).

Genetic correlations between TD-MY and fertility traits

Genetic and phenotypic correlations between TD-MY and fertility traits are shown in Table 4-3.

Table 4-3. Heritabilities¹ of fertility trait, genetic and phenotypic correlations between TD-MY and fertility traits for selected DIM; posterior standard deviations are in parentheses

Parameter	Traits ²	DTFS	DFLS	DO	CI	NSPC	FSC	P90
Heritability		0.02 (0.01)	0.03 (0.01)	0.05 (0.02)	0.05 (0.01)	0.02 (0.02)	0.02 (0.01)	0.02 (0.03)
Genetic correlation	TD-MY at DIM							
	5	0.74 (0.11)	0.42 (0.17)	0.51 (0.16)	0.17 (0.13)	-0.45 (0.13)	0.62 (0.10)	0.29 (0.10)
	65	0.68 (0.13)	0.39 (0.16)	0.45 (0.16)	0.16 (0.11)	-0.39 (0.11)	0.42 (0.13)	0.30 (0.13)
	125	0.63 (0.13)	0.30 (0.17)	0.38 (0.16)	0.08 (0.11)	-0.43 (0.11)	0.42 (0.14)	0.35 (0.14)
	185	0.59 (0.13)	0.19 (0.17)	0.30 (0.16)	-0.11 (0.11)	-0.55 (0.10)	0.53 (0.14)	0.44 (0.14)
	245	0.56 (0.13)	0.08 (0.17)	0.23 (0.16)	-0.19 (0.10)	-0.70 (0.10)	0.67 (0.14)	0.54 (0.14)
	305	0.60 (0.13)	0.09 (0.17)	0.26 (0.16)	-0.22 (0.10)	-0.79 (0.10)	0.77 (0.14)	0.63 (0.14)
	365	0.79 (0.12)	0.35 (0.17)	0.52 (0.16)	0.00 (0.10)	-0.73 (0.09)	0.72 (0.13)	0.69 (0.13)
Phenotypic correlation	TD-MY at DIM							
	5	-0.12 (0.01)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.00 (0.01)	0.01 (0.02)	-0.02 (0.01)
	65	-0.12 (0.01)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)	0.01 (0.01)	0.00 (0.01)	-0.03 (0.01)
	125	0.00 (0.01)	0.03 (0.01)	0.03 (0.01)	0.03 (0.01)	0.00 (0.01)	0.00 (0.01)	-0.02 (0.01)
	185	0.02 (0.01)	0.03 (0.01)	0.04 (0.01)	0.03 (0.01)	0.00 (0.01)	0.00 (0.01)	-0.02 (0.01)
	245	0.04 (0.01)	0.04 (0.01)	0.06 (0.01)	0.04 (0.01)	0.00 (0.01)	0.00 (0.01)	-0.02 (0.01)
	305	0.05 (0.01)	0.05 (0.01)	0.08 (0.01)	0.07 (0.01)	0.02 (0.01)	-0.02 (0.01)	-0.04 (0.01)
	365	0.04 (0.01)	0.04 (0.01)	0.10 (0.01)	0.10 (0.01)	0.06 (0.01)	-0.07 (0.01)	-0.08 (0.01)

¹Estimates of heritabilities are from univariate analyses

²DTFS = days from calving to first service; DFLS = days between first and last service DO = days from calving to successful conception; CI = calving interval; NSPC = number of service per conception; FSC = conception at first service; Pregnancy within 90 after first service (P90); TD-MY = test-day milk yield

The estimated correlations varied depending on the particular fertility trait and the stage of lactation considered. Genetic correlations between TD-MY and interval fertility traits (DTFS, DFLS, DO and CI) were mostly positive, ranged from -0.22 to 0.79, with the exception of correlation between TD-MY and CI in mid to late lactation (185-365 d) which were negative values to zero. Genetic correlations were moderate to high and favorable between TD-MY and ordinal or binary fertility traits (NSPC, FSC, and P90). Genetic correlations between TD-MY and NSPC was all negative varied from -0.79 to -0.39, whereas genetic correlations between TD-MY and FSC and between TD-MY and P90 were all positive, ranged from 0.42 to 0.77 and from 0.29 to 0.69. However, all phenotypic correlation estimated were close to zero.

The unfavorable genetic correlation between TD-MY and DTFS, DFLS, DO and CI indicated that selection for increased milk production is associated with longer DTFS, DFLS, DO and CI especially in early lactation. The results are also in agree with most previous reports such as in upgraded dairy cattle (Hoekstra et al., 1994), in Holstein (Dematawewa and Berger, 1998; Kadarmideen et al., 2000), in Swedish red and white dairy cattle (Roxström et al., 2001) and in Irish dairy cattle (Evans et al., 2002). Although DO and CI are almost the same traits, but genetic correlations between TD-MY and DO and between TD-MY and CI are different value which are different from other studied. This might be because of the different definition of the pregnancy period in different studies. However, this study has found that the trend of genetic correlation of both traits (between TD-MY and DO and between TD-MY and CI) from day 5 to 305 of DO and CI are about the same.

The negative genetic correlation between TD-MY and NSPC and positive genetic correlation between TD-MY and FSC and P90 in this study result different from literatures that summarized by Pryce et al. (2004). This result may be explained by the different of genetic base of Thai dairy crossbred from dairy European dairy purebred, which implies that in Thai dairy crossbred population, genes that positively affect milk production are likely to reduce number of service per conception and increase first service conception and pregnancy within 90 d. However, the phenotypic correlation between TD-MY

and these fertility traits were close to zero, implying that animals that produce more milk have not associated with high NSPC or low FSC and P90. This relationship was, therefore, due to environment, management, or non-additive genetic factors rather than genetic factors. In addition, in this study, most of dairy farmers allowed the cows to be bred after 60 days postpartum which is in the after peak lactation period, in accordance with extension officers' advice. Hence, only one service to conceive was expected. As a consequence, FSC is relatively high, leading to decreasing NSPC, especially in mid to late lactation. However, some studies have reported no and low correlations between milk yield and fertility (Raheja et al., 1989; Weller, 1989).

Genetic correlations between TD-FPR and fertility traits

Genetic and phenotypic correlations between TD-FPR and fertility traits are shown in Table 4-4. The correlations between TD-FPR and fertility traits varied depending on the particular fertility trait and the stage of lactation considered. In general, genetic correlations between TD-FPR and the most of fertility traits (DFLS, DO, CI, NSPC, FSC and P90) were moderate to high, ranged from -0.98 to 0.98 except for DTFS which were moderate negative values. The correlations in early lactation (5-65 DIM) were higher than that found in mid to late lactation. These results indicate that cows with relatively higher TD-FPR are the cows in NEB status. As a consequence, such cows tend to have longer in DFLS, DO, and CI, higher NSPC and lower FSC and P90. This result is in accordance with many other studies (Jorritsma et al., 2003; Buttchereit et al., 2010; Jamrozik and Schaeffer, 2012; Negussie et al., 2013) which found that an antagonistic relationship exists between genetic for milk yield and reproduction, causing by the increasing of NEB in early lactation.

However, the moderate negative genetic correlations between TD-FPR and DTFS (range from -0.61 to -0.14) could indicated that cows with higher TD-FPR trend to have shorter DTFS. This result contradicted to the theory and could be explained by the norm of practice. In Thailand most of dairy farmers, which is smallholder allow the cows to be bred after 60 days postpartum in accordance with

extension officer recommendation. Some farmers also believe that the cows should be bred after 90 day postpartum to get higher pregnancy rate. So the voluntary waiting period (**VWP**) of Thai dairy crossbred is around 60-90 days or more. As a result, there was confounded in measurement of the DTFS.

The phenotypic correlations between TD-FPR and fertility traits were very low and all estimates are in the same trend as genetic correlations.

