Institute of Animal Science

Department of Animal Genetics and Breeding

Prof. Dr. Jörn Bennewitz

UNIVERSITY OF
HOHENHEIM

Analyses of quantitative traits in varying environments in pigs and Brown Swiss cattle

Dissertation

submitted in fulfilment of the regulations to acquire the degree

Doktor der Agrarwissenschaften

(Dr. sc. agr. in Agricultural Science)

to the

Faculty of Agricultural Science

presented by

Nina Annik Imort-Just

born in Marl, North Rhine-Westphalia, Germany

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GENERAL INTRODUCTION

One of the main objectives in animal breeding is to make genetic progress in quantitative traits. To achieve this objective, complex breeding programmes are developed. These programmes are used worldwide and are in principle similarly structured, independent of species and breed. They are always characterised by successive steps: (1) a breeding goal definition for specific production systems, environments and species, (2) the recording of phenotypes, (3) the acquisition of kinship information, (4) the estimation of breeding values for specific traits and animals, (5) the selection process of high value animals to breed the next generation based on complex total merit indices and (6) the dissemination of genetics into the production tier.

For several reasons, those programmes need to be reviewed and adjusted on a regular basis. Alongside with findings from research, future challenges, like climate change, and the effective use of resources need to be considered. Furthermore, social and ethical influences are important, notably regarding animal welfare, food production and consumers demands. In addition, political regulations, e.g. for specific production systems, and economic aspects, like the profit generated by genetic gain, are crucial for the success and evaluation of breeding programmes (European Commission, 2008 a, 2008 b).

The breeding goal includes multiple traits, combined in a total merit index, and is developed for long-term improvement of the population. In the last decades, most breeding strategies in pigs and cattle focused on production traits and high yields, as a result of their economic value. Negative genetic correlations between those yield traits and functional traits led to a decline in fitness traits (Lucy, 2001; Knol et al., 2002; Grandinson, 2005). This is criticised by consumers, the general society as well as certain farmers. In order to put more emphasis on fitness traits, these have to be weighted to higher degree in the total merit index and/or new traits have to be considered (Egger-Danner et al., 2014). For pigs, mothering ability traits are becoming increasingly important because it has become evident that a good mothering ability is one of the prerequisites for low piglet mortality.

Breeding animals are selected based on the total merit index. The latter combines the single trait breeding values and the economic importance of the traits or trait complexes and is another important step in breeding programmes. Different objective and non-objective approaches can be

used to determine economic weights for traits. Those depend on data, monetary evaluation of traits and questioning, like the consideration of specific environmental effects or the maximisation aim (Nielsen and Amer, 2007; Teegen et al., 2008; Fuerst-Waltl et al., 2010).

Changing environments pose the question about genotype by environment interactions (GxE). Ignoring GxE effects might result in diminished genetic gain (Mulder and Bijma, 2005; Mulder, 2007). Therefore, breeding programmes need to be optimised in the presence of GxE, to breed animals which are capable of a reliable performance in a variety of environments. This is important, because well performing animals in a specific environment do not necessarily perform as good in another, more different environment (Falconer and Mackay, 1996). There are different concepts to estimate GxE interactions, like the estimation of genetic correlations between performances in different environments or the reaction norm approach, which uses continuous environmental descriptors (Hayes et al., 2016).

In the present thesis, several aspects of classical, common and novel quantitative traits in pigs and, in different environments, in cattle are analysed.

In **Chapter 1** phenotypic data of new mothering ability traits in pigs, recorded on an ordinal scale, were used to estimate genetic parameters. Heritabilities and repeatabilities were estimated by applying generalised linear mixed and threshold models. Bivariate analyses were used to estimate genetic correlations. Subsequently, the data recording approach, the fitted models and the possible inclusion of the investigated traits in existing breeding schemes were discussed.

Chapter 2 focuses on the economic aspect of cattle breeding programmes. A discrete choice experiment was used to evaluate the importance of commonly included and new, not yet monetarily evaluated, traits in total merit indices of Brown Swiss cattle. Selection decisions and farm management environments of surveyed breeders were considered. A conditional logit model was used to derive relative economic weights and estimate the marginal willingness to pay for six trait complexes, the semen price and interactions between traits. Finally, the, not strictly economic and non-objective, discrete choice approach, and its regular use in breeding programmes and results were discussed.

In **Chapter 3** possible GxE for production and functional traits of Brown Swiss cattle and their effect on existing breeding programmes were examined. Bivariate sire models were used to

estimate genetic correlations between environments on a trait level. Furthermore, total merit indices (TMI) for sires were calculated using environment-specific relative economic weights to determine possible GxE effects at TMI level. Subsequently, results and their impact on existing breeding programmes were discussed.

Chapter 4 investigates GxE interactions for various production and functional traits of Brown Swiss cattle using reaction norm models. Milk energy yield was used as a continuous environmental descriptor, combining the average herd effects of milk, fat and protein yield of phenotyped animals. A reaction norm model was used, including a random regression of a specific sire on the environmental descriptor and heterogeneously modelled residuals. In addition, breeding values for sires were estimated to provide insight into putative reranking effects. The results and possible effects on existing breeding schemes of Brown Swiss were discussed.

A **general discussion** will connect the different Chapters. It discusses the applied methods, the results and their use for existing breeding programmes of pigs and Brown Swiss cattle. Moreover, possibilities for the implementation of results and findings in current breeding schemes will be analysed and prospects for future research are presented.

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GENERAL SUMMARY (ENGLISH)

Complex breeding programmes are used worldwide to achieve genetic progress in quantitative traits. These programmes are basically similarly structured, independent of breed and species, and are characterised by successive steps. The adjustment and revision of breeding programmes is of ongoing interest due to several reasons, e.g. research findings and various political, economic, social and ethical aspects. For the long-term improvement of livestock populations, multiple traits are included in the breeding goals of such programmes. Unfavourable genetic correlations between economically important production traits and functional traits compromise the genetic progress in animal health and welfare. Novel functional and behavioural traits and the adjustment of relative economic weights for the optimisation of total merit indices are investigated in research projects. In addition, genotype by environment interactions (GxE) can influence the genetic improvement of livestock populations. The consideration of these interactions is crucial due to the globalisation of breeding structures and the associated varying production environments.

The main objectives of this thesis were 1) to investigate novel behavioural traits in pig breeding, 2) to derive environmental-specific relative economic weights based on consumers preferences for Brown Swiss cattle, 3) to estimate GxE at a trait and an index level by applying bivariate sire models in Brown Swiss cattle and 4) to analyse GxE for different production and functional traits in Brown Swiss cattle using reaction norm models.

In **Chapter 1** genetic parameters for mothering ability traits were estimated, based on field-recorded data on a five-point ordinal scale. Heritabilities (h^2) were estimated by applying a linear mixed model and a threshold model, ranging between 0.02 to 0.07 and 0.05 to 0.15, respectively. The slightly higher estimates for the repeatability ranged from 0.05 to 0.09 and from 0.08 to 0.17 (same models applied) and indicate the influence of the permanent environment. Highest h^2 were found for the group- and nursing behaviour of the sows. Correlations, estimated by bivariate analyses, were positive. Highest genetic correlations were found between group-/nursing behaviour and litter balance and piglet weaning weight with estimates between 0.71 and 0.86. The results indicate that the threshold model seems to be more suitable for the data used. Accelerating genetic gain for improved mothering ability in sows is possible. For the implementation of results in breeding programmes, a most objective definition of traits is necessary. Furthermore, the

investigation of correlations between mothering ability traits and common production traits is required.

In **Chapter 2**, the importance of breeding traits of Brown Swiss cattle in terms of selection decisions of farm managers were evaluated by using a discrete choice experiment (DCE). Environment-specific relative economic weights (REW) and the marginal willingness to pay were estimated by using a conditional logit model. Several trait complexes, the semen price, interactions between these traits and specific characteristics of the farms were included. Farmers showed highest preferences for the milk value, conformation/udder and fitness. Interactions indicated a great importance of the fitness trait complex for organically managed farms compared to conventional farmers. The latter weighted the milk value and the trait complex conformation/udder high. The DCE is flexible regarding the modelling of heterogeneous farmers' preferences for a limited number of trait complexes. Derived environmental-specific REW can be used for the development of an environmental-specific total merit index (TMI). The method is suitable to judge farmers' preferences for specific traits, especially those which have not yet been monetarily evaluated. The results can be used by breeding organisations in their decision-making processes to include traits in the TMI. Further, a comparison of currently used REW and the DCE-derived REW indicated, that they agree to a large extent, but farmers want to include the new trait perinatal sucking behaviour in the TMI. The combination of the DCE and purely profit-oriented approaches is recommended.

Chapter 3 investigated GxE at a trait and an index level for Brown Swiss sires. Bivariate sire models were used to estimate genetic correlations between organic and conventional production systems and two altitude level of the farms for milk production traits and several functional traits. Furthermore, to determine possible GxE and rerankings at an index level, total merit indices for the sires were calculated, based on breeding values and environmental-specific REW. The genetic correlations were high between the analysed environments, ranging from $r_g=0.79$ (first insemination to conception between the different altitude level of the farms) to $r_g=0.99$ (calving to first insemination, cystic ovaries, maternal stillbirth between the production systems). The results indicate no severe GxE at a trait level and thus, no adjustment of the existing breeding programme. Between the environmental-specific TMIs of the Brown Swiss sires for organic and conventional production systems, no severe reranking was found. Consequently, no putative GxE effects were found for the production system environments at an index level.

In **Chapter 4**, GxE for various production and functional traits in Brown Swiss cattle were analysed using random regression reaction norm models. The continuous environmental descriptor milk energy yield (MEY) was calculated as a linear combination of average herd effects, obtained from the routine breeding value estimation, of milk-, fat- and protein yield. The applied reaction norm model included a random sire effect (intercept) and a random sire slope effect (environmental sensitivity), i.e. the random regression coefficient of the regression of a specific sire on the environmental descriptor MEY. To investigate putative GxE effects, breeding values for the sires were estimated. Results showed no severe GxE for the functional traits but for the production trait fat yield. In addition, the slope variances as descriptors of the environmental sensitivity and the Spearman rank correlations between the estimated breeding values of the sires at different environmental levels indicate no severe GxE for the investigated traits. The results imply no substantial benefit of the consideration of GxE given the environmental descriptor and traits for the Brown Swiss breeding programme.

GENERAL SUMMARY (GERMAN)

Weltweit werden komplexe Zuchtprogramme eingesetzt, um genetische Fortschritte bei quantitativen Merkmalen zu erzielen. Diese Programme sind unabhängig von Nutztierart und Rasse grundsätzlich ähnlich strukturiert und zeichnen sich durch aufeinander folgende Schritte aus. Die Anpassung und Überarbeitung dieser Zuchtprogramme ist von anhaltendem Interesse und erfolgt aus ganz unterschiedlichen Perspektiven und mit variierenden Zielvorstellungen, so gilt es etwa, aktuelle Forschungsergebnisse einzubinden oder verschiedene politische, wirtschaftliche, soziale und ethische Aspekte zu berücksichtigen. Zur langfristigen Optimierung der Nutztierpopulationen sind in den Zuchtzielen solcher Programme komplexe Zusammenstellungen an Merkmalen enthalten. Gerade diese Komplexität und die genannten äußeren Aspekte führen dazu, dass sich die Rahmenbedingungen der Programme stetig ändern. Dieser Wandel muss von der Forschung begleitet werden, um zum Beispiel ungünstige genetische Korrelationen zwischen wirtschaftlich wichtigen Produktionsmerkmalen und neuen funktionalen Merkmalen aufzudecken, die den genetischen Fortschritt, insbesondere in Bezug auf die Tiergesundheit und den Tierschutz, beeinträchtigen können. Dementsprechend wird in Forschungsprojekten neben neuartigen funktionalen Merkmalen und Verhaltensmerkmalen auch die Anpassung von relativen ökonomischen Gewichten zur Optimierung von Gesamtzuchtwerten untersucht. Die Optimierungsprozesse der Zuchtprogramme beziehen darüber hinaus die Genotyp-Umwelt-Interaktionen (GxE) mit ein, welche die genetische Verbesserung von Nutztierpopulationen beeinflussen. Die Berücksichtigung dieser Interaktionen ist in Folge der Globalisierung der Zuchtstrukturen und der damit verbundenen, variierenden Produktionsumgebungen von entscheidender Bedeutung.

Die zentralen Zielsetzungen dieser Dissertation waren 1) die Untersuchung neuer Verhaltensmerkmale in der Schweinezucht, 2) die Ableitung umweltspezifischer, relativer wirtschaftlicher Gewichte auf der Grundlage von Züchterpräferenzen für Braunvieh, 3) die Schätzung von Genotyp-Umwelt-Interaktionen auf Merkmals- und Gesamtzuchtwertebene unter Anwendung bivariater Vatermodelle beim Braunvieh und 4) die Analyse von Genotyp-Umwelt-Interaktionen für verschiedene Produktionsmerkmale und funktionale Merkmale beim Braunvieh unter Verwendung von Reaktionsnormmodellen.

In **Kapitel 1** wurden genetische Parameter für Mütterlichkeitsmerkmale bei Schweinen auf der Grundlage von Felddaten, erfasst auf einer Fünf-Stufen-Skala, geschätzt. Die Heritabilitäten (h^2) wurden sowohl unter Anwendung eines linear gemischten Modells als auch eines Schwellenwertmodells geschätzt und lagen zwischen 0,02 und 0,07 bzw. 0,05 und 0,15. Die etwas höheren Schätzungen für die Wiederholbarkeit lagen zwischen 0,05 und 0,09 bzw. 0,08 und 0,17 und weisen auf einen Einfluss der permanenten Umwelt hin. Für das Gruppen- und Säugeverhalten der Sauen wurden die höchste Heritabilitäten geschätzt. Die Korrelationen zwischen den Mütterlichkeitsmerkmalen, geschätzt mit einer bivariaten Erweiterung des linear gemischten Modells, waren positiv. Die höchsten genetischen Korrelationen wurden zwischen dem Gruppen-/ Säugeverhalten und der Wurfhomogenität sowie dem Absetzgewicht der Ferkel gefunden, mit Schätzungen zwischen $r_g = 0,71$ und $r_g = 0,86$. Eine züchterische Optimierung des mütterlichen Verhaltens von Sauen erscheint aussichtsreich. Die Ergebnisse legen nahe, dass sich das Schwellenwertmodell für die verwendeten ordinalen Daten besser eignet. Für die Umsetzung der Ergebnisse in Zuchtprogrammen ist eine möglichst objektive Definition der Merkmale erforderlich. Ferner ist die Untersuchung von Korrelationen zwischen Mütterlichkeitsmerkmalen und allgemeinen Produktionsmerkmalen von Interesse.

In **Kapitel 2** wurden Züchterpräferenzen für ausgewählte Merkmale beim Braunvieh mit Hilfe eines Discrete Choice Experiments (DCE) untersucht. Umweltspezifische, relative ökonomische Gewichte (REW) und die marginale Zahlungsbereitschaft („marginal willingness to pay") wurden unter Verwendung eines bedingten Logit-Modells geschätzt. Berücksichtigt wurden klassische und neue Merkmalskomplexe, der Samenpreis der Bullen, spezifische Charakteristika der Betriebe sowie Interaktionen zwischen den genannten Attributen. Die Betriebsleiter zeigten die größten Präferenzen für die Merkmalskomplexe Milchwert, Exterieur/ Euter sowie Fitness. Interaktionen wiesen auf eine große Bedeutung des Fitnesskomplexes für ökologisch wirtschaftende Betriebe im Vergleich zu konventionell wirtschaftenden Betrieben hin. Letztere gewichteten den Milchwert und den Merkmalskomplex Exterieur/ Euter hoch. Das DCE ist flexibel in Bezug auf die Modellierung heterogener Präferenzen der Landwirte für eine begrenzte Anzahl von Merkmalskomplexen. Abgeleitete, umweltspezifische REW können für die Entwicklung eines umweltspezifischen Gesamtzuchtwertes (TMI) verwendet werden. Die Methode eignet sich zur Beurteilung der Präferenzen der Landwirte für bestimmte Merkmale, insbesondere solche, die noch nicht monetär bewertet wurden. Die Ergebnisse können von Zuchtorganisationen in ihre

Entscheidungsprozesse eingebunden werden, um vielversprechende Merkmale in den Gesamtzuchtwert aufzunehmen. Ein Vergleich der derzeit verwendeten REW und der von dem DCE abgeleiteten, umweltspezifischen REW ergab, dass sie weitgehend übereinstimmen. Die befragten Landwirte zeigten jedoch ein gesteigertes Interesse an dem neuen Merkmal „perinatales Saugverhalten" und möchten dieses in den TMI aufnehmen. Die Kombination von DCE und strikt gewinnorientierten Ansätzen wird empfohlen.

