

Dedication

This thesis is dedicated to my family and
tribute to my late teachers in animal breeding and genetic;
Prof. Dr. Seno Johari M.Sc. and Prof. Dr. Irene Sumediana K., M.S.
Specific contributions of others are acknowledged.

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Abstract

Genetic parameter for reproductive traits in artificial insemination record were estimated from total 7,941 record of 2,161 heifers and three parities of 2,078 cows. The animals were daughters of 171 sires and whose ancestors were traced back to five generations using pedigree information. The total number of animals in the pedigree was 15,600. Reproductive traits included 56 days non-return rate (NRR), success in first insemination (SFI), number of insemination (IN), days from first to successful insemination (FS), gestation length (GL), age at calving (AC), days from calving to first insemination (CF), days open (DO), pregnancy rate (PR) and calving interval (CI).

Genetic study for reproductive traits of heifers

The genetic parameters of five reproductive traits in Japanese Black heifers were estimated by restricted maximum likelihood (REML) with the use of univariate animal model and the environmental factors strongly associated were identified by GLM. Averages of reproductive traits over eleven years were assessed, and significant effects of farm, year, month, artificial insemination (AI) technician and interaction of farm \times year on the traits were identified. Estimated heritability of FS was very low and that of age of first calving (AFC) was higher than that of the other traits. A close genetic relationship was observed among NRR, IN and FS; however, their heritabilities were very low.

Genetic study for reproductive traits of three parities of cows using multiple-trait model

Data across three parities of cows were analyzed by multiple-trait model under which the performance of a trait in different parities was treated as a different trait. AC comprises age at first calving (AFC), age at second calving (ASC) and age at third calving (ATC). Genetic parameters were estimated by REML via multiple-trait model. Estimated

heritability of the traits showed little variation among parities. Heritability of AC was higher than that of the other traits, although it was lower in later parities; 0.158, 0.107 and 0.088 for AFC, ASC and ATC, respectively. The genetic correlations between the same traits across parities were generally high, ranging from 0.72 to 0.99.

Genetic study for reproductive traits of three parities of cows using repeatability model

Data for three parities of cows were treating as repeated measurements. Heritability ranged from 0.013 for NRR to 0.059 for CF. The highest repeatability was observed for CF (0.142) and the lowest for FS (0.036). The lowest genetic correlation in absolute value was observed between CF and IN (-0.075) and the highest between DO and CI (0.957).

Relationship between reproductive traits of heifers with reproductive traits of cows

Two-trait animal model was used to estimate genetic correlation between reproductive traits of heifers with reproductive traits of cows. Reproductive traits for heifers were coded as NRR-h, IN-h, FS-h and GL-h, respectively. Reproductive traits for cows were four traits same as in heifers, which were coded as NRR-c, IN-c, FS-c, GL-c, and CF, DO, PR and CI. AC has individual traits at each parity such as AFC, ASC and ATC. The highest and the lowest genetic correlations were between FS-h and FS-c (0.795) and between GL-h and PR (0.065), respectively. AFC was more favorable compared with ASC and ATC. Due to the fact that AFC is a trait measured early, it shows high genetic correlations with IN-c and FS-c (0.661 and 0.634, respectively) and moderate genetic correlations with NRR-c, GL-c, CF, DO, PR and CI.

Determination of penalty methods for interval from first to successful insemination

Five penalty methods created for handling 206 missing records (8.7%) of FS in heifers were: C1 (FS average according to the number of inseminations), C2 (constant number of days; 359), C3 (maximum number of FS days to each insemination), C4

(average of FS at the last insemination and FS of C2) and C5. C5 was generated by adding a constant number (21d) to the highest number of FS days in each contemporary group. The bootstrap method was used to compare among the 5 methods in terms of bias, mean squared error (MSE) and coefficient of correlation between estimated breeding value (EBV) of non-censored data and censored data. MSE in C4 heritability was 0.633×10^{-4} , 0.879×10^{-4} , 0.876×10^{-4} and 0.866×10^{-4} for 5, 8.7, 10 and 15%, respectively, of the missing records. Thus C4 showed the lowest and the most stable MSE of heritability; the coefficient of correlation for EBV was 0.88; 0.93 and 0.90 for heifer, sire and dam, respectively.

Estimated genetic parameters for binary traits using Bayesian approach via Gibbs sampling

The genetic parameters of NRR and SFI were estimated using Bayesian approach via Gibbs sampling to determine the best model for analysis of binary traits. The variance covariance components were estimated via Bayesian procedure by GIBBS1F90 and THRGIBBS1F90, respectively for linear and threshold model. Estimated heritability for SFI-h was similar to that for NRR-h by linear model. When threshold model was applied, heritability of SFI-h was slightly higher than that of NRR-h. Estimated heritability for SFI-c was higher than heritability for NRR-c on either linear or threshold model have applied.

In conclusion, AFC is potentially more useful for genetic improvement of female reproductive traits. Selection by AFC will provide high genetic improvement in reproductive performance of Japanese Black heifers and cows. The repeatability model seems to be more appropriate for estimating reproductive traits of cows because it yields a low standard error in estimated parameters. We concluded that C4 was the best penalty method for missing records of FS due to the stable value of estimated parameters and the

highest coefficient of correlation. For estimated genetic parameter of binary traits, threshold model was concluded to be better than linear model because BIC value for NRR and SFI estimated by threshold model were lower than that by linear model for both records of heifers and cows.

要約

黒毛和種繁殖形質の遺伝学的分析を行った。繁殖形質は子牛の生産性に直接関係するだけでなく、農家経営を持続可能なかたちで発展させるうえでも重要である。分析対象は、7,941件の人工授精記録である。血統情報は、5世代前までさかのぼり、分析に含まれる牛の総数は15,600頭であった。分析対象形質はノンリターン率 (NRR)、初回授精率 (SFI)、授精回数 (IN)、初回授精から受胎までの日数 (FS)、妊娠期間 (GL)、分娩時月齢 (AC)、分娩から初回授精の日数 (CF)、空胎期間 (DO)、受胎率 (PR)、分娩間隔 (CI) の10形質である。まず、未經産牛における5つの繁殖形質について要因分析を行い、農家、年、月、人工授精師、農家と年の相互作用が有意であることを確認した。遺伝率推定値は、FSが非常に低い一方、初産月齢 (AFC) の遺伝率は比較的高いことを明らかにした。また、NRR、IN、FSの間に密接な遺伝的關係があった。次に多形質モデルにより経産牛データを分析した。形質の遺伝率推定値は各産次の間ではほぼ変動を示さなかった。ACの遺伝率は他の形質より高かったが、AFCで最も高く、後の産次になるほど低くなる傾向がみられた。各産次の同じ形質間の遺伝相関は一般的に高く、範囲は0.72から0.99であった。反復率モデルによる遺伝率推定では、NRRの0.013からCFの0.059の範囲にあった。最も高い反復率はCF (0.142) でみられ、最も低い反復率はFS (0.036) でみられた。絶対値が最も低い遺伝相関はCFとIN (-0.075) であり、最も高い遺伝相関はDOとCI (0.957) であった。比較的高い反復率を持つCFでは、永続的環境効果が大きいことが示唆された。未經産牛 (-h) と経産牛 (-c) の繁殖形質の遺伝相関を推定すると、遺伝相関の高いものはIN-hとDO (0.931) であり、低いものはGL-hとPR (0.065) であった。AFCはIN-cとFS-cにおいて高い遺伝相関を示し (それぞれ0.661、0.634)、NRR-c、GL-c、CF、DO、PR、CIにおいて中程度の遺伝相関を示した。AFCは早期に測定される形質であ

ることから世代間隔の面でも有利であり、有効な遺伝的形質であることが明らかとなった。未経産牛のFSの欠測値の補正法として、ブートストラップ法によりC1(授精回数によるFSの平均)、C2(一定の日数である359)、C3(各授精のFS日の最大値)、C4(最後の授精時のFSとC2のFSの平均)、C5(各グループのFS日の最大値に定数の21日を追加)の5つのペナルティ法について比較した結果、C4の遺伝率の平均平方誤差(MSE)は最も低く安定した結果を示し、推定育種価(EBV)の相関係数でも最大値を示し、最適なペナルティ法であることを明らかにした。最後にバイナリ形質であるNRRとSFIの遺伝的パラメータを閾値モデルと線形モデルで比較した。いずれも閾値モデルの遺伝率が高く推定され、またベイズ情報量基準(BIC)においても閾値モデルは線形モデルより優れていることを明らかにした。以上の結果、黒毛和種繁殖形質の改良において、AFCが最も有用な形質であるとの結論が得られた。

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List of abbreviations

AC	-	Age at Calving
AFC	-	Age at First Calving
ASC	-	Age at Second Calving
ATC	-	Age at Third Calving
AI	-	Artificial Insemination
CD	-	Calving Date
CF	-	Days from Calving to First Insemination
CI	-	Calving Interval
CIH	-	Confidence Interval of Heritability
CV	-	Coefficient of Variation
DIC	-	Deviance Information Criterion
DO	-	Day Open
EBV	-	Estimated Breeding Value
FS	-	Days from First to Successful Insemination
GL	-	Gestation Length
GLM	-	General Linear Model
HI	-	Heat Interval
IN	-	Number of Insemination
LSM	-	Least Square Mean
MCE	-	Error of Monte Carlo Chain
MSE	-	Mean Squared Error
NC	-	Number of Calves
NRR	-	Non-Return Rate

PR	-	Pregnancy Rate
REML	-	Restricted Maximum Likelihood
SAS	-	Statistical Analysis System
SFI	-	Success in First Insemination
SD	-	Standard Deviation
SE	-	Standard Error
VWP	-	Approximate Voluntary Waiting Period

Chapter 1

General introduction

1.1 Female reproductive traits

Production trait, especially carcass characteristics has been a primary object in Japanese Black cattle. Reproductive trait is secondary in the breeding program, whereas it directly influence biological and economical efficiencies of cow-calf production (Dickerson, 1970; Costa et al., 2015). Female reproductive trait is a complex trait in beef production systems and genetic evaluation procedures, which varies according to breed, farm location, climate, nutritional management and mating system (Lopez et al., 2006). Since the liberalization of domestic beef market in April 1991, beef farmers of Japanese Black cattle commonly tend to pursue low production cost, and reproductive ability of Japanese Black cows is one of the most critical element to achieve this target (Uchida et al., 2002).

The common mating system applied in Japan is AI, According to AI record and calving event, female reproductive traits have been classified into three categories as listed below.

1.1.1 Interval traits

Interval traits which commonly used in beef breeding programs are CI, DO, GL, FS and CF (Oyama et al., 2002; Goyache et al., 2005; Yaque et al., 2009). CI is the complex trait defined as ability of animals to resume normal post-calving cyclicity, to express oestrus of sufficient intensity to be detected, to conceive and establish pregnancy in addition to maintain consistent gestation length (Berry et al., 2014). Interval trait defined in heifers was FS, GL and AFC (Gutiérrez et al., 2002; Martínez-Velázquez et al., 2003).

1.1.2 Binary traits

Binary traits are those with only two outcomes, for example success is coded as 1 or fail is coded as 0. NRR and SFI are the most common binary traits in cattle (Jamrozik et al 2005; Sun and Su, 2010) but limited reports on beef cattle have been published. In terms of genetic parameters estimation, the threshold model was assumed to be relevant to binary trait because the threshold model is based on the assumption of an underlying unobservable continuous response variable that follows the assumptions of a latent normal distribution (Gianola and Foulley, 1983).

1.1.3 Count traits

The most common count trait is IN (Veerkamp et al., 2001; Yaque et al., 2009), under ideal situation it would be possible for a cow to obtain one viable calf in one year (365 days). Often in farms arises a situation that the first insemination after calving is delayed and in some cases, AI needs to be repeated. The increased number of services per conception indicates the problems of reproductive ability of a cow which considerably brings negative impact on farm profitability making farm management difficult (LeBlanc, 2007; Honarvar et al., 2010).

1.2 Present situation in genetic research of female reproductive traits

Improvements in reproductive performance can be more important than improvements in production traits in a conventional cow-calf operation because profit comes from selling weaning calves at market (Melton, 1995). Production traits including growth and carcass traits are focused in beef breeding system program because availability of records and analysis procedures have been improved (Evans et al., 1999). On the other hand, genetic improvement of reproductive traits is still challenging area because it is difficult in measuring and slow response of selection (Gutierrez et al., 2002; Ibi et al., 2008).

Genetic parameters which represent genetic structure of animal population could be changed over time by strong inbreeding, cross breeding and selection. Among them, selection enjoy main course for improving genetic of traits. Essential parameters which characterize population are heritability and genetic correlation. Heritability is the proportion of genetic variation on phenotypic variation and is based on the alleles that are inherited. The effect of alleles depends on their frequency in the population (Falconer and Mackay, 1996). Because it is not often possible to have phenotypes between two generations (parents and offspring), heritability is often measured across one generation (Lynch and Walsh, 1998). A genetic correlation is defined as the proportion of genetic covariation that is shared between two traits divided by the square root of the product of genetic variation for each trait (Neale, 2016). Both heritability and genetic correlation are not only required in research but also needed for designing effective breeding program.

1.2.1 Heritability for reproductive trait of beef cattle

In a review of 30 studies for estimated heritability of reproductive traits in beef cattle, the average heritability for female reproductive traits is described generally low because of a large, unexplainable portion of residual variation and considerable influence of farm management (Cammack et al., 2009). Some traits have moderate heritability and favorable genetic correlations with other reproductive traits and production traits.

CD reported to have moderate heritability (0.20) in Hereford cattle by Buddenberg et al. (1990). Heritability of NC was reported by Meyer et al. (1990) in Zebu cross (0.357), by Morris and Cullen (1994) in Angus cattle (0.33). Moderate heritability of AFC was reported ranging from 0.20 to 0.28 by Morris et al., (1992; 2000), Frazier et al. (1999) and Martínez-Velázquez et al (2003) in Angus cattle. Among them, AFC was reported to have favorable genetic relationship with economical important traits.

1.2.2 Heritability for reproductive traits of Japanese Black cattle

Genetic studies for reproductive traits in Japanese Black cattle were limited. Among these studies, GL was reported to have high heritability (0.40) by Oyama et al. (2004) and (0.53) by Ibi et al. (2008). But, GL did not show favorable genetic relationship with other reproductive traits and carcass traits in their studies. AFC of Japanese black cattle was also moderately heritable. Some results for estimated heritability of AFC were 0.109 by Uchida et al. (2001), 0.215 by Oyama et al. (2002) and 0.20 by Oyama et al. (2004). In their studies, moderate genetic correlation was also reported between AFC and CI, however heritability of CI was very low (0.047).

Low heritabilities for many reproductive traits do not indicate that reproductive traits have less economical value. As stated by Dickerson (1970), economical and biological efficiencies of cow-calf production are largely dependent on success of reproduction. Furthermore, a trait with high heritability and favorable genetic correlation is absolutely necessary as a basis for the selection decision to achieve successful genetic improvement of all economically traits (Meyer et al., 1990). Our study focused on determining reproductive trait which can be measured early, has high heritability and favorable genetic relationship with important traits such as IN.