Table 4-4. Heritability¹ of fertility trait, genetic and phenotypic correlations between TD-FPR and fertility traits for selected DIM; posterior standard deviations are in parentheses

Parameter	Traits ²	DTFS	DFLS	DO	CI	NSPC	FSC	P90
Heritability		0.02 (0.01)	0.03 (0.01)	0.05 (0.02)	0.05 (0.01)	0.02 (0.02)	0.02 (0.01)	0.02 (0.03)
Genetic correlation	TD-FPR at DIM							
	5	-0.45 (0.16)	0.60 (0.19)	0.67 (0.10)	0.63 (0.10)	0.88 (0.07)	-0.86 (0.07)	-0.97 (0.07)
	65	-0.53 (0.15)	0.63 (0.14)	0.53 (0.12)	0.55 (0.10)	0.96 (0.04)	-0.84 (0.07)	-0.93 (0.07)
	125	-0.58 (0.15)	0.63 (0.13)	0.44 (0.12)	0.50 (0.11)	0.97 (0.03)	-0.81 (0.07)	-0.87 (0.07)
	185	-0.61 (0.15)	0.61 (0.12)	0.39 (0.13)	0.47 (0.11)	0.98 (0.03)	-0.83 (0.07)	-0.85 (0.07)
	245	-0.60 (0.15)	0.56 (0.12)	0.37 (0.13)	0.44 (0.11)	0.97 (0.03)	-0.87 (0.07)	-0.86 (0.07)
	305	-0.41 (0.15)	0.46 (0.12)	0.37 (0.13)	0.42 (0.12)	0.93 (0.03)	-0.94 (0.06)	-0.89 (0.07)
	365	-0.14 (0.15)	0.28 (0.12)	0.38 (0.13)	0.35 (0.12)	0.82 (0.03)	-0.98 (0.06)	-0.90 (0.07)
Phenotypic correlation	TD-FPR at DIM							
	5	0.02 (0.01)	0.03 (0.01)	0.04 (0.01)	0.04 (0.01)	0.03 (0.01)	-0.02 (0.01)	-0.04 (0.01)
	65	0.01 (0.01)	0.02 (0.01)	0.03 (0.01)	0.03 (0.01)	0.02 (0.01)	-0.02 (0.01)	-0.03 (0.01)
	125	0.00 (0.01)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	-0.01 (0.01)	-0.02 (0.01)
	185	-0.00 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	-0.01 (0.01)	-0.02 (0.01)
	245	-0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	-0.01 (0.01)	-0.02 (0.01)
	305	-0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	-0.02 (0.01)	-0.03 (0.01)
	365	-0.00 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	-0.03 (0.01)	-0.04 (0.01)

¹Estimates of heritabilities are from univariate analyses.

²DTFS = days from calving to first service; DFLS = days between first and last service DO = days from calving to successful conception; CI = calving interval; NSPC = number of service per conception; FSC = conception at first service; Pregnancy within 90 after first service (P90); TD-FPR = test-day milk fat-to-protein ratio.

CONCLUSION

Based on the moderate to high antagonistic correlations between TD-FPR and fertility traits and between TD-MY and fertility traits, as well as, the positive correlation in early lactation between TD-MY and TD-FPR indicated that selection for lower fat-to-protein ratio would decrease NSPC, and increase FSC and P90. In addition, cow selection based only on high milk production has strong effects to prolong DTFS, DO and CI. On the other hand, a very low TD-FPR is known to be an indicator for the subclinical rumen acidosis. Therefore, TD-FPR may be a useful trait for selection to improve fertility and yields traits of Thai dairy crossbred by including optimum value of TD-FPR in breeding program with an appropriate economic weights. However, inclusion of TD-FPR in breeding programs in Thai dairy cattle at the current state of knowledge might be premature. Further studies should be conducted to get the suitable range of TD-FPR in Thai dairy crossbred population.

Chapter V

Genetic analysis of the rates of conception using a longitudinal threshold model with random regression in dairy crossbreeding within a tropical environment

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INTRODUCTION

The incidence of health and fertility problems in tropical area including Thailand has an important impact on the overall profitability of dairy cattle industry. Low fertility results in higher insemination, labor and veterinary costs, decrease of milk production (fewer progeny born), slippage in dairy pattern, less intensive selection and increase replacement rate due to involuntary culling (Hodel et al., 1995; Roche, 2006).

The dairy cattle in Thailand have been developed through the national sire selection and AI mating program since 1956, focusing on milk production (Buaban et al., 2015). Upgrading Thai native cattle by purebred HF frozen semen as the predominant breed according to the size and milk production that considered being suited to local marketing system and socio-economic conditions of Thailand was practiced. Currently, the majority of the dairy population are >75% HF blood (Department of Livestock Development, 2015). The gene fraction of HF varies widely even within farms. The continued selection for increased milk yield has induced a decrease in fertility performance (Pryce and Veerkamp, 2001) because of the antagonistic genetic relationship between milk yield and fertility traits (Roxström et al., 2001; Liu et al., 2008). Therefore, an inclusion of the fertility traits in the breeding goal is considered to be necessary to optimize the genetic improvement of dairy cattle in Thailand.

The traits used in measuring fertility range from binary (discrete) responses, to continuous traits; such as days (from calving) to first service, days between first and last service, number of services per conception, non-return rate within 56 days after first service, success at first insemination, calving interval, and days open (Jorjani, 2007; Abe et al., 2009; Sun et al., 2009b). Although several traits are being used for genetic evaluation of fertility, binary responses such as the outcome of an insemination event seems to be the trait of choice; as it is conveniently measured, and taken in early to mid-stages of lactation. Recently, the outcome of first insemination (first conception rate), has been commonly evaluated. However, only a single record per cow within lactation is used. Thus, additional breeding

records of cows having more than one insemination are not considered, and have led to information loss. The use of the random regression model (**RRM**) allows us to analyze the outcome of an insemination event (CR) along the stage of lactation. Averill et al. (2004) proposed RP-THM in first lactation, where all insemination events of a cow in a breeding season were considered as repeated observation. Averill et al. (2006) extended their initial study via a random coefficient-based model. Tsuruta et al. (2009) used bivariate analysis of conception rates and test-day milk yields in Holsteins using a RR-THM. Their model showed the probability of conception rate as a function of the shape of the lactation curve and the relationships among various days in milk production. An additional advantage of RRM is the joint accountability of service sire and female fertility for all insemination events along the breeding period, which provided greater accuracy in predicting breeding values at any point along lactation.

Nevertheless, knowledge of these performances in dairy cattle within a tropical zone had not been reported. The objectives of this study, therefore, were 1) to estimate genetic parameters and breeding values for CR using RP-THM and RR-THM, and 2) to implement and compare different random coefficient functions for modeling the additive genetic and permanent environmental effects in a RR-THM. As a case study, longitudinal binary fertility traits of Thai dairy cows were analyzed using AI data from the national recording database.

MATERIALS AND METHODS

Data and trait definitions

First parity service records of both pregnant and non-pregnant Thai dairy cows, calving between 1996 and 2011, were obtained from the dairy cattle database of the Bureau of Biotechnology for Livestock Production (BBLP), DLD, Thailand. The fertility data, defined as the outcome of all insemination events, characterized a successful service conception event with '1' and an unsuccessful

service conception event with '0'. Pregnant status was confirmed either by pregnancy check or by identifying the next calving date. Non pregnant cows that had insemination events within an opportunity period between 20 and 365 days after calving were used. Cows with inconsistent identification, having more than one successful insemination per lactation, or an unrealistic interval between consecutive inseminations were removed. In addition, they were from a herd-year of insemination subclass, with at least one complete fertility contemporary record. The days to first service were between 20 and 250 days; and age at first calving, between 18 and 48 months. All cows had mated sire identification.

The final data set consisted of a total of 55,789 cows with 130,592 service records, averaging 2.34 inseminations per cow, 997 AI service sires, and 28,360 herd-year contemporary groups. The average for the number of inseminations per service sire was 131.

A pedigree file was constructed by tracing back three generations of ancestors, included 108,982 individuals. Breed groups of cows were classified into 4 classes considering percentage of Holstein blood: <81.25%, 81.25 to 87.49%, 87.50 to 93.74%, and $\geq 93.75\%$. Age at first calving was classified into seven classes with three month intervals, with <25 months as the first class, and >39 months as the last class. The day in milk to insemination (**DIM**) class had 16 classes with 21 day intervals (estrus cycle). The first class was 20-50 and the last was 345-365. A more detailed description of the data is presented in Table 5-1.

Statistical analysis

In this study, the outcome of an insemination event (referred to as the conception rate, or CR) is defined as a binary trait when estimating parameters using the following model: 1) RP-THM, and 2) RR-THM. In RP-THM, the outcomes of inseminations after calving during the breeding period were considered as repeated observations, therefore the animal's additive genetic effects (AG), the permanent environmental effects (PE), and residual effects were modeled constant. For RR-THM, the basic underlying idea consists of modeling the AG (or other random effects in the model) as a function of an

observed dependent variable (i.e., DIM) through a set of random coefficients. The equation for analyzing all models was written as such:

$$\mathbf{l} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_h\mathbf{h} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_p\mathbf{p} + \mathbf{Z}_s\mathbf{s} + \mathbf{e}$$

where \mathbf{l} is a vector of unobserved liabilities for service records from a binary outcome of insemination events (1 = success or 0 = failure); $\boldsymbol{\beta}$ is a vector of fixed effects (year-month of insemination, breed x DIM class and age at calving); \mathbf{h} is a vector of the contemporary groups (CG) random effects, defined as the effects of the herd-year of insemination; \mathbf{a} is a vector of random AG for all animals in the pedigree [for RR-THM, a random regression curve was modeled by the second-order (**RR-L2-THM**), the third-order (**RR-L3-THM**), and the fourth-order (**RR-L4-THM**) of Legendre polynomials]; \mathbf{p} is a vector of random PE for all animals with records (for RR-THM, a random regression curve was modeled in the same way as AG); \mathbf{s} is a vector of random service sire effects; \mathbf{e} is a vector of random residual effects; \mathbf{X} is the incidence matrix for fixed effects; and \mathbf{Z}_h , \mathbf{Z}_a , \mathbf{Z}_p , and \mathbf{Z}_s are the incidence matrices for random effects. The covariance structures were assumed as:

$$Var \begin{bmatrix} \mathbf{h} \\ \mathbf{a} \\ \mathbf{p} \\ \mathbf{s} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} I\sigma_h^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & A\sigma_a^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & I\sigma_p^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & I\sigma_s^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & I\sigma_e^2 \end{bmatrix}, \quad \text{for the RP-THM}$$

$$Var \begin{bmatrix} \mathbf{h} \\ \mathbf{a} \\ \mathbf{p} \\ \mathbf{s} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} I\sigma_h^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_0 \otimes A\sigma_a^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{P}_0 \otimes I & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & I\sigma_s^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & I\sigma_e^2 \end{bmatrix}, \quad \text{for the RR-THM}$$

where \mathbf{A} is the additive relationship matrix among animals, \mathbf{I} is the identity matrix, \otimes is a Kronecker product, \mathbf{G}_0 and \mathbf{P}_0 are covariance matrices of random regression coefficients for AG and PE effects, respectively; and $\sigma_h^2, \sigma_a^2, \sigma_p^2, \sigma_s^2$ and σ_e^2 are herd-year, additive genetic, permanent environment, service sire, and residual variances, respectively. The reason for using herd-year as the random effect, instead of herd-year-month as CG was due to the small number of records in the CG and, consequently, the large number of classes containing all successes or failures.

The j^{th} normalized Legendre polynomial, P_j is calculated as Kirkpatrick et al. (1990) with the following formula:

$$P_j(t) = \frac{1}{2^j} \sqrt{\frac{2j+1}{2}} \cdot \sum_{m=0}^{[j/2]} (-1)^m \binom{j}{m} \binom{2j-2m}{j} (t)^{j-2m}$$

where j is the order of the polynomial, m is an index number needed to determine the j^{th} polynomial, and t is the standardized day in milk to insemination, with values ranging from -1 to 1. The standardized day in milk to insemination were computed as

$$t = -1 + 2 \left(\frac{t_i - t_{\min}}{t_{\max} - t_{\min}} \right)$$

where t_{\min} and t_{\max} are the earliest and latest day in milk to insemination represented in data ($t_{\min} = 20, t_{\max} = 365$).

Computation of (co) variance components

Estimates of (co) variance components were calculated by a Bayesian implementation via Gibbs sampling. Computations were carried out using the program THRGIBBS1F90 (Tsuruta and Misztal, 2006). Uniform prior distribution was assumed for each location parameter and variance component.

The number of iterations was set to 300,000. The first 30,000 samples were discarded as burn-in, and every 10th sample was kept thereafter. Post-Gibbs analysis by the POSTGIBBSF90 (Tsuruta and Misztal, 2006) program was conducted to obtain posterior distribution statistics for verification of the parameter estimates. All parameter estimates for CR were on a liability scale.

For model that used random regression curve with Legendre polynomials, the genetic (co)variance, on the liability scale, between success and failure of inseminations at times t_i and t_j is given by

$$g(t_i, t_j) = \mathbf{z}(t_i) \mathbf{G}_0 \mathbf{z}(t_j),$$

where \mathbf{G}_0 is matrix of genetic variance between random regression coefficients, $\mathbf{z}(t_i)$ and $\mathbf{z}(t_j)$ are the vectors of covariates evaluated at times t_i and t_j from the sub-model fitted to the AG effect (the second-, third-, and fourth-order of Legendre polynomials). The same procedure was applied to the PE effect.

Heritability (h_t^2) and repeatability (R_t) on the liability scale at time t were defined as

$$\begin{aligned} h_t^2 &= \frac{\sigma_a^2}{\sigma_h^2 + \sigma_a^2 + \sigma_p^2 + \sigma_s^2 + 1}, & \text{for RP-THM} \\ h_t^2 &= \frac{\mathbf{z}(t)' \mathbf{G}_0 \mathbf{z}(t)}{\sigma_h^2 + \mathbf{z}(t) \mathbf{G}_0 \mathbf{z}(t) + \mathbf{z}(t) \mathbf{P}_0 \mathbf{z}(t) + \sigma_s^2 + 1}, & \text{for RR-THM} \\ R_t &= \frac{\sigma_a^2 + \sigma_p^2}{\sigma_h^2 + \sigma_a^2 + \sigma_p^2 + \sigma_s^2 + 1}, & \text{for RP-THM} \\ R_t &= \frac{\mathbf{z}(t)' \mathbf{G}_0 \mathbf{z}(t) + \mathbf{z}(t) \mathbf{P}_0 \mathbf{z}(t)}{\sigma_h^2 + \mathbf{z}(t) \mathbf{G}_0 \mathbf{z}(t) + \mathbf{z}(t) \mathbf{P}_0 \mathbf{z}(t) + \sigma_s^2 + 1}, & \text{for RR-THM} \end{aligned}$$

Correlations on the liability scale between times i and j for RP-THM and RR-THM were computed as the ratio of the covariance to the square root of the products of the variances of time i and time j .

$$\begin{aligned}\hat{r}_g(t_i t_j) &= \frac{cov(t_i t_j)}{\sqrt{\hat{\sigma}_{a_{t_i}}^2 \hat{\sigma}_{a_{t_j}}^2}}, & \text{for RP-THM} \\ \hat{r}_g(t_i t_j) &= \frac{\hat{z}(t_i) \mathbf{G}_0 \mathbf{z}(t_j)}{\sqrt{\hat{z}(t_i) \mathbf{G}_0 \mathbf{z}(t_i) * \hat{z}(t_j) \mathbf{G}_0 \mathbf{z}(t_j)}}, & \text{for RR-THM}\end{aligned}$$

where $cov(t_i t_j)$ are the genetic covariance between success and failure of inseminations at times t_i and t_j , and $\hat{\sigma}_{a_{t_i}}^2, \hat{\sigma}_{a_{t_j}}^2$ are the genetic variance of the success and failure of inseminations at times t_i and times t_j , respectively.

Breeding value estimation

For the estimation of best linear unbiased prediction (**BLUP**) breeding values (**EBV**) were solved by BLUPF90 (Miszta et al., 2014) with the posterior means of (co) variance components at their estimated values. Solutions for AG effects can be used to form EBV corresponding to service day after calving (DIM). Thus, the EBV for animal i was calculated as follow:

Under RP-THM, it provides a single estimate of the additive genetic effect of an animal (\hat{a}_i) that is constant for a whole lactation. Consequently, the breeding value in any service day after calving (U_{RP-THM}) is equal to the AG effect obtained on a daily basis:

$$EBV_{RP-THM} = \hat{a}_i,$$

Under RR-THM, function of solutions is the EBV for the random regression coefficients ($\hat{\mathbf{G}}$), which are not very useful for ranking or selecting animals. Therefore it should be calculate EBV for each animal by method of Jamrozik and Schaeffer (1997). An EBV in service day after calving (D_{t_i}), EBV_{RR-THM} , is obtained by summing the EBV for each DIM. That is

$$\begin{aligned}EBV_{RR-THM} &= D_{t_i}, \\ D_{t_i} &= \hat{\mathbf{G}} \hat{\mathbf{z}}(t_i).\end{aligned}$$

Model comparison

The models were compared by using 3 criteria: 1) measure goodness of fit (**GOF**), 2) test of predictive ability (**PA**) for random set of observations, and 3) test of the predicted results of animal (**PRA**). The GOF and PA were tested as Matos et al. (1997a).

The GOF for different models were compared in terms of the mean squared error statistic (**MSE**) and the empirical correlation (ρ) between the observed and predicted value. The model with the lowest MSE and high correlation were assumed to give the best fit.