Kapitel 3 untersuchte Genotyp-Umwelt-Interaktionen (GxE) sowohl auf Merkmals- als auch auf Gesamtzuchtwerteben für Braunviehbullen. Bivariate Vatermodelle wurden angewendet, um genetische Korrelationen zwischen ökologischen und konventionellen Produktionssystemen sowie unterschiedlichen geografischen Höhenniveaus der Betriebe für verschiedene Milchproduktionsmerkmale und funktionale Merkmale zu schätzen. Um mögliche GxE- und Rangverschiebungen auf Indexebene zu bestimmen, wurden auf der Grundlage von Zuchtwerten und umweltspezifischen REW Gesamtzuchtwerte für die Braunviehbullen berechnet. Die genetischen Korrelationen zwischen den untersuchten Umwelten waren hoch und lagen zwischen $r_g = 0,79$ (Verzögerungszeit zwischen den unterschiedlichen Höhenniveaus der Betriebe) und $r_g = 0,99$ (Rastzeit, Zysten, maternale Totgeburtenrate zwischen den Produktionssystemen). Die Ergebnisse deuten auf keine wesentlichen GxE auf Merkmalsebene hin und bestätigen somit die bestehenden Zuchtprogramme. Zwischen den umweltspezifischen Gesamtzuchtwerten der Braunviehbullen für ökologische und konventionelle Produktionssysteme konnten keine gravierenden Rangverschiebungen festgestellt werden. Folglich konnten keine wesentlichen Genotyp-Umwelt-Interaktionen zwischen den untersuchten Produktionssystemen auf Indexebene gefunden werden.

In **Kapitel 4** wurden Genotyp-Umwelt-Interaktionen für ausgewählte Produktionsmerkmale und funktionale Merkmale bei Braunvieh mithilfe von Reaktionsnormmodellen analysiert. Der kontinuierliche Umweltdeskriptor Milchenergiemenge (MEY) wurde als eine lineare Kombination von durchschnittlichen Herdeneffekten für die Milch-, Fett- und Proteinmenge berechnet, die aus der routinemäßigen Zuchtwertschätzung stammten. Das angewandte Reaktionsnormmodell beinhaltete einen zufälligen Vatereffekt (intercept) und einen Vater-Slope-Effekt (Umweltsensitivität), d. h. den zufälligen Regressionskoeffizienten der Regression eines bestimmten Bullens auf den Umweltdeskriptor MEY. Um mögliche GxE-Effekte zu untersuchen, wurden Zuchtwerte für die Bullen geschätzt. Die Ergebnisse zeigten keine wesentlichen GxE für

die funktionalen Merkmale, jedoch für das Produktionsmerkmal Fettmenge. Weder die Varianzen der Steigung der Reaktionsnormen als Beschreiber für die Umweltsensitivität noch die Spearman-Rangkorrelationen zwischen den geschätzten Zuchtwerten der Bullen auf verschiedenen Umweltebenen weisen auf relevante Genotyp-Umwelt-Interaktionen für die untersuchten Merkmale hin. Aufgrund der Ergebnisse scheint eine Berücksichtigung von Genotyp-Umwelt-Interaktionen unter Verwendung des Umweltdeskriptors MEY und den betrachteten Merkmalen für das aktuelle Braunvieh-Zuchtprogramm nicht nötig.

CHAPTER ONE

Genetic analyses of mothering ability in sows using field-recorded observations

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Abstract

The improvement of the postpartum survival rate of piglets is important for pig breeding nowadays. For the improvement, breeding for good mothering abilities of sows offer a promising strategy. The aim of the following study was to estimate genetic parameters for mothering ability traits recorded on an five-point ordinal scale (1="best" to 5="worst"). Information of 48,028 litters and 15,688 sows belonging to different lines and crosses was available. Genetic parameters were estimated by applying a linear mixed- and a threshold model. Pairwise bivariate analyses were conducted for the linear mixed model (LMM) in order to calculate correlations.

The estimates for the heritability (repeatability) using the LMM are between 0.02 and 0.07 (0.05 and 0.09). With the threshold model the heritability (repeatability) estimates are between 0.05 and 0.15 (0.08 and 0.17). The difference between repeatability and heritability points to a huge impact of the permanent environment. The threshold model seems to be more suitable for analysing the data. The heritability estimated for group - and nursing behaviour with the threshold model was highest (0.15 and 0.10). All the correlations were positive and the genetic correlations were in accordance with the phenotypic correlation. The genetic correlation for piglet vitality and estrus behaviour was zero. The highest genetic correlations were estimated between nursing – (group behaviour) and litter balance and piglet weaning weight. For nursing behaviour and piglet weaning weight the genetic correlation was 0.86.

Accelerating genetic gain for good mothering abilities of sows will be possible. Especially nursing - and group behaviour seem to be promising traits. For the implementation in breeding programs, clearly defined traits are required and correlations between mothering ability and common production traits (e.g. daily weight gain) should be investigated.

Keywords: pure breed and cross breed sows; linear mixed - and threshold models; genetic parameters; mothering ability

1. Introduction

From an economical point of view pig production is highly dependent on the productivity of the sow, defined as the number of piglets weaned per sow per year. A main objective is to achieve high numbers of piglets in balanced litters with a high survival rate of piglets. Piglet losses before

weaning are the reason why productivity cannot be measured immediately after birth (Lund et al., 2002). A low heritability for survival rate of piglets until weaning, the ongoing breeding for high leanness, high growth rates and a good feed efficiency have led to a slight decrease in piglet (Grandinson et al., 2002; Grandinson, 2005; Kerr and Cameron, 1996; Knol et al., 2002; Roehe and Kalm, 2000). Moreover the present development in the field of sow management (more opened husbandry systems, growing farm structures) as well as ongoing debates about animal welfare have increased the demand for sows with better mothering ability.

Because of this issue the search for improvement options of the survival rate of piglets moves in the focus of breeding tasks. Breeding for good mothering ability of sows offer an important and promising strategy to improve the postpartum survival rate of the piglets (Grandinson et al., 2003; Lund et al., 2002). Numerous characteristics for a comprehensive description of sow maternity were already pinpointed and genetically evaluated in some studies (Grandinson et al., 2003, 2005; Gäde et al., 2008a, 2008b; Hellbrügge et al., 2006a, 2006b, 2008a, 2008b; Løvendahl et al., 2005, Vangen et al., 2005). All those studies have in common that the estimates of the heritability are general low.

For practical operations an easy and immediate data recording is needed. To fulfil these essential requirements the pig breeding association "Schweinezuchtverband Baden-Württemberg e.V." (SZV) has developed a practical possibility to develop a comprehensive data base. Since 2011, the data of seven mothering ability traits, were recorded on farms in Germany and Switzerland. The sows were evaluated based on a given catalogue, designed by the breeding association, including definitions and corresponding classifications of the traits (Table 1). Based on an internet platform a continuous data transfer from the farms to the SZV is guaranteed.

The aim of this study was to make use of their comprehensive data base to estimate genetic parameters of mothering ability traits by applying suitable linear mixed- and threshold models. Recommendations for the practical application in pig breeding programs will be given.

Table 1 Mothering ability traits as well as their abbreviations (in parenthesis) with description. The definitions are only shown for the best (1) and worst (5) category on the five-point scale.

Traits	Description	Definition
Estrus behaviour (EB)	Clarity, intensity, period	1: Estrus on time, distinct tolerance 5: Bad/no estrus, bad/no tolerance
Group behaviour (GB)	Inconspicuous, dominant, aggressive	1: Calm 5: Aggressive, dominant
Farrowing behaviour (FB)	Behaviour during farrowing, aggressiveness towards piglets, mothering abilities	1: Sow remains lying during farrowing, is not biting or snapping, rapid parturition /no help is needed 5: Sow stands up frequently during farrowing, is biting or snapping, heavily delayed parturition
Piglet vitality (PV)	Lively, lethargic, birth weight, colostrum intake	1: Birth weight >1,2 kg, piglets suckle immediately and stimulate the udder well 5: Birth weight <1 kg, many piglets have problems in locating the udder or are even not able to find it
Nursing behaviour (NB)	Nursing behaviour, quality of teats including	1: Sow feeds the piglets until satiation, all udder complexes are fully developed and functional 5: Sow is laying on the udder, feeds the piglets short, injured/ non-functional udder complexes
Litter balance (LB)	Homo-/heterogeneity of piglets in litter	1: No underweight piglets, litter is balanced 5: Many underweight piglets, litter is unbalanced

Piglet weaning weight (PW)	Average weight of piglets in the litter	1: Weight: 4 weeks: >8 kg
		          3 weeks: >6.5 kg
		5: Weight: 4 weeks: <8 kg
		          3 weeks: <6.5 kg

2. Materials and Methods

2.1. Animals

The sows were kept on 90 farms in Germany and Switzerland between 2011 and 2014. Most of the farms worked in a three week rhythm. The parities of the sows ranged from 1 to 18. Information of 48,028 litters and 15,688 sows was available. In the first litter 26% of the sows provide data for the mothering ability traits. In the second litter 21% of the sows had observations, in the third litter 16% and in litters ≥4 approximately 37% had observations.

The sows belong to different lines and crosses. From the pure breed sows, German Landrace (GL, 33%) and Large White (LW, 28%) were most frequently represented followed by Piétrain (PI, 14%). From the cross breed sow 19% belong to the cross Leicoma (LC) x GL and 3.5% belong to the crosses LW x (LC x GL) and LW x GL. The pedigree of the sows was augmented with ancestral information from up to eighteen generations back and comprises information from 38,013 sires and dams, depending on the breed. The founder animals were assigned to six genetic groups.

2.2. Mothering ability traits

Before data collection started, a meeting of the farmers with the pig breeding association "Schweinezuchtverband Baden-Württemberg e.V." (SZV) was arranged to give detailed instructions for data recording during routine farm work. To fulfil the essential requirements of an easy and immediate data recording the pig breeding association "Schweinezuchtverband Baden-Württemberg e.V." (SZV) has developed a practical possibility to develop a comprehensive data base. Each farmer received a catalogue, including classifications and corresponding trait definitions of the mothering ability and recorded the data. Based on an internet platform a continuous data transfer from the farms to the SZV is guaranteed. Vangen et al. (2005) showed that collecting data on maternal behaviour with questionnaires seems to work in a large scale under field conditions.

Data recording was done using a five-point ordinal scale including categories 1 until 5. The traits with description and definitions of the best (1) and worst category (5), representing biological extremes, are listed in Table 1. The categories 2 and 4 have been added on the catalogue by the SZV in 2013. This was done because a quantitative genetic background of the traits is assumed, which is better represented by more detailed categories. This is in accordance with the study of Gäde et al. (2008a) who also used 5 categories.

Table 2 Absolute and relative number of observations for mothering ability traits in the five categories.

Traits[a]	Absolute number of observation	Proportion in the categories				
		1	2	3	4	5
		Good		Not good		
EB	31,449	87.83	2.26	7.04	0.68	2.18
GB	13,905	87.62	3.50	8.22	0.23	0.42
FB	34,711	77.34	4.15	12.26	1.97	4.29
PV	31,450	78.61	5.05	12.92	1.33	2.09
NB	29,924	81.07	4.09	11.25	1.25	2.34
LB	32,906	74.33	5.37	15.30	1.81	3.19
PW	32,487	74.60	5.36	15.43	1.45	3.15

Combination of categories 1 and 2 (good) and categories 3, 4 and 5 (not good).

[a] For trait abbreviation see Table 1.

The following seven mothering ability traits were available: Estrus behaviour (EB), group behaviour (GB), farrowing behaviour (FB), piglet vitality (PV), nursing behaviour (NB), litter balance (LB) and piglet weaning weight (PW). The absolute number of observations for the seven behaviour traits as well as their proportion in the five categories are included in Table 2. The number of observations from the seven mothering ability traits recorded for the sows ranged from 13,905 for GB to 34,711 for FB. Most obvious are the low proportions of observations in categories 2 and 4 for all the traits. Therefore the observations for these traits were transformed into 0/1 (not good/good). Categories 1 and 2 were combined into the category "good" whereas 3, 4 and 5 were combined in the category "not good", which was done by summing up the proportions in categories 3, 4 and 5 (1 and 2) for all the traits. The proportions on the binary scale can be calculated from the proportions in the 5 categories listed in Table 2.

2.3. Statistical models

For the genetic analysis two statistical models were applied; a linear mixed model (LMM) and a threshold model (e.g. McCullagh and Nelder, 1989; Tempelman, 1998); Gäde et al. (2008a) have shown that the effects of the parity and of the combined farm season, influence the behaviour of

sows. For the analysis parities ≥4 were combined. The farm in the combined farm season effect was included to account for the effect of the farmer. Each of the three seasons comprises 4 months. For EB and GB (FB, PV, NB, LB and PW) the service (farrowing) period was considered in the season to take account for the recording period. Both systematic environmental effects were tested for significance, before inclusion in the statistical models.

In the first step the observations were assumed to be normal distributed and the following linear mixed model was applied for the analysis of the seven mothering ability traits:

$$y_{ijl} = FxS_i + P_j + a_l + pe + e_{ijl} \qquad (1)$$

where the response variable y_{ijl} is the observation of sow l, coded with 0 or 1. The fixed effects FxS_i represent the systematic environment of the ith farm season and P_j of the lth litter, which are included only if they were significant. pe is the random permanent environment effect of the lth sow, with a covariance structure as $pe\sim N(0, I\sigma_{pe}^2)$ where σ_{pe}^2 is the permanent environmental variance, a_l is a random additive-genetic effect of the sow, with a covariance structure as $a_{ilk}\sim N(0, A\sigma_a^2)$ where σ_a^2 is the additive genetic variance and A is the numerator relationship matrix derived from the pedigree and I is an identity matrix. e_{ijl} is the random residual, with a covariance structure as $e_{ijl}\sim N(0, I\sigma_e^2)$ where σ_e^2 is the residual variance.

In further analyses the 0/1 observations were assumed to be binomial distributed and a single threshold model with a probit link function was applied, including the same fixed and random effects as stated above. In the analysis the residual variance was fixed at σ_e^2=1.

The statistical analyses were performed separately for each trait in order to estimate the repeatability and the heritability of the traits. The repeatability was calculated as $t = \frac{\sigma_a^2+\sigma_u^2}{\sigma_a^2+\sigma_u^2+\sigma_e^2}$ and the heritability as $h^2 = \frac{\sigma_a^2}{\sigma_a^2+\sigma_u^2+\sigma_e^2}$. Pairwise bivariate analyses were conducted in order to estimate genetic and phenotypic correlations. For these analysis the LMM was used.

3. Results

3.1. Univariate analyses

The effect of the combined farm season interaction and of the litter was significant for all seven mothering ability traits in both models (p≤0.001, not shown) and was included for the genetic analysis.

The results of the univariate analyses are given in Table 3. In the LMM, the repeatability of the traits raged between 0.05 for PV and 0.09 for FB, NB and PW. The corresponding heritability ranged from 0.02 for EB to 0.07 for NB. EB, PV, LB and PW revealed the lowest heritability, followed by FB, GB and NB.

Table 3 Heritability ($\hat{h}^2$) and repeatability ($\hat{t}$) of mothering ability traits (standard errors in parenthesis), results from univariate analyses.

Traits[a]	LMM		Threshold model	
	$\hat{t}$	$\hat{h}^2$	$\hat{t}$	$\hat{h}^2$
EB	0.07 (0.01)	0.02 (0.01)	0.12 (0.01)	0.08 (0.02)
GB	0.08 (0.01)	0.05 (0.01)	0.17 (0.03)	0.15 (0.06)
FB	0.09 (0.01)	0.04 (0.01)	0.12 (0.01)	0.07 (0.01)
PV	0.05 (0.01)	0.03 (0.01)	0.08 (0.01)	0.07 (0.02)
NB	0.09 (0.01)	0.07 (0.01)	0.12 (0.01)	0.10 (0.02)
LB	0.08 (0.01)	0.03 (0.01)	0.12 (0.01)	0.05 (0.01)
PW	0.09 (0.01)	0.03 (0.01)	0.11 (0.01)	0.05 (0.01)

[a] For trait abbreviation see Table 1.

In the threshold, the repeatability for the traits raged between 0.08 for PV and 0.17 for GB. The corresponding heritability ranged from 0.05 for LB and PW to 0.15 for GB (Table 3). LB, PW, NB, PV, and EB revealed the lowest heritability, followed by NB and GB. The repeatability and the heritability were lower in the LMM compared to the threshold model.

3.2. Pairwise bivariate analyses

The results from pairwise bivariate analyses are shown in Table 4. All the correlations are positive. The phenotypic correlations are in an interval between 0.02 (for EB and all the other traits except GB as well as for GB and PV) and 0.41 (for PV and NB). The genetic correlations were largest for PW and NB (0.86). For the pair PV and EB the genetic correlation was zero, which is in accordance with the phenotypic correlation.