1.3 Objectives

1. Identify non-genetic factors strongly associated with reproductive traits and to estimate genetic parameters of reproductive traits in Japanese Black heifers.
2. Estimate heritability of reproductive trait for cows at different parity and genetic correlation between same traits among parity.
3. Estimate heritability, repeatability and genetic correlation for reproductive traits of three parities of cows.
4. Estimate genetic correlation between reproductive traits of heifer and age at calving

and reproductive traits of cows.

5. Determine the best approach for handling missing records of heifer reproductive traits, for estimating the genetic parameters and for predicting the breeding value of FS in Japanese Black heifers.
6. Estimate genetic parameters for binary traits using Bayesian approach via Gibbs sampling.

Chapter 2

Genetic study for reproductive traits of heifers

2.1 Introduction

Reproductive traits in heifers can be measured at a relatively early stage of their reproductive life; thus the inclusion of heifer reproductive traits in genetic evaluation programs increases potential of genetic improvement. But studies on reproductive performance of Japanese Black heifer are scarce.

Most reproductive traits in heifers are of low heritability in dairy cattle (Abe et al., 2009; Liu et al., 2008; Tiezzi et al., 2012) and in beef cattle (Gutiérrez et al., 2002; Martínez-Velázquez et al., 2003; Morris et al., 2000). The number of reports on reproductive traits of Japanese Black heifers is relatively small. Low heritability of reproductive traits is attributed to non-genetic effects, especially farm management practice that largely affects the reproductive performance of heifers (Bolacali and Öztürk, 2008).

Selection of reproductive traits in heifers based on genetic parameters may potentially solve reproduction problems. Therefore designing breeding programs at an early stage necessitates selection of a reproductive trait with high heritability and favorable genetic correlations with other reproductive traits. The objective of this part of study is to identify non-genetic factors strongly associated with traits and to estimate genetic parameters of reproductive traits in Japanese Black heifers.

2.2 Materials and Methods

2.2.1 Reproductive data

Reproduction records of Japanese Black heifers were obtained from the Artificial Insemination Center of Northern Okinawa: data comprised artificial insemination and

calving events. A data set included reproduction records of heifers born between 2004 and 2014, first insemination occurring between 2005 and 2015, less than 10 services and farms with a minimum of five records. Heifers with incomplete records, embryo transfer donor or recipient, and bearing twin calves were excluded from the data set. Edited records of 2161 heifers with NRR and 2047 heifers with FS, IN, AFC and GL were analyzed. To evaluate the effects of age at first insemination, heifers were classified into three age groups: <16, 16 to 19 and >19 month (Liu et al., 2008). Eight AI technicians carried out the artificial insemination on the heifers from 164 farms. The number of animals in the pedigree was 15,600.

2.2.2 Traits in study

The traits studied were NRR to 56 days (coded one when no subsequent insemination occurred until 56 days after the first insemination, and zero otherwise); FS being the number of days between the first insemination and the successful insemination which resulted conception, IN, AFC defined as the difference between the heifer's date of birth and the date of birth of her first calf, and GL being the interval in days from the last insemination to the subsequent calving.

2.2.3 Statistical analysis

The GLM procedure of SAS 9.3 software (SAS, 2011) was used to test the significance of reproductive traits. The linear model for NRR, FS, IN and GL was as follows:

$$y_{ijklmop} = F_i + Y_j + M_k + T_l + A_m + F_i \times Y_j + s_o + e_{ijklmop},$$

where $y_{ijklmop}$ is the observation of NRR, FS, IN and GL, F_i the i^{th} fixed effect of farm, Y_j the j^{th} fixed effect of year of insemination, M_k the k^{th} fixed effect of month of insemination, T_l the l^{th} fixed effect of AI technicians, A_m the m^{th} fixed effect of age at first insemination, s_o the o^{th} random effect of sire, and $e_{ijklmop}$ the random residual of $y_{ijklmop}$.

The following model was used for AFC:

$$y_{ijklop} = F_i + Y_j + M_k + T_l + F_i \times Y_j + s_o + e_{ijklop},$$

where y_{ijklop} is the observation of AFC. F_i , T_l , and s_o are as described in the previous model where two effects were defined differently, Y_j the j^{th} fixed effect of year of birth, M_k the k^{th} fixed effect of month of birth and e_{ijklop} the random residual of y_{ijklop} . The GLM procedure of SAS 9.3 software (SAS, 2011) was used to estimate the LSM of the year effect. The univariate animal model by REML of the Asreml software (Gilmour et al., 2015) was used to estimate the genetic parameters. The linear model for the analysis was as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{G}\mathbf{u} + \mathbf{e},$$

where

\mathbf{y} = a vector of reproductive traits,

\mathbf{b} = a vector of fixed effect,

\mathbf{X} = an incidence matrix for the fixed effects,

\mathbf{u} = a vector of random genetic additive effect,

\mathbf{Z} = an incidence matrix for the random effect and

\mathbf{e} = a vector of random residuals.

The expectations for \mathbf{y} , \mathbf{u} and \mathbf{e} are

$$E \begin{bmatrix} \mathbf{y} \\ \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{X}\mathbf{b} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} .$$

The variance-covariance structure of random effects was

$$V \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix} ,$$

where \mathbf{A} is the numerator relation matrix, \mathbf{I} the identity matrix, σ_a^2 and σ_e^2 the additive genetic variance and residual variance, respectively.

2.3 Results

Table 2.1 presents the averages of the reproductive traits over eleven years were 67%, 1.76, 36.33 days, 25.8 months and 288.22 days for NRR, IN, FS, AFC and GL, respectively.

Table 2.1 The descriptive statistic of reproductive traits Japanese Black heifers

Trait ^a	No. of records	Mean	SD	Minimum	Maximum
NRR	2161	0.67	0.47	0	1
IN	2047	1.76	1.08	1	10
FS (days)	2047	36.33	69.88	0	363
AFC (months)	2047	25.8	5.39	19.67	43.27
GL (days)	2047	288.22	4.94	263	303

^a)NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, AFC: age at first calving, GL: gestation length.

Farm effect was significant in all traits, year effect was significant in NRR, FS, GL and AFC, and month effect was significant in only GL. The effect of AI technician was significant in FS and AFC, whereas age at first insemination was not significant in any of the traits; furthermore, the interaction of farm × year effect was significant in FS, AFC and GL (Table 2.2).

Table 2.2 Significance of factors affecting heifer reproductive traits

Source	df	NRR		IN		FS (days)		AFC (months)		GL (days)	
		F-value	<i>P</i>	F-value	<i>P</i>	F-value	<i>P</i>	F-value	<i>P</i>	F-value	<i>P</i>
Farm	163	1.27	0.0151	1.48	0.0002	1.81	<.0001	3.07	<.0001	4.27	<.0001
Year	10	2.73	0.0016	1.5	0.1259	2.46	0.0048	3.16	0.0002	3.01	0.0005
Farm×year	636	1.04	0.2632	0.95	0.7883	1.33	<.0001	1.38	<.0001	1.43	<.0001
Month	11	0.96	0.4796	1.13	0.3319	0.93	0.514	0.85	0.5848	3.64	<.0001
Technician	7	1.19	0.3124	1.43	0.2105	2.31	0.0423	2.95	0.0117	0.38	0.8635
Age	2	0.45	0.6399	1.73	0.1783	2.26	0.1049	-	-	0.98	0.3767

^a) NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, AFC: age at first calving, GL: gestation length.

Table 2.3 presents yearly trend of LSM of heifer reproductive traits. The highest LSM for NRR was observed in 2010, and for IN and FS in 2005. The longest GL was observed in 2010. Heifers born in 2010 showed the highest LSM for AFC.

Table 2.3 Yearly trend of LSM (\pm SE) of heifer reproductive traits

Year ^a	Trait ^b				
	NRR	IN	FS	AFC	GL
2004	-	-	-	26.28 \pm 0.45	-
2005	0.64 \pm 0.04	1.99 \pm 0.11	100.83 \pm 10.76	25.55 \pm 0.43	287.20 \pm 0.42
2006	0.69 \pm 0.04	1.85 \pm 0.10	53.58 \pm 9.92	26.03 \pm 0.35	287.00 \pm 0.39
2007	0.62 \pm 0.03	1.83 \pm 0.09	66.48 \pm 8.80	26.16 \pm 0.35	288.45 \pm 0.34
2008	0.72 \pm 0.03	1.77 \pm 0.08	73.08 \pm 8.07	26.05 \pm 0.34	288.59 \pm 0.31
2009	0.68 \pm 0.03	1.71 \pm 0.08	49.05 \pm 7.91	26.24 \pm 0.33	288.80 \pm 0.31
2010	0.74 \pm 0.03	1.79 \pm 0.08	61.35 \pm 7.95	26.43 \pm 0.38	289.54 \pm 0.31
2011	0.65 \pm 0.03	1.98 \pm 0.09	73.05 \pm 8.71	25.26 \pm 0.44	288.93 \pm 0.34
2012	0.73 \pm 0.04	1.75 \pm 0.10	64.13 \pm 9.51	25.50 \pm 0.44	288.50 \pm 0.37
2013	0.70 \pm 0.04	1.77 \pm 0.11	52.77 \pm 10.46	25.36 \pm 0.39	287.94 \pm 0.41
2014	0.60 \pm 0.03	1.85 \pm 0.10	42.11 \pm 9.55	24.10 \pm 0.42	286.90 \pm 0.37
2015	0.67 \pm 0.03	1.63 \pm 0.10	31.26 \pm 9.40	-	287.57 \pm 0.37

a) Year of insemination for NRR, IN, FS and GL; year of birth for AFC.

b) NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, AFC: age at first calving, GL: gestation length.

Table 2.4 presents genetic parameters of heifer reproductive traits. Estimated heritability of FS was the lowest, and that of AFC was higher than of the other traits

Table 2.4 Genetic parameters (\pm SE) of heifer reproductive traits

Trait ^a	σ_a^2	σ_e^2	h^2
NRR	6.05x10 ⁻³ \pm 0.005	0.21 \pm 0.007	0.027 \pm 0.024
IN	3.07x10 ⁻² \pm 0.093	1.58 \pm 0.068	0.019 \pm 0.023
FS	121.85 \pm 0.332	1026 \pm 0.532	0.011 \pm 0.018
AFC	5.26 \pm 0.061	24.17 \pm 0.012	0.180 \pm 0.028
GL	1.42 \pm 0.016	15.91 \pm 0.094	0.081 \pm 0.024

a) NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, AFC: age at first calving, GL: gestation length.

σ_a^2 : additive genetic variance, σ_e^2 : residual variance, h^2 : heritability.

Table 2.5 presents genetic correlations and phenotypic correlations among reproductive traits. The highest and the lowest genetic correlations were between FS and NRR and between FS and GL, respectively, in absolute values. AFC showed moderate genetic correlation with NRR and GL, but high with IN and FS. The phenotypic correlation between NRR and GL was the lowest, whereas that between FS and AFC was the highest

Table 2.5 Genetic correlation (\pm SE) above diagonal and phenotypic correlation (\pm SE) below diagonal among reproductive traits

Trait ^a	NRR	IN	FS	AFC	GL
NRR		-0.636 \pm 0.031	-0.913 \pm 0.028	-0.351 \pm 0.009	-0.569 \pm 0.047
IN	-0.551 \pm 0.016		0.874 \pm 0.025	0.625 \pm 0.048	0.226 \pm 0.026
FS	-0.162 \pm 0.023	0.708 \pm 0.011		0.798 \pm 0.034	0.183 \pm 0.008
AFC	-0.057 \pm 0.022	0.511 \pm 0.018	0.881 \pm 0.008		0.299 \pm 0.021
GL	-0.037 \pm 0.024	0.080 \pm 0.022	0.043 \pm 0.025	0.129 \pm 0.024	

^a) NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, AFC: age at first calving, GL: gestation length.

2.4 Discussion

In the present study, NRR after the first service was slightly lower (67%) than estimates in published results: 74% in Canadian Holstein heifers (Jamrozik et al., 2005), and 73.9% in Holstein Friesian heifers in the Netherlands (Haer, 2013). FS of Japanese Black heifers in Okinawa was 36.33 days and slightly longer than average reported for the Rubia Gallega breed (30.60 days) (Yagüe et al., 2009). The average IN of Japanese Black cows has been 1.41 (Sasaki et al., 2016), whereas it was lower than the average in the present study; on the other hand, GL was consistent with their average (288 days). In this study, AFC was 25.8 months, being slightly longer than 24.4, 25.1 and 24.98 months compared with the previous report reports (Baco et al., 1998; Oyama et al., 2002; Uchida et al., 2002, respectively), and records in Okinawa prefecture between 1990 and 2009

have shown that AFC was 26.93 months, being longer than in the present study (Oikawa, 2017).

In the present study, analysis of variance showed that farm had a significant effect on all reproductive traits of Japanese Black heifers in Okinawa, indicating that different management practices on farms influenced heifer reproductive traits significantly. Animal management standards on farms have a significant effect on the number of services to Holstein heifers (M'Hamdi et al., 2011). Better reproductive performance of cows on large farms relative to those on small farms is attributable to high standard equipment and operating procedures (Dargatz et al., 2004). In the present study, the year of insemination had a significant effect on NRR, FS and GL, and the year of birth had a significant effect on AFC. A similar study on the Simmental breed, has shown that the year effect is strong on female reproductive traits, the effect of the AI technician is significant on FS and AFC, but age at first insemination is not significant in any of the traits (Bolacali and Öztürk, 2008). By contrast, reproductive traits in dairy heifers are influenced by age at first insemination: heifers inseminated at an older age for the first time have a slightly higher rate of success at first insemination and, as a result, require a smaller number of services (Jamrozik et al., 2005). Furthermore, environmental variations, employment of an estrus detector and the expertise of the AI technician may play major roles in a successful first insemination (Bormann et al., 2006).

Previous studies on Holstein heifers have shown that genetic variance in binary and count traits are lower than those in interval traits (Guo et al., 2014; Liu et al., 2017). The linear statistical model is appropriate and common for genetic analysis of interval traits; however, it is not optimal for genetic analysis of binary traits, the nature of which violates assumptions of normality under which the linear model is valid (Kadarmideen et al., 2000). On the other hand, the threshold model has proved to be appropriate for evaluating

binary traits, and heritabilities obtained with the model has usually been higher than that obtained with the linear model for the same trait (Jamrozik et al., 2005). Nonetheless, a disadvantage of the threshold model is that it produces biased estimates for variances of random effects when categorical traits are analyzed together with interval traits for estimating variance components (Boettcher et al., 1999; Luo et al., 2001). In the present study, five reproductive traits were analyzed, only one of which was binary. Genetic correlation among reproductive traits is difficult to estimate when pairs of trait are analyzed under different models; therefore, the linear model was used to estimate genetic parameters in this study.