The mean squared error statistic was defined as:

$$MSE = \sum_{i=1}^m \sum_{j=1}^s (y_{ij} - \hat{y}_{ij})^2 / \sum_{i=1}^m \sum_{j=1}^s n_{ij}$$

where y_{ij} is a observed value and \hat{y}_{ij} is a predicted value of animal i at service day j after calving (DIM) , n_{ij} are the number of observations, m is number of animals, s is number of service day, written as:

$$\hat{y}_{ij} = \begin{cases} 1 & \text{if } 1 - \Phi(\hat{l}_{ij}) > 0.5 \\ 0 & \text{otherwise} \end{cases}$$

where $\Phi(\cdot)$ is the cumulative standard normal distribution of \hat{l}_{ij} and \hat{l}_{ij} is obtained from:

$$\hat{l} = X\hat{\beta} + Z_h\hat{h} + Z_a\hat{a} + Z_p\hat{p} + Z_s\hat{s}$$

where \hat{l} are predicted liability values of l described in above section. In RP-THM, \hat{a}_{ij} and \hat{p}_{ij} of animal i were constant across DIM until service day j after calving. In RR-THM, the covariate functions of Legendre polynomials were included in the liability prediction equation, therefore, \hat{a}_{ij} and \hat{p}_{ij} of

animal i were calculated as BV and PE along DIM function until service day j after calving. The cumulative normal distribution was defined as:

$$\Phi(\hat{l}) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^l \exp\left\{-\frac{1}{2}(t - \mu)^2\right\} dt$$

To assess PA in this study, the whole data set was reduced randomly into a half. This procedure would be repeated ten times. Then, fixed and random effects from any reduced data set were estimated base on the variance estimates of the whole data set with different model. The predictive distributions were conditional on the variance estimates, and the whole data set was used because estimates obtained from any reduced data set would have been unreliable. To compare the agreement between the predicted value from reduced data set and the observed value from whole data set, the MSE and the correlation statistics were used to measure in a similar fashion as goodness of fit. Average for MSE and correlations were calculated from the ten partitioned data sets for each model.

To assess PRA in this study, the reliability (R^2) of predicted result conception of animal at different DIM (60, 90, 120, 150 and 180) in different models (RP-THM and RR-THM) from the whole data set were compared the agreement by considering in term of each animal.

The reliability was defined as

$$R^2 = 1 - MSE$$

RESULTS AND DISCUSSION

Data description

The means of CR at first, second, third and subsequent services, and total services are shown in Table 5-1. The overall CR is 33.45%, and the average numbers of services per cow was 2.34 (130,592 records/5, 5789 cows). The intervals from first to second, and from second to third insemination were 47.32 ± 37.94 and 41.77 ± 31.37 days; similar to the Holstein population in New York State (Tsuruta et

al., 2009). The long estrous cycle found in this study may be explained through breeding management, such as timed AI programs for convenience, low or erroneous heat detection, or expression.

Table 5-1. A descriptive summary of the edited data

Item	Number of records			
	Total	1 st service	2 nd service	≥ 3 rd service
Cows	55,789			
Service Sires	997			
Records	130,592	54,083	33105	43404
Successful	43,679	17,916	11,867	13,896
Failed	86,913	36,167	21,238	29,508
Conception rate ¹ (%)	33.4	33.1	35.8	32.0

¹the proportion of successful services to the total number of services

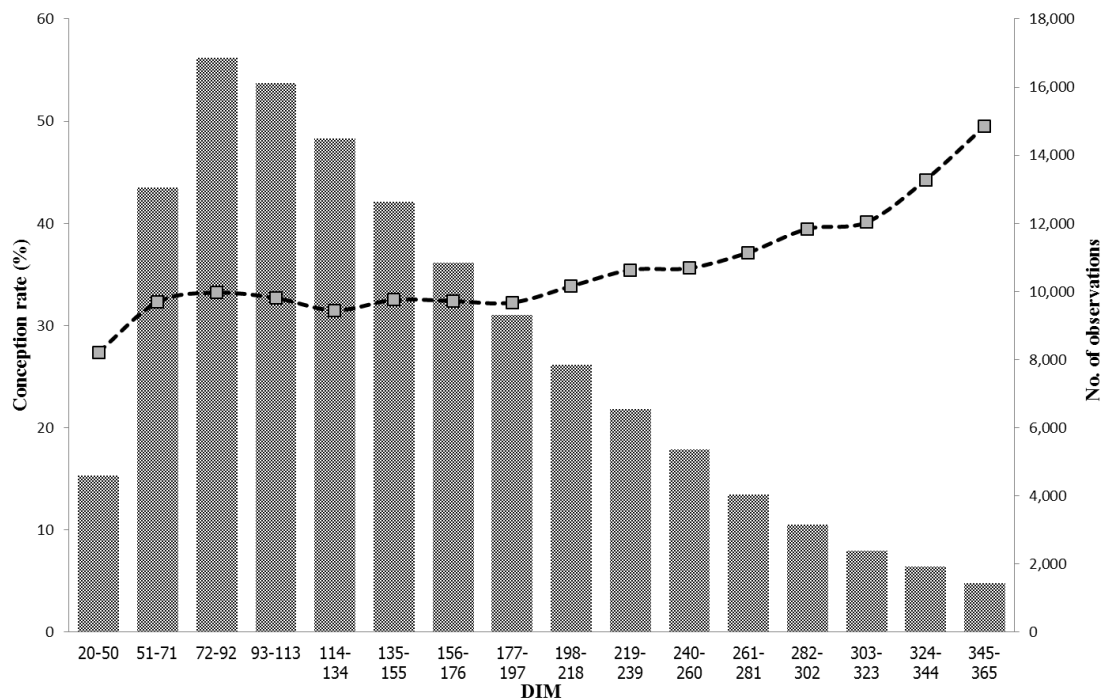


Figure 5-1. Distribution of phenotypic cow conception rates (broken line) defined as the percentage of success insemination by DIM classes in Thai dairy cattle. The column indicate the number of observations in each DIM class.

Distribution of records by DIM-classes and phenotypic CR over DIM are shown in Figure 5-1.

The number of observations was extremely low where DIM were below 51 and above 260. The CR

showed an obvious increase from DIM class 177-197 to the last class, DIM 345-365. This may be due to the fact that most small Thai dairy farmers were instructed by the AI officers that, in order to achieve successful breeding within a single insemination, their cows should be bred after 60 days postpartum; which is after the peak lactation period. Hence, only one service to conceive was expected.

Variance components and parameters

The posterior mean and standard deviation of (co)variance components, heritability, and repeatability for CR from 20 to 365 DIM using different models, are shown in Table 5-2.

Table 5-2. Averages of posterior means and SD (in parenthesis) of variance components and heritability and repeatability for conception rate (CR) along 20 to 365 days to insemination after calving for Thai dairy cattle

Parameters ¹	Model ²			
	RP-THM	RR-L2-THM	RR-L3-THM	RR-L4-THM
σ_a^2	0.066 (0.010)	0.058 (0.016)	0.079 (0.042)	0.098 (0.079)
σ_p^2	0.012 (0.007)	0.110 (0.068)	0.128 (0.107)	0.172 (0.194)
σ_h^2	0.092 (0.005)	0.094 (0.005)	0.096 (0.006)	0.097 (0.006)
σ_s^2	0.012 (0.002)	0.012 (0.002)	0.012 (0.002)	0.013 (0.002)
σ_e^2	1.002 (0.006)	1.002 (0.006)	1.002 (0.006)	1.002 (0.006)
h^2	0.056 (0.010)	0.045 (0.012)	0.058 (0.024)	0.065 (0.032)
R	0.070 (0.009)	0.129 (0.047)	0.150 (0.073)	0.175 (0.110)

¹ σ_a^2 = the additive genetic variance; σ_p^2 = permanent environmental variance; σ_h^2 = herd x year of service variance; σ_s^2 = service variance; σ_e^2 = residual variance; h^2 = heritability; and R = repeatability.

²RP-THM = repeatability model; and RR-L2-THM, RR-L3-THM and RR-L4-THM = random regression with the second-, third-, and fourth-order of Legendre polynomials, respectively.

AG variances were in a range of 0.066-0.098 (0.066, 0.058, 0.079, and 0.098 for RP-THM, RR-L2-THM, RR-L3-THM, and RR-L4-THM; respectively). PE variances of RR-THM with the second-to fourth-order Legendre polynomials were in a range of 0.110 to 0.172, which is almost twice that of the AG variance. Notice that in this study, the RR-THM gave a higher estimate of PE variance than RP-THM. Therefore, repeatability in all RR-THM for CR was higher than that in RP-THM. Herd-year variance of RR-THM are also higher than RP-THM. Although AG variances estimated from all models were not much different, the RRM was more precise in PE variance estimates, due to the adjustment of

the environmental effects, given the expected change over time on the day of service. This led to improved accuracy of the genetic evaluation of the reproductive performance of cows (Averill et al., 2004). Service sire and residual variances were not different among all models.

The average heritability estimates for CR in RR-L3-THM (0.058) and RR-L4-THM (0.065) were slightly higher than that in RP-THM (0.056). These heritability estimates were close to 0.058, reported by Averill et al. (2006) using RRM with the Ali and Schaeffer function (Ali and Schaeffer, 1987). However, they proved higher than the 0.024 calculated by Weller and Ron (1992), the 0.028 reported by Averill et al. (2004) using RP-THM, the 0.032 presented by Averill et al. (2006) using RRM with a quadratic linear function, and the 0.032 estimated by Kawahara et al. (2010) using RP-THM. However, it should be kept in mind that a comparison of heritability across literary reports is difficult to gauge, due to the different trait definitions and different models applied; as well as to the genetic origin of the dairy cattle used in the studies.