Table 4 Phenotypic (above the diagonal) and genetic (below the diagonal) correlations ($\hat{r}_p$ and $\hat{r}_g$) between mothering ability traits (standard errors in parenthesis), results from bivariate analyses.

Trait[a]	EB	GB	FB	PV	NB	LB	PW
EB	-	0.23 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)
GB	0.12 (0.19)	-	0.03 (0.01)	0.02 (0.01)	0.03 (0.01)	0.04 (0.01)	0.04 (0.01)
FB	0.05 (0.17)	0.26 (0.17)	-	0.22 (0.01)	0.25 (0.01)	0.13 (0.01)	0.13 (0.01)
PV	0.00 (0.18)	0.12 (0.16)	0.32 (0.13)	-	0.41 (0.01)	0.22 (0.01)	0.22 (0.01)
NB	0.06 (0.15)	0.34 (0.13)	0.55 (0.09)	0.60 (0.09)	-	0.30 (0.01)	0.30 (0.01)
LB	0.07 (0.18)	0.71 (0.13)	0.56 (0.12)	0.61 (0.12)	0.85 (0.06)	-	n.c.[b]
PW	0.10 (0.18)	0.71 (0.12)	0.52 (0.12)	0.67 (0.10)	0.86 (0.06)	n.c.[b]	-

[a] For trait abbreviation see Table 1.

[b] n.c.: not converged.

The largest phenotypic correlations were calculated for FB/PV and NB (0.25/0.41) as well as for NB and LB/PW (0.30/0.30). For FB/PV and NB (0.55/0.60) and for NB and LB/PW (0.85/0.86) the genetic correlations were also large. The highest genetic correlations were calculated for the pairs LB/PW and all other traits except EB, ranging from 0.52 to 0.86.

4. Discussion

There is a difficulty in the interpretation and the comparison of the results with other studies. On the one side there is huge amount of traits describing the mothering abilities mentioned in the literature, on the other side there are distinct differences in trait recording, scaling and analysing of the data. Besides practical recording methods, e.g. using questionnaires (Vangen et al., 2005), there are more complex methods, e.g. using special behaviour tests, to judge the behaviour and the reaction of the animals (Grandinson et al., 2003). However also the analyses of the data were done using different models. Some authors used threshold models (Gäde et al., 2008a, 2008b; Kaufmann et al., 2000; Vangen et al., 2005) others used linear models (Løvendahl et al., 2005; Quiniou et al., 2002; Roehe, 1999) and Grandinson et al. (2002) used both kind of models.

Subsequently a comparison was done for the genetic parameters of traits which were also analysed in the literature and for the models.

4.1. Comparison with the literature

In general the difference between the repeatability and the heritability indicate that a huge part of the between individual variance is due to the permanent environment. This was also supported by Gäde et al. (2008a) who estimated a moderate repeatability of 0.24 and a low heritability of 0.07 for the GB of the sows. For GB and NB the estimates of the heritability were highest with the LMM and threshold model.

For GB the repeatability and heritability estimated with the LMM (threshold model) in our study was 0.08 and 0.05 (0.17 and 0.15). In the study of Løvendahl et al. (2005) the heritability estimated for GB was low until moderate. However they used a trait definition for GB, which differentiates between animals behaving aggressive (h^2=0.04) and the ones receiving the aggression (h^2=0.24). For EB the heritability estimated with the LMM (threshold model) was 0.02 (0.08). Although Gäde et al. (2008b) used a different trait definition for EB of the sow and estimated a similar heritability of 0.09.

For the FB and NB the heritability estimated with the LMM (threshold model) was 0.04 and 0.07 (0.07 and 0.10). For the maternal abilities of the sow, comprising among others FB, NB Gäde et al. (2008a) estimated a similar heritability of 0.05. The low heritability estimates reflect the results

of the study of Vangen et al. (2005) where a different scaling and scored was used. The "exposing of the sows udder to the piglets at suckling" (h^2=0.07) and the "interruptions and nervousness of the sow during suckling" (h^2=0.08) were analysed separately.

For PV the piglet birth weight, the ability of the piglet to locate the udder and the colostrum intake are taken into account. The estimated heritability for PV was 0.03 for the LMM and 0.07 for the threshold model. Grandinson et al. (2002); Kaufmann et al. (2000); Knol et al. (2002) and Roehe (1999) estimated a heritability between 0.15 and 0.22 for birth weight of piglets. Selecting on sows with heavy piglets during birth could reduce the piglet losses postpartum (Quiniou et al., 2002). The lower heritability estimates in our study suggests that a combination of the aspects describing the PV possibly has an effect on the heritability. Maybe analysing the aspects of PV separately might increase the heritability estimates and accelerate the genetic gain.

4.2. Comparison of the models

When using a threshold model, the heritabilities are estimated on the assumed underlying scale and are expected to be higher than heritabilities estimated on the observed scale (Dempster and Lerner, 1950). In general the heritability estimates for the traits were higher with the threshold model than with the LMM. However those kind of models involve a higher computational effort because they are susceptible for the *extreme category problem* (ECP). This problem occurs if there is insufficient trait variation in the fixed effect classes and hinders the continuous genetic parameter estimation (Sorensen and Gianola, 2002).

At the moment the heritability was estimated using a threshold model with a single-threshold because of the lack of data in categories 2 and 4. A single-threshold is suitable for the analysis to avoid problems in obtaining convergence, or a valid set of estimates (Gianola and Foulley, 1983). However with an increase in the proportions of records in categories 2 and 4, the application of a model with multiple thresholds might become possible in the future. Gäde et al. (2008a) analysed GB and maternal ability of sows using a multiple threshold model.

4.3. Pairwise bivariate analyses

The genetic correlations are between $r_g = 0$ (PV and EB) and $r_g = 0.86$ (PW and NB). Associations between an inconspicuous and calm GB of the sows and the other mothering traits are in agreement

with the results of other studies. Andersen et al. (2005) reported that sows which are more inconspicuous in the group, were more protective to their piglets and showed less crushing. Furthermore the handling of an inconspicuous and calm sows can be of benefit.

The positive genetic correlations between FB of the sow and PV ($r_g = 0.32$), NB ($r_g = 0.55$), LB ($r_g = 0.56$) and PW ($r_g = 0.52$) are in agreement with other studies. A positive, peaceful FB is commonly associated with a good NB of the sow and an increase in the postpartum PV. As a consequence the litters are more homogeneous with high average weights of the piglets at weaning. If the sow remains lying during farrowing, it is more likely that the piglets start sucking behaviour. As a result of this stimulating behaviour, the sows organism releases oxytocin to promote milk ejection. This has a positive impact on the vitality of the offspring and support piglet growth (Algers, 1993; Valros, et al., 2002). This results in an increase of the economy of the production and improves the welfare of the sows and piglets (Cronin and van Amerongen, 1991; Grandinson, et al., 2003; Herskin, et al., 1998; Valros, et al., 2002; Wechsler and Hegglin, 1997).

The high genetic correlations between NB and PV ($r_g = 0.60$) as well as between NB and LB ($r_g = 0.85$) and NB and PW ($r_g = 0.86$) support the causal chain. Valros et al. (2002) confirmed that the FB of the sow is positive correlated with the growth of the piglets.

To shed some light in the complexity of mothering ability traits, structural equation models (SEM) can be applied (Gianola and Sorensen, 2004). The causal structures for the SEM can be pre-selected based on prior biological knowledge (e.g. different recording periods).

Furthermore the estimation of correlations between mothering ability and common production traits (e.g. daily weight gain) should be investigated in ongoing studies.

5. Conclusion

A noticeable part of the between-individual variance is captured by the permanent environment, as can be seen for the traits EB, FB, LB and PW. In comparison with the LMM, the threshold model offers higher heritability estimates for the traits. This is most obvious for the traits EB and GB.

The highest heritability in both models was estimated for the traits NB and GB, which seem to be promising traits for the selection of mothering abilities of the sows. However the estimates of

heritability are still not high. That means accelerating the genetic gain will be possible but time-consuming.

Maybe more clearly defined traits might help to increase the heritability and improve the genetic gain. However correlations between mothering ability and common production traits (e.g. daily weight gain) should also be investigated to give recommendation of how to implement mothering ability traits in breeding programs.

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CHAPTER TWO

Estimation of relative economic weights and the marginal willingness to pay for breeding traits of Brown Swiss cattle using discrete choice experiments

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ABSTRACT

Breeding traits are usually combined in a total merit index according to their economic weights to maximize genetic gain based on economic merit. However, this maximization may not always be the aim of the selection decisions by farm managers. A discrete choice experiment was used to evaluate the importance of traits in terms of the selection decisions of farm managers operating in different environments. Six trait complexes, the semen price, the interactions between these traits, and significant characteristics of the farms were included in a conditional logit model to estimate relative economic weights and the marginal willingness to pay for all traits. Milk value, conformation/udder, and fitness were the most important traits for the farmers, and significant interactions indicated that fitness is of greater importance on organically managed farms than on conventional farms. Farm managers with an advanced education placed more weight on the milk value trait than farm managers without advanced education. On conventional farms, managers weighted the traits milk value and conformation/udder highly. The conformation/udder and fitness trait complexes were important on organic farms. A new trait called perinatal sucking behavior of newborn calves should be included in the total merit index.

Keywords: economic weight, discrete choice experiment, Brown Swiss cattle

INTRODUCTION

The definition of breeding goals is one of the most important steps in the development of efficient breeding programs. Trait selection for inclusion in a breeding goal depends on trait heritability and genetic correlations with other traits as well as the costs and labor required to record phenotypic data and the economic importance of the trait. For many breeds, a total merit index (**TMI**) is established that includes both the traits and their relative economic weights (**REW**). Several methods are available to estimate REW, the most common of which are strictly economic in nature and include objective and profit-oriented methods, such as the herd model (Amer et al., 1996; Fuerst-Waltl et al., 2010), or direct costing and profit functions, which are based on the costs and profits of a production system (Brascamp et al., 1985; Nielsen and Amer, 2007). Critical aspects of these methods are the lack of information on some traits, especially functional traits and new traits that have not been validated monetarily, and the assumption that the sole objective of breeders and farmers is profit maximization. However, the choices of farmers may not be

affected only by economic factors, especially on organic farms, where particular importance may be attached to noneconomic aspects such as animal welfare, environmental impacts, and other individual operational characteristics (Nielsen and Amer, 2007).

Alternatively, REW may be derived via nonobjective methods that are based on the subjective assessments and empirical values of experts, breeders, farmers, or consumers. Teegen et al. (2008) and von Rohr et al. (1999) applied the contingent valuation method to estimate REW in horse and pig breeding, respectively. A simple and intuitive approach is to analyze the frequency of the use of sires for AI and link it to the EBV of their traits, which would yield some realized REW (i.e., the relative importance of trait EBV in the past selection of the sires). However, such an approach would fail for new traits, and more sophisticated methods have to be used. Choice experiments are frequently applied to study farmers' preferences for traits. For example, Martin-Collado et al. (2015) applied pairwise comparisons of traits in an online survey to study Australian dairy farmers' preferences for 13 traits. The authors showed that the preferences are heterogeneous with respect to farmer characteristics - that is, they differed for production-focused, functionality-focused, and type-focused farmers. The farmer characteristics were identified by using principal component analysis followed by hierarchical cluster analysis. A similar approach was used by Slagboom et al. (2016a, b) to identify farmers' characteristics. An interesting result of Martin-Collado et al. (2015) was that the heterogeneity was intrinsic to farmers and not to production systems or breeds. The results of the study were used in the design of new breeding objectives and selection indices tailored for these 3 farmer types in Australia (Byrne et al., 2016). Choice experiments have also been applied in other species, such as sheep (Byrne et al., 2012; Ragkos and Abas, 2015), pigs (Roessler et al., 2012), and chickens (Bett et al., 2011) and frequently to study farmers' preferences in developing countries (Duguma et al., 2011). Ahlman et al. (2014) and Slagboom et al. (2016a, b) used choice experiments to study Swedish and Danish dairy farmers' preferences for breeding traits, respectively, considering heterogeneous preferences among farmers (i.e., organic and conventional farmers).

A challenge is the proper design of the choice sets. The discrete choice experiment (**DCE**) has a well-defined theoretical basis in random utility theory (Louviere et al., 2010) and is closely related to natural decision processes. Respondents are given a questionnaire consisting of multiple questions called choice sets, and they are required to choose one alternative from each set, which enables researchers to examine comprehensive decisions. In animal breeding, this method can be

used to study farmers' preferences for breeding traits and, based on this, to derive REW by allowing breeders to choose among hypothetical sires with different EBV and semen prices. The assumption is that the sire chosen from the questionnaire will represent the greatest utility for the breeder. This utility is affected by the levels of the attributes of the sires (i.e., hypothetical EBV and semen prices) and by operational characteristics of the farm (e.g., conventional or organic systems). The latter allows for the consideration of heterogeneous preferences among farmers. Naturally, the utility comprises economic aspects but also values the experience, informal background, or future orientation of the farmers. Interactions between the trait EBV of the sires and the characteristics of farms or farmers can be used to determine heterogeneous REW, which is termed "environment-specific REW" throughout this article. These can be used to define environment-specific breeding goals.

The DCE can also be used to calculate the marginal willingness to pay (**MWTP**), which describes the amount of money a respondent is willing to pay to obtain an additional nonmonetary attribute (Aizaki et al., 2015) - in this case an improvement in a certain trait by 1 genetic standard deviation. This broadens the assessment of trait importance to include a monetary perspective.

The Brown Swiss cattle breed is a milk-type, dual-purpose breed that is commonly used in southern Germany, and it is reared in conventional as well as organic farming systems, which have their own TMI with different REW. The aim of the present study was to estimate REW and the MWTP using a DCE for Brown Swiss cattle in the state of Baden-Wuerttemberg in southern Germany. The REW were subsequently used to establish an environment-specific TMI and were compared with the REW used in the current TMI for this breed.

MATERIALS AND METHODS

Survey Design and Data

A choice experimental design was created with 18 choice sets consisting of 3 hypothetical sires each; 1 sire had to be chosen by the breeder to serve as an average cow in the herd. Seven attributes were defined for the sires; namely, the price for 1 portion of semen (monetary element in euros) and breeding values for the following 6 trait complexes. The milk production value trait complex represented milk, protein, and fat yield. The general beef production value represented daily gain, carcass quality, and slaughter yield. The conformation/udder trait complex consisted of exterior and

health of claw, leg, and udder. The fitness trait complex comprised the remaining functional traits (i.e., calving ease, stillbirth, functional longevity, persistency, fertility). The show type trait denoted all exterior traits except udder, claw, and leg exterior. The final trait, perinatal sucking behavior (**PSB**), was included because insufficient PSB is a serious problem in this breed and shows significant heritability (Maltecca et al., 2007). According to a survey, approximately 7% of newborn Brown Swiss calves exhibit insufficient PSB in Germany, and the heritability is about 0.15 (C. Dreher and J. Bennewitz, Institute of Animal Science, University Hohenheim, Germany, personal communication). This trait is a putative novel breeding trait. The admissible levels of the breeding values were 100 (mean breeding value), 112 (1 SD above the mean), and 124 (2 SD above the mean), and no breeding value was assumed to be below the mean. The prices for 1 portion of semen were set at €6 (low cost), €12 (moderate cost), and €18 (higher cost). The analytical design was created with the R package "support.CEs" (Aizaki, 2012).

Table 1. Example of a discrete choice set[1]

Trait	Sire 1	Sire 2	Sire 3
Milk value	++	++	O
Beef value	+	++	+
Conformation/udder	O	O	++
Show type	+	O	O
Fitness	O	+	+
Perinatal sucking behavior	++	+	++
Price[2]	12	18	18
Choice	6	12	18

[1] O, +, and ++ = hypothetical breeding values (mean, 1 SD, and 2 SD, respectively) for the traits of hypothetical sires.
[2] Hypothetical values for the sires' semen (€/portion).

Seven orthogonal main effects arrays (1 for each trait and 1 for the semen price) were used to define the first alternative of each choice set, and the same was done for the second and third alternatives. Assignments were performed randomly with different seeds. For each of the 1,000 designs resulting from the different seeds, 500 DCE were simulated, and the average standard errors and the average correlations were recorded between the estimated and true effects. The design with the smallest

standard error and highest correlation was chosen for the study, and of the 18 choice sets, 2 questionnaires (A and B) with 9 choice sets each were randomly created to limit the number of choice sets the farmers had to consider. On-farm trial interviews were conducted using the questionnaires to evaluate their comprehensibility, and the results revealed that no adaptation of the initial questionnaires was necessary. Additionally, the reactions of the farmers were generally very positive, indicating a general willingness to cooperate. Following the trial interviews, the questionnaires were sent to 230 managers (respondents) of both conventionally and organically managed farms in southern Germany (Alb region of the state of Baden-Wuerttemberg). Farmers were randomly assigned either questionnaire A or questionnaire B, and every farmer was required to complete 9 choice sets. An example of a choice set is given in Table 1. Questionnaires were sent by mail and were accompanied by an explanation letter with instructions and additional questions about the farming system (e.g., organic or conventional, feeding, daily milking frequency) and the characteristics of the respondents (e.g., level of education). A total of 166 completed surveys were returned and used for the statistical analyses, which resulted in 4,482 data sets [9 choice sets (A or B) × 3 alternatives × 166 respondents].