In this study, heritability of NRR (0.027) was slightly higher than the estimate (0.012) for dairy heifers (Liu et al., 2008) with the use of a linear model, whereas it was 0.019 for IN and 0.011 for FS, which were in agreement with previous studies on dairy heifers, ranging between 0.013 and 0.026 and between 0.013 and 0.017 for IN and FS, respectively (Liu et al., 2017, 2008; Tiezzi et al., 2012). Furthermore, in the present study, the estimated heritability of GL (0.081) was consistent with that in Japanese Black cows (0.080) (Ibi et al., 2008), whereas it is lower (0.037) in the Rubia Gallega breed (Yagüe et al., 2009). In our study, AFC was the reproductive trait that demonstrated the highest heritability (0.180), which was consistent with (0.215) in Japanese Black cattle (Oyama et al., 2002), whereas higher heritability (0.28) was shown in Angus heifers (Martínez-Velázquez et al., 2003), and lower heritability (0.09) was in the Tabapuã beef breed (Bernardes et al., 2015).

In the present study, genetic correlations among pairs of the traits varied substantially: NRR showed negative and moderate genetic correlations with IN (-0.636) and GL (-0.569). Genetic correlation between NRR and IN was slightly lower than those estimated in Chinese Holstein heifers (-0.87)(Liu et al., 2017). NRR showed negative and

high correlation with FS (-0.913), being similar to estimated value (-0.780) in Canadian Holstein by Jamrozik et al. (2005), whereas the genetic correlation for NRR and GL was low (0.25) in their study. The genetic correlation between FS and IN was favorably high (0.874) in the present study (Table 2.5), but slightly lower than a previous estimate of over 0.90 in dairy cows (Ghiasi et al., 2011; Jamrozik et al., 2005; Liu et al., 2017). These high correlations seem to be attributable to the strong correlation between IN and FS. The genetic correlations between GL and IN and between GL and FS were low in the present study, but consistent with those in Rubia Gallega cows (-0.138) and (0.106), respectively (Yagüe et al., 2009). IN and FS were recorded before conception, however GL is trait related to the capability of heifers to maintain pregnancy to calving day. Thus, these low genetic correlation indicates which these two traits (IN and FS) are genetically unrelated to GL and may be influenced by different groups of genes. Consequently, selection of one of the traits would have little effect on the other.

IN and FS showed high genetic correlations with AFC, whereas genetic correlations between AFC and NRR, and AFC and GL were moderate in absolute values. High genetic correlation seems to be due to the pleiotropic effect of genes, where a group of genes may simultaneously have a common genetic effect on these three traits (IN, FS and AFC). Heifers that calve early tend to have fewer IN and shorter FS. AFC is genetically correlated with calving interval in Japanese Black cows (Oyama et al., 2002). Heifers that conceive and drop the first calf early are expected to require a small number of inseminations and to undergo a short calving interval.

2.5 Conclusion

The present study suggests that low heritability of the most reproductive traits in Japanese Black heifers is strongly influenced by farm management practices, and that large residual variance makes genetic evaluation difficult. NRR, IN and FS demonstrated

close genetic relationship with one another, although their heritabilities were very low. Among the reproductive traits, AFC has the highest heritability and favorable genetic correlations with IN and FS.

Chapter 3

Genetic study for reproductive traits of three parities of cows using multiple-trait model

3.1 Introduction

The number of calves born in life of a cow is related to calf productivity, which depends on calving interval and productive lifetime (Silva et al., 2015). Cows with superior fertility tend to resume reproductive cycles early and show high possibility of subsequent successful pregnancies (Schneider et al., 2005; Pravia et al., 2014; Naya et al., 2017). Thus, the reproductive performance of cows is crucial for high calf productivity and for economical efficiency in cow-calf production systems. Furthermore, improvement of reproductive trait is very important.

Reproductive performance is measured more than one time over their lifetime. For these observation, a multiple-trait model is a natural choice for analyzing traits across parity. Whereas computationally the task may not be simple. Aspects of multiple-trait analyses discussed include genetic evaluations for each parity and genetic correlation between same trait among different parity. A multiple-trait analysis should theoretically improve the accuracy of ranking animals for genetic merit of each trait (Schaeffer, 1983).

Analysis reproductive traits using multiple-trait model was conducted in dairy cows (Liu et al., 2017; Tiezzi et al., 2012; Zink et al., 2011). Nevertheless, only limited results are available on reproductive traits across parities in beef cattle. The aim of this part of study was to estimate heritability of reproductive trait for cows at different parity and genetic correlation between same traits among parity.

3.2 Materials and Methods

3.2.1 Reproductive data

Field records of artificial insemination and calving events for the first three parities

of cows were collected from 184 farms. The data set was edited by the following criteria: cows born between 2004 and 2014, age at first calving between 20 and 36 months, less than ten inseminations per parity, and FS less than 365 days. The final data set available for the first three parities of cows was 2,078, 1,840 and 1,822, respectively, and the total number of animals in pedigree was 15,600.

3.2.2 Traits in study

Nine traits studied: NRR was coded as one when no subsequent insemination occurred for 56 days after the first insemination, otherwise coded as zero, IN, FS was interval between the first insemination and the successful insemination that resulted in conception, GL was the interval in days from the last insemination to the subsequent calving, CF was the interval between previous calving to first inseminations in the subsequent breeding, DO was interval between previous calving to subsequent conception, PR, CI and AC. PR was a count as described (Oseni et al. 2004): $1/[(DO - VWP)/HI + 1]$, where VWP was set at 50 days and HI was set at 21 days. AC was divided into three traits: AFC, ASC and ATC.

3.2.3 Statistical analysis

Animal models were used to estimate the variance and covariance components of female reproductive traits. Data across multiple parities were analyzed using the multiple-trait model in which the performance of a trait in different parities was treated as different traits. The linear model of the three-trait model is as follows:

$$\begin{bmatrix} \mathbf{y}_2 \\ \mathbf{y}_3 \\ \mathbf{y}_4 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_3 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X}_4 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_3 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_4 \end{bmatrix} \begin{bmatrix} \mathbf{a}_2 \\ \mathbf{a}_3 \\ \mathbf{a}_4 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_2 \\ \mathbf{e}_3 \\ \mathbf{e}_4 \end{bmatrix} ,$$

where \mathbf{y}_i is the vector of observations ($i=2,3,4$) representing parities 2,3 and 4 of cows in model; \mathbf{b}_i the vector of fixed effects for the i th trait, including farm, month and year of insemination (for NRR, FS, IN and GL) or month and year of calving (for CF, DO,PR

and CI), month and year of birth (for AFC, ASC and ATC) and AI technician; \mathbf{a}_i the vector of random additive genetic effect for the i th trait; and \mathbf{e}_i the vector of random residuals for the i th trait. \mathbf{X}_i , and \mathbf{Z}_i are incidence matrices connecting \mathbf{b}_i , and \mathbf{a}_i , to \mathbf{y}_i . It was assumed that

$$\begin{bmatrix} \mathbf{a}_1 \\ \vdots \\ \mathbf{a}_n \end{bmatrix} \sim N \left(\mathbf{0}, \mathbf{A} \begin{bmatrix} \sigma_{a_1}^2 & \cdots & \sigma_{a_1 a_n} \\ & \ddots & \vdots \\ & & \sigma_{a_n}^2 \end{bmatrix} \right),$$

$$\begin{bmatrix} \mathbf{e}_1 \\ \vdots \\ \mathbf{e}_n \end{bmatrix} \sim N \left(\mathbf{0}, \mathbf{I} \begin{bmatrix} \sigma_{e_1}^2 & \cdots & \sigma_{e_1 e_n} \\ & \ddots & \vdots \\ & & \sigma_{e_n}^2 \end{bmatrix} \right),$$

where \mathbf{A} is the numerator relationship matrix of additive genetic relationships between individuals in the pedigree; \mathbf{I} the identity matrix; $\sigma_{a_i}^2$, and $\sigma_{e_i}^2$ the additive genetic variance and residual variance of the i th trait, respectively; σ_{a_n} and σ_{e_n} the additive genetic covariance and residual covariance among the trait in n th parity. The variance covariance components were estimated by REML using Asreml 4.1 software (Gilmour et al., 2015).

3.3 Results

Table 3.1 presents descriptive statistic of reproductive traits for each parity of cows. The range of means among parities was 0.71-0.74 for NRR; 1.47-1.52 for IN; 27.11-28.08 days for FS; 288.94-289.76 days for GL; 72.34-74.11 days for CF; 100.84-104.65 days for DO; 0.66-0.70 for PR, 390.73-393.75 days for CI, and 39.65 and 52.93 months for ASC and ATC, respectively. (Table 3.1).

Table 3.2 presents variance covariance component and heritability using multiple-trait model. Estimated heritability did not show variation among parities except for AC, whereas heritability of NRR was low and the lowest was shown in the fourth parity. Heritability of AC was higher than of the other traits but tended to turn lower at later parity, being 0.107 and 0.088 for ASC and ATC, respectively. Genetic correlation between

the same traits across parities by the multiple-trait model was generally high, ranging between 0.72 and 0.99 (Table 3.3).

Table 3.1 The descriptive statistic of reproductive traits in Japanese Black cows

Traits ^a	Second parity		Third parity		Fourth parity	
	Means	CV	Means	CV	Means	CV
NRR	0.71	0.63	0.73	0.59	0.74	0.59
IN	1.52	0.60	1.47	0.58	1.49	0.55
FS, days	27.11	2.21	28.01	2.25	28.08	2.08
GL, days	288.94	0.02	289.76	0.02	289.21	0.02
CF, days	74.11	0.51	73.31	0.49	72.34	0.50
DO, days	104.65	0.71	102.16	0.70	100.84	0.73
PR	0.66	0.47	0.67	0.48	0.70	0.54
CI, days	393.75	0.19	391.73	0.18	390.73	0.19
AC*, months	25.8 ¹	0.21	39.65 ²	0.19	52.93 ³	0.17

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval.

* AC: ¹age at first, ²second and ³third calving.

3.4 Discussion

A comparison of the average performance of reproductive traits in Japanese Black cows between the present study and previous studies showed that CF (73.25 days) and DO (102.55 days) in this study were shorter than the interval of 80 days and 112 days, respectively, reported by Sasaki et al. (2016); CI (392.07 days) was shorter than the interval (401 days) reported by Oyama et al. (2002); IN (1.49) was similar to the number of inseminations (1.48) reported by Uchida et al. (2002); GL (289.31 days) was three day longer than the average (286.51 days) reported by Ibi et al. (2008); FS (27.73 days) was slightly shorter than (30.60 days) in Rubia Gallega beef cows reported by Yagüe et al. (2009); NRR (73%) was almost 15% higher than the values reported in dairy populations (Jamrozik et al., 2005; Liu et al., 2017, 2008; Tiezzi et al., 2012); and PR (0.67) was lower

Table 3.2 Variance covariance component and heritability (\pm SE) of reproductive traits using multiple-trait model

Parameter ^b	Traits ^a								
	NRR	IN	FS	GL	CF	DO	PR	CI	AC*
$\sigma_{a_2}^2$	0.389 $\times 10^{-2}$	0.209 $\times 10^{-1}$	98.924	1.119	51.143	207.569	0.319 $\times 10^{-2}$	248.188	6.361 ¹
$\sigma_{a_3}^2$	0.259 $\times 10^{-2}$	0.179 $\times 10^{-1}$	106.013	0.933	43.820	154.169	0.143 $\times 10^{-2}$	196.605	5.304 ²
$\sigma_{a_4}^2$	0.239 $\times 10^{-2}$	0.150 $\times 10^{-1}$	75.684	0.897	66.070	159.702	0.293 $\times 10^{-2}$	235.827	5.608 ³
$\sigma_{e_2}^2$	0.188	0.754	3418.64	26.159	929.061	4765.93	0.053	4755.88	33.804 ¹
$\sigma_{e_3}^2$	0.177	0.692	3766.16	17.970	889.411	4340.85	0.061	4358.99	44.151 ²
$\sigma_{e_4}^2$	0.181	0.630	3306.53	17.957	845.529	4612.26	0.136	4607.69	57.762 ³
h_2^2	0.020(0.029)	0.027(0.028)	0.028(0.053)	0.041(0.045)	0.052(0.047)	0.042(0.044)	0.027(0.038)	0.049(0.048)	0.158(0.039) ^a
h_3^2	0.014(0.022)	0.025(0.038)	0.027(0.033)	0.049(0.056)	0.047(0.057)	0.034(0.052)	0.023(0.034)	0.043(0.045)	0.107(0.037) ^b
h_4^2	0.013(0.034)	0.023(0.029)	0.022(0.031)	0.047(0.027)	0.072(0.057)	0.034(0.033)	0.021(0.036)	0.048(0.042)	0.088(0.028) ^c

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval.

^b $\sigma_{a_i}^2$ (i=2,3,4) additive genetic variance of *i*th parity, $\sigma_{e_i}^2$ (i=2,3,4) residual variance of *i*th parity, h_i^2 (i=2,3,4) heritability of *i*th parity.

* AC: ¹age at first, ²second and ³third calving.

Table 3.3 Genetic correlations (\pm SE) between reproductive traits in different parities using multiple-traits model

Traits ^{a,b}	NRR	IN	FS	GL	CF	DO	PR	CI	AC
$r_{a_2a_3}$	0.965(0.173)	0.972(0.077)	0.887(0.059)	0.908(0.046)	0.981(0.044)	0.923(0.087)	0.882(0.066)	0.969(0.071)	0.805(0.037)
$r_{a_2a_4}$	0.926(0.154)	0.913(0.070)	0.872(0.037)	0.938(0.035)	0.973(0.049)	0.989(0.056)	0.889(0.065)	0.943(0.058)	0.721(0.031)
$r_{a_3a_4}$	0.936(0.157)	0.964(0.043)	0.870(0.032)	0.985(0.037)	0.938(0.060)	0.927(0.077)	0.903(0.059)	0.988(0.052)	0.956(0.044)

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval and AC: age at calving.

^b $r_{a_i a_j}$ genetic correlation between performance of trait in parities i and j.

than in beef cattle (0.75) reported by Martínez-Velázquez et al. (2003).

In multiple-trait analyses, the estimated heritability of AC (0.088-0.158) was higher than that of the other reproductive traits; furthermore, that of AFC (0.158) was the highest in this study but slightly lower than the estimated 0.215 in Japanese Black cows reported by Oyama et al. (2002). On the other hand, range of estimated heritability of cow reproductive traits from 0.013 for NRR in the fourth parity to 0.072 for CF in fourth parity was consistent with estimates in a previous study on Japanese Black cattle (Oyama et al., 2002) and other beef populations (Goyache et al., 2005; Yagüe et al., 2009). In a review of 30 studies on the estimated heritability of reproductive traits in beef cattle, the average heritability for female reproductive traits is described as generally low because of a large, unexplainable portion of residual variation and considerable influence of farm management on many of these traits (Cammack et al., 2009).