The course of AG and PE variance for insemination outcome (CR) as a function of time (DIM) using RR-THM with random coefficient of the second-, third- and fourth-order of Legendre polynomials and RP-THM, are shown in Figure 5-2 (a) and (b). The variations of heritability and repeatability are shown in Figures 5-2 (c) and (d). For RR-L3-THM and RR-L4-THM, the courses of posterior means of additive genetic variances were similar in pattern, which quite high in the beginning and later phases, and slightly stable in the middle intervals; whereas the results were found to be flat in RR-L2-THM. However, the courses of posterior means of PE variances of all models were also similar in pattern except RP-THM, which decreased continuously from day 20 to approximately day 80 after calving and increased continuously to the end of lactation. The change over time in heritability of the CR indicated a trend similar to the AG variance, whereas the repeatability trends were similar to the pattern of PE variance. Heritability ranged from 0.032 to 0.067, from 0.037 to 0.165, and from 0.045 to 0.218; whereas repeatability ranged from 0.060 to 0.259, from 0.073 to 0.407, and from 0.078 to 0.579; for RR-L2-THM, RR-L3-THM, and RR-L4-THM, respectively. The heritability and repeatability

estimates of CR for RP-THM were constant through the trajectory of curve, at 0.056 and 0.070, respectively.

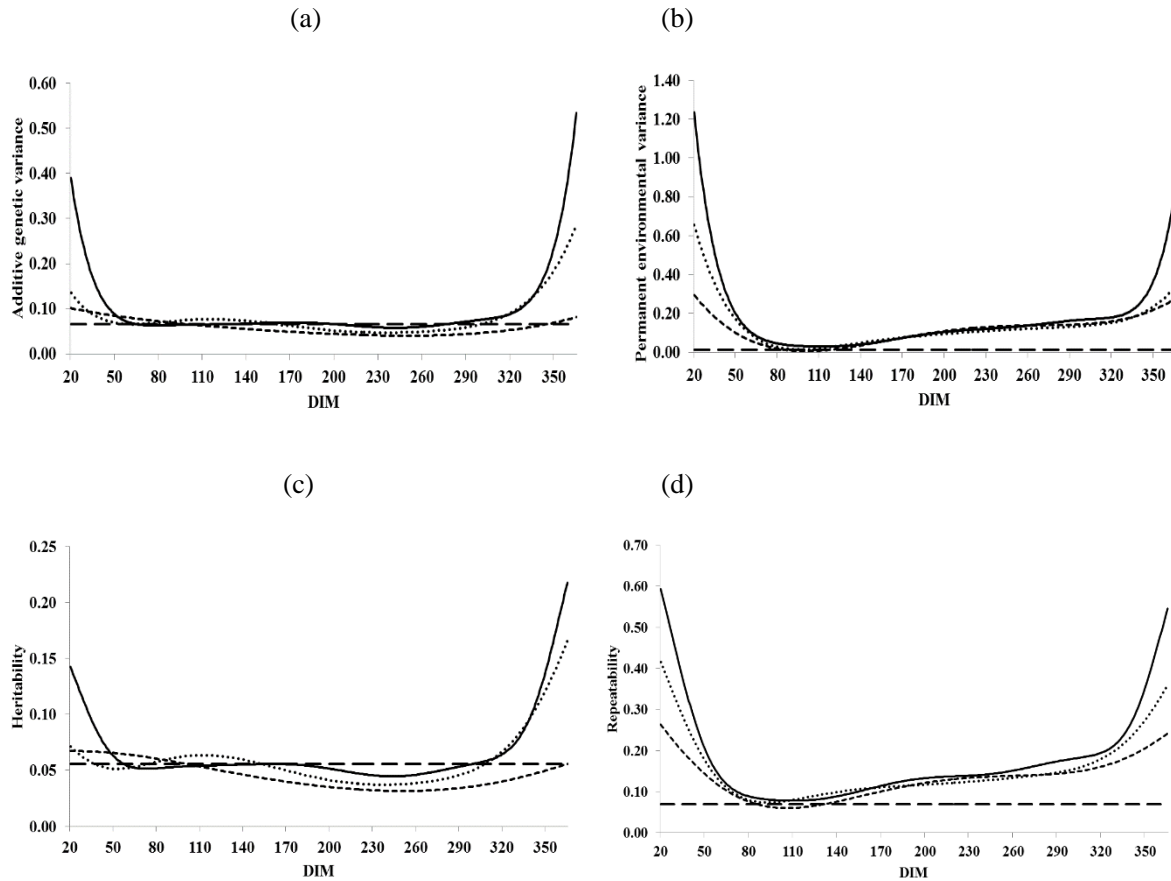


Figure 5-2. Additive variance (a), permanent environmental variance (b), heritability (c), and repeatability (d) of conception rate using RP-THM (---) and RR-THM as a function of time with the second- (-----), third- (.....) and fourth- (——) order of Legendre polynomials.

The heritability found in this study was in the range of estimates reported by Tsuruta et al. (2009) using the second-order of Legendre polynomials, by Averill et al. (2006) using quadratic linear function (0.03-0.04), and the Ali and Schaeffer function (0.03-0.07), and Brügemann et al. (2013) using the third-order of Legendre polynomials as a function of thermal humidity index (THI) (<0.05); though slightly higher. This difference may be explained by the difference of structure and order of covariance function models.

The higher heritability for CR at the extreme ends of the DIM scale may be attributed to several reasons. First, random regression models are sensitive when a complex covariance function is estimated from a limited number of observations (Jamrozik and Schaeffer, 1997; Yin et al., 2012; Gernand et al., 2013). In this study, the higher heritability at DIM<50 and DIM>320 might be affected by a low number of observations (Figure. 5-1). Second, is the nature of the Legendre function, which is likely to affect both the beginning and end of the curve. Third, changes are based on the genetic background and mechanism of gene expression. Generally, for production traits, phenotypic expression of the genetic potential was hampered in harsh environments. Brügemann et al. (2012) applied RR-THM, and found the tendency for decreasing AG variances and heritability for protein yield with increasing heat stress levels.

In CR evaluation, the consequence of higher heritability and AG variance at the end of lactation is somehow less significant because we generally considered evaluating the CR genetics of cows during early to mid-stages of lactation after calving. Opposite to milk yield or milk composition evaluation, the EBV was usually estimated from the whole area under the curve for genetic comparisons.

Correlations

The genetic and phenotypic correlations for CR at different time points are shown in Table 5-3 and Figure 5-3. The correlations between points of time after calving changed with the different order of Legendre polynomials. A decrease in correlations was found when the order increased. The high genetic correlations among time points were found until 170 days after calving for all RR-THM. These results were different from research of Tsuruta et al. (2009) which the correlation among CR at different DIM were close to zero or even negative when the distance was 100 days or larger. The genetic correlation of conception after calving seemed to decrease after 170 days. This may indicate that various gene control CR in different stage of lactation. However, the strong correlation among earlier days of service after

calving suggests that the genetic ability of conception should be evaluated within that time frame. Based on EBV, therefore, animals could be differentiated for selecting or culling with greater accuracy.

Table 5-3. Posterior means of genetic correlations (above the diagonal) and phenotypic correlations (below the diagonal) between specific time points using RR-THM with the second-, third-, and fourth-order of Legendre polynomials

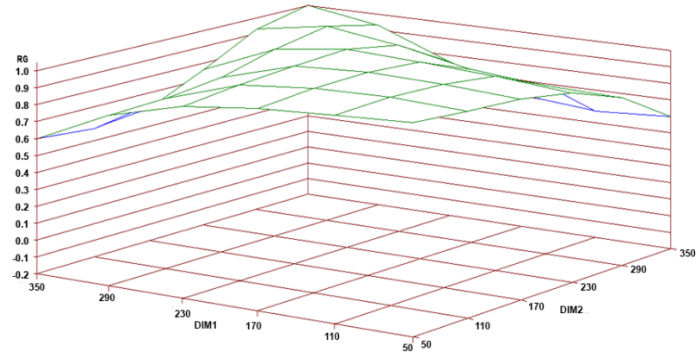
Time points, d	50	110	170	230	290	350
----- RR-L2-THM ¹ -----						
50	-	0.98	0.96	0.91	0.80	0.60
110	0.05	-	0.99	0.95	0.81	0.57
170	-0.01	0.06	-	0.98	0.85	0.61
230	-0.04	0.05	0.11	-	0.94	0.76
290	-0.03	0.04	0.09	0.13	-	0.93
350	0.01	0.02	0.04	0.08	0.14	-
----- RR-L3-THM ² -----						
50	-	0.76	0.73	0.81	0.77	0.49
110	0.02	-	0.98	0.83	0.70	0.68
170	-0.04	0.07	-	0.91	0.75	0.64
230	-0.04	0.05	0.10	-	0.91	0.60
290	0.00	0.04	0.08	0.12	-	0.79
350	0.03	0.07	0.08	0.09	0.15	-
----- RR-L4-THM ³ -----						
50	-	0.65	0.69	0.77	0.46	0.09
110	0.01	-	0.88	0.82	0.72	0.44
170	-0.02	0.06	-	0.91	0.56	0.54
230	-0.02	0.04	0.11	-	0.77	0.36
290	-0.04	0.05	0.07	0.12	-	0.35
350	-0.08	0.03	0.09	0.07	0.09	-

¹SD of genetic correlations ranged from 0.002 to 0.070; SD of phenotypic correlations ranged from 0.009 to 0.026.