Conditional Logit Model

The questionnaires were analyzed with a conditional logit model as follows: $y_{nki} = 1$ if person n chose alternative i from the kth choice set completed by the person, and $y_{nkj} = 0$ for the other alternatives, $j \neq i$. It is assumed that random variables U_{nki} exist such that

$$y_{nki} = \begin{cases} 1 & \text{if } U_{nki} > U_{nkj} \text{ for all } j \neq i \\ 0 & \text{otherwise} \end{cases}$$

The value U_{nki} is the utility (or benefit) that person n obtained from choosing alternative i from the kth choice set. It is assumed that the utility can be decomposed as

$$U_{nki} = (\beta + \textstyle\sum_s \gamma_s \delta_{ns})' a_{nki} + \varepsilon_{nki}$$

where the vector a_{nki} contained the attributes of alternative i from the kth choice set completed by farmer n; β is the vector of the effects of the traits; γ_s is the vector of interactions between characteristic s describing the farms and the traits; and $\delta_{ns} = 1$ if the farm managed by farmer n has characteristic s. The variable ε_{nki} captures the effect of all unobserved factors that affect the choice of the farmer. As a shorthand,

$$V_{nki} = (\beta + \sum_s \gamma_s \delta_{ns})' a_{nki}$$

where V_{nki} is called the observable component of the benefit farmer n obtained from choosing alternative i in the kth choice set C_k. The probability for choosing the alternative i is

$$P_n(i|C_k) = \frac{\exp(V_{nki})}{\sum_{j \in C_k} \exp(V_{nkj})}$$

In this conditional logit model, the MWTP for the nonmonetary variable (i.e., the 6 traits) included in the DCE was calculated as

$$\text{MWTP} = -\frac{b_{fm}}{b_m}$$

where b_{fm} is the estimated coefficient of the nonmonetary variable and b_m is the estimated coefficient of the monetary variable price per portion of each sire's semen. Twelve euros per portion of semen was taken as a basis, and the results were reported in euros for a portion of semen and per genetic standard deviation of the specific trait. To estimate the coefficients for all traits as well as the interactions, the R package "survival" and the function "clogit" were used (Aizaki, 2012). Interactions with $P > 0.01$ were excluded from the model step by step, but if the interaction between a farm characteristic and a trait was significant, the interaction of this characteristic with all traits was retained. To derive the MWTP, the R function "mwtp" was used (Aizaki et al., 2015). Farm managers were classified as educated (**EF**; basic 3-yr apprenticeship) or advanced educated (**AEF**; basic 3-yr apprenticeship plus 2 yr of extra schooling), and the farming systems were classified as conventional or organic.

RESULTS

Table 2 shows the coefficients and P-values estimated for the 7 attributes (6 traits and the semen price) and 2 significant interactions (i.e., between the trait fitness and the farming system and between the trait milk value and the education level of the farm manager) using the conditional logit regression model.

Table 2. Estimated coefficients for traits and significant interactions between traits and the individual and operational characteristics of the respondents using a conditional logit regression model

Item	Coef[1]	SE (Coef)	P-value
Milk value	0.76	0.09	< 0.001
Beef value	-0.07	0.06	0.219
Conformation/udder	1.13	0.06	< 0.001
Show type	0.12	0.06	0.055
Fitness	0.59	0.06	< 0.001
Perinatal sucking behavior	0.56	0.06	< 0.001
Price	-0.31	0.07	< 0.001
Fitness × organic	0.73	0.25	0.004
Milk value × advanced farmer education	0.42	0.11	< 0.001

[1] Coef = estimated coefficients for traits and significant interactions from the discrete choice experiment using a conditional logit regression model.

Five of the attributes (milk value, conformation/udder, fitness, PSB, and the monetary element price for 1 portion of semen) showed a significant effect on the choice behavior of the respondents ($P < 0.001$). The 2 traits of beef value and show type were not significant. The conformation/ udder trait complex showed the highest estimated coefficient followed by the trait complexes of milk value and fitness and the trait PSB (in descending order), and a negative coefficient was estimated for the price. The coefficient for the interaction between organic farming systems and the fitness trait complex was 0.73, and coefficient for the interaction between the milk value trait and AEF was 0.42. Based on the 2 significant interactions, REW were calculated for 4 environments, which were defined by the combinations of conventional and organic farming systems and EF and AEF (Table 3). Conventional AEF considered the trait of milk value to be 9% more important than conventional EF, and AEF of organic farms assigned a weight of 17% to the milk value, also 9% higher than EF of organically managed farms. The highest REW were estimated for the conformation/udder trait complex for the environment of conventional farming system and EF. Organic farm managers weighted the conformation/udder trait complex approximately 30%, and they weighted the fitness trait complex approximately 35%, which was twice the weight given by conventional farm

managers. The REW for the trait PSB were between 14 and 21%, and this trait seemed to be more important for EF, whereas no difference was observed between the 2 farming types.

Table 3. Environment-specific relative economic weights (%) of traits depending on the farming system and level of education of the farm manager[1] using discrete choice experiment data

Trait	Conventional		Organic	
	EF	AEF	EF	AEF
Milk value	25	34	8	17
Beef value	-2	-2	3	2
Conformation/udder	35	33	30	29
Show type	4	3	4	3
Fitness	17	18	35	34
Perinatal sucking behavior	21	14	20	15

[1] EF = farm manager without an advanced education; AEF = farm manager with an advanced education.

Show type was not very important in any environment, and beef value was even less so. The REW for beef value was slightly negative for conventional and slightly positive for organic farming systems. Table 4 shows the REW estimated in this study, the REW used in the current conventional TMI (Bayrische Landesanstalt für Landwirtschaft, 2016; Fuerst-Waltl et al., 2016), and the REW used in the current organic TMI (Bayrische Landesanstalt für Landwirtschaft, 2017). The REW for fitness and constitution derived from the DCE were in similar range as the current conventional TMI and organic TMI. In the conventional system, the DCE REW for fitness was approximately 6% higher than in the current TMI. The DCE-derived REW included the new traits PSB and show type, which were not included in the current TMI; the addition of these traits reduced the REW of milk value and beef value compared with the current TMI. The DCE REW of the milk value is lower in both systems, and the DCE REW for beef value equals one quarter of the currently used REW in the organic TMI.

Table 4. Relative economic weights (%) of traits depending on the farming system compared with current relative economic weights (%) used for the conventional and organic total merit index (TMI)

Trait	Conventional TMI		Organic TMI	
	Current[1]	DCE[2]	Current[3]	DCE
Milk value	50	29.5	25	12.5
Beef value	5	-2	10	2.5
Fitness/constitution[4]	45	51.5	65	64
Show type	-	3.5	-	3.5
Perinatal sucking behavior	-	17.5	-	17.5

[1] Bayrische Landesanstalt für Landwirtschaft (2016).

[2] Discrete choice experiment (this study).

[3] Bayrische Landesanstalt für Landwirtschaft (2017).

[4] Fitness (term in the current conventional TMI) and constitution (term in the current organic TMI) are comparable trait complexes.

Table 5 shows the results of the MWTP estimation. Farm managers were willing to pay approximately €3.60 more for a portion of semen and an improvement of 1 genetic standard deviation of the conformation/ udder trait complex independent of farming system and level of education. The AEF group of conventional farms were willing to pay €3.95 more for the trait of milk value, whereas the EF group of organic farms were willing to pay only €0.88 more for a portion of semen. Managers of organic farms were willing to pay approximately €0.35 more for the sires' semen and an improvement of 1 standard deviation of the beef value trait, whereas managers of conventional farms were not willing to pay for a genetic gain in the trait (−€0.23). Managers of organic farms were willing to pay more than twice as much money as conventional farm managers for an improvement in fitness. For the trait of PSB, AEF managers, independent of farming system, were willing to pay approximately €1.80 more for a portion of semen to improve the trait by 1 genetic standard deviation, whereas EF managers were willing to pay approximately €2.19 more.

Table 5. Marginal willingness to pay[1] (€) for the traits depending on the farming system and level of education of the farm manager[2] using discrete choice experiment results

Trait	Conventional		Organic	
	EF	AEF	EF	AEF
Milk value	2.58	3.95	0.88	2.25
Beef value	-0.21	-0.25	0.37	0.33
Conformation/udder	3.54	3.90	3.34	3.70
Show type	0.43	0.34	0.46	0.36
Fitness	1.68	2.10	4.00	4.40
Perinatal sucking behavior	2.09	1.70	2.28	1.90

[1] Mean price for 1 portion of a sire's semen with €12 as a basis. Results are in euros for 1 portion of semen and per genetic SD of the trait.

[2] EF = farm manager without an advanced education; AEF = farm manager with an advanced education.

DISCUSSION

A DCE approach was used to determine the REW and the MWTP for trait complexes in Brown Swiss cattle in southern Germany. In discussing the results of the study, it is important to note that this approach is not purely economically motivated, so if the aim of cattle breeding is to maximize profit, the results of the DCE should be considered with some caution. Profit-oriented methods aim to maximize profit for farmers but do not always reflect the farmers' aims. In the DCE method, the opinions of farmers can be included, so the estimated REW are more likely to reflect the aspirations of the farmers. At the same time, the amount of money a farmer is willing to pay may not completely represent the effects of trait improvements on the profitability of the farm. Thus, DCE could be used to complement profit-oriented methods to obtain REW, and the putative differences in the results of these 2 alternative approaches can be evaluated and discussed with the farmers.

DCE Questionnaire Structure

Considering the collection of the data for the DCE, the selection of the traits to be included in the questionnaires was particularly important. The chosen traits should not be random, meaning that

they should be known or of special interest to breeders, and trait complexes, such as the milk value (milk yield, protein, and fat content), should be commonly understood or otherwise explained to the respondents. In addition, the scope of the choice sets should not be too complex, as too many traits per set can overwhelm the respondents, which may negatively affect the choice behavior (Auspurg and Liebe, 2011). As a result, the respondent might too often choose the one alternative with the greatest personal utility or might refuse to participate completely. Therefore, to ensure cooperation, it is necessary to select meaningful traits, perform trial interviews in person on the farm, explain the motivation for this kind of experiment, and limit the scope of the questionnaire sets. It seems that the number of traits in the present DCE was not too high, which can be deduced from the relatively high number of returned questionnaires and from the results of the on-farm trial interviews. However, it would naturally be better to include more traits in the questionnaires to obtain a more differentiated picture of single-trait REW. For example, the milk value trait in this study included milk fat and protein yield, but it can reasonably be assumed that the REW of these 3 subtraits would differ, and the same holds true for the functional traits. A weak point of the DCE questionnaire design was that the trait PSB was the only trait that was not embedded in a trait complex. This was done because before this experiment, it was unknown whether breeders would prefer to have PSB included as a new trait in the TMI. Including PSB as a subtrait in a trait complex would not have informed us about the farmers' preferences for this specific trait. However, it is reasonable to assume that the REW of PSB would be lower if other traits in the TMI were treated separately and not included in trait complexes. This, however, would greatly increase the number of traits, risking the problems associated with too many choices as listed above.

Results of the DCE

The results of this study confirm the heterogeneity in the farmers' trait preferences (Tables 2–4), which was also found by, for example, Martin-Collado et al. (2015), Ahlman et al. (2014), and Slagboom et al. (2016a, b). The farms were classified using external information (i.e., production system and level of farmers' education). More sophisticated classification methods were applied by Martin-Collado et al. (2015) and Slagboom et al. (2016a, b). This requires the collection of farmers and farm profile factors, which were not included in our questionnaires.

The managers of organic farming systems placed more weight on the fitness trait complex and less on milk value, and the MWTP for the fitness trait complex was twice as high compared with

conventional farm managers. This might be due to the need for more robust cows because medical treatment options are reduced in organic systems. In addition, a high genetic milk value is less important in organic systems because there are generally fewer opportunities to realize high milk yield due to feeding restrictions. The conformation/udder trait complex is very important for both farming systems. Ahlman et al. (2014) investigated the differences for traits between organic and conventional farming systems in Sweden using questionnaires. In general, the same traits were important in both systems, with some differences in the relative importance of traits. Organic farm managers put more weight on health traits and less on milk production, which is in agreement with the results of the present study. Slagboom et al. (2016a) identified a higher priority of production traits for organic farmers compared with conventional farmers in Denmark, which is in contrast to the results of Ahlman et al. (2014) and to our results. The explanations for these results given by Slagboom et al. (2016a) were that farmers wanted to improve the traits that are more problematic in their herds. Because the average milk yield and the disease incidences were both lower in organic herds compared with the conventional herds included in their study, organic farmers ranked milk yield higher than the conventional farmers did.

In the present study, the second tier of the farm characteristics was the education of the farmers. The AEF gave more weight to milk value and less to the new trait of PSB. One explanation could be that insufficient PSB is less severe on farms with AEF, but this could not be demonstrated in the current study.

The currently used TMI was recently adjusted based on newly estimated economic weights of traits and discussions with the breeders (Fuerst-Waltl et al., 2016). In general, both REW (the currently used and the DCE REW) agree to a large extent for both farming systems (Table 4). However, it seems that farmers wish to include the new trait PSB, which goes mainly at the costs of the weight of milk in the TMI. Currently, routine data recording is implemented for the trait PSB by the breeding organization, and farmers must assess the sucking behavior of newborn calves using 4 categories (no, weak, normal, and strong sucking reflex). Once a suitable data structure and genetic evaluation (i.e., EBV calculation) have been established, this trait will be included in the TMI, and the results of the current DCE might be used to determine the weight that this trait should receive in the adjusted TMI.

CONCLUSIONS

The DCE is a suitable choice experiment method to derive REW for a limited number of trait complexes. It can be viewed as a bottom-up approach because the REW are based on the responses of farmers to structured questionnaires. Thus, this method is not strictly economically driven and can be used in combination with purely profit-orientated approaches. The DCE is flexible in the sense that heterogeneous farmers' preferences can be modeled straightforwardly. Thus, it allows for the estimation of environment-specific REW, which can in turn be used to develop an environment-specific TMI. It is a suitable method to judge the importance of traits for farmers, especially traits that have not been economically evaluated, and hence might guide breeding organizations in their decisions to include these traits in the TMI. Furthermore, the DCE can be regularly used to assess whether the current TMI reflects the expectations of farmers and to indicate where adjustments are needed. By comparing the REW obtained by the DCE with those that are currently used in the German Brown Swiss population, it became obvious that they agree to a large extent except that farmers wish to have the new trait PSB included in the TMI. The addition of PSB would reduce the REW for the milk trait complex.

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CHAPTER TWO

CHAPTER THREE

Genotype by environment interactions at a trait level and an index level in German Brown Swiss cattle

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CHAPTER THREE

ABSTRACT

Production and functional traits in the dairy-emphasized dual-purpose cattle breed Brown Swiss improved due to the optimization of breeding and management in recent decades. The breed is used in a wide range of different production environments in the state of Baden-Wuerttemberg, southern Germany. Regarding sustainability aspects and consumer preferences, more extensive production systems and environments are popular. In comparison to other production environments, these production environments contain more extensive, organic systems and more intensive, conventional systems. Additionally, due to the topography of southern Germany, the altitude of the farms (e.g., Swabian Alb and Black Forest) is of interest and chosen as the other environment. The aim of the study was to estimate the genotype by environment interaction (GxE) for Brown Swiss sires in terms of milk production traits (milk yield, protein yield and fat yield) and functional traits (longevity, nonreturn rate 56, calving to first insemination, first insemination to conception, cystic ovaries, calving ease and stillbirth rate). This approach was conducted by applying bivariate sire models. Furthermore, total merit indices (TMIs) for sires were calculated based on breeding values estimated with different models and environment-specific relative economic weights (REW) to determine a possible GxE at TMI levels and rerankings of sires. In general, genetic correlations at the trait level were high for differently defined environments and ranged from $r_g=0.79$ (first insemination to conception for altitude) to $r_g=0.99$ (calving to first insemination, cystic ovaries and maternal stillbirth rate). The majority of genetic correlations were above 0.8, indicating no severe GxE at the trait level and no need for an adjustment to the breeding programs to account for different environments for Brown Swiss cattle. Due to the results of the rank correlations between the different environment-specific TMIs, no severe reranking was shown, and no GxE at the TMI level was induced by the results at the trait level.