Compared with estimate by multiple-trait model in dairy cattle, heritabilities of CF (0.052-0.072), DO (0.034-0.042) and CI (0.043-0.049) were also consistent with that of previous studies reported by Liu et al. (2017) and Tiezzi et al. (2012). Interval traits of FS, CF, DO and CI may be influenced by management decisions such as the length of the voluntary waiting period or estrus synchronization applied at the farm (Ghiasi et al., 2011).

In this study, the threshold model was assumed to be relevant for binary trait NRR. The linear model is directly based on the assumption of normal distribution, whereas the threshold model is based on the assumption of an underlying unobservable continuous response variable which follows the assumptions of a mixed linear model (Gianola and Foulley, 1983). Nonetheless, the threshold model involves bias in the estimation of the variance component when the number of fixed effects is high (Tempelman, 1998; Varona et al., 1999). When estimating the binary trait by using the threshold model, heritability appears high (Ghiasi et al., 2011; Kadarmideen et al., 2000). Heritability of NRR (0.013)

in our study was lower than 0.04 estimated by Muir et al. (2004) using the threshold model.

Genetic correlation between the same reproductive traits in a pair of parities of cows was high (over 0.87) with the exception for AC, for which the genetic correlation between AFC and ASC was 0.805 and between AFC and ASC was 0.721 but with a relatively large standard error, consistent with results by Bagnato and Oltenacu (1993) and Roxström et al. (2001) in dairy cows. Although genetic correlation among different parities within the same trait was high, additive genetic variance of DO and CI in the second parity was larger than that in later parities. The same result was reported by Liu et al. (2017) for FS, CF and DO.

3.5 Conclusion

The results from this part of study suggest that reproductive traits in the different parity of cow should be treated separately to increase reliability and reduce bias in routine genetic evaluations. Moreover, high genetic correlation between traits in different parities of cows indicated that trait across parity could be analysed as repeated measurement.

Chapter 4

Genetic study for reproductive traits of three parities of cows using repeatability model

4.1 Introduction

Government survey reveals that reproductive performance in Japanese Black cow declined consistently in recent decade. As reported by Sasaki et al. (2016), one of the reasons for the gradual hike in the price of calves is the decline in reproductive performance. The factor of this declining of reproductive performance is still unclear, however, one of solution for that problem is genetic improvement of it. Incorporating reproductive traits in breeding program is important as a way to improve production efficiency because it is effective to stabilize farm management, also it has a direct effect on total production costs (Costa et al., 2015; Schmidt et al., 2019). In addition of genetic improvement, prediction of future calf crop is required for sustainable farm production. In this situation, repeatability is important to quantifying the reproductive trait of same cow, same farm with parity as a repetition.

The repeatability model assumes a genetic correlation of unity between all pairs of records and equal variance for all records (Pereira et al., 2001). The low estimates of repeatability for a trait indicated low genetic and permanent environmental variances to temporary environmental variance ratios for that traits and reflected differences in their response to the existing environmental conditions. This indicated that selection on the basis of first record is not advisable. The subject of this part of study is to estimated heritability, repeatability and genetic correlation reproductive traits of three parities of cows.

4.2 Materials and Methods

4.2.1 Reproduction on records

The records have been used in Chapter 3 were analyzed. A total of 5,780 records were available from three parities of 2,078 cows.

4.2.2 Traits in study

Reproductive traits were analyzed by treating records in three parities as repeated measurements, except AC. It is difficult to accept AC as a repeatable trait as latter AC has the former AC as its component.

4.2.3 Statistical Models

Animal model was used to estimate the variance and covariance components of female reproductive traits. The records were analyzed based on the repeatability model by treating records in multiple parities as repeated measurements.

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{pe} + \mathbf{e} \quad (1)$$

The correlation between a pair of cow traits was estimated by using the following two-trait animal model:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{W}_2 \end{bmatrix} \begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}, \quad (2)$$

where \mathbf{y} is the vector of observations, \mathbf{y}_1 and \mathbf{y}_2 representing pair of reproductive traits in model (2); \mathbf{b}_i the vector of fixed effects for the i th trait, including farm, month and year of insemination (for NRR, FS, IN and GL) and month and year of calving (for CF, DO, PR and CI), AI technician and parity; \mathbf{a}_i the vector of random additive genetic effect for the i th trait; \mathbf{pe}_i the vector of permanent environmental effects for the i th trait; and \mathbf{e}_i the vector of random residuals for the i th trait. \mathbf{X}_i , \mathbf{Z}_i and \mathbf{W}_i are incidence matrices connecting \mathbf{b}_i , \mathbf{a}_i , and \mathbf{pe}_i to \mathbf{y}_i . In matrix notation, the model can be written as:

$$E \begin{bmatrix} \mathbf{a} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} .$$

$$V \begin{bmatrix} \mathbf{a} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & I\sigma_{pe}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & I\sigma_e^2 \end{bmatrix} ,$$

where A is the numerator relationship matrix of additive genetic relationships between individuals in the pedigree; I the identity matrix; σ_a^2 , σ_{pe}^2 and σ_e^2 the additive genetic variance, permanent environmental variance and residual variance of the i th trait, respectively. The variance covariance components were estimated by REML using Asreml 4.1 software (Gilmour et al., 2015).

4.2 Results

The mean for each trait was (0.73) for NRR, (1.48) for IN, (28.21) for FS, (289.42) for GL, (73.82) for CF, (102.63) for DO, (0.67) for PR and (392.12) for CI. Large coefficients of variation in NRR, IN, FS, CF, DO and PR indicated that these traits displayed large proportions of phenotypic variation (Table 4.1). Heritability ranged from 0.013 for NRR to 0.059 for CF. The highest repeatability was observed at CF (0.142) and the lowest for FS (0.036) (Table 4.2).

Table 4.1 The descriptive statistic of reproductive traits in three parities of cows

Traits ^a	Number of records	Means	SD	Minimum	Maximum
NRR	5740	0.73	0.61	0	1
IN	5315	1.48	0.58	1	9
FS, days	5315	28.21	2.77	0	364
GL, days	5311	289.42	0.02	261	312
CF, days	4537	73.82	0.49	20	228
DO, days	4208	102.63	0.71	22	572
PR	4208	0.67	0.47	0.04	1
CI, days	4208	392.12	0.19	301	860

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval form calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval.

Table 4.2 Genetic variance, permanent environmental variance, residual variance, heritability (\pm SE) and repeatability for cow reproductive traits using single-trait animal model

Parameter ^b	Traits ^a							
	NRR	IN	FS	GL	CF	DO	PR	CI
$\sigma_{a_{234}}^2$	0.242 $\times 10^{-2}$	0.187 $\times 10^{-1}$	93.845	1.021	57.469	193.668	0.191 $\times 10^{-1}$	235.103
$\sigma_{pe_{234}}^2$	0.639 $\times 10^{-2}$	0.229 $\times 10^{-1}$	37.749	0.591	79.231	213.579	0.343 $\times 10^{-1}$	239.766
$\sigma_{e_{234}}^2$	0.171	0.697	3548.91	20.403	823.303	4947.06	0.793	4545.85
h_{234}^2	0.013(0.017)	0.025(0.017)	0.025(0.019)	0.046(0.020)	0.059(0.029)	0.036(0.021)	0.022(0.007)	0.047(0.009)
<i>rep</i>	0.049(0.018)	0.056(0.017)	0.036(0.018)	0.073(0.018)	0.142(0.022)	0.076(0.021)	0.063(0.012)	0.095(0.016)

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate and CI: calving interval.

^b $\sigma_{a_{234}}^2$: additive genetic variance for cows traits, $\sigma_{pe_{234}}^2$: permanent environmental variance for cow traits, $\sigma_{e_{234}}^2$: residual variance for cow traits, h_{234}^2 : heritability for cow traits, *rep*: repeatability for cow traits.

Table 4.3 Genetic (above the diagonal) and phenotypic (below the diagonal) correlations (\pm SE) among reproductive traits

Trait ^a	NRR	IN	FS	GL	CF	DO	PR	CI
NRR		-0.319(0.016)	-0.708(0.013)	0.347(0.039)	0.628(0.092)	-0.194(0.062)	0.378(0.062)	-0.122(0.083)
IN	-0.615(0.009)		0.903(0.014)	-0.184(0.007)	-0.075(0.053)	0.481(0.019)	-0.598(0.076)	0.525(0.032)
FS	-0.197(0.014)	0.715(0.007)		-0.133(0.036)	0.255(0.063)	0.917(0.018)	-0.807(0.014)	0.866(0.017)
GL	-0.024(0.015)	0.018(0.014)	-0.011(0.014)		0.233(0.033)	0.081(0.013)	-0.402(0.011)	0.697(0.016)
CF	0.034(0.017)	-0.021(0.016)	0.180(0.021)	-0.078(0.016)		0.427(0.007)	-0.487(0.018)	0.498(0.011)
DO	0.126(0.095)	0.714(0.016)	0.831(0.082)	0.192(0.046)	0.382(0.069)		-0.924(0.013)	0.957(0.008)
PR	0.173(0.012)	-0.322(0.017)	-0.247(0.024)	0.019(0.025)	0.096(0.018)	-0.881(0.043)		-0.825(0.017)
CI	-0.053(0.019)	0.629(0.021)	0.691(0.036)	0.158(0.034)	0.479(0.067)	0.916(0.021)	-0.823(0.029)	

^a NRR: non-return rate, IN: number of inseminations, FS: interval from first to successful insemination, GL: gestation length, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate and CI: calving interval.

The lowest genetic correlation in absolute value was observed between CF and IN (-0.075) and the highest between DO and CI (0.957). Phenotypic correlation among reproductive traits ranged from 0.011 (between FS and GL) to 0.916 (between DO and CI) (Table 4.3).

4.3 Discussion

Estimated heritabilities of cow reproductive traits by using the repeatability model ranged from 0.013 for NRR to 0.059 for CF. Heritability of DO (0.036) and CI (0.047) were consistent with the estimates in a previous study on Japanese Black cattle (0.05) by Oyama et al. (2004) but lower than (0.135) for DO and (0.106) for CI reported on Asturiana de los Valles beef cattle by Goyache et al. (2005), where the cow was raised in pasture and they were mated by natural mating. Heritability of FS (0.025) and IN (0.025) were lower than those for FS (0.078) and for IN (0.071) reported by Yagüe et al. (2009) in Rubia Gallega beef cattle for which paddock mating were applied. Whereas heritability of CF (0.059) and GL (0.046) were similar to their estimates (0.050) and (0.037) for CF and GL, respectively. Heritability of NRR (0.013) in our study was lower than the estimate (0.04) by Muir et al. (2004) estimated by the threshold model.

The benefit of repeatability model is provide an estimate of permanent environmental effect on a trait (Schaeffer, 2011). In this study, repeatability for DO (0.076) and CI (0.095) was consistent with previous estimates of 0.087 and 0.092, respectively (Oyama et al., 2002), but repeatability for GL (0.073) was considerably lower than their estimate (0.403). That difference seems to be due to fixed effects fitted to the mixed model; the high repeatability in their study may be attributable to specific practices on the farm especially that common environmental effect may influence their estimation. In our study, the range of repeatability for interval traits (0.036-0.142) was generally consistent with a previous study on other beef populations (0.082-0.147; Yagüe et al., 2009). Compared

with a study on dairy cattle, the repeatability estimate for NRR (0.049) in our study was higher than 0.010 estimated by Tiezzi et al. (2012). For IN, the estimated repeatability (0.056) in our study agreed with the range (0.022 to 0.080) reported by Kadarmideen et al. (2000), Demeke et al. (2004), Estrada-León et al. (2008) and M'Hamdi et al. (2010).

Our phenotypic correlation was consistent with that in previous studies (Kadarmideen et al., 2003; Liu et al., 2017). CF and FS were component traits of DO, and DO and GL were component traits of CI. Among these, CF is a trait that indicates ability to recover estrus after calving, and FS is a trait that indicates ability of the cycling cow to conceive. CF is a trait strongly affected by artificial factors such as delay of insemination at the first estrus postpartum and failure of heat detection. PR showed high phenotypic correlations with DO and CI, and moderately high correlations with IN, FS, CF and AC. The high correlation between PR and DO may to be related because PR was calculated based on the DO interval and CI has a close genetic relation to DO.

The genetic correlation among pairs of cow traits varied substantially. NRR showed negative genetic correlation with FS and IN, (-0.708 and -0.319 respectively), and agreed well with -0.78 for NRR-FS (Jamrozik et al., 2005) and -0.51 for NRR-IN (Liu et al., 2017). On the other hand, the genetic correlation of FS with IN was favorably high (0.903), being consistent with the results (higher than 0.90) of several previous studies on dairy cows (Ghiasi et al., 2011; González-Recio and Alenda, 2005; Jamrozik et al., 2005; Liu et al., 2017). As this high correlation indicates that IN is actually recorded at the end of the FS period, cows with longer FS generally undergo a large number of IN and vice versa. In our study, the genetic correlation of NRR with DO and CI was low and negative (-0.194 and -0.122, respectively). Low genetic correlation may be caused by the hypothesis that a group of genes affecting NRR are different from one affect DO and CI. These results agree with those of Liu et al. (2008) (-0.18) for NRR-DO and of Muir et al. (2004) (-0.09)

for NRR-CI.

In our study, the genetic correlation of IN with DO and CI (0.481 and 0.525, respectively) was in good agreement with another study on beef cattle (Yagüe et al., 2009). Our genetic correlation of FS with DO and CI was favorably high (0.917 and 0.866, respectively); Yagüe et al. (2009) has also reported high genetic correlation of FS-DO and FS-CI. The genetic correlation between FS and DO, in our study, was consistent with previous estimates ranging from 0.78 to 0.99 (Ghiasi et al., 2011; González-Recio and Alenda, 2005; Liu et al., 2017, 2008).

In our study, the genetic correlation of CF with IN was negatively low (-0.075) but that with NRR, DO and CI was positively moderate, ranging from 0.427 to 0.628. These results were consistent with previous reports by Gredler et al. (2007) for NRR-CF and Guo et al. (2014) for CF-DO and CF-CI. Yagüe et al. (2009), however, have reported lower genetic correlation (0.304 and 0.383) for CF-DO and CF-CI, respectively, while González-Recio and Alenda (2005) and Ghiasi et al. (2011) have reported a higher genetic correlation, ranging from 0.76 to 0.98. In our study, the genetic correlation of CF-FS was low (0.255) and consistent with 0.27 estimated by Jamrozik et al. (2005), but slightly lower than estimates of 0.500 and 0.580 by González-Recio and Alenda (2005) and Ghiasi et al. (2011), respectively. The low genetic correlation between CF and FS indicates that these two traits are influenced by different groups of genes. FS was measured before calving and described as the capability of cows to conceive, whereas CF was measured after calving and described as the capability of cows to recover estrus after calving.

The negatively low correlation of GL-IN (-0.184) and GL-FS (-0.133), in our study, was consistent with that in studies on another beef population (Yagüe et al., 2009) and on dairy population (Jamrozik et al., 2005). GL showed low genetic correlation with NRR, CF and DO, which could be due to NRR, CI, DO, FS and IN being measurements for

efficiency of conception, whereas GL is the interval from the day of conceiving to the day of calving. Furthermore, the genetic correlation between GL and CI was higher than that among the other traits. As stated by Goyache et al. (2005), CI is a complex trait that includes not only GL as a component trait but also variation in the ability of cows to conceive.