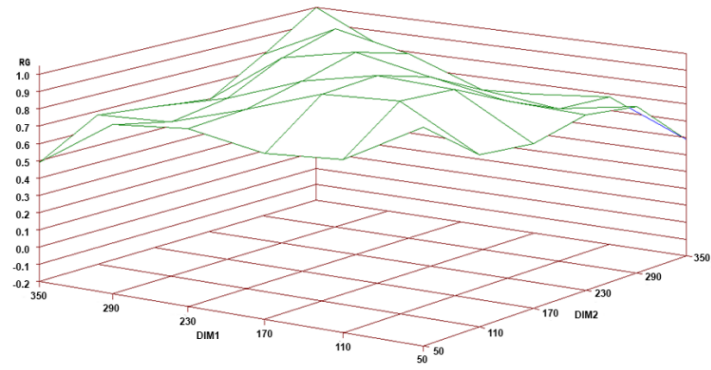
²SD of genetic correlations ranged from 0.003 to 0.172; SD of phenotypic correlations ranged from 0.010 to 0.033.

³SD of genetic correlations ranged from 0.006 to 0.164; SD of phenotypic correlations ranged from 0.009 to 0.030.

(a)



(b)



(c)

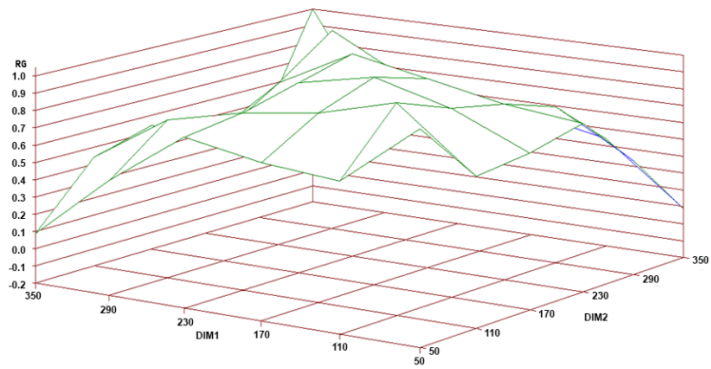


Figure 5-3. The genetic correlation among day 50 to 350 after calving using the second- (a), third- (b) and fourth- (c) order of Legendre polynomials.

Model selection criteria

GOF statistics and the PA results of the different models are presented in Table 5-4. In general, GOF of RP-THM was poorer, in terms of both MSE and correlations between predicted and observed values, than that of RR-THM. Within the RR-THM, a slightly increasing value of GOF was found as the order polynomial for the AG and PE effect increase. This confirmed that high order of Legendre polynomials were more efficient in fitting model. These results were in agreement with the results presented by Brotherstone et al. (2000), López-Romero and Carabano (2003) and Albuquerque and Meyer (2005), studied in milk production traits.

PA results, in terms of MSE and correlations between observed and predicted values from full and reduced data set of the models showed the same trend as GOF analysis.

Table 5-4. Statistics for goodness of fit (GOF) and the predictive ability (PA) results of the different models (RR_THM with the second-, third- and fourth-order of Legendre polynomials and RP_THM

Model ¹	Covariance structure	GOF		PA	
		MSE	$\rho_{y,\hat{y}}^2$	MSE	$\rho_{y,\hat{y}}^3$
RR-L2-THM	3x3	0.23	0.57	0.25	0.49
RR-L3-THM	4x4	0.22	0.59	0.24	0.51
RR-L4-THM	5x5	0.21	0.61	0.23	0.52
RP-THM	1x1	0.27	0.48	0.27	0.45

¹RP-THM = repeatability model; and RR-L2-THM, RR-L3-THM and RR-L4-THM = random regression with the second-, third-, and fourth-order of Legendre polynomials, respectively.

²correlation between the observed and the predicted value.

³correlation between the observed from the whole data set and predicted value from the reduced data set.

The PRA from the different models at day 60, 90, 120, 150 and 180 after calving (DIM) in term of reliability are shown in Table 5-5. Reliabilities were calculated from the observed and predicted values of animals in the whole data set. The PRA from the predicted service result at day 60 to day 180 using RR-THM were higher than that of RP-THM. However, the PRA tentatively decreased when DIM increased from day 60 to day 180; due to the more numerous environmental effects involved in the services. Within the RR-THM at all DIM, a decreasing trend of PRA was also found when the order

decrease except the second- and third-order of day 60 and the third- and fourth-order of day180 with values were similar. This pattern is in agreement with the pattern of GOF and PA analysis.

Table 5-5. Reliability of the predicted service results of animals (PRA) from RR-THM and RP-THM at day 60, 90, 120, 150 and 180 after calving

Model ¹	Covariance structure	D60	D90	D120	D150	D180
RR-L2-THM	3x3	0.98	0.90	0.85	0.83	0.82
RR-L3-THM	4x4	0.98	0.91	0.86	0.84	0.84
RR-L4-THM	5x5	0.99	0.92	0.87	0.85	0.84
RP-THM	1x1	0.96	0.87	0.83	0.81	0.80

¹RP-THM = repeatability model; and RR-L2-THM, RR-L3-THM and RR-L4-THM = Random regression with the second-, third-, and fourth-order of Legendre polynomials, respectively.

Based on GOF, PA and PRA criteria showed that the MSE, correlations and R^2 accordingly, RR-THM was better than RP-THM. The best model was RR-L4-THM. However, when consider only RR-THM together with the heritability of different DIM (Figure 5-2 (c)) and correlations among day 50 to day 350 (Figure 5-3), the RR-L2-THM was recommended according to the smoothing plot and non-oscillation of heritability and genetic correlation with slightly different of GOF, PA, PRA to RR-L4-THM.

CONCLUSION

A longitudinal analysis in this study allows for the inclusion of breeding information over a specific period with threshold model. The repeatability model and random regression models having different parameter functions were compared. The application of an RRM for binary longitudinal data using a time dependent covariate accounts for the variation in genetic variance for outcome of insemination events over time, as well as the order in which they were used, potentially leading to more precise estimates and more realistic modeling compared with the repeatability model. This comparison was also proved based on goodness of fit, predictive ability and the predicted results of animal. However, a higher order of Legendre polynomials of the random regression model with a limited amount of data maybe the main reason of upward bias of AG, PE variance, and heritability in the extreme ends of the DIM-scale. Estimates of heritability using the third- and fourth-order of Legendre polynomials were upwardly biased in comparison to those expected for fertility traits; especially at the end of the lactation. Moreover, higher orders of polynomials require higher capacity and take time in analysis. Estimates of genetic parameters from all models studied here indicated the possibility that reproductive performance can be genetically improved through selection using the second-order of Legendre polynomials.

Chapter VI

General conclusion and recommendation

The overall objective of this dissertation was to study the genetic evaluation of female fertility traits of Thai dairy cattle by applying appropriate methodology and introducing it into Thailand national genetic evaluation. The dissertation carried out different studies on the various aspects of fertility in dairy cattle under tropical conditions. The studied population was Thai dairy cattle, which were crossbred of *Bos indicus*, such as Sahiwal, Brahman, and Thai Native cattle upgraded by Holstein Frisian (HF), raised in a smallholder system all over Thailand. Different aspects and concerns were focused in the female fertility analysis.

The first step, the investigated fertility traits were defined as ordered categorical, binary traits and continuous traits (time interval traits). These traits included the following: age at first service (AFS), age at first calving (AFC), days from calving to first service (DTFS), days between first and last service (DFLS), days open (DO), calving interval (CI), number of services per conception (NSPC) and conception at first service (FSC). In addition, fertility measures were considered as different traits if they were taken over the different parities. We defined heifer fertility traits, primiparous cow fertility traits, and multiparous cow fertility traits. Genetic parameters were estimated for these traits providing an indication of the expected response to selection in dairy herds. Gibbs sampling was employed to obtain (co)variance components using both univariate and bivariate analyses with linear and threshold animal models. Results showed that, virgin heifers had better fertility performance than primiparous and multiparous cows. The reproductive performance in primiparous cows was inferior compared with multiparous cows. Cows with higher HF blood showed lower reproductive efficiency. Heritability estimates for most of the fertility traits were 0.04 or less except for AFS (0.26) and AFC (0.25). The estimated genetic correlations among fertility traits within parity indicated that selection for cows with high conception rate could lead to shortened DO and CI, as well as DTFS. The FSC and NSPC could be

used as the best indicators for heifer and cow fertility and could be complemented by other traits such as DTFS and DFLS in terms of a fertility index. This would enable efficient selection programs for better fertility. Genetic correlations for fertility traits in primiparous and multiparous cows were very high (>0.90), but those between heifers and cows were lower (0.03 to 0.83). The latter results indicated that fertility traits of heifers and cows should be considered as different traits.