Keywords: Genotype by environment interaction, Brown Swiss cattle, organic production systems, total merit indices

1. INTRODUCTION

In the state of Baden-Wuerttemberg, southern Germany, 2016 approximately 343,720 dairy cows are milked, of which approximately 8,5 % are housed in organically managed systems (Statistisches Bundesamt, 2017; Statistisches Landesamt Baden-Wuerttemberg, 2018). Brown Swiss cattle are one of the predominant breeds used for milk production in Baden-Wuerttemberg. Recent surveys regarding breeder preferences and breeding objectives revealed that in comparison to conventional farmers, organic farmers put more weight on fitness traits (Steininger et al., 2012; Steinwidder and Krogmeier, 2014; Just et al., 2018). This conclusion is based on the publication of two types of total merit indices (TMIs) for Brown Swiss cattle in Germany: the conventional TMI with relative economic weights of 50 %, 5 % and 45 % for milk, beef and fitness traits, respectively, and the organic TMI with weights of 25 %, 10 % and 65 % for milk, beef and fitness (56 % fitness and 9 % conformation) traits, respectively (Fuerst-Waltl et al., 2016; LfL, 2018). However, to date, it has been unclear whether a genotype x environment interaction (GxE) exists between organic and conventional farming systems for breeding traits. In addition, how the ranking of sires would change if a GxE at a trait level or at a TMI level are taken into account is unknown. In addition to trait GxE, the TMI level also considers the different economic weights. In Baden-Wuerttemberg, variation in the production environment also is due to the fact that some farms are located on low mountain ranges, such as the Swabian Alb or the Black Forest, which results in a noticeable altitudinal range with regard to farm locations. In general, the environmental conditions are relatively more severe on these farms than on lowland farms. To date, it is unknown whether GxE interactions are present between these two environments. If undetected GxE interactions exist, then the evaluated genetic performance of sires for a specific environment (e.g., conventional production system) might not be valid for their offspring in other environments. This scenario could lead to an inefficiency of breeding programs and hence to reduced genetic improvement (Mulder and Bijma, 2005; Hammami et al., 2009). Even though there are numerous studies on GxE, only a few studies address GxE in different production systems, such as organic and conventional systems, or at a topographic level, such as altitude of the farms where the performance is evaluated. Nauta et al. (2006) found GxE for milk production traits for organically and conventionally managed Holstein Friesians in the Netherlands, and Sundberg et al. (2010) showed similar results for fertility traits in Swedish Holstein/Swedish Red. Pfeiffer et al. (2016) investigated GxE between different production systems for milk yield and functional traits in Austrian Fleckvieh (dual-

purpose Simmental) and found no severe GxE. Studies considering different altitudes as environments are rare. Williams et al. (2012) investigated the growth and survival of Angus cattle in the U.S. at differing altitudes and found minor GxE for high mountain disease.

In Germany, only a few GxE studies have been conducted. Koenig et al. (2005) defined geographical region and herd size as environmental factors. Genetic correlations between eastern and western Germany were between 0.9 and 0.95 for protein yield. Larger effects were reported when herd size was considered as an environmental factor. Streit et al. (2012, 2013) investigated GxE effects for German Holsteins using reaction norm models. Similar to the results of Koenig et al. (2005), they found little GxE. A study by Simianer et al. (2007) investigated GxE at the trait level between organically and conventionally managed farms in Switzerland and selected farms in Germany for Brown Swiss cattle. They found no severe GxE for different milk production and functional traits.

The aim of this study was to investigate GxE at the trait level for two different environments, i.e., production system and altitude of the farms, for milk production traits and functional traits in German Brown Swiss cattle using a multiple-trait sire model. These results were subsequently used to create a TMI for organic and conventional production systems according to the economic weights used in the routine breeding program to detect putative GxE effects at the TMI level.

2. MATERIAL AND METHODS

2.1. Animals, Traits and Environments

This study was based on trait records from twelve production and functional traits and pedigree data of Brown Swiss cows born between 2006 and 2014 in southern Germany in the state Baden-Württemberg. In total, 52,013 cows and 132 sires were evaluated in this study; however, the number of individuals was smaller for some analyses (see below). The pedigree contained 185,439 animals. The milk production traits investigated were milk, fat and protein yield. The analyses of functional traits included longevity, nonreturn rate 56, calving to first insemination, first insemination to conception, cystic ovaries, maternal and paternal calving ease and maternal and paternal stillbirth rate. Pfeiffer et al. (2015a, b) proposed estimating breeding values in a routine application and subsequent extract derivates such as yield deviations (YDs) or deregressed estimated breeding values (dEBV) and using these in multivariate GxE analysis. This approach has

computational advantages because in a GxE study, simple models can be applied. We followed this approach and used YDs obtained by the best prediction method (Cole et al., 2012) during routine genetic evaluations for the milk production traits, which are described in Fuerst et al. (2019). For the functional traits, we used dEBV. Fertility traits were deregressed using a multivariate deregression based on the approach of Jairath et al. (1998) and Schaeffer (2001), which is implemented in the program packages MiX99 (Lidauer et al., 2013). The deregression for calving ease and stillbirth rate was performed using the Garrick method (Garrick et al., 2009). The genetic evaluation system for functional traits is described in Fuerst et al. (2019).

Table 1 Number of cows, farms and sires (with at least five daughters) in each of the production systems[1] and farm locations based on altitude[2] for selected traits in Brown Swiss cattle.

traits	number	production system		altitude of farm	
		organic	conventional	< 800 m ASL	> 800 m ASL
milk production traits	cows	3,783	48,230	43,434	1,214
	farms	173	1,706	1,651	171
	sires	132		56	
functional traits	cows	3,486	45,115	39,629	928
	farms	129	1,196	1,251	57
	sires	127		51	
calving ease	cows	3,453	46,072	40,074	850
	farms	149	1,504	1,478	117
	sires	131		44	
stillbirth rate	cows	3,229	43,643	37,377	740
	farms	141	1,399	1,382	95
	sires	122		41	

[1] organic production system according to commission regulation (EC) No 889/2008 (European Commission, 2008).

[2] farm location based on altitude; classification according to comparison areas (LEL, 2017).

The two types of environment, production system and altitude of farm location, with two levels each, were considered. These two production systems considered were conventionally and organically managed farms, and the two farm locations were located below and above 800 meters above sea level (ASL) (LEL, 2017). Above 800 ASL was considered because many farms above 800 ASL are mainly located in mountainous regions with relatively severe environmental conditions, e.g., in food quality, and they are mainly grassland-based feeding regimes. Only sires with at least five daughters with trait records at each level within an environmental class were used in the statistical analysis. Table 1 gives an overview of the number of cows, sires and farms for the selected traits or trait complexes and the four environmental classes.

2.2.   Univariate sire model

All variance component analyses were performed using the package ASReml 3.0 in R 3.2.3. (Butler, 2009; R Core Team, 2015). For the estimation of non-environmental-specific breeding values, a univariate sire model was applied. This estimation was determined as a reference scenario using the following equation:

$$y = \mu + Zs + e \tag{1}$$

where y is a vector containing the trait phenotypes (i.e., YD or dEBV), μ is the overall mean, and s is a vector of random sire effects. The distribution of the sire effects is assumed to be $s \sim N(0, A\sigma^2 s)$, where A is the sire additive genetic relationship matrix and σ_s^2 is the sire variance. Z denotes the incidence matrix relating the cow observations to the corresponding sire effect. The vector e contains the random residuals, with $N(0, I\sigma^2 e)$, where I is the identity matrix and σ_e^2 is the residual variance.

2.3.   Analysis of GxE at a trait level using bivariate sire models

Equation (2) is a bivariate extension of equation (1), and equation (2) modelled the trait records collected in different environments as different but correlated traits. The model was applied separately for each environmental class (i.e., production system and altitude of farm location) with the two levels as different environments within the classes. The equation was as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} I_1 & 0 \\ 0 & I_2 \end{bmatrix} \begin{bmatrix} \mu_1 \\ \mu_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} s_1 \\ s_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \qquad (2)$$

where y_1 and y_2 are vectors with trait phenotypes (i.e., YD or dEBV) from daughters in environments 1 and 2, respectively. I_1 and I_2 are the identity matrices linking the phenotypes to the environment level means (μ_1 and μ_2). Z_1 and Z_2 are the incidence matrices relating the trait records to the random sire effects (vectors s_1 and s_2) for the corresponding environmental level. The covariance structure of these two random effects is $\mathrm{Var} \begin{bmatrix} s_1 \\ s_2 \end{bmatrix} = C \otimes A, \; with \; C = \begin{bmatrix} \sigma^2 s_1 & \sigma s_{1,2} \\ \sigma s_{1,2} & \sigma^2 s_2 \end{bmatrix}$, where A is the sire additive relationship matrix; $\sigma_{s_1}^2$ and $\sigma_{s_2}^2$ the sire variances for environment 1 and 2, respectively; and σ_{s_1,s_2} is the corresponding covariance. The vectors e_1 and e_2 contained the random residuals, where $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ are the residual variances for environment 1 and environment 2, respectively. The genetic correlation between the trait records, collected at different environmental levels, was estimated using standard notations.

2.4. Analysis of GxE on a total merit index level

To estimate putative GxE effects for the production system environment at an index level, the sire EBV for organic and conventional production systems were estimated using equation (2). In addition, these values were estimated in equation (1), i.e., without considering GxE. Relative economic weights (REWs) for the two environments were approximated by the weighting factors used in routine applications (LfL, 2016; LfL, 2018) and recent studies about breeder preferences for common traits, novel traits and traits that are not yet monetarily evaluated in cattle breeding (Steinwidder and Krogmeier, 2014; Fuerst-Waltl et al., 2016; Just et al., 2018).

The REWs used to create the environment-specific total merit index (TMI) of a sire are shown in Table 2. In summary, in the organic production system, the milk production traits jointly received a weight of only 36 %, while in the conventional system, this value was 54 %. The REW for longevity was 24 % (16 %) in the organic (conventional) system. Additionally, the remaining functional traits were weighted higher in the organic system than in the conventional system. Notably, the somatic cell score as a proxy trait to improve udder health was not considered in this study.

Table 2 Environmental-specific relative economic weights[1] (%, rounded) of specific traits used for the calculation of total merit indices of Brown Swiss cattle, managed in organic and conventional production systems[2].

trait complexes	traits	production system	
		organic	conventional
milk production traits	milk yield	12	18
	fat yield	12	18
	protein yield	12	18
functional traits	longevity	24	16
	nonreturn rate 56	8	6
	calving to first insemination	8	6
	first insemination to conception	8	6
	cystic ovaries	8	6
calving ease	maternal	4	3
	paternal	4	3

[1] The relative economic weights applied in this study were approximated, using routine applications as a basis (LfL, 2016; LfL, 2018).

[2] organic production system according to commission regulation (EC) No 889/2008 (European Commission, 2008).

For each sire, four different TMIs were calculated. For the conventional production system, the TMI for a sire was calculated as follows:

$$TMI_{con} = \sum_{t=i}^{10} EBV_{con,t} * REW_{con,t} \tag{3}$$

where TMI_{con} is the conventional TMI of a sire, $EBV_{con,t}$ is the sire EBV for trait t obtained from model (2) and $REW_{con,t}$ is the conventional REW of trait t. Similarly, for the organic production system, the sire TMI was calculated as follows:

$$TMI_{org} = \sum_{t=i}^{10} EBV_{org,t} * REW_{org,t} \qquad (4)$$

where the subscript organic (org) denotes the corresponding values valid for the organic production system. In comparison, a TMI_{conv} (TMI_{org}) was additionally calculated by using the EBV obtained from equation (1) in equations (3) and (4), i.e., the difference in these two TMIs is solely due to the use of different REWs. Rank correlations between sire TMIs were calculated to detect the putative GxE reranking effect at an index level.

3. RESULTS

3.1. GxE at the trait level

The genetic correlation estimates are shown in Table 3. The genetic correlations between organically and conventionally managed farms were close to one for calving to first insemination, cystic ovaries, and maternal and paternal stillbirth rates and approximately $r_g = 0.95$ for first insemination to conception, longevity, milk yield, protein yield, fat yield, nonreturn rate 56 and paternal calving ease. For maternal calving ease, the genetic correlation was below $r_g = 0.90$. The correlations of all the traits were slightly smaller for altitude of farm than for production system. All standard errors (SEs) were small.

A similar pattern was observed for the genetic correlations between low and high altitude farms. The genetic correlations for nonreturn rate 56 and maternal stillbirth rate were close to one. Most correlations ranged between $r_g = 0.85$ and $r_g = 0.95$. For the trait first insemination to conception, the lowest correlation was found ($r_g = 0.79$). Except for the traits stillbirth rate and first insemination to conception, the SEs were small.

3.2. GxE at the TMI level

The rank correlations between weighted TMIs of all organically and conventionally produced sires, using EBVs from the univariate and bivariate models, respectively, are shown in Table 4. All rank correlation coefficients were between 0.96 and 1.

Table 3 Genetic correlations (r_a) and standard errors (SE; in brackets) of selected traits between the levels of the production system[1] (organic and conventional) and farm location based on altitude[2] (< 800 m ASL and > 800 m ASL, resp.) in Brown Swiss cattle, calculated with the bivariate sire model.

trait complexes	traits	production system	altitude of farm
		organic - conventional	< 800 m - > 800 m ASL
milk production traits	milk yield	0.95 (0.03)	0.91 (0.06)
	fat yield	0.95 (0.02)	0.93 (0.06)
	protein yield	0.93 (0.03)	0.87 (0.08)
functional traits	longevity	0.96 (0.07)	0.92 (0.09)
	nonreturn rate 56	0.94 (0.07)	0.98 (0.08)
	calving to first insemination	0.99 (0.04)	0.95 (0.11)
	first insemination to conception	0.97 (0.05)	0.79 (0.15)
	cystic ovaries	0.99 (0.03)	0.90 (0.08)
calving ease	maternal	0.84 (0.10)	n.c.[3]
	paternal	0.92 (0.11)	n.c.[3]
stillbirth rate	maternal	0.99 (0.04)	0.97 (0.32)
	paternal	0.98 (0.05)	0.94 (0.11)

[1] organic production system according to commission regulation (EC) No 889/2008 (European Commission, 2008).

[2] farm location based on altitude; classification according to comparison areas (LEL, 2017).

[3] not converged.

Table 4 Rank correlations ($r_{Spearman}$) between the organic[1] and conventional total merit indices of all 123 Brown Swiss sires, calculated with the univariate and the bivariate estimated breeding values as a basis.

	TMI_{uo}[2]	TMI_{uc}[3]	TMI_{bo}[4]	TMI_{bc}[5]
TMI_{uo}	1			
TMI_{uc}	0.972	1		
TMI_{bo}	0.983	0.966	1	
TMI_{bc}	0.970	0.998	0.965	1

[1] organic production system according to commission regulation (EC) No 889/2008 (European Commission, 2008).

[2] TMI_{uo}: total merit index, univariate estimation, organic weighting.

[3] TMI_{uc}: total merit index, univariate estimation, conventional weighting.

[4] TMI_{bo}: total merit index, bivariate estimation, organic weighting.

[5] TMI_{bc}: total merit index, bivariate estimation, conventional weighting.

4. DISCUSSION

4.1. GxE at the trait level

The genetic correlations for milk production traits found in this study ranged from approximately 0.94 (production system) to 0.90 (farm altitude). All correlations were higher than 0.8, indicating no severe GxE or demand for independent breeding programs for those environments (Boelling et al., 2003; Robertson, 1959; Mulder et al., 2006). Similar results for differing production systems were found in several other studies. Nauta et al. (2006) estimated genetic correlations between organic and conventional production systems in Dutch Holstein. For the traits milk yield, fat yield and protein yield, the correlations were $r_g = 0.80$, $r_g = 0.88$ and $r_g = 0.71$, respectively, indicating a moderate GxE. Gerber et al. (2006) conducted a study in Fleckvieh cattle and estimated genetic correlations for milk production traits between farms with different levels of management intensity. In that study, minor GxE interactions were found ($r_g = 0.94$, $r_g = 0.95$ and $r_g = 0.88$ for milk yield, fat yield and protein yield, respectively). For Swedish Holstein/Swedish Red, the genetic correlations for milk production traits between organic and conventional production systems were close to one, indicating no occurrence of a GxE (Sundberg et al., 2010).

In a project to detect a GxE for different production and functional traits measured in organic and conventional production systems in Switzerland and Germany, Simianer et al. (2007) calculated genetic correlations of $r_g = 0.89$, $r_g = 0.86$ and $r_g = 0.89$ for milk yield, fat yield and protein yield, respectively, in Brown Swiss cattle. These results suggest only a minor GxE. For the functional trait calving to first insemination, a genetic correlation of $r_g = 0.69$ was estimated. The authors noted that this significant GxE should be interpreted with caution because of the data structure and very divergent variances of permanent environmental effects in both environments.