PR showed moderate genetic correlation with NRR, IN, GL and CF, but high genetic correlation with FS, DO and CI. These genetic correlations seem to be caused by the pleiotropic effect of genes, where a group of genes may have common genetic effect on the four traits (FS, DO, CI and PR) simultaneously. The estimated genetic correlation between DO and CI in this study (0.957) was similar to that reported in both dairy cows (Ghiasi et al., 2011; Guo et al., 2014) and beef cattle (Goyache et al., 2005), thus, the present result supports the argument that DO is an earlier alternative to CI.

4.5 Conclusion

The repeatability model seems to be more appropriate for estimating reproductive traits because it yields a low standard error in estimated parameters. As an additional information, the repeatability model provides an estimate of permanent environmental effect on a trait. In this part of study, CF is showed the highest repeatability. However, the lowest genetic correlation was observed between CF and IN.

Chapter 5

Relationship between reproductive traits of heifers with reproductive traits of cows

5.1 Introduction

Good reproductive performance is a basis to improve lifetime productivity. Reproductive traits of heifer can be measured early, so they have advantage of early evaluation and shorter generation interval as a consequence. A heifer trait with high heritability and favorable genetic relationship with cow trait is desirable to conduct earlier selection. Selection of reproductive trait of heifer will bring faster genetic improvement of reproductive performance and calf cropping productivity (Abe et al., 2009).

Several studies reported genetic correlations of reproductive traits between heifers and cows in dairy cattle (Andersen Ranberg et al., 2005; Jamrozik et al., 2005; Abe et al., 2018; Liu et al., 2008, Tiezzi et al., 2012). Estimated genetic correlations between reproductive traits in heifers and cows were required in a study for designing selection program. They indicated that selection of heritable reproductive traits in heifers may improve reproductive performance during their lifetime. In Japanese Black cattle genetic correlations between reproductive traits of heifer and cow have not been reported. Objective of this study is to estimate genetic correlations between reproductive traits of heifers and cows.

5.2 Materials and Methods

5.2.1 Reproductive data

A data set consists of reproduction records of heifers which have been also used in Chapter 2 and reproductive records of three parities of cows in Chapter 4 were analyzed in this part study.

5.2.2 Traits in study

Four reproductive traits for heifers, eight reproductive traits for cows and three traits of age at calving were included in this study. Reproductive traits for heifers were NRR, IN, FS, and GL, then denoted as NRR-h, IN-h, FS-h and GL-h, respectively. Reproductive traits for cows were four traits same as in heifer, which denoted as NRR-c, IN-c, FS-c, GL-c, and CF, DO, PR and CI. Age at calving were individual traits at each parity such as AFC, ASC and ATC.

5.2.3 Statistical Models

Two-trait animal model was used to estimate genetic correlation between reproductive traits for heifer and age at calving with reproductive traits of cows.

The two-trait model was:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} ,$$

where \mathbf{y}_1 is the vector of reproductive traits of heifers or age at calvings, and \mathbf{y}_2 the vector of reproductive traits of cows; \mathbf{b}_i the vector of fixed effects for the i th trait, including farm, month and year of insemination (for NRR, FS, IN and GL of heifers and cows), month and year of calving (for CF, DO, PR and CI of cows) and month and year of birth (for AFC, ASC and ATC), parity (for reproductive trait of cows) and AI technician; \mathbf{a}_i the vector of random additive genetic effect for the i th trait; and \mathbf{e}_i the vector of random residuals for the i th trait. \mathbf{X}_i , and \mathbf{Z}_i are incidence matrices connecting \mathbf{b}_i and \mathbf{a}_i to \mathbf{y}_i . The variance covariance components were estimated by REML using Asreml 4.1 software (Gilmour et al., 2015).

5.3 Results

Genetic correlations between reproductive traits of heifers and cows varied from low to high: the highest and the lowest genetic correlations were between FS-h and FS-c and

Table 5.1 Genetic correlations (\pm SE) between heifer traits and cow traits

Heifer trait ^b	Cow traits ^a							
	NRR-c	IN-c	FS-c	GL-c	CF-c	DO	PR	CI
NRR-h	0.417(0.021)	-0.574(0.023)	-0.327(0.016)	-0.568(0.037)	0.369(0.015)	0.434(0.017)	-0.422(0.031)	0.390(0.017)
IN-h	-0.592(0.028)	0.734(0.018)	0.455(0.016)	0.427(0.026)	0.335(0.016)	0.431(0.031)	-0.152(0.019)	0.456(0.021)
FS-h	-0.388(0.036)	0.485(0.015)	0.795(0.024)	0.538(0.026)	0.281(0.013)	0.597(0.018)	-0.142(0.017)	0.371(0.026)
GL-h	-0.290(0.025)	0.289(0.011)	0.077(0.015)	0.087(0.015)	-0.333(0.039)	0.292(0.018)	0.065(0.016)	0.276(0.016)

^a NRR-c: non-return rate of cows, IN-c: number of inseminations of cows, FS-c: interval from first to successful insemination of cows, GL-c: gestation length of cows, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval.

^b NRR-h: non-return rate of heifers, IN-h: number of inseminations of heifers, FS-h: interval from first to successful insemination of heifers, GL-h: gestation length of heifers.

Table 5.2 Genetic correlations (\pm SE) between age at calving with cow traits

Age at calving ^b	Cow traits ^a							
	NRR-c	IN-c	FS-c	GL-c	CF-c	DO	PR	CI
AFC	-0.396(0.027)	0.661(0.024)	0.634(0.026)	-0.279(0.035)	0.422(0.019)	0.533(0.018)	-0.505(0.014)	0.436(0.025)
ASC	0.251(0.024)	0.584(0.029)	0.221(0.023)	-0.166(0.019)	0.580(0.015)	0.627(0.021)	-0.375(0.019)	0.483(0.021)
ATC	-0.072(0.031)	0.402(0.259)	0.598(0.019)	-0.086(0.032)	0.521(0.024)	0.441(0.023)	-0.202(0.022)	0.402(0.025)

^a NRR-c: non-return rate of cows, IN-c: number of inseminations of cows, FS-c: interval from first to successful insemination of cows, GL-c: gestation length of cows, CF: interval from calving to first insemination, DO: days open, PR: pregnancy rate, CI: calving interval.

^b AFC: age at first calving, ASC: age at second calving and ATC: age at third calving.

between GL-h and PR, respectively, in absolute values (Table 5.1).

AFC showed high genetic correlation with FS-c and IN-c but moderate correlations with others reproductive traits of cows. ASC indicated low genetic correlation with FS-c and GL-c and high genetic correlations with DO, whereas ATC showed low to moderate genetic correlations with reproductive traits of cows (Table 5.2).

5.4 Discussion

The inter trait genetic correlations between IN-h with IN-c and FS-h with FS-c were high (0.734 and 0.795, respectively) however, genetic correlation between heifer and cow traits ranged from low to high (0.065-0.795). This agreed with results of several studies on dairy cows (Jamrozik et al., 2005; Liu et al., 2008; Tiezzi et al., 2012).

The low genetic correlation of PR with IN-h, FS-h and GL-h may be due to physiological and genetic factors. As a physiological factor, the metabolic pathway shows large change after the first calving. One of the key aspects of the change related to reproduction is milk production that is associated with increased metabolism of the steroid hormone (Wiltbank et al., 2006). As a genetic factor, gene expression in heifers might be different from that in cows (Tiezzi et al., 2012). The differential expression pattern of genes between heifers and cows may potentially play a role in the low genetic correlation between heifer traits and PR of cows, indicating that reproduction traits of heifers and cows should be evaluated as different traits. Thus reproductive traits of heifers and cows need to be evaluated separately, although most reproductive traits in heifers genetically correlate strongly with reproductive traits in subsequent parities (Liu et al., 2017).

In term of common practice in Japan, heifers undergo the first insemination when they are older than 12 months or their body height reaches more than 118 cm. Based on that fact,

AC is closely related to reproductive efficiency because delay of calving indicates that cows need more than one insemination for their conception. Fourth groups of reproductive traits for cows defined based on the patterns of genetic correlations with AC.

The first trait group measured abilities of cows to recycle after calving, indicated by CF in the present study, which had genetic correlations with AC ranging from 0.422 to 0.580. The second group of traits described the capacities of cows to conceive at subsequent breeding, including NRR-c, IN-c and FS-c. Genetic correlations between these traits with AC were moderate to high, ranging from 0.221 to 0.661 in absolute values, except for the genetic correlations of NRR-c with AFC (-0.396) and ATC (-0.072). The third group of traits described the capacities of cows for maintaining pregnancy, indicated and GL-c, which had negative low genetic correlations with AC (-0.279 to -0.086). The fourth group of the traits was DO, PR and CI which measured the combined abilities to recycle, conceive and maintain pregnancy. Most genetic correlations between these traits with AC were moderate to high, ranging from 0.202 to 0.627 in absolute values.

In the present study, AFC was considered to be the most useful for genetic improvement of reproductive traits, compared with ASC and ATC. Since AFC is a trait measured early, it shows high genetic correlation with IN-c and FS-c (0.661 and 0.634, respectively) and moderate genetic correlation with NRR-c, GL-c, CF, DO, PR and CI. Based on that result, AFC can be used as an early indicator of ability of cows to maintain regular reproductive cycle. Furthermore, AFC is a trait routinely recorded in breeding programs for reproductive traits in beef cows (Gutiérrez et al., 2002; Oyama et al., 2002; Martínez-Velázquez et al., 2003). AFC is suggested to be the most promising trait for genetic improvement of reproductive traits.

5.5. Conclusion

In this study, AFC was considered to be most favorable compared with ASC and ATC. Since AFC is a trait measured early, AFC also indicated moderate to high genetic correlations with traits which measured the abilities to recycle, conceive and maintain pregnancy. Based on the result, AFC can be used as an early indicator for ability of cows to maintain regular reproductive cycle.

Chapter 6

Determination of penalty methods for interval from first to successful insemination

6.1 Introduction

Reproductive traits of heifers are measured relatively early in their productive life and have positive genetic correlations with reproductive and yield traits in dairy cows (Abe et al., 2009). Thus genetic analysis of reproductive traits in heifers should be conducive to the improvement of reproductive performance without loss of genetic progress in yield traits. A problem in evaluating FS of heifers is the high number of unsuccessful inseminations termed “open heifer”. Farmers tend to cull heifers that do not conceive after a series of inseminations in that early culling can reduce the cost of feeding the animals. In the present study, heifers that did not conceive were culled and categorized under “missing FS record”. Thus, records of all animals are crucial for valid genetic analysis.

For solving the problem of missing records, several penalty methods have been proposed by animal geneticists: Adding 21 days to the largest record within a contemporary group, has been proposed based on the estrous cycle of female cattle (Johnston and Bunter, 1996). Adding a constant number of 30, 60 or 90 days to a missing record, has been proposed, based on the number of months after the last insemination (Bormann and Wilson, 2010). In this study, we set up one approach based on the number of inseminations and another based on the estrous cycle of female cattle. The objective of this study is to determine the best approach for handling missing records of heifer reproductive traits, for estimating the genetic parameters and for predicting the breeding value of FS in Japanese Black heifers.

6.2. Materials and Methods

6.2.1 Data set

A data set consisted of records of artificial insemination, calving events and FS in heifers. The data set was edited by the following requirement: heifers born between 2003 and 2015, first insemination of heifers between 2005 and 2016, and farms with a minimum of five records. The final data set comprised 2367 records of heifers from 164 farms, including 206 (8.7% of the total) missing records. The data structure is presented in (Table 6.1). FS is computed as the interval in days between the first insemination date and the last insemination date that resulted in conception. Three percentages (5%, 10% and 15%) of the records were investigated with the use of a random censoring scheme.

Table 6.1 Structure of source data

Class	Number
Heifer with data	2,161
Open heifer	206
Sire	101
Dam	1,317
Farm	164
Age*	3
Animal in pedigree	15,600

*Age class : <16, 16 to 19 and >19 month

6.2.2 Penalty method

Two penalty approaches were used in this study: 1) based on the number of inseminations, 2) based on the estrous cycle of female cattle. FS days tend to be prolonged with the increasing number of inseminations, and based on this relationship, four penalty methods, coded C1, C2, C3 and C4, were set up. The last penalty method (C5) was based on the estrous cycle of female cattle (Johnston and Bunter, 1996). When P is days of penalty, the methods

are:

1. C1 : average FS according to the number of inseminations.

$P = n_x$, where n_x is the average number of FS days at the number of times till the last insemination plus one.

2. C2 : constant number of days (359), derived from the highest expectation of FS in the

records, $P = n_m$, where $n_m = 359$.

3. C3 : maximum number of FS days to each insemination.

$P = n_n$, where n_n is the maximum number of FS days to the n th insemination.

4. C4 : average of n_x and n_m , where n_x is the average number of FS days at the number of times till the last insemination.

5. C5 : a constant number (21d) was added to the highest number of FS days in each contemporary group. $P = n_g + 21$, where n_g is the maximum number of FS in each contemporary group.

6.2.3 Bootstrap method

The bootstrap method is one of the most powerful variance estimation techniques applied to complex sample statistics, whereby simulation is conducted to generate multiple data sets from an original data set (Efron and Tibshirani, 1993). The principle of bootstrap is based on resampling of records from a current data set, that is composed of pseudo samples distributed according to the same distribution as of the original sample. A data set with missing values is generated by a random sampling scheme from the original data by replacement. Although each resampled data set has the same number of observations as the original sample, the composition of the data set is different. Therefore, each of these data sets randomly deviates from the original data set.

In the present study, the bootstrap method was used to compare five penalty methods in terms of bias, MSE and the accuracy of EBV. Resampling was generated 100 times from the original data. The bias and error variance computation requires between 50 and 200 resamplings (Efron, 1990). The number of bootstrap replications suggested is a minimum of 100 for standard error estimation (Thai et al., 2013). Nonetheless, an approach using the bootstrap technique has been proposed for obtaining robust estimates of heritability (Reverter et al., 1998; Rao and Prabhakaran, 2001). In the present study, the steps of bootstrap were as follows:

- (1) Generate a resampled data set 100 times from the original (non-censored) data.
- (2) Choose 8.7% of missing records within each resampling data set by the random censoring scheme.
- (3) Estimate genetic parameters and predict EBV for each data set.
- (4) Calculate the average of genetic parameters and predicted EBV.
- (5) Compare the penalty methods by bias and MSE of heritability and correlation of EBV with a non-censored data set.
- (6) Repeat steps 1 to 5 for three other percentages (5%, 10% and 15%) to assess the influence of different proportions of missing records on the inference.

6.3 Results

The mean FS in C5 was higher than in the other methods. On the other hand, among the methods based on the number of inseminations, the highest and the lowest mean FS was observed in C2 and C3, respectively (Table 6.2).