The second step, the test-day milk fat-to-protein ratio (TD-FPR) could serve as a measure of the energy balance status and might be used as a criterion to improve metabolic stability and fertility through genetic selection. Therefore, genetic parameters for fertility traits, test-day milk yield (TD-MY) and TD-FPR, as well as, their relationships during different stages of lactation were estimated. Gibbs sampling algorithms were implemented to obtain (co)variance components using both univariate linear and threshold animal models and bivariate linear-linear and linear-threshold animal models with random regression. Average TD-MY and TD-FPR were 12.60 and 1.15. Heritability estimates for TD-MY, TD-FPR and selected fertility traits ranged from 0.31 to 0.58, 0.17 to 0.19 and 0.02 to 0.05 respectively. The moderate to high antagonistic correlations between TD-FPR and fertility traits and between TD-MY and fertility traits, as well as, the positive correlation in early lactation between TD-MY and TD-FPR indicated that selection for lower fat-to-protein ratio would decrease NSPC, and increase FSC and pregnancy within 90 days after the first service (P90). In addition, cow selection based only on high milk production has strong effects to prolong DTFS, DO and CI. On the other hand, a very low TD-FPR is known to be an indicator for the subclinical rumen acidosis. Therefore, TD-FPR may be a useful trait for selection to improve fertility and yields traits of Thai dairy crossbred by including optimum value of TD-FPR in breeding program with an appropriate economic weights.

The third step, the investigated fertility traits were defined as the longitudinal binary responses such as the outcome of an insemination (call conception rate, CR). A longitudinal analysis in this study allows for the inclusion of breeding information over a specific period with threshold model. The repeatability model and random regression models (RRM) having different parameter functions were

compared. The application of an RRM for binary longitudinal data using a time dependent covariate accounts for the variation in genetic variance for outcome of insemination events over time, as well as the order in which they were used, potentially leading to more precise estimates and more realistic modeling compared with the repeatability model. Heritability estimates of CR ranged from 0.032 to 0.067, 0.037 to 0.165, and 0.045 to 0.218 for RR-THM with the second, third, and fourth-order of Legendre polynomials, respectively. The heritability estimated from RP-THM was 0.056. Model comparisons based on goodness of fit, predictive abilities, predicted service results of animal, and pattern of genetic parameter estimates, indicated that the model which fit the desired outcome of insemination was the RR-THM with two regression coefficients.

In these studies, there were also some major different results which has never been identified of heifers and cows in tropical conditions from those in temperate climate such as the mean of AFS was higher than those in temperate condition. Also the reproductive performance in primiparous cows was inferior compared with multiparous cows. The longer AFS in Thai dairy cattle could be due to the environmental condition, particularly feeding level. The latter might be due to the norm of practice of small dairy farmers in Thailand who traditionally raise their female calves, heifers, and pregnant heifers less intensively than cows providing income at the moment. Consequently, these animals are always neglected under improper nutrition management. In addition, the mean of FPR in this study was a little bit lower than the range showed in the literatures which infer that Thai dairy crossbred cows may be subjected to subclinical rumen acidosis due to daily feed ration is based heavily on concentrates, especially in winter and summer. The time that roughage shortage happened every year and most of the farmers tried to solve the problem by using higher proportion of commercial mixed ration instead.

In conclusion, female fertility is a complex set of traits, confounded with each other, strongly influenced by data quality and affected by both genetic and environmental factors. Although heritability estimates are low, ranging from 1% for FSC and DFLS in heifers to 26% for age at first service, additive genetic variation still exists. It seems to be difficult for selection of this trait but it is possible.

Genetic correlations between different fertility traits indicate that there is not likely a single characteristic that would serve well for selection purposes. Selection for cows with high conception rate could lead to shortened DO and CI, as well as DTFS. The FSC and NSPC could be used as the best indicators for heifer and cow fertility and could be complemented by other traits such as DTFS and DFLS in terms of a fertility index. This would enable efficient selection for better fertility. Fertility traits of heifers and cows should be considered as different traits. The moderate to high antagonistic correlations between TD-FPR and fertility traits and between TD-MY and fertility traits, as well as, the positive correlation in early lactation between TD-MY and TD-FPR indicated that selection for lower fat-to-protein ratio would decrease NSPC, and increase FSC and pregnancy within 90 d after first service (P90). In addition, cow selection based only on high milk production has strong effects to prolong DTFS, DO and CI. Therefore, TD-FPR may be a useful trait for selection to improve fertility and yield traits by including TD-FPR with optimum weighting in a multi-trait selection index for the overall breeding objective of dairy cattle. The binary response such as the outcome of an insemination event seems to be the trait of choice in genetic evaluation of female fertility traits of Thai dairy cattle with considering the suitable model. As it is conveniently measured, taken in early to mid-stages of lactation and included of breeding information over a specific period.

Nevertheless, creating a fertility data set as production level (high & low) or the farm size (large & small) are necessary for future research.

This study has high potential for applying in genetic evaluation for selection of fertility traits in Thai dairy cattle which will be highly beneficial for Thai dairy industry as well as other dairy industries in tropical areas. Since the fertility is low heritable trait and reliable data is difficult to achieve, further study on genomic wide association in dairy crossbred for genomic evaluation would be recommended.

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ABTRACT

Fertility is of great economic importance in the dairy industry. It has overwhelm impact on herd productivity and overall profitability in dairy farming. Including the fertility in breeding objective is considered to be an appropriate strategy to optimize the result of genetic improvement of dairy cattle. In Thailand, a national genetic evaluation system for female fertility is not yet available. Hence, the overall objective of this dissertation is to study the genetic evaluation of female fertility traits of Thai dairy cattle by applying appropriate methodology and introducing it into Thai dairy cattle national genetic evaluation. There were specific objectives conducted in following three studies.

The objective of the first study was to estimate genetic parameters for various fertility traits on Thai dairy heifers and cows in a smallholder system under tropical conditions using data sets from the Thailand AI national recording scheme. The data consisted of 68,555, 34,401, and 54,004 records on heifers, primiparous, and multiparous cows, respectively, calving between 1996 and 2011. The analysis provided insight (co)variance components and genetic parameters of the investigated traits [age at first service (**AFS**); age at first calving (**AFC**); days from calving to first service (**DTFS**); days between first and last service (**DFLS**); days open (**DO**); calving interval (**CI**); number of services per conception (**NSPC**); and conception at first service (**FSC**)]. Gibbs sampling was employed using both univariate and bivariate analyses with linear and threshold animal models. Virgin heifers had better fertility performance than primiparous and multiparous cows. The reproductive performance in primiparous cows was inferior compared with multiparous cows. Cows with higher Holstein-Friesian blood showed lower reproductive efficiency. Heritability estimates for most of the fertility traits were 0.04 or less except for AFS (0.26) and AFC (0.25). The estimated genetic correlations among fertility traits within parity indicated that selection for cows with high conception rate could lead to shortened DO and CI, as well as DTFS. The FSC and NSPC could be used as the best indicators for heifer and cow fertility and could be complemented by other traits, which were genetically considered as different traits such as

DTFS and DFLS in terms of a fertility index. This would enable efficient selection for better fertility. Genetic correlations for fertility traits in primiparous and multiparous cows were very high (>0.90), but those between heifers and cows were lower (0.03 to 0.83). The latter result indicated that fertility traits of heifers and cows should be considered as different traits.

The objective of the second study was to estimate genetic parameters for fertility traits, test-day milk yield (**TD-MY**) and test-day fat-to-protein ratio (**TD-FPR**) as well as their relationship during different stages of lactation using random regression models (**RRM**) on Thai dairy cows in a smallholder system under tropical condition. Data on fertility traits and monthly test-day record of milk production and milk compositions consisted of 25,968 primiparous cows, calving between 1996 and 2011. Gibbs sampling algorithms were implemented to obtain (co)variance components using both univariate linear and threshold animal models and bivariate linear-linear and linear-threshold animal models with random regression. Average TD-MY and TD-FPR were 12.60 kg and 1.15. Heritability estimates for TD-MY, TD-FPR and selected fertility traits ranged from 0.31 to 0.58, 0.17 to 0.19 and 0.02 to 0.05 respectively. Genetic correlations among TD-FPR and TD-MY, TD-FPR and fertility traits, and TD-MY and fertility traits ranged from 0.05 to -0.44, -0.98 to 0.98 and -0.22 to 0.79, respectively. Selection for lower TD-FPR would decrease NSPC, and increase FSC and pregnancy within 90 days after the first service (**P90**). In addition, cow selection based only on high milk production had strong effects to prolong DTFS, DO and CI. Therefore, TD-FPR might be a useful trait for selection to improve fertility and yield traits of Thai dairy crossbred by including optimum value of TD-FPR in breeding program with an appropriate economic weights.

The objectives of the third study were 1) to estimate genetic parameters and breeding values for conception rates (**CR**) of Thai dairy cows using the repeatability threshold model (**RP-THM**) and random regression threshold models (**RR-THM**) and 2) to compare covariance functions for modeling the additive genetic (**AG**) and permanent environmental (**PE**) effects in the RR-THM. A data set of 130,592 first-lactation insemination records of 55,789 primiparous cows, calving between 1996 and

2011, was used in the analyses. The CR was defined as the outcome of an insemination. A longitudinal analysis in this study allowed inclusion of breeding information over a specific period with threshold model. The RP-THM and RR-THM with different parameter functions were compared. Variance components were estimated using a Bayesian method via Gibbs sampling. Heritability estimates of CR ranged from 0.03 to 0.07, 0.04 to 0.17, and 0.05 to 0.22 for RR-THM with the second, third, and fourth-order of Legendre polynomials, respectively. The heritability estimated from RP-THM was 0.06. Model comparisons based on goodness of fit (**GOF**), predictive abilities (**PA**), predicted service results of animal (**PRA**), and pattern of genetic parameter estimates indicated that the model which fit the desired outcome of insemination was the RR-THM with two regression coefficients.

In conclusion, female fertility is a complex set of traits affected by both genetic and environmental factors. Although heritability estimates is low, additive genetic variation still exists. Therefore, genetic improvement for cows' fertility through selection seems to be possible. Genetic correlations between different fertility traits indicate that there is not likely a single characteristic that would serve well for selection purposes. The FSC and NSPC could be used as the best indicators for heifer and cow fertility and could be complemented by other traits such as DTFS and DFLS in terms of a fertility index. This would enable efficient selection for better fertility. Fertility traits of heifers and cows should be considered as different traits. Since the TD-FPR was found highly correlated with all fertility traits in this study, the TD-FPR might be a useful trait for selection to improve fertility by including TD-FPR with optimum weighting in a multi-trait selection index for the overall breeding objective of dairy cattle. The binary response such as the outcome of an insemination event seems to be the trait of choice in genetic evaluation of female fertility traits of Thai dairy cattle with considering the suitable model. As it is conveniently measured, taken in early to mid-stages of lactation and included of breeding information over a specific period. In the studied model which fits the desired the outcome of an insemination is the RR-THM with two regression coefficients.

要旨

繁殖性は酪農において経済的に非常に重要であり、酪農経営において生産性と収益に大きな影響を及ぼす。改良目標に繁殖性を含めることは、乳用牛の遺伝的改良の結果を最適化するための適切な戦略である。タイにおいて、雌牛の繁殖性に関する国内遺伝的能力評価は、現在のところ実現していない。そこで、本論文の主題は、タイ乳用牛の雌牛繁殖形質の遺伝的能力評価に応用できる最適な手法について研究し、タイの国内遺伝的能力評価へ導入することである。以下の3つの研究を実施した。

第一の研究の目的は、タイ国内人工授精記録事業データを使用し、熱帯条件下の小規模経営における未経産および経産牛に対する種々の繁殖形質の遺伝的パラメータを推定するための研究である。データは、1996年から2011年までに分娩した個体について、未経産、初産および2産以上でそれぞれ、68,555、34,401および54,004記録を含む。分析では、調査形質〔初回授精月齢（AFS）、初産分娩月齢（AFC）、分娩から初回授精までの日数（DTFS）、初回および最終授精までの日数（DFLS）、空胎日数（DO）、分娩間隔（CI）、受胎あたりの授精回数（NSPC）、および初回授精受胎率（FSC）〕の（共）分散成分および遺伝的パラメータを推定した。単変量および線形-閾値多変量アニマルモデルに Gibbs Sampling 法を応用した。未経産牛は、初産および2産以上の経産牛との比較において繁殖能力が優れていた。初産牛における繁殖能力は、2産以上の経産牛より低かった。ホルスタイン・フリージアン種の血統濃度が高い雌牛は、繁殖効率が低かった。ほとんどの繁殖形質の遺伝率推定値は、AFS（0.26）および AFC（0.22）を除き、0.04以下であった。産次内の繁殖形質間の遺伝相関推定値は、受胎率を高める方向への選抜が DO、CI および DTFS を短期化することを示唆し

た．FSC および NSPC は，繁殖性指数において DTFS および DFLS のような遺伝的に異なると考えられている他の形質を補完できることから，未經産牛および経産牛の繁殖性に関する最適な指標であろう．これは，繁殖性に関する効果的な選抜を可能にする．初産および2産以上の経産牛に関する繁殖形質間の遺伝相関は非常に強かった (>0.90) が，未經産牛および経産牛間のそれらはより弱かった (0.03 から 0.83) ．このことは，未經産牛と経産牛の繁殖形質が異なる形質であることを示唆した．

第二の研究の目的は，熱帯条件下の小規模経営におけるタイの乳用交雑種に対し，変量回帰検定日モデル (RRM) を使用し，繁殖形質，検定日乳量 (TD-MY) および検定日 P/F 比 (TD-FPR) の遺伝的パラメータ，および各泌乳ステージにおけるそれら間の関係を推定することである．繁殖形質および毎月の検定日乳量と乳成分のデータは，1996 年から 2011 年までに分娩した 25,968 頭の初産雌牛の記録を使用した．Gibbs sampling アルゴリズムは，単形質線形または閾値アニマルモデル，および二変量の線形-線形および線形-閾値変量回帰アニマルモデルを使用して分散成分を推定するために使用された．平均 TD-MY および TD-FPR は，12.60 および 1.15 であった．TD-MY，TD-FPR および繁殖形質の遺伝率推定値は，それぞれ，0.31 から 0.58，0.17 から 0.19 および 0.02 から 0.05 の範囲であった．TD-FPR と TD-MY 間，TD-FPR と繁殖形質間，および TD-MY と繁殖形質間の遺伝相関は，それぞれ，0.05 から -0.44，-0.98 から 0.98，および -0.22 から 0.79 の範囲であった．TD-FPR を低くする方向への選抜は，受胎あたりの授精回数を減少させ，FSC および分娩後 90 日以内の受胎を増加させるであろう．さらに，乳量を増加させる方向への選抜は，DTFS，DO および CI を大きく増加させる．そのため，TD-FPR は，育種プログラムの経済的重み付けにおいて最適な重み付けを与えることにより，タイ交雑種の繁殖性と泌乳形質を改良する方向への選抜に利用できる形質である．

第三の研究の目的は、1) 反復閾値モデル (RP-THM) および変量回帰閾値モデル (RR-THM) を用いた CR の遺伝的パラメータおよび育種価を推定すること、2) 相加的血縁 (AG) および恒久的環境 (PE) の共分散を比較することである。データは、1996 年から 2011 年までに分娩した 55,789 頭の初産雌牛からの 130,592 記録を使用した。CR は、授精ごとの結果と定義した。本研究において、閾値モデルによる育種価の推定は、長期にわたる分析期間を必要とした。RP-THM と RR-THM の推定値を比較した。分散成分は、Bayesian 法による Gibbs Sampling を使用して推定した。CR の遺伝率推定値は、2 次、3 次および 4 次の Legendre 多項式を用いた RR-THM について、それぞれ、0.03 から 0.07、0.04 から 0.17、および 0.05 から 0.22 の範囲であった。RP-THM による遺伝率推定値は 0.06 であった。適合度、予測性能、個体の授精結果の予測、および遺伝的パラメータ推定値のパターンから、授精結果について 2 次の RR-THM が望ましいと判断した。

結果として、雌牛の繁殖性は遺伝と環境の要因が影響する複雑な形質であった。遺伝率推定値は低い、相加的遺伝分散が存在した。そのため、選抜による雌牛の繁殖性の改良は可能であろう。異なる繁殖形質間の遺伝相関は、ひとつの形質が選抜目標をすべて満たすような都合の良い形質が存在しないことを示唆した。FSC と NSPC は、未経産牛および経産牛の繁殖性のための最良の指標であり、繁殖指数において TDFS および DFLS のような他の形質を補完できる。このことは、繁殖性改良のための効果理的な選抜を可能とする。未経産牛および経産牛の繁殖形質は異なる形質とみなされた。TD-FPR は、本研究におけるすべての繁殖形質との間に高い遺伝相関が認められたため、乳用牛の総合指数において、最適な重み付けで含めることによって繁殖性改良のための選抜に適するであろう。授精結果のような閾値による観測値は、泌乳初期から中期に得られ、育種情報として利用できる。そのため、この形質は、最適なモデルを使用することでタ

イ乳用牛の雌牛繁殖形質の遺伝的能力評価形質における選択支となるであろう。
本研究において、2次のRR-THMは授精結果への適合度が優れていた。