The results of an Austrian GxE analysis in Fleckvieh cattle were similar to the results from the previously described studies. Pfeiffer et al. (2016) investigated GxE effects for milk yield as well as different functional traits in production environments with varying management intensities (organic and conventional farming at low and high farm intensities). All estimated genetic correlations were close to one, e.g., $r_g = 0.98$ for milk yield, indicating no GxE effects.

For the trait longevity, high genetic correlations of $r_g = 0.96$ and $r_g = 0.92$ were estimated for production system and altitude of farm location, respectively, which confirm the findings of Pfeiffer et al. (2016) and Ahlman et al. (2011). In both studies, correlations for longevity were above 0.8, suggesting no severe GxE. Ahlman et al. (2011) found that the traits considered indicated a higher longevity and consequently a lower replacement rate in organic production systems than in conventional production systems in Sweden. Longevity is a key issue for farmers because a longer productive life and selection for improved fertility leads to reduced replacement rates and costs (Pritchard et al., 2013).

For the functional traits nonreturn rate 56, calving to first insemination and cystic ovaries, high genetic correlations for both environmental descriptors were estimated. Pfeiffer et al. (2016) found similar results for the traits nonreturn 56 (average $r_g = 0.94$) and cystic ovaries ($r_g = 1.0$) between organic and different conventional production systems in Austrian Fleckvieh cattle. Haile-Mariam et al. (2008) analysed the GxE of functional traits in Australian Holstein Friesians considering different calving systems and regions as environments. They found slight GxE effects for nonreturn rates in extreme environments (continuous environmental descriptors such as herd size) and groups of herds that were approximately $r_g = 0.6$. Sundberg et al. (2010) estimated a genetic correlation for calving to first insemination collected during different lactation events that was close to one in Swedish Holstein/Swedish Red. Describing the environment according to different calving months

and geographic locations, Ismael et al. (2016) showed GxE effects for geographic location ($r_g = 0.8$) in the Scandinavian Holstein population.

In the present study, the only genetic correlation below 0.8 was estimated for the functional trait first insemination to conception when the environment was classified by farm location altitude. No GxE effects were found with respect to the production systems.

For the traits calving ease and stillbirth rate, high genetic correlations were estimated. No correlations could be estimated for maternal calving ease because the equation did not converge. Genetic correlations for Holstein populations estimated between different countries as part of the Interbull Organization ranged between $r_g = 0.58$ (maternal calving ease) and $r_g = 0.59$ (maternal stillbirth), indicating GxE effects for those traits and environments (Mark, 2004). For the trait maternal calving ease, the evaluated genetic correlations between seven core populations of Holstein were $r_g = 0.84$. Similar to the results of Mark (2004), lower correlations between all populations and countries might be due to trait definitions and data evaluation procedures but not solely due to GxE effects.

As the dataset used in this study is a representative sample of the farm structure for Brown Swiss breeders and was not further preselected to obtain a balanced data structure, there was a relatively large difference regarding the number of individuals, farms and sires between the certain environmental classes. This scenario might have compromised the detection of GxE effects. However, the data structure reflected the reality of GxE in these environments. Since an environmental descriptor has a strong influence on the results of GxE studies, alternative environmental descriptors may lead to noticeable interactions, but alternative environmental descriptors were not focused on in this study. Further studies should be conducted using continuously scaled environmental descriptors and/or genotype data to obtain a detailed view of GxE and to analyse GxE at the QTL level.

4.2. GxE at the TMI level

The TMIs for sires, using their EBV for organic and conventional production systems (see 2.4.), were estimated to determine whether there are putative GxE effects for production system environments at an index level. The rank correlations for all sires were close to unity, indicating no reranking at an index level. A reranking across environments is more important for animal

breeding than scaling effects, indicating that the best sire in one environment is not necessarily the best in other environments, leading to losses in genetic gain. Several studies have investigated the reranking of animals due to GxE effects for different environments, genotypes and traits by looking at the magnitude of GxE due to the extent of genetic correlations or estimated rank correlations.

Pfeiffer et al. (2016) found no severe rank effects (rank correlations were close to unity) for Austrian Fleckvieh for milk yield between organic and conventional production systems according to sire EBVs. Similar results were shown for different management systems in the U.S., different grazing systems in the Netherlands, different fertility categories and continuous herd average fertility performances in New Zealand (Kearney et al., 2004; van der Laak et al., 2016; Craig et al., 2018).

Streit et al. (2012) estimated GxE for different milk-production traits using reaction norm models in German Holstein and found only a minor GxE. Estimated rank correlations between EBV showed no severe reranking of sires, even if a slight GxE was found.

Only a few studies found rerankings of animals due to a GxE between varying environments. Nauta et al. (2006) estimated genetic correlations below 0.8 for milk production traits in Dutch Holstein between organic and conventional production systems. Estimated breeding values of specific sires resulted in a reranking with respect to milk yield. Ismael et al. (2016) investigated GxE for the environments calving month and geographic location for Danish and Swedish Holstein. They found minor rerankings of sires due to differences from unity for estimated correlations for calving to first insemination between calving months. No reranking could be observed between different locations and the same trait.

Hayes et al. (2003) observed only small rerankings of bulls for milk-yield traits and the environmental descriptor temperature-humidity index in Australian Holstein Friesian.

The rank correlations in the present study indicate no reranking at the TMI level for the investigated production systems and traits. Only minor effects could be observed for the top 10 organic sires between production systems. These results suggest that selection decisions will not be affected, and no putative GxE effects at the TMI level are present.

The results at the trait level and TMI level suggest no separate breeding programs are needed for the investigated production environments. The provision of an organic TMI (ÖZW; LfL, 2018) for Brown Swiss sires is a helpful tool for breeders. These environmentally specific TMIs allow organic breeders to select animals in accordance with their production environment and maximize genetic and economic merit based on their preferences for fitness traits.

5. CONCLUSIONS

In general, no severe GxE was found at a trait level or at an index level. This result suggests that no separate breeding programs are needed for the investigated environments and traits in German Brown Swiss cattle.

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CHAPTER THREE

CHAPTER FOUR

The extent of genotype-by-environment interactions for milk production and functional traits in Brown Swiss dairy cattle using random regression reaction norm models

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IMPLICATIONS

Genotype-by-environment interactions are one source of variance in environment-sensitive quantitative traits. In animal breeding, ignoring this variance component can result in scaling and reranking effects of estimated breeding values for these traits. This, in turn, might compromise the response to selection and, hence, the efficiency of animal breeding schemes. In the present study, genotype-by-environment interactions in Brown Swiss dairy cattle for sixteen milk production and functional traits were investigated by applying random regression reaction norm models. The aim was to determine if and to what extent genotype-by-environment interactions are present and whether these have a potential impact on the estimated breeding values.

INTRODUCTION

The sensitive reaction of a genotype to environmental changes can be one source of quantitative trait variation. Some production traits, but particularly functional traits, are of low heritability and strongly influenced by environmental factors. For these traits, genotype-by-environment interactions (GxE) are more likely than for traits that depend, mostly, on the genetics of an animal. To determine GxE and to infer how these might impact selection and breeding schemes in livestock, bivariate and multivariate analyses as well as reaction norm models were frequently applied. In the latter approach, the environment is modelled as a continuously scaled variable, such as temperature-humidity index, herd disease level or farm input level as recently reviewed by Hayes et al. (2016). Several studies found GxE in different cattle breeds using different environmental descriptors (e.g. Hayes et al., 2003; El-Tarabany and Nasr, 2015; Ha et al., 2017) and the suitability of different reaction norm models was investigated (e.g. Calus et al., 2002; Kolmodin et al., 2002; Lillehammer et al., 2009).

As sires are usually selected according to their estimated breeding value, GxE may affect values for certain traits, which can eventually result in scaling effects or a reranking of sires. Recent studies revealed that GxE influence the breeding value estimation of traits with significant GxE. Including information on environmental sensitivity led to an increased accuracy of estimated breeding values, especially if genomic data was available (Zhang et al., 2019; Bohlouli et al., 2018). If GxE is one source of the variability of certain traits in a specific breed, this would reduce the response to selection and, hence, compromise the efficiency of breeding schemes.

GxE always depend on the applied environmental descriptor. Larger environmental sensitivity can be observed when the range of the environmental descriptor is wide, which especially concerns across breed and across country evaluations. Brown Swiss is one of the most important dairy cattle breeds in southern Germany and Austria. The topography, the farm size, the management and the feeding regimes can differ substantially, and the environmental ranges are therefore expected to be large. Imort-Just et al. (2019, submitted) conducted GxE studies in the German-Austrian Brown Swiss population using bivariate sire models to infer GxE considering environments classified by farm altitude (above and below 800 m ASL) and farming system (organic and conventional). Since sires are usually selected according their total merit index, they investigated GxE effects on trait and on total merit index level. They found minor GxE effects for one functional trait (first insemination to conception interval). No reranking of sires was observed, neither on trait nor on total merit index level.

The objective of the present study was to investigate GxE effects in Brown Swiss cattle using random regression reaction norm models. A continuously scaled environmental descriptor capturing a wide range of herd environments was used, which has successfully been done in other studies (e.g. Calus et al., 2002; Strandberg et al., 2009; Streit et al., 2012). The results were expected to determine traits affected by GxE and to infer roughly the potential impact on estimated breeding values and currently used breeding schemes.

MATERIAL AND METHODS

Individuals and environmental descriptor

This study is based on phenotype and pedigree data from a sample of the German-Austrian Brown Swiss dairy population. The dataset contained the averaged performance of first lactating cows, born between 2006 and 2014, with at least 7 herd-test-day records. Individuals with a lack of sire information or that descend from sires with less than five female offspring in the dataset were discarded from the analyses.

The investigated traits were the milk production traits milk yield (MY), fat yield (FY) and protein yield (PY) as well as milk energy yield (EY) as a linear function of the three traits (Nostitz and Mielke, 1995). Further, the functional traits longevity (LON), non-return rate 56 of heifers (hNRR) and cows (cNRR), calving to first insemination interval (CFI), first insemination to conception

interval of heifers (hFIC) and cows (cFIC), cystic ovaries (CO), fertility disorders (FD), maternal and paternal calving ease (mCE, pCE) and maternal and paternal stillbirth rate (mSB, pSB) were examined.

For analyses, the cows' yield deviations (YD) were derived from their averaged first lactation performances of the routine genetic evaluation using an animal test day model (Fuerst et al., 2019). The YDs were not adjusted for heterogeneous variances. This approach ensured that the phenotypes were not pre-corrected for potential GxE effects captured by heterogeneous herd variances (Lidauer et al., 2002) and concerned the milk production traits and LON. For all other traits, breeding values, obtained from the routine genetic evaluations (Fuerst et al., 2019), were deregressed following Garrick et al. (2009) and considered as phenotypes in the subsequent analyses.

For the application of reaction norm models, a continuously scaled parameter is required to describe the production environment of individuals. Herd-test-day solutions of milk production traits have frequently been used successfully as environmental descriptors (e.g. Streit et al., 2012). Therefore, in the present study, averaged herd effects (AHE) obtained during routine breeding value estimation were used, not corrected for heterogeneous herd variances. According to Streit et al. (2012), who proposed to rather use one single environmental descriptor instead of three correlated descriptors, milk energy yields (MEY, in MJ) were calculated as a linear combination of the AHE of MY, FY and PY following Nostitz and Mielke (1995). Assuming a constant lactose content of 4.8 % per kg milk yield, and with the evidence of high correlations between the traits, the following formula was applied to calculate the environmental descriptor for each cow j:

$$MEY_j = 0.802 * MY_j + 38.4 * FY_j + 23.6 * PY_j \tag{1}$$

To ensure that the environmental descriptor is representative for the overall Brown Swiss herd's environments, individuals showing most extreme milk energy yields (2.5% of the data) were discarded from further analyses. Depending on the respective trait, 52,545 to 60,441 cows descending from 1,095 to 1,235 bulls remained in the evaluation dataset after quality control.

Statistical analyses

The phenotypes and milk energy yields (environmental descriptor variable) were scaled to a mean of zero and a standard deviation of one. Following Kolmodin et al. (2002) and Lillehammer et al.

(2009), the following random regression reaction norm model was applied using the R package ASReml-R (Butler et al., 2017):

$$y_{ijk} = \mu + b * MEY_k + s_{ai} + s_{bi} MEY_k + e_{ijk} \tag{2}$$

with y being the YD of the j-th daughter of sire i in environment k (details see below), μ the overall mean and b the fixed effect of the environment. s_{ai} denotes the random sire effect (intercept) and s_{bi} the sire slope effect (environmental sensitivity), which is the random regression coefficient of the regression of sire i on the environmental descriptor MEY. The variance-covariance structure of the sire intercept and slope effects is defined as $var \begin{bmatrix} s_a \\ s_b \end{bmatrix} = A \otimes \begin{bmatrix} \sigma_{s_a}^2 & \sigma_{s_a,s_b} \\ \sigma_{s_a,s_b} & \sigma_{s_b}^2 \end{bmatrix}$, with A being the pedigree-derived relationship matrix. The residuals were modelled heterogeneously within 10 equally sized groups according to the milk energy yield (Lillehammer et al., 2009). The fixed effect of the environment was tested for significance using Wald test statistics (Kenward and Roger, 1997). The random effects (intercept, slope) were tested for significance applying z-statistics at a significance level of $\alpha = 0.01$.

Following Lynch and Walsh (1998) the sire variance as a function of the environment was calculated as

$$\sigma_{s|MEY}^2 = \sigma_{s_a}^2 + 2MEY\sigma_{s_a,s_b} + MEY^2 \sigma_{s_b}^2 \tag{3}$$

for each trait, with $\sigma_{s_a}^2$ ($\sigma_{s_b}^2$) being the estimated intercept (slope) variance component, σ_{s_a,s_b} their covariance and MEY, a vector containing the realisations of the continuously scaled environmental descriptor variable. Genetic correlations between the sire variance given MEY_{min} and MEY_{max}, the 10- and 90% - quantile of MEY, and the 25- and 75% - quantile of MEY, respectively, were computed. Generally, considering two environments MEY_1 and MEY_2, the correlation is

$$r_{g_{MEY_1,MEY_2}} = \frac{\sigma_{MEY_1,MEY_2}}{\sigma_{MEY_1} \sigma_{MEY_2}} \tag{4}$$

and the covariance was defined as

$$\sigma_{MEY_1,MEY_2} = \sigma_{s_a}^2 + \sigma_{s_a,s_b}MEY_1 + \sigma_{s_a,s_b}MEY_2 + \sigma_{s_b}^2 MEY_1 MEY_2 \tag{5}$$

Using the random effect estimates of sire i, the sires' reaction norm R across all environments was calculated as

$$R_i = s_{ai} + s_{bi}\, MEY \tag{6}$$

and its estimated breeding value (EBV) in environment E then was

$$EBV_{i|E} = s_{ai} + s_{bi}\, MEY_E \tag{7}$$

To infer whether putative GxE effects affect the EBV ranking of bulls, and if certain EBV ranges are more affected than others, Spearman rank correlations were calculated for different sire subsets. According to their intercept value (i.e. EBV_i irrespective the environment), the following sires were chosen and their $EBV_{i|E}$ reranking was investigated for the different values of MEY_E described above for the genetic correlation: the ten bulls with the highest (best 10 sires) and the lowest (worst 10 sires) intercept EBVs, the sire with the median EBV ± five bulls (medium sires), and all the sires in the study.

RESULTS

The reaction norm model (Formula 2) did not reach convergence for the traits hNRR, hFIC, FD, mCE, pCE and mSB. For the remaining traits, the results of the variance component estimation can be taken from Table 1. The sire intercept variance was significant for all traits, ranging from 0.026 (cNRR) to 0.203 (MY), and was generally much lower for the functional traits compared to the milk production traits. In contrast, the estimated slope variance was only significant for FY. Overall, the sire slope variances were notably small (across all traits the intercept variance was on average 27-fold larger). Except for cNRR and LON, the covariance between the intercept and slope was negative. However, the covariance estimates were close to zero and not significant for all investigated traits.

The standard errors of the estimated variance components were large when the estimated variance was close to zero, which concerned almost all non-significant variance components. For the milk production traits and functional traits, the sire variance, expressed as a function of the environment, is visualised in Figure 1 and Figure 2, respectively.

Table 1 Variance component estimates obtained from ASReml. The sire intercept variance ($\sigma_{s_a}^2$), sire slope variance ($\sigma_{s_b}^2$) and their covariance (σ_{s_a,s_b}) as well as the standard errors (SE) are shown for the investigated traits; [*] highlight significant components ($\alpha = 0.01$). For clarity, the estimates were multiplied by the factor 100.