Table 6.2 Basic statistics of FS in the penalty methods at each percentage of missing records

Method	Percentage of missing							
	5%		8.7%		10%		15%	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C1	59.34	72.64	64.78	78.12	65.69	91.63	70.73	92.33
C2	72.18	82.34	78.18	86.47	80.21	87.58	93.03	95.84
C3	60.26	71.02	64.93	75.52	68.16	78.13	72.89	82.88
C4	64.83	78.36	68.45	80.29	71.87	81.43	78.15	87.52
C5	107.43	120.60	111.35	123.04	113.23	124.97	119.12	131.26

The estimated genetic variance, residual variance and heritability of the non-censored data set were 136.15; 10,527; 0.012, respectively. C1 showed high heritability ranging between 0.011 ± 0.019 and 0.014 ± 0.016 . The lowest heritability was 0.009 ± 0.017 and the highest was 0.015 ± 0.019 in C2. C3 also showed heritability ranging between 0.008 ± 0.019 and 0.015 ± 0.019 . C4 demonstrated medium heritability, whereas C5 showed unstable heritability. All penalty methods showed large standard errors of heritability (Table 6.3).

Bias of estimated heritability in five penalty methods is presented in Table 6.4. C1 and C2 had bias ranging between 0.61 and 1.91 and between 0.54 and 2.71, respectively. The same trend was observed in both methods, where the lowest bias occurred in 10% and the highest in 15% of the missing records. The bias in C3 ranged between 0.79 and 2.54, with the lowest in 5% and the highest in 10%; in 8.7% it was lower than in the other penalty methods. The bias in C4 ranging between 0.48 and 2.49, demonstrated fluctuation within different percentages of the missing records. C5 showed the highest bias among the penalty methods at all percentages of missing records.

Table 6.3 Genetic variance, error variance and heritability (\pm SE) of FS for non-censored data and data set with missing FS in five penalty methods.

Percentage of missing	Method	σ_a^2	σ_e^2	h^2
non-censored data		136.15	10,527	0.012 \pm 0.016
5%	C1	193.76	13,808	0.014 \pm 0.016
	C2	199.07	14,669	0.013 \pm 0.019
	C3	172.65	13,190	0.013 \pm 0.019
	C4	140.31	11,366	0.012 \pm 0.018
	C5	891.07	61,925	0.015 \pm 0.023
8.7%	C1	210.95	14,654	0.014 \pm 0.020
	C2	250.54	16,743	0.015 \pm 0.019
	C3	197.07	13,887	0.015 \pm 0.019
	C4	151.25	13,260	0.011 \pm 0.018
	C5	1051.6	104,080	0.010 \pm 0.021
10%	C1	217.59	15,943	0.013 \pm 0.019
	C2	224.08	18,066	0.012 \pm 0.017
	C3	113.86	13,599	0.008 \pm 0.019
	C4	171.63	16,469	0.010 \pm 0.018
	C5	1694.5	111,500	0.015 \pm 0.021
15%	C1	231.04	20,307	0.011 \pm 0.019
	C2	199.11	21,068	0.009 \pm 0.017
	C3	263.13	16,743	0.008 \pm 0.019
	C4	139.81	14,035	0.010 \pm 0.019
	C5	2033.8	161,740	0.012 \pm 0.022

σ_a^2 : additive genetic variance, σ_e^2 : residual variance, h^2 : heritability.

MSE of estimated heritability in five penalty methods is presented in Table 6.5. The result showed that C1 had the highest MSE in 8.7%, and a variable MSE between different percentages of missing records. C2 showed a moderate MSE, ranging between 1.047 and 1.552, and the trend increased as the percentage of missing records became higher. C3 showed a low MSE, the lowest occurring in 5% and increasing as missing records increased. The highest MSE was observed at 15% of missing records. C4 showed a moderate MSE of estimated heritability, ranging between 0.633 and 0.879. C5 had a larger MSE ranging

between 1.423 and 1.876.

Table 6.4 Bias of estimated heritability ($\times 10^{-3}$) in five penalty methods

Method	Percentage of missing			
	5%	8.7%	10%	15%
C1	1.47	1.12	0.61	1.91
C2	0.64	1.17	0.54	2.71
C3	0.79	1.05	2.91	2.54
C4	0.48	2.12	0.57	2.49
C5	2.18	2.39	2.53	2.67

The average correlation between the EBV of the five penalty methods and the EBV from the non-censored data set is shown in Table 6.6. The correlation in C1 in 8.7% of the missing records was 0.82, 0.84 and 0.83 for heifer, sire and dam, respectively. The correlation between C1 and non-censored data was high in 5% and decreased as the percentage of missing records increased. C2 and C3 showed moderate correlation in 8.7% (0.81, 0.87 and 0.83) and (0.86, 0.90 and 0.86) for heifer, sire and dam, respectively. The highest correlation was found in C4 (0.88, 0.93 and 0.90) for heifer, sire and dam, respectively. C5 showed the lowest correlation (0.41, 0.46 and 0.41) for heifer, sire and dam, respectively, with the same trend as in C1, C2 and C3 in terms of different missing records.

Table 6.5 MSE ($\times 10^{-4}$) of estimated heritability in five penalty methods

Method	Percentage of missing			
	5%	8.7%	10%	15%
C1	0.776	1.899	1.344	1.453
C2	1.047	1.334	1.337	1.552
C3	0.786	1.266	1.345	2.781
C4	0.633	0.876	0.879	0.866
C5	1.442	1.876	1.423	1.775

Table 6.6 Average of correlation between EBV of five penalty methods and EBV of non-censored data set in FS

Percent of missing	Method	Heifer	Sire	Dam
5%	C1	0.89	0.87	0.90
	C2	0.87	0.85	0.86
	C3	0.92	0.94	0.92
	C4	0.92	0.95	0.93
	C5	0.50	0.60	0.52
8.7%	C1	0.82	0.84	0.83
	C2	0.81	0.87	0.83
	C3	0.86	0.90	0.86
	C4	0.88	0.93	0.90
	C5	0.41	0.46	0.41
10%	C1	0.79	0.82	0.79
	C2	0.77	0.85	0.80
	C3	0.82	0.87	0.84
	C4	0.87	0.91	0.89
	C5	0.43	0.44	0.41
15%	C1	0.69	0.71	0.73
	C2	0.71	0.81	0.73
	C3	0.73	0.81	0.76
	C4	0.78	0.87	0.83
	C5	0.39	0.42	0.38

6.4 Discussion

6.4.1 Estimated parameters

Heifers that have a true FS are those with successful insemination, gestation and calving. Eliminating an open heifer from the data set would yield biased or underestimated genetic parameters (Liu et al., 2017). In the present study, genetic and error variances tended to be large when the penalty data were included, and those in C4 were the lowest among the five penalty methods in 8.7%, whereas those in C5 were the highest. The effect of 30, 60 and 90 penalty days on calving day and age at first calving in the Angus heifer has demonstrated that genetic and error variance increase when a high penalty score is included in the analysis (Bormann and Wilson, 2010). They have concluded that the smallest number of penalty days

is recommended in genetic analysis because their result showed that the lowest standard error of heritability was estimated at the smallest penalty score.

In the present study, heritability of a non-censored data set was 0.012 ± 0.016 , lower than the average estimates in C1, C2 and C3, but slightly higher than those in C4 and C5. Standard errors of heritability of penalty methods were all higher than the heritability of a non-censored data set. Compared with previous reports, our heritability estimates were within the range of estimates in the literature. For Holstein heifers (Liu et al., 2008; Haer et al., 2013) and Ayrshire heifers (Fogh et al., 3003), FS heritability has ranged between 0.01 and 0.02.

In the present study, all of the penalty methods showed positive bias in heritability estimates. The bias in C5 was higher than that in the other penalty methods, making its error variance five times higher than the other penalty methods.

MSE is the most important criterion in evaluating the performance of a predictor or an estimator; it is also useful in acquiring the concepts of bias and accuracy in statistical estimations (Maiti et al., 2014). Estimates with a small MSE are better because they are closer to the real value (Burnham and Anderson, 2002). Taking those aspects into consideration in the present study, MSE was calculated to compare the penalty methods: C4 showed the lowest MSE; however, C1 and C5 were both higher, demonstrating that C4 was better than the other methods.

6.4.2 Percentage of missing records

In the present study, 8.7% of the records were missing, and 5%, 10% and 15% were designed to assess the influence of the missing records. The genetic and error variances in C1 and C5 tended to increase as the percentage of missing records increased; in C2, C3 and C4 they were inconsistent in the 10% and 15% missing records; in C4 they were the lowest

in 5%, 8.7% and 15% as compared with the other methods; however, in 10% of the missing records, the lowest variance was observed in C3. The reason for the fluctuation in genetic and error variances in 10% and 15% of the missing records was attributable to changes in pedigree structure. This phenomenon may be due to the deletion of key animals with regard to pedigree.

C1 showed the lowest MSE in 5% and the highest in 8.7% compared with the other percentages. In C2 MSE tended to be similar to those in C3 and C4, where the lowest MSE occurred in 5% and increased as the percentage of missing records became higher. In C4 MSE was lower than in the other methods at all percentages of missing records. C5 showed the highest and the most unstable MSE among the different percentages. When the percentage of missing records rises up to 15%, heritability tends to be lower because genetic variance decreases, while error variance increases. The change in genetic and error variances is reinforced with higher missing percentages in conjunction with changes in the data structure (Guo et al., 2001).

6.4.3 Prediction of EBV of heifer and parent

The coefficient correlation of EBV for heifer was lower than that for sire and dam, whereas it was higher for sire in 8.7%, 10% and 15 % of the missing records. In 5% of the missing records, it was higher in C1 for heifer than for sire, whereas in C2 it was higher for heifer than for dam or sire. In the other percentages, it was lower for heifer than for sire or dam, which may be attributable to the decreased accuracy for heifer EBV at higher percentages of missing records.

The coefficient correlation in C3 was lower than in C4 but higher than in the other three methods. In C4 it was consistent and highest for heifers, sires and dams at all the percentages

of missing records. In C5 it was the lowest for heifer and parents among the five penalty methods. The penalty in C5 was based on the highest number of FS days, as identified in each contemporary group plus the constant number (21d). Thus the penalty by the simple addition of certain days resulted in a less accurate EBV and a lower correlation than the other methods. This phenomenon could be due to changes in EBV ranking when penalty data are implemented (Newcom et al., 2005). Smaller changes in EBV ranking may result in C4 attaining the highest correlation with a non-censored data set, demonstrating that the penalty data in C4 are the most appropriate for handling missing records of FS in genetic analysis.

6.5 Conclusion

This study indicates that C4 is the best penalty method for missing records because it has the lowest MSE and average standard errors of heritability. It also demonstrated the highest accuracy for EBV and consistent results for all the percentages of missing records. C1 and C2 are inadequate because they are too extreme to infer true FS, whereas C4 seems to have properties that reflect true FS. True FS of heifers with missing records may be higher than the average FS at the number of times till the last insemination but lower than the highest expectation of FS in the records.

Chapter 7

Estimated genetic parameters for binary traits using Bayesian approach via Gibbs sampling

7.1 Introduction

NRR and SFI have been used to evaluate reproductive performance in dairy cattle (González-Recio et al., 2005; Chang et al., 2006; Liu et al., 2008; Tiezzi et al., 2012). Nevertheless only limited studies evaluated NRR and SFI for reproductive performance in Japanese Black cows.

NRR could be used to assess the ability of female cattle to conceive and maintaining pregnancy in early period of gestation. The advantage of NRR is a property which can be measured early and NRR is less biased due to fewer missing record than other reproductive traits (Andersen-Ranberg et al., 2005; Sun and Su, 2010). NRR has disadvantage that a cow which does not return within 56 might be pregnant or showing no return without pregnancy. In this case SFI can be used as an alternative trait for evaluating the ability of female cattle to conceive and maintain gestation.

NRR and SFI are both binary traits. Theoretically, threshold model is more appropriate than linear model for estimating genetic parameter of this type of traits. Linear model is based on assumption of normal distribution, whereas threshold model is based on the assumption of an underlying unobservable continuous response variable that follows normal distribution (Gianola and Foulley, 1983). On the other hand, Tempelman (1998) and Varona et al. (1999) reported that threshold model has bias in the estimation of variance component when the number of fixed effects is large. The objective of this study was to estimate heritability of NRR and SFI using Bayesian approach via Gibbs sampling.

7.2 Materials and Methods

7.2.1 Data Set

Field records of artificial insemination and calving events for heifers and the first three parities of cows were collected from 184 farms. The data set was edited by the following criteria: cows born between 2004 and 2014, age at first insemination more than 12 months and age at first calving between 16 and 36 months.

Table 7.1 Structure of source data for NRR and SFI

Traits	Heifer	Cow
NRR		
0	672	1437
1	1489	4343
SR		
0	1002	2206
1	1159	3574
Total numbers of records	2161	5780

NRR was coded as one when there was no subsequent insemination at 56 days after the first insemination and zero otherwise. SFI was coded as one if the cow was inseminated only once and had a subsequent calving and zero otherwise. Traits of heifers were denoted as NRR-h and SFI-h, whereas that for cow denoted as NRR-c and SFI-c. The final data set available after editing were 2161 of heifers and 5780 of cows. The detailed information of the datasets is presented in Table 7.1.

7.2.2 Statistical model

7.2.2.1 Linear Model

Single trait linear animal model used for NRR and IN separately for heifers and cows data were:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}, \quad (1)$$

and

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{pe} + \mathbf{e}. \quad (2)$$

In the above model, \mathbf{y} is vector of observations of particular reproductive traits for heifers (model 1) and cows (model 2); \mathbf{b} is vector of fixed effects including farm, month and year of insemination, AI technician and age at first calving and parity (only for model 2); \mathbf{a} is vector of random additive genetic effect; the \mathbf{pe} is vector of permanent environmental effects (only for model 2); and \mathbf{e} is vector of random residuals for the i th trait. \mathbf{X} , \mathbf{Z} and \mathbf{W} are incidence matrices connecting \mathbf{b} , \mathbf{a} , and \mathbf{pe} to \mathbf{y} .

7.2.2.2 Threshold model

The single trait threshold animal model assumed an underlying liabilities (\mathbf{L}) of NRR and SFI (\mathbf{y}) with the same effects as linear animal model, but the response of observation was modeled with the following distribution:

$$\begin{aligned} f(\mathbf{y}|\mathbf{L}) &= \prod_{i=1}^n f(\mathbf{y}_i | \mathbf{L}_i) \\ &= \prod_{i=1}^n [I(\mathbf{L}_i < \mathbf{t}_i)I(\mathbf{y}_i = \mathbf{0}) + I(\mathbf{t}_i < \mathbf{L}_i < \mathbf{t}_1)I(\mathbf{y}_i = \mathbf{1})] \end{aligned}$$

where \mathbf{t}_i is threshold that define the two categories of response and I is an indicator function that takes value one if the condition specified is true, otherwise the value is zero. The genetic parameters were estimated via a Bayesian procedure (Wang et al., 1993) assuming that the normal distribution with density as:

$$p(\mathbf{a}|\sigma_a^2)\sim N(0, A\sigma_a^2),$$

$$p(\mathbf{pe}|\sigma_{pe}^2)\sim N(0, A\sigma_{pe}^2),$$

$$p(\mathbf{e}|\sigma_e^2)\sim N(0, A\sigma_e^2),$$

where A is the numerator relationship matrix of additive genetic relationships between individuals in the pedigree; I the identity matrix; σ_a^2 , σ_{pe}^2 (only for cows) and σ_e^2 the additive genetic variance, permanent environmental variance and residual variance, respectively.

The variance covariance components were estimated via Bayesian procedure by GIBBS1F90 and THRGIBBS1F90, respectively for linear and threshold model (Misztal, 2002). After burn-in of the first 1,000,000 samples and taken apart at every 250 cycles (sampling interval), resulting posterior distribution with 4,000 samples in which inferences were performed. Value from burn-in step and sampling interval were evaluated through the POSTGIBBS1F90, which uses the Geweke diagnostic test (Geweke, 1992) based on the Z test of average equality of the conditional distribution data logarithm.

7.3 Results

Estimated heritability for SFI-h was similar to that for NRR-h when it was analyzed by linear model. When threshold model was applied, heritability of SFI-h was slightly higher than of NRR-h (Table 7.2).

Table 7.2 Genetic variance, error variance and heritability (posterior SD) for NRR-h and SFI-h for analysis using linear and threshold models

Trait	Model	σ_a^2	σ_e^2	h^2
NRR-h	Linear	0.0056	0.2148	0.025(0.066)
	Threshold	0.0314	0.9421	0.032(0.038)
SFI-h	Linear	0.0064	0.2379	0.026(0.074)
	Threshold	0.0375	0.9341	0.039(0.022)

σ_a^2 : additive genetic variance, σ_e^2 : residual variance, h^2 : heritability.

Estimated heritability for SFI-c was higher than heritability for NRR-c even if either linear or threshold model was applied (Table 7.3). In general, threshold model showed lower posterior standard deviation than linear model.

Table 7.3 Genetic parameters for NRR-c and SFI-c for analysis using linear and threshold models.

Trait	Model	σ_a^2	σ_{pe}^2	σ_e^2	h^2
NRR-c	Linear	0.0029	0.0074	0.1726	0.016(0.091)
	Threshold	0.0219	0.0329	1.0173	0.020(0.025)
SFI-c	Linear	0.0048	0.0096	0.2139	0.021(0.036)
	Threshold	0.0312	0.0801	1.0249	0.027(0.013)

σ_a^2 : additive genetic variance, σ_e^2 : residual variance, σ_{pe}^2 : permanent environmental variance, h^2 : heritability.

The estimated heritability for all traits both in heifers and cows showed low values of Geweke (p-value) ranged (0.012-0.022) and MCE ranged (0.001-0.004). They also represented narrow interval of CIH. DIC of estimates heritability by linear model were ranged from 3173.27 to 7997.49, while those by threshold model were lower, ranging from 2086.90 to 4683.37 (Table 7.4).

Table 7.4 MCE, CIH and DIC for heritability estimates by linear and threshold models

Model	Trait	Geweke (p-value)	MCE	CIH	DIC
Linear	NRR-h	0.017	0.003	0.000-0.038	3173.27
	SFI-h	0.022	0.004	0.000-0.044	3674.31
	NRR-c	0.013	0.001	0.000-0.024	6259.84
	SFI-c	0.016	0.001	0.000-0.035	7497.49
Treshold	NRR-h	0.015	0.001	0.016-0.045	2086.90
	SFI-h	0.018	0.002	0.018-0.050	2401.25
	NRR-c	0.012	0.002	0.008-0.032	4618.09
	SFI-c	0.014	0.002	0.012-0.031	4683.37

7.4 Discussion

7.4.1 Estimates of heritabilities

Linear model produces a heritability estimate in observed scale, while threshold model provides a heritability estimates in underlying scale (liability). A direct comparison on estimated heritabilities of NRR and SFI in beef cattle is not available at the present. The estimates of heritability for NRR and SFI were slightly higher than those reported in dairy cattle. For NRR, Wall et al. (2003) and Veerkamp et al. (2001) reported heritability estimates of 0.018 and 0.019, respectively, using linear model, but Sun and Su (2010) and Andersen-Ranberg et al. (2005) reported lower heritability (0.011 and 0.010). Using threshold model, the estimates in the range of 0.014 to 0.050 were reported by Sun and Su (2010), Heringstad et al. (2006) and González-Recio et al. (2005).

For SFI, the estimates ranging between 0.010 and 0.017 were reported by Veerkamp et al. (2001), Kadarmideen et al. (2003), De Haas et al. (2007) and Sun and Su (2010), using linear model. Whereas, González-Recio and Alenda (2005) and Sun and Su (2010) estimated slightly higher heritability of 0.040 and 0.020, respectively by threshold model.

7.4.2 Comparison between heifers and cows

The estimates of heritability for NRR and SFI in heifers ranged between 0.025 and 0.039 slightly higher than those in cows (0.016-0.027). This result was similar to estimated heritability for NRR using linear model reported by Liu et al. (2017) in dairy cattle. This difference between heifers and cows may be resulted by genetic and physiological factors. This result suggested that NRR and SFI are different trait when measured on heifers and cows. The interpretation of this result is that, given a pool of genes affecting reproductive of an individual, gene expression in heifers might be different from that in cows (Tiezzi et al., 2012). Physiological status of female cattle changes considerably after the first calving. When the cows start to produce milk, metabolism of the steroid hormone increase and affect reproductive performance as a consequence (Wiltbank et al., 2006).

7.4.3 Model comparison

Geweke criteria and error of Monte Carlo chain (MCE) were used to monitor the convergence. They were obtained by calculating the variance of samples for each component divided by the number of samples (Geweke, 1992). Low values of Geweke criterion and MCE for both linear and threshold models indicated that the amount of a posteriori for heritability estimate was valid for binary trait. Furthermore, the low value indicated that chain size for the particular Bayesian analyses was confirmed to reach convergence (Figueiredo Filho et al., 2018).

CIH estimated by threshold model showed narrower interval than that estimated by linear model. This result indicated that threshold model showed higher reliability of the estimates. DIC is a parameter which makes model comparison being based on a posteriori distribution of the likelihood ratio. Model with smaller value of DIC is better in terms of

heritability estimates (Spiegelhalter et al., 2002). Based on the value of DIC, threshold model is better than linear model for estimated genetic parameter for binary traits. DIC value for NRR and SFI estimated by threshold model were lower than that by linear model for both heifers and cows data set.

SFI showed more appropriate for evaluation of first insemination. Besides SFI showed slightly higher heritability than NRR, the records of success or fail of the data is more reliable. Thus the result of this study suggested that NRR and SFI on heifers and cows should be analyzed separately as a different traits. In term of model comparison for estimated heritability of binary traits, threshold model showed more reliable results than linear model.

7.5 Conclusion

The result of this study suggested that NRR and SFI on heifers and cows should be analyzed separately as a different trait. SFI showed more relevant for evaluation of first insemination. Besides SFI showed slightly higher heritability than NRR, the records of success or fail of the data is more reliable. The values of Geweke criteria and MCE indicated that chain size for the particular Bayesian analyses for either linear or threshold models was confirmed to reach their convergence. Whereas, narrow interval of CIH and smaller value of DIC suggested that threshold model was more appropriate than linear model for estimate genetic parameters of binary traits.

Chapter 8

General Conclusion

The study of reproductive traits in heifers suggests that low heritability of reproductive traits is strongly influenced by farm management practices, and that large residual variance makes genetic evaluation difficult. NRR, IN and FS demonstrated close genetic relationship with one another, although their heritabilities were very low. Among the reproductive traits of heifer, AFC has the highest heritability and favorable genetic correlations with IN and FS.

Estimated heritability of most female reproductive traits in three parities of Japanese Black cows is low. Multiple-trait analysis showed that genetic correlations between same traits among different parities of cows were high. Whereas, repeatability model seems to be more appropriate for estimating reproductive traits because it yields a low standard error in estimated parameters. The repeatability model have additional benefit to provide permanent environmental effect on a trait.

In the study of relationship between reproductive trait of heifers and cows, AFC was considered to be the most desirable trait compared with ASC and ATC. Since AFC is a trait measured early, it AFC also indicate moderate to high genetic correlations with traits which measured the abilities to recycle, conceive and maintain pregnancy.

Study of penalty methods for FS indicated that C4 was the best penalty method for missing records because it had the lowest MSE and average standard errors of heritability. It also demonstrated the highest accuracy for EBV and consistent results for all the percentages of missing records. Furthermore, C4 seemed to have properties that reflect true FS because the value was in interval between C1 and C2. While, C1 and C2 were too extreme to infer

true FS. Then study of different model for binary traits using Bayesian approach via Gibbs sampling resulted that values of Geweke criteria and MCE indicated that chain size for the particular Bayesian analyses for either linear or threshold models was confirmed to reach their convergence. Whereas narrow interval of CIH and smaller value of DIC suggested that threshold model is more appropriate than linear model for estimating genetic parameters of binary traits.

AFC is considered a key trait in the reproductive cycle of and as an indicator of sexual maturity in female cattle. Improvement of AFC will play an important role for increasing reproductive performance in subsequent parities. Based on favorable genetic correlations with important traits such as IN and FS, AFC can be used as an early indicator of ability of cows to maintain regular reproductive cycle. Selection by AFC will provide consistent genetic improvement in reproductive performance of Japanese Black cows.

REFERENCES

- Abe H., Masuda Y., Suzuki M. 2009. Relationships between reproductive traits of heifers and cows and yield traits for Holsteins in Japan. *Journal of Dairy Science* **92**: 4055-4062.
- Andersen-Ranberg I.M., Klemetsdal G., Heringstad B., Steine T. 2005. Heritabilities, genetic correlations and genetic change for female fertility and protein yield in Norwegian dairy cattle. *Journal of Dairy Science* **88**: 348-355.
- Baco S., Harada H., Fukuhara R. 1998. Genetic relationships of body measurements at registration to a couple of reproductive traits in Japanese Black cows. *Animal Science and Technology (Jpn)* **69**:1-7.
- Bagnato A., Oltenacu P.A. 1993. Genetic study of fertility traits and production in different parities in Italian Friesian cattle. *Journal of Animal Breeding and Genetics* **110**: 126-134.
- Bernardes P.A., Grossi D.A., Savegnago R.P., Buzanskas M.E., Urbinati I., Bezerra L.A.F., Lobo R.B., Munari D.P. 2014. Estimates of genetic parameters and genetic trends for reproductive traits and weaning weight in tabapuã cattle. *Journal of Animal Science* **93**: 5175-5185.
- Berry D.P., Wall E., Pryce J.E. 2014. Genetics and genomics of reproductive performance in dairy and beef cattle. *Animal* **8**: 105-121.
- Boettcher P.J., Jairath L.K., Dekkers J.C.M. 1999. Comparison of methods for genetic evaluation of sires for survival of their daughters in the first three lactations. *Journal of Dairy Science* **82**:1034-1044.
- Bolacali M., Öztürk Y. 2017. Effect of non-genetic factors on 305-days milk yield in Simmental cows reared in subtropical climate condition. *The Journal of Animal and*

Plant Sciences **27**:1420-1425.

Bormann J.M., Totir L.R., Kachman S.D., Fernando R.L., Wilson D.E. 2006. Pregnancy rate and first-service conception rate in Angus heifers. *Journal of Animal Science* **84**: 2022-2025.

Bormann J.M., Wilson D.E. 2010. Calving day and age at first calving in Angus heifers. *Journal of Animal Science* **88**:1947-1956.

Buddenberg B.J., Brown C.J., Brown A.H. 1990. Heritability estimates of calving date in Hereford cattle maintained on range under natural mating. *Journal of Animal Science* **68**:70-74.

Burnham K.P., Anderson D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach (second edition). Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, USA.

Cammack K.M., Thomas M.G., Enns R.M. 2009. Reproductive traits and their heritabilities in Beef cattle. *The Professional Animal Scientist* **25**: 517-528.

Chang Y.M., Andersen-Ranberg I.M., Heringstad B., Gianola D., Klemetsdal G. 2006. Bivariate analysis of number of service to conception and days open in Norwegian Red using a censored threshold-linear model. *Journal of Dairy Science* **89**: 772-778.

Costa R.B., Camargo G.M.F., Diaz I.D.P.S., Irano N., Dias M.M., Carvalheiro R., Boligon A.A., Baldi F., Oliveira H.N., Tonhati H., Albuquerque L.G. 2015. Genome-wide association study of reproductive traits in Nelore heifers using Bayesian inference. *Genetics Selection Evolution* **47**: 67-75.

Dargatz D.A., Dewell G.A., Mortimer R.G. 2004. Calving and calving management of beef cows and heifers on cow-calf operations in the United States. *Theriogenology* **61**: 997-

- 1007.
- De Haas, Y., Janss, L.L., Kadarmideen, H.N. 2007. Genetic correlations between body condition scores and fertility in dairy cattle using bivariate random regression models. *Journal of Animal Breeding and Genetics* **124**: 277-285.
- Demeke S., Neso F.W.C., Schoeman S.J. 2004. Estimates of genetic parameters for Boran, Friesian, and crosses of Friesian and Jersey with the Boran cattle in the tropical highlands of Ethiopia: Milk production traits and cow weight. *Journal of Animal Breeding and Genetics* **121**: 163-175.
- Dickerson G.E. 1970. Efficiency of animal production-molding the biological components. *Journal of Animal Science* **30**: 849-859.
- Efron B., Tibshirani R.J. 1993. *An Introduction to the Bootstrap*, Chapman & Hall, New York.
- Efron B. 1990. More efficient bootstrapping computation. *Journal of the American Statistical Association* **85**: 79-89.
- Estrada-León R.J., Magana J.G., Segura-Correa J.C. 2008. Genetic parameters for reproductive traits of Brown Swiss cows in the tropics of Mexico. *Journal of Animal and Veterinary Advances* **7**: 124-129.
- Evans J.L., Golden B.L., Bourdon R.M., Long K.L. 1999. Additive genetic relationships between heifer pregnancy and scrotal circumference in Hereford cattle. *Journal of Animal Science* **77**: 2621-2628.
- Falconer D.S., Mackay T. F.C. 1996. *Introduction to quantitative genetics* (fourth edition). Longman, Harlow, United Kingdom.
- Figueiredo Filho L.A.S., Sarmento J.L.R., Campelo J.E.G., Almeida M.J.O., Sousa Júnior A., Santos N.P.S., Costa M.S., Torres T.S., Sena L.S. 2018. Genetic parameters for marbling

- and body score in Anglonubian goats using Bayesian inference via threshold and linear models. *Asian-Australasian Journal of Animal Science* **31**: 1407-1414.
- Fogh A., Roth A., Pedersen O.M., Eriksson J.Å., Juga J., Toivonen M., Ranberg I.M.A., Steine T., Nielsen U.S., Aamand G.P. 2003. A joint Nordic model for fertility traits. *Interbull Bulletin* **31**: 52-55.
- Frazier E.L., Sprott L.R., Sanders J.O., Dahm P.F., Crouch J.R., Turner J.W. 1999. Sire marbling score expected progeny difference and weaning weight maternal expected progeny difference associations with age at first calving and calving interval in Angus beef cattle. *Journal of Animal Science* **77**: 1322-1328.
- Geweke J. 1992. Evaluating the accuracy of sampling-based approaches to calculating posterior moments. *Bayesian Statistics*. Oxford University Press Oxford, UK.
- Ghiasi H., Pakdel A., Nejati-Javaremi A., Mehrabani-Yeganeh H., Honarvar M., González-Recio O., Carabano M.J., Alenda R. 2011. Genetic variance components for female fertility in Iranian Holstein cows. *Livestock Science* **139**: 277-280.
- Gianola D., Foulley J. 1983. Sire evaluation for ordered categorical data with a threshold model. *Genetics Selection Evolution* **15**: 201-224.
- Gilmour A.R, Gogel B.J, Cullis B.R, Welham S.J, Thompson R. 2015. ASReml User Guide Release **4.1** Structural Specification, VSN International Ltd, Hemel Hempstead, HP1 1ES, UK.
- González-Recio O., Alenda R. 2005. Genetic parameters for female fertility traits and a fertility index in Spanish dairy cattle. *Journal of Dairy Science* **88**: 3282-3289.
- Goyache F., Gutiérrez J.P., Fernández I., Royo L.J., Álvarez I. 2005. Short communication: Genetic analysis of days open in beef cattle. *Livestock Production Science* **93**: 283-289.