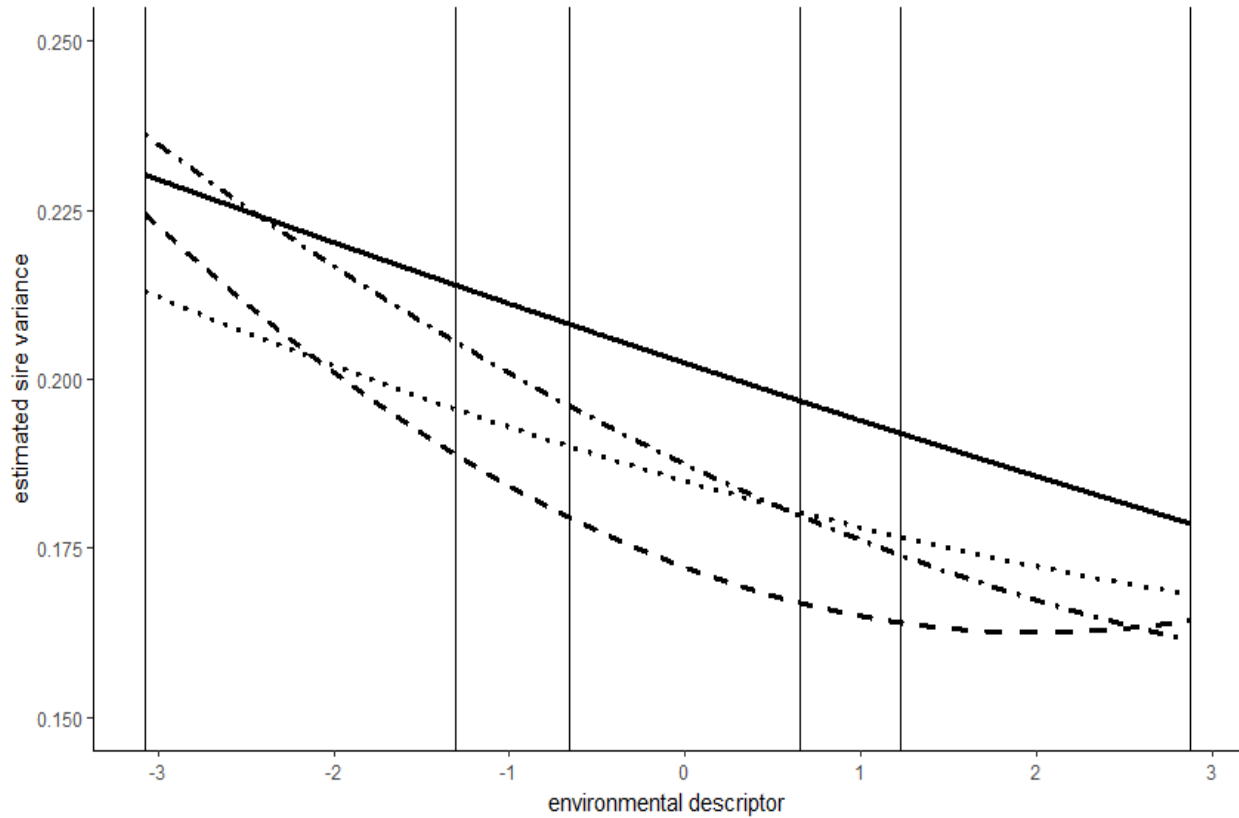| Trait[1]	$\sigma_{s_a}^2 * 10^2$ (SE)	$\sigma_{s_b}^2 * 10^2$ (SE)	$\sigma_{s_a,s_b} * 10^2$ (SE)
MY	20.240 (1.123)[*]	0.014 (0.023)	-0.433 (0.207)
FY	17.220 (1.033)[*]	0.240 (0.083)[*]	-0.481 (0.275)
PY	18.494 (1.063)[*]	0.055 (0.035)	-0.371 (0.233)
EY	18.742 (1.081)[*]	0.115 (0.052)	-0.618 (0.253)
cNRR	2.614 (0.289)[*]	0.018 (0.025)	0.030 (0.071)
CFI	5.071 (0.474)[*]	0.028 (0.028)	-0.253 (0.120)
cFIC	2.367 (0.281)[*]	0.006 (0.023)	-0.090 (0.070)
LON	2.866 (0.340)[*]	0.052 (0.040)	0.021 (0.106)
CO	6.179 (0.514)[*]	0.007 (0.024)	-0.112 (0.113)
pSB	7.135 (0.615)[*]	0.049 (0.037)	-0.121 (0.160)

[1] Milk yield (MY), fat yield (FY), protein yield (PY), milk energy yield (EY), non-return rate 56 of cows (cNRR), calving to first insemination interval (CFI), first insemination to conception interval of cows (cFIC), longevity (LON), cystic ovaries (CO), paternal stillbirth rate (pSB)

It shows that the estimated sire variance was higher for the milk production traits and larger differences in sire variance across environments were apparent for these traits. For traits with a positive covariance between the sire intercept and slope variance, the estimated sire variance decreased with increasing values of the environmental variable. The opposite was observed for the trait cNRR. For LON, the estimated sire variance decreased while the environmental descriptor was less than MEY = -0.406 and subsequently increased up to the maximal value of the environmental descriptor.

Nevertheless, all genetic correlations that were calculated between different percentiles of the environment were positive for all traits and ranged from 0.992 to 1 (from 0.972 to 1), considering the 25th and 75th (10th and 90th) percentile. A smaller genetic correlation was present for the traits LON (0.845) and FY (0.886) between the two most extreme environments (see Table 2).
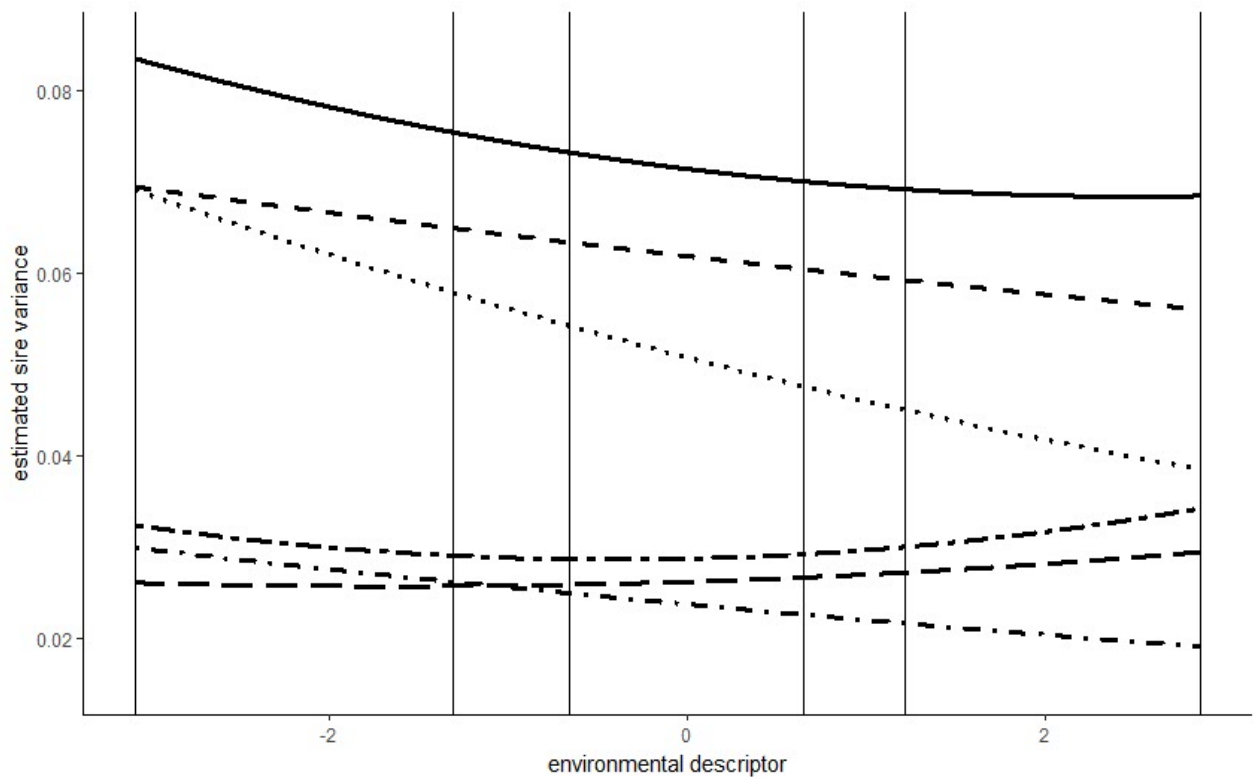
Figure 1 Estimated sire variance as a function of the environmental descriptor milk energy yield (MEY, Formula 1) for the investigated milk production traits. The plot illustrates the estimated sire variance as a function of the environmental descriptor for the milk production traits milk yield (solid line), milk energy yield (dot-dashed), protein yield (dotted) and fat yield (dashed). The vertical lines correspond to the minimum, 10th percentile, 25th percentile, 75th percentile, 90th percentile and the maximum (from left to right) of the environmental descriptor.

Figure 2 Estimated sire variance as a function of the environmental descriptor milk energy yield (MEY, formula 1) for the investigated functional traits. The plot illustrates the estimated sire variance as a function of the environmental descriptor for the functional traits paternal stillbirth rate (solid line), cystic ovaries (dashed), calving to first insemination interval (dotted), longevity (two-dashed), first insemination to conception rate in cows (dot-dashed) and a cows' non-return rate 56 (long-dashed). The vertical lines correspond to the minimum, 10th percentile, 25th percentile, 75th percentile, 90th percentile and the maximum (from left to right) of the environmental descriptor.

Figure 3 Reaction norms of the best 10 sires (left), medium sires (middle) and worst 10 sires (right) for the traits fat yield (top) and cystic ovaries (bottom). The vertical lines correspond to the minimum, 10th percentile, 25th percentile, mean, 75th percentile, 90th percentile and the maximum (from left to right) of the environmental descriptor milk energy yield (MEY, formula 1).
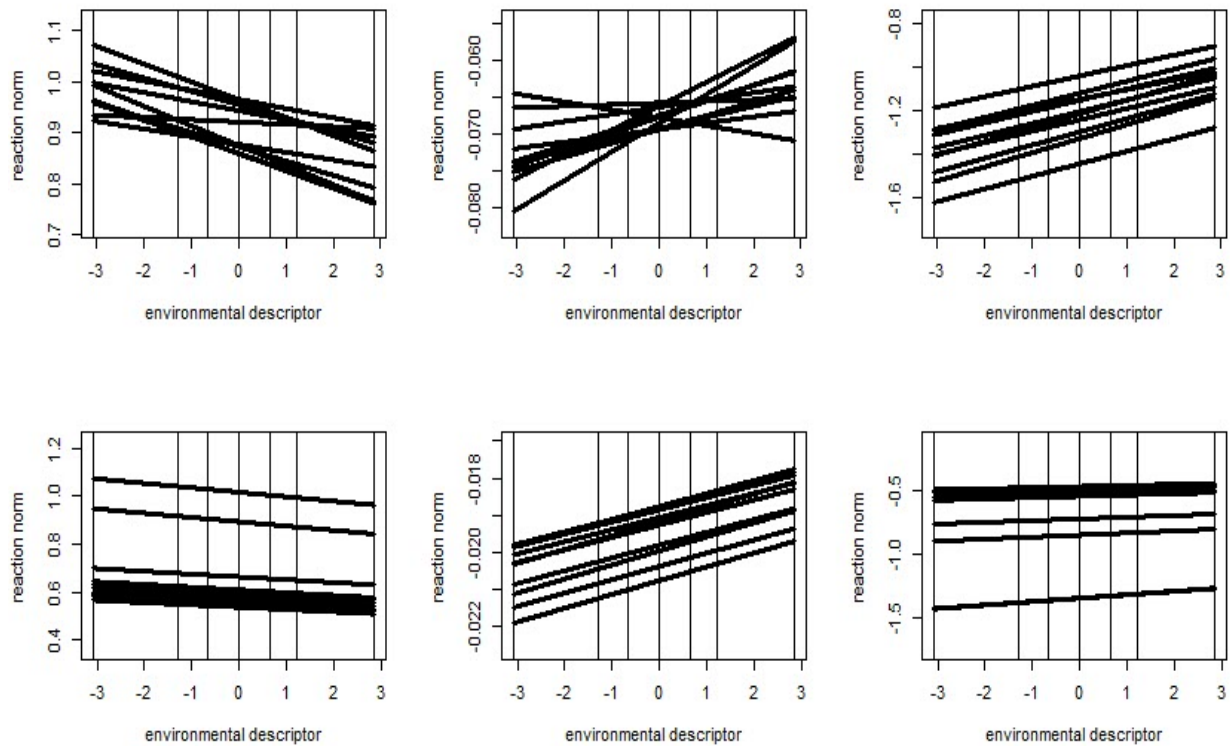
Table 2 Genetic correlations (r_g) between the minimum and maximum, the 10th and 90th percentile and the 25th and 75th percentile of the environmental descriptor milk energy yield (MEY, formula 1), respectively, are shown for the investigated traits.

Trait[1]	$r_g(min, max)$	$r_g(p10, p90)$	$r_g(p25, p75)$
MY	1.000	1.000	1.000
FY	0.886	0.980	0.994
PY	0.980	0.996	0.999
EY	0.962	0.993	0.998
cNRR	0.942	0.990	0.997
CFI	0.991	0.998	1.000
cFIC	1.000	1.000	1.000
LON	0.845	0.972	0.992
CO	0.995	0.999	1.000
pSB	0.944	0.990	0.997

[1] For trait abbreviations, see Table 1.

Table 3 provides the Spearman rank correlations between the estimated breeding values of all sires, calculated for different environments based on the estimated sire intercept and slope effects (Formula 7). The rank correlations were above 0.995 for all traits and all environments compared. Even for the trait FY, that showed significant GxE, no severe reranking was present. This changes when the rank correlations of the sire cohort's best 10 sires (Table S1), medium sires (Table S2) and worst 10 sires (Table S3) were investigated separately. Generally, the rank correlations were slightly reduced for the best 10 sires (-0.039) and worst 10 sires (-0.018) and dropped remarkably in the subset of medium sires (-0.262). This shows that reranking effects predominantly occur between sires with estimated intercept breeding values close to the mean. Across all traits, the ranking differences increased, the more the environment differed. This was especially evident for the traits FY and LON, but also evident for EY, cNRR, CFI and pSB in the medium sire cohort.

The reaction norms of the sires within the sire subsets, exemplarily displayed for the traits FY and CO in Figure 2, support these findings. Further, they provide additional information about the size

of the estimated breeding value across the continuously scaled environmental variable. It is clearly visible that small to moderate scaling effects can be observed for all bulls. In contrast, reranking effects only affected a fraction of sires and were most pronounced when comparing the medium sires (e.g. FY, see Figure 3).

Table 3 Spearman rank correlations between the estimated breeding values irrespective of the environment based on the intercept estimates (EBV_i) and the estimated breeding values in a certain environment E ($EBV_{i|E}$) (see Formula 7) for all of the sires in the study and the investigated traits. The rank correlations (ρ) are shown for the estimated breeding values given the minimum ($\rho_{(EBV_{i|min})}$), maximum ($\rho_{(EBV_{i|max})}$), 10th ($\rho_{(EBV_{i|p10})}$), 25th ($\rho_{(EBV_{i|p25})}$), 75th ($\rho_{(EBV_{i|p75})}$) and 90th ($\rho_{(EBV_{i|p90})}$) percentile of the environmental descriptor milk energy yield (MEY, formula 1).

Trait[1]	$\rho_{(EBV_{i|min})}$	$\rho_{(EBV_{i|p10})}$	$\rho_{(EBV_{i|p25})}$	$\rho_{(EBV_{i|p75})}$	$\rho_{(EBV_{i|p90})}$	$\rho_{(EBV_{i|max})}$
MY	1.000	1.000	1.000	1.000	1.000	1.000
FY	0.996	0.999	1.000	1.000	0.999	0.995
PY	1.000	1.000	1.000	1.000	1.000	1.000
EY	0.999	1.000	1.000	1.000	1.000	0.999
LON	0.996	0.999	1.000	1.000	0.999	0.997
cNRR	0.999	1.000	1.000	1.000	1.000	0.999
CFI	1.000	1.000	1.000	1.000	1.000	1.000
cFIC	1.000	1.000	1.000	1.000	1.000	1.000
CO	1.000	1.000	1.000	1.000	1.000	1.000
pSB	0.999	1.000	1.000	1.000	1.000	0.999

[1] For trait abbreviations, see Table 1.

Table S1 Spearman rank correlations of the best 10 sires. Spearman rank correlations between the estimated breeding values irrespective the environment based on the intercept estimates (EBV_i) and the estimated breeding values in a certain environment E ($EBV_{i|E}$) (see Formula 7). The rank correlations (ρ) are shown for the estimated breeding values given the minimum ($\rho_{(EBV_{i|min})}$), maximum ($\rho_{(EBV_{i|max})}$), 10th ($\rho_{(EBV_{i|p10})}$), 25th ($\rho_{(EBV_{i|p25})}$), 75th ($\rho_{(EBV_{i|p75})}$) and 90th ($\rho_{(EBV_{i|p90})}$) percentile of the environmental descriptor milk energy yield (MEY, Formula 1) and were calculated for each trait across the best ten sires (ranked according to their intercept breeding values).

Trait[1]	$\rho_{(EBV_{i|min})}$	$\rho_{(EBV_{i|p10})}$	$\rho_{(EBV_{i|p25})}$	$\rho_{(EBV_{i|p75})}$	$\rho_{(EBV_{i|p90})}$	$\rho_{(EBV_{i|max})}$
MY	0.988	1.000	1.000	1.000	1.000	1.000
FY	0.636	0.855	0.939	0.988	0.976	0.842
PY	0.988	1.000	1.000	1.000	1.000	1.000
EY	0.964	0.988	0.988	1.000	0.988	0.988
LON	0.564	0.867	0.939	0.927	0.927	0.842
cNRR	0.964	1.000	1.000	0.988	0.988	0.964
CFI	0.988	1.000	1.000	1.000	1.000	0.988
cFIC	1.000	1.000	1.000	1.000	1.000	1.000
CO	1.000	1.000	1.000	1.000	1.000	1.000
pSB	0.818	0.915	0.988	0.964	0.964	0.927

[1]For trait abbreviations, see Table 1.

Table S2 Spearman rank correlations of the medium sires. Spearman rank correlations between the estimated breeding values irrespective of the environment based on the intercept estimates (EBV_i) and the estimated breeding values in a certain environment E ($EBV_{i|E}$) (see Formula 7). The rank correlations (ρ) are shown for the estimated breeding values given the minimum ($\rho_{(EBV_{i|min})}$), maximum ($\rho_{(EBV_{i|max})}$), 10th ($\rho_{(EBV_{i|p10})}$), 25th ($\rho_{(EBV_{i|p25})}$), 75th ($\rho_{(EBV_{i|p75})}$) and 90th ($\rho_{(EBV_{i|p90})}$) percentile of the environmental descriptor milk energy yield (MEY, formula 1) and were calculated for each trait across sires with medium intercept breeding values (the sire having the median intercept breeding value ± 5 bulls, ranked according to their intercept breeding values).

Trait[1]	$\rho_{(EBV_{i|min})}$	$\rho_{(EBV_{i|p10})}$	$\rho_{(EBV_{i|p25})}$	$\rho_{(EBV_{i|p75})}$	$\rho_{(EBV_{i|p90})}$	$\rho_{(EBV_{i|max})}$
MY	1.000	1.000	1.000	0.991	0.991	0.991
FY	0.490	0.745	0.864	0.755	0.527	0.209
PY	0.818	0.918	0.955	0.982	0.982	0.900
EY	0.718	0.855	0.882	0.845	0.618	0.209
LON	0.527	0.536	0.573	0.027	-0.191	-0.364
cNRR	0.727	0.900	0.927	0.755	0.455	0.127
CFI	-0.109	0.277	0.964	1.000	0.909	0.791
cFIC	0.855	0.973	0.991	0.982	0.936	0.891
CO	0.982	0.991	1.000	1.000	1.000	0.991
pSB	0.309	0.773	0.909	0.945	0.918	0.909

[1] For trait abbreviations, see Table 1.

Table S3 Spearman rank correlations of the worst 10 sires. Spearman rank correlations between the estimated breeding values irrespective the environment based on the intercept estimates (EBV_i) and the estimated breeding values in a certain environment E ($EBV_{i|E}$) (see Formula 7). The rank correlations (ρ) are shown for the estimated breeding values given the minimum ($\rho_{(EBV_{i|min})}$), maximum ($\rho_{(EBV_{i|max})}$), 10th ($\rho_{(EBV_{i|p10})}$), 25th ($\rho_{(EBV_{i|p25})}$), 75th ($\rho_{(EBV_{i|p75})}$) and 90th ($\rho_{(EBV_{i|p90})}$) percentile of the environmental descriptor milk energy yield (MEY, formula 1) and were calculated for each trait across the worst ten sires (ranked according to their intercept breeding values).

Trait[1]	$\rho_{(EBV_{i|min})}$	$\rho_{(EBV_{i|p10})}$	$\rho_{(EBV_{i|p25})}$	$\rho_{(EBV_{i|p75})}$	$\rho_{(EBV_{i|p90})}$	$\rho_{(EBV_{i|max})}$
MY	0.988	0.988	1.000	1.000	1.000	1.000
FY	0.976	1.000	1.000	0.988	0.976	0.976
PY	1.000	1.000	1.000	1.000	1.000	1.000
EY	0.988	1.000	1.000	1.000	1.000	1.000
LON	0.806	0.952	0.976	0.952	0.952	0.891
cNRR	0.964	0.988	1.000	1.000	1.000	1.000
CFI	0.988	0.988	1.000	0.988	0.988	0.976
cFIC	1.000	1.000	1.000	1.000	1.000	0.952
CO	1.000	1.000	1.000	1.000	1.000	1.000
pSB	0.842	0.939	0.952	1.000	0.988	0.976

[1] For trait abbreviations, see Table 1.

DICUSSION

A previous study examining GxE in the same population applying bivariate analyses revealed no severe interactions (Imort-Just et al. 2019, submitted). Since the detection of GxE effects in that study was compromised by the classification in two distinct environments, which resulted in strongly unbalanced datasets, it was suggested to investigate GxE by using a continuously scaled environmental descriptor and reaction norm models as used in the present study.

Random regression reaction norm models to infer the sources of variability, particularly GxE, are complex and need a suitable data structure and sufficient trait variability to gain reasonable estimates. Small variation or a lack of information may result in high standard errors as well as

poor convergence of the model or parameter estimates that are outside the parameter space (Misztal, 2008). Although convergence issues are usually less evident in sire models (Misztal and Legarra, 2017), the variance in question was not sufficiently large in some of the functional traits (hNRR, hFIC, FD, mCE, pCE and mSB) to estimate reliable variance components given the model parameterisation in the present study (Table 1). However, since the model contained all relevant sources and could not be reduced any further, GxE investigations for these traits should be conducted using larger datasets or increasing the minimum number of daughters of sires in the evaluation. This, in turn, might also decrease the partially high standard errors of the estimates. Still, increasing the minimum number of daughters per sire would have reduced the general dataset. This would not represent reality since there are always sires with little offspring information included in the routine genetic evaluations. Further, but more importantly, this might have compromised the detection of GxE effects in other traits caused by losses in variation of the environmental descriptor. Alternatively, non-linear reaction norm models can be applied as done by Streit et al. (2012); however, it did not substantially improve the results in their study as the reaction norms were almost linear and the first order effect explained the environmental sensitivity sufficiently. Regarding the reaction norms of the sires (Figure 2), their findings might also be valid for the present study.

The estimates of the sire variance irrespective of the environment (intercept variance) was significant for all traits and remarkably larger for the milk production traits than for the functional traits (Table 1). This was expected since this variance component is roughly equivalent to the sire variance obtained from models without an interaction term, and it has been shown in previous studies that there is genetic variation in the relevant functional and production traits in this breed. Among others, Loberg et al. (2015) conducted variance component estimations in several Brown Swiss cattle populations and estimated moderate to high heritabilities for milk production traits whereas the heritabilities for functional traits were small (e.g. $h^2 = 0.03$ for maternal calving ease, for which the reaction model in this study did not converge). The influence of the environment is strong in traits with a low heritability and, hence, GxE are more likely to impact the expression of a phenotype in such traits. In agreement, the results of Kolmodin et al. (2002) suggest that GxE effects may be more present in functional traits. Still, no GxE were found for the functional traits in the present study, but for the milk production trait FY. Derivates of the milk production traits were used to calculate the environmental descriptor MEY, and FY had the highest weight in this

variable (Formula 1). Thus, the environmental descriptor was probably more suitable to detect GxE effects for this particular trait than for others. This was also discussed by Streit et al. (2012), who analysed GxE for milk production traits using either milk energy yield or somatic cell score as the environmental descriptor. Generally, GxE are more pronounced if the range of the environmental descriptor is very large (i.e. temperature-humidity index) or in across country evaluations of breeds (Hayes et al., 2016).

The estimates of the slope variance, which denotes the measure of the environmental sensitivity of genotypes, were generally small across all traits (Table 1), indicating no GxE in the German-Austrian Brown Swiss population (only marginal GxE for the trait FY). This either results from the fact that the individuals are not particularly sensitive to the environment, i.e. robust, or of a small environmental variance, i.e. the herd production levels across the environments are very homogeneous, or both. In the present study, the reasons could not be further quantified due to the lack of single herd-test-day information. Instead of averaged herd effects across the first lactation herd-test-days, these would probably have been more suitable to capture the production environment.

The results of GxE studies imply that a low covariance between the intercept and the slope comes along with larger reranking effects (e.g. Santana et al., 2013). Zhang et al. (2019) discussed that this holds true for a high covariance, given that the variance components are significant and the range of the environment is large. In the present study, the slope variances were close to zero for all traits which naturally leads to low covariances irrespective of potential reranking effects. Even though FY revealed minor GxE, across all individuals no severe reranking was observed in the German-Austrian Brown Swiss sires for all traits (Table 3).

In the separately investigated sire subsets' best 10 sires, medium sires and worst 10 sires (defined in the Material & Methods section), reranking was only considerably present for the subset of sires with intercept sire effects close to the mean (which was close to zero due to standardizing the data) for some of the investigated traits. Here, the breeding value of a sire is dominated by the slope effect, even if this effect is minimal and following the breeding value changes (almost) completely with changes of the environment. Further, sires with an EBV close to the mean are rarely selected and, hence, barely contribute to the next generation.

For all bulls in the study, slight EBV scaling effects were observed for each of the traits. A negative (positive) covariance between the intercept and slope (Table 1) resulted in negative (positive) slopes of the reaction norms of sires with a high (low) intercept breeding value (Figure 3). These relations should be interpreted with caution since the covariance estimates were significant. Differences in daughter performance caused by these scaling effects should not be expected.

The trait LON showed different results compared to the other traits. Whereas otherwise no significant GxE were found (Table 1), the reranking of bulls, especially of sires with the highest and lowest intercept breeding values for LON, was most evident and resulted in the smallest Spearman rank correlations (Table S1 and Table S3). Petersson et al. (2005) found significant GxE for this trait in dairy cattle as well. These results suggest that further GxE investigations in LON, using a larger dataset and herd-test-day records, might be promising in this Brown Swiss population.

As Zhang et al. (2019) pointed out, the estimation of breeding values is affected by the environment for traits with significant GxE and consequently shows genetic correlations that significantly differ from unity between certain environments. In this case, the exclusion of GxE could cover reranking effects whereas the inclusion of GxE information increased the accuracy of EBVs, especially when genomic data was available (Bohlouli et al., 2018; Zhang et al., 2019).

The results of the present study imply that the routine animal evaluation and breeding scheme of the German-Austrian Brown Swiss population would not substantially benefit from the consideration of GxE given the environmental descriptor applied. Similar results could be observed when applying bivariate models and considering farming systems or the altitude of farm location as environments in the same population, especially if sire selection is based on the total merit index (Imort-Just et al. 2019, submitted).

CHAPTER FOUR

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CHAPTER FOUR

GENERAL DISCUSSION

This study investigates different aspects of breeding programmes in pigs and Brown Swiss cattle. Maintaining the major objective of animal breeding, the superiority of the next generation over the present through genetic gain, is one of the key aspects of any breeding programme, independent of breed or species. The successive steps of breeding programmes, starting with the definition of a breeding goal in a specific production environment and ending with the dissemination of genetics by selecting animals based on their outstanding total merit indices, need to be edited on a regular basis due to exogenous aspects. Those influencing factors might be research findings or future economic, political, environmental and social circumstances. A variety of starting points arise from these factors to optimise currently used breeding programmes.

Novel traits and the estimation of environmental-specific relative economic weights (Chapter 1 and 2)

Traits considered in breeding programmes can roughly be characterised as production and functional traits, whereby the former maximise the profit by a higher output, for example the milk yield of dairy cows or the feed utilisation and growth rate in pigs. Functional traits reduce costs of input and thus increase the efficiency of animal production. Common traits are for instance health and the calving ease in cows or the rates of losses (e.g. number of weaned piglets) in pigs (Groen et al., 1997; Swalve, 2003; Tarrés et al., 2006).

Research findings revealed negative genetic correlations between production and functional traits, leading to a decline in health and functionality of animals as a consequence of selection for high productivity (Simianer et al., 1991; Gäde, 2006). Due to these findings, political influences, consumers' and farmers' demands, and various other aspects, novel functional and behavioural traits (Dreher et al., 2019; Egger-Danner et al., 2014; Kramer et al., 2013) gain importance. Common problems related to these kinds of traits are the difficulties in recording, due to the subjective perception, varying trait definitions, the non-normal distribution related to the common classification in categories and especially the dependency on the motivation of the data collector, e.g. veterinarian or farmer (e.g. Gäde, 2006; Hellbrügge, 2007; Løvendahl, 2005; Gernand et al., 2012). In addition, various mathematical and statistical approaches for quantitative genetic

analyses (e.g. linear mixed models, threshold models) are available. These factors make a reliable, objective phenotyping and the comparison with other studies difficult.

The results of **Chapter 1** showed highest heritabilities for the nursing behaviour and the group behaviour of sows, making those promising traits for a selection for improved mothering ability of sows. A significant part of between-individual variance is captured by the permanent environment, most obvious for the estrus behaviour, farrowing behaviour, the balance of the litter and the average weight of the piglets in the litter. Comparing the estimates of the linear mixed model and the threshold model, it becomes clear that the latter offers higher heritability estimates, which is most evident for the estrus and the group behaviour. Nevertheless, the threshold model is a more elaborate method that requires a higher computational effort (Sorensen and Gianola, 2002). Even though estimates are higher, they are still low, indicating that an acceleration of genetic gain is possible for certain traits, but will be time-consuming.

The results of this study are based on field-recorded observations. For large amounts of data, on-farm phenotyping replaces stationary assessments of only a small number of animals. This approach requires the motivation of breeders/farmers, a practical and easy recording of data, and transfer, but is also closer to practical conditions and not as cost intensive as stationary assessments (Grandinson et al., 2003; Vangen et al., 2005). The approach of field-recording and online data transmission by the pig breeding association "Schweinezuchtverband Baden-Württemberg e.V." shows that collecting reliable on-farm data by trained farmers is possible on a large scale, and can provide big data for quantitative genetic analyses whether it is for behavioural traits or other new traits.

Breeding associations deal with behavioural traits of sows to address legal requirements, e.g. open housing systems, related animal welfare issues and consumers' and breeders' demands for a more animal oriented food production. The cooperation of the "Schweinezuchtverband Baden-Württemberg e.V." with the French breeding association AXIOM, concerning the improvement of mothering abilities of sows, indicate a decline of piglet losses due to teat quality of the sows (German Genetic, 2018).

Various studies investigated new functional and behavioural traits in dairy cows to adapt to future circumstances and optimise current breeding schemes. The utility of direct health traits for breeding programmes, such as mastitis diagnoses, was shown by Egger-Danner et al. (2012) for Austrian

Fleckvieh cattle and Heringstad et al. (2007) for Norwegian red cattle. Koeck et al. (2010) and Urioste et al. (2010) investigated newly defined udder health traits in Fleckvieh and Norwegian Red cattle, like the prolonged elevated somatic cell score, and found higher genetic correlations with mastitis in comparison to the commonly used somatic cell score. Many studies deal with reproduction traits, e.g. calving and mating behaviour information, artificial insemination, fertility disorders and body conditioning score (Egger-Danner et al., 2014; Pryce et al., 2001; Løvendahl and Chagunda, 2010). Other traits relate to the cows' behaviour, such as temperament during milking or the sucking behaviour of the cow or calf (Kramer et al., 2013; Fuerst-Waltl et al., 2010a; Dreher et al., 2019). Due to future climate protection, a special focus lays on traits optimizing the methane emission of dairy cows, like the methane emission predicted from the residual feed intake (De Haas et al., 2011).

For the investigation of new and behavioural traits, clear and objective definitions need to be established. This may help to allow large scale data collection on-farm by trained farmers. Several studies showed that this approach is expedient and data quality is similar to those of expert staff, e.g. veterinarians (e.g. Gernand et al., 2012; Grandinson et al., 2003). Furthermore, clear definitions of traits can increase the calculated parameters of quantitative genetic analyses, e.g. heritabilities, and simplify the decision-making process over including new traits in existing breeding schemes, regarding achievable genetic gain in an appropriate time. Moreover, genetic correlations to economically important production traits should be considered and investigated to avoid economic losses.

Apart from the investigation and implementation of new traits in existing breeding programmes, the economic component of breeding schemes can be optimised. The ideal weighting of existing or new traits in total merit indices to estimate values of animals and, therefore, their potential for selection is crucial regarding