- Gredler B., Fuerst C., Sölkne, J. 2007. Analysis of new fertility traits for the joint genetic evaluation in Austria and Germany. *Interbull Bulletin* **37**: 152-155.
- Guo S.F., Gianola D., Rekaya R., Short T. 2001. Bayesian analysis of lifetime performance and prolificacy in Landrace sows using linear mixed model with censoring. *Livestock Production Science* **72**: 243-252.
- Guo G., Guo X., Wang Y., Zhang X., Zhang S., Li X., Liu L., Shi W., Usman T., Wang X., Du L., Zhang Q. 2014. Estimation of genetic parameters of fertility traits in Chinese Holstein cattle. *Canadian Journal of Animal Science* **94**: 281-285.
- Gutiérrez J.P., Alvarez I., Fernández I., Royo L.J., Díez J., Goyache F. 2002. Genetic relationships between calving date, calving interval, age at first calving and type traits in beef cattle. *Livestock Production Science* **78**: 215-222.
- Haer de L.C.M., de Jong G., Vessies P.J.A. 2013. Estimation of genetic parameters of fertility traits, for virgin heifers in the Netherlands. *Interbull Bulletin* **47**: 23-25.
- Heringstad B., Andersen-Ranberg I.M., Chang Y.M., Gianola D. 2006. Genetic analysis of nonreturn rate and mastitis in first-lactation Norwegian red cows. *J Journal of Dairy Science* **89**: 4420-4423.
- Honarvar M., Nejati J.A., Miraei A.S.R., Dehghan B.M. 2010. A simulation study: Effect of length of productive life on genetic trend of milk production and profitability. *African Journal of Biotechnology* **9**: 3000-3010.
- Ibi T., Kahi A.K., Hirooka H. 2008. Genetic parameters for gestation length and the relationship with birth weight and carcass traits in Japanese Black cattle. *Animal Science Journal* **79**: 297-302.
- Jamrozik J., Fatehi J., Kistemaker G.J., Schaeffer L.R. 2005. Estimates of genetic parameters

- for Canadian Holstein female reproduction traits. *Journal of Dairy Science* **88**: 2199-2208.
- Johnston D.J., Bunter K.L. 1996. Days to calving in Angus cattle: genetic and environmental effects, and covariances with other traits. *Livestock Production Science* **45**:13-22.
- Kadarmideen H.N., Thompson R., Simm G. 2000. Linear and threshold model genetic parameters for disease, fertility and milk production in dairy cattle. *Animal Science* **71**: 411-419.
- Kadarmideen H.N., Thompson R., Coffey M.P., Kossaibati M.A. 2003. Genetic parameters and evaluations from single- and multiple-trait analysis of dairy cow fertility and milk production. *Livestock Production Science* **81**: 183-195.
- LeBlanc S. 2007. Economics of improving reproductive performance in dairy herds. *WCDS Advances in Dairy Technology* **19**: 201 – 214.
- Liu Z., Jaitner J., Reinhardt F., Pasman E., Rensing S., Reents R. 2008. Genetic evaluation of fertility traits of dairy cattle using a multiple-trait animal model. *Journal of Dairy Science* **91**: 4333-4343.
- Liu A., Lund M.S., Wang Y., Guo G., Dong G., Madsen P., Su G. 2017. Variance components and correlations of female fertility traits in Chinese Holstein population. *Journal Animal Science and Biotechnology* **8**:1-9.
- Lopez R., Thomas M.G., Hallford D.M., Keisler D.H., Silver G.A., Obeidat B.S., Garcia M.D., Krehbiel C.R. 2006. Case study: Metabolic hormone profiles and evaluation of associations of metabolic hormones with body fat and reproductive characteristics of Angus, Brangus, and Brahman heifers. *The Professional Animal Scientist* **22**:273-282.
- Luo M.F., Boettcher P.J., Schaeffer L.R., Dekkers J.C. 2001. Bayesian inference for

- categorical traits with an application to variance component estimation. *Journal of Dairy Science* **84**: 694-704.
- Lynch M., Walsh B. 1998. *Genetics and Analysis of Quantitative Traits*, Sinauer, Sunderland, Massachusetts.
- M'Hamdi N., Aloulou R., Brar S.K., Bouallegue M., Hamouda M.B. 2010. Phenotypic and genetic parameters of reproductive traits in Tunisian Holstein cows. *Biotechnology Animal Husbandry* **26**:297-307.
- Maiti T., Ren H., Sinha S. 2014. Prediction error of small area predictors shrinking both means and variances. *Scandinavian Journal of Statistics* **41**: 775-790.
- Martínez-Velázquez G., Gregory K.E., Bennett G.L., Van Vleck L.D. 2003. Genetic relationships between scrotal circumference and female reproductive traits. *Journal of Animal Science* **81**: 395-401.
- Melton B.E. 1995. Conception to consumption: The economics of genetic improvement. *Proceedings of 27th Beef Improvement Federation Annual Meeting and Symposium*. Sheridan, USA. p.40.
- Meyer K., Hammond K., Parnell P.F., Mackinnon M.J., Sivarajasingam S. 1990. Estimates of heritability and repeatability for reproductive traits in Australian beef cattle. *Livestock Production Science* **25**:15-30.
- Misztal J. 2002. Fortran programs [Internet]. Athens, GA, USA: University of Georgia; Available from: <http://nce.ads.uga.edu/wiki/doku.php?id=readme.gibbs3>.
- Morris C.A., Baker R.L., Cullen N.G. 1992. Genetic correlations between pubertal traits in bulls and heifers. *Livestock Production Science* **31**:221-234.
- Morris C. A., Cullen N.G. 1994. A note on genetic correlations between pubertal traits of

- males or females and lifetime pregnancy rate in beef cattle. *Livestock Production Science* **39**: 291-297.
- Morris C.A., Wilson J.A., Bennett G.L., Cullen N.G., Hickey S.M., Hunter J.C. 2000. Genetic parameters for growth, puberty, and beef cow reproductive traits in a puberty selection experiment. *New Zealand Journal of Agricultural Research* **43**:83-91.
- Muir B.L., Fatehi J., Schaeffer L.R. 2004. Genetic relationships between persistency and reproductive performance in first-lactation Canadian Holsteins. *Journal of Dairy Science* **87**: 3029-3037.
- Naya H., Peñagaricano F., Urioste J.I. 2017. Modelling female fertility traits in beef cattle using linear and non-linear models. *Journal of Animal Breeding and Genetics* **134**: 202-212.
- Neale B.M. 2016. Genomics, circuits and pathways in clinical neuropsychiatry, Chapter 9- Association strategies: 133-139.
- Newcom D.W., Baas T.J., Stalder K.J., Schwab C.R. 2005. Comparison of three models to estimate breeding values for percentage of loin intramuscular fat in Duroc swine. *Journal of Animal Science* **83**: 750-756.
- Oikawa T. 2017. Effect of heat stress on age at first calving of Japanese Black cows in Okinawa. *Animal Science Journal* **88**: 439-444.
- Oseni S., Tsuruta S., Misztal I., Rekaya R. 2004. Genetic parameters for days open and pregnancy rates in US Holsteins using different editing criteria. *Journal of Dairy Science* **87**: 4327-4333.
- Oyama K., Katsuta T., Anada K., Mukai F. 2002. Heritability and repeatability estimates for reproductive traits of Japanese Black cows. *Asian-Australasian Journal of Animal*

- Science **15**: 1680-1685.
- Oyama K., Katsuta T., Anada K., Mukai F. 2004. Genetic parameters for reproductive performance of breeding cows and carcass traits of fattening animals in Japanese Black (Wagyu) cattle. *Animal Science* **78**: 195–201.
- Pereira J.A.C., Suzuki M., Hagiya K., Yoshizawa T., Tsuruta S., Misztal I. 2001. Method R for estimates of heritability and repeatability for milk, fat and protein yields of Japanese Holstein. *Animal Science Journal* **72**: 372-377.
- Pravia M.I., Ravagnolo O., Urioste J.I., Garrick D.J. 2014. Identification of breeding objectives using a bioeconomic model for a beef cattle production system in Uruguay. *Livestock. Science.* **160**: 21-28.
- Rao A.R., Prabhakaran V.T. 2001. A bootstrap method of estimating heritability from varietal trial data. *Indian Journal of Genetic and Plant Breeding* **61**: 87-91.
- Reverter A., Kaiser C.J., Mallinckrodt C.H. 1998. A Bootstrap Approach to Confidence Regions for Genetic Parameters from Method R Estimates. *Journal of Animal Science* **76**: 2263-2271.
- Roxström A., Strandberg E., Berglund B., Emanuelson U., Philipsson J. 2001. Genetic and environmental correlations among female fertility traits and milk production in different parities of Swedish red and white dairy cattle. *Acta Agriculturae Scandinavica, Section A – Animal Science* **51**: 7-14.
- Sasaki Y., Uematsu M., Kitahara G., Osawa T. 2016. Reproductive performance of Japanese Black cattle: Association with herd size, season, and parity in commercial cow-calf operations. *Theriogenology* **86**: 2156–61.
- SAS Institute Inc. 2011. Base/STAT SAS® 9.3 User’s Guide. SAS Institute Inc., Cary, NC

USA.

Schaeffer L.R. 1983. Effectiveness of model for cow evaluation intra herd. *Journal of Dairy Science* **66**: 874-880.

Schaeffer L.R., 2011. Cumulative permanent environmental effects for repeated records animal models. *Journal of Animal Breeding and Genetics* **128**: 95-99.

Schmidt P.I., Campos G.S., Roso V.M., Souza F.R.P., Boligon A.A. 2019. Genetic analysis of female reproductive efficiency, scrotal circumference and growth traits in Nelore cattle. *Theriogenology* **128**: 47-53.

Schneider M. del P., Strandberg E., Ducrocq V., Roth A. 2005. Survival analysis applied to genetic evaluation for female fertility in Dairy cattle. *Journal of Dairy Science* **88**: 2253-2259.

Silva L.N., Gasparino E., Torres Júnior R.A.A., Euclides Filho K., Silva L.O.C., Alencar M.M., Souza Júnior M.D., Battistelli J.V.F., Silva S.C.C. 2015. Repeatability and genotypic correlations of reproductive and productive traits of crossbred beef cattle dams. *Genetic and Molecular Research* **14**: 5310-5319.

Spiegelhalter D.J., Best N.G., Carlin B.P., Van der Linde A. 2002. Bayesian measures of model complexity and fit. *Journal of Royal Statistic Society* **64**: 583-616.

Sun C., Su G. 2010. Comparison on model for genetic evaluation of non-return rate and success in first insemination of the Danish Holstein cows. *Livestock Science* **127**: 205-210.

Tempelman R.J. 1998. Generalized linear mixed models in dairy cattle breeding. *Journal of Dairy Science* **81**: 1428-1444.

Thai H.T., Mentre F., Holford N.H., Veyrat-Follet C., Comets E. 2013. A comparison of

- bootstrap approaches for estimating uncertainty of parameters in linear mixed-effects models. *Pharmaceutical Statistics* **12**: 129-140.
- Tiezzi F., Maltecca C., Cecchinato A., Penasa M., Bittante G. 2012. Genetic parameters for fertility of dairy heifers and cows at different parities and relationships with production traits in first lactation. *Journal of Dairy Science* **95**:7355-7362.
- Uchida H., Kobayasi J., Inoue T., Suzuki K., Oikawa T. 2002. Current level of reproductive performances in Japanese Black cows. *Asian-Australasian Journal of Animal Science* **15**: 1098-1102.
- Varona L., Misztal I., Bertrand J.K. 1999. Threshold-linear versus linear-linear analysis of birth weight and calving ease using an animal model: II. Comparison of models. *Journal of Animal Science* **77**: 2003-2007.
- Veerkamp R.F., Koenen E.P.C., De Jong G. 2001. Genetic correlations among body condition score, yield, and fertility in first-parity cows estimated by random regression models. *Journal of Dairy Science* **84**: 2327-2335.
- Wall E., Brotherstone S., Woolliams J.A., Banos G., Coffey M.P. 2003. Genetic evaluation of fertility using direct and correlated traits. *Journal of Dairy Science* **86**: 4093-4102.
- Wang C.S., Rutledge J.J., Gianola D. 1993. Marginal inferences about variances components in a mixed linear model using Gibbs sampling. *Genetics Selection Evolution* **25**: 41-62.
- Wiltbank M., Lopez H., Sartori R., Sangsritavong S., Gümen A. 2006. Changes in reproductive physiology of lactating dairy cows due to elevated steroid metabolism. *Theriogenology* **65**: 17-29.
- Yagüe G., Goyache F., Becerra J., Moreno C., Sánchez L., Altarriba J. 2009. Bayesian estimates of genetic parameters for pre-conception traits, gestation length and calving

interval in beef cattle. *Animal Reproduction Science* **114**: 72-80.

Zink V., Štípková M., Lassen J. 2011. Genetic parameters for female fertility, locomotion, body condition score, and linear type traits in Czech Holstein cattle. *Journal of Dairy Science* **94**: 5176-5182.

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黒毛和種人工授精記録による雌繁殖形質の遺伝学的研究

Doctoral Thesis

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2020

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A dissertation submitted to the United Graduate School of Agricultural Sciences
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Doctor of Philosophy

by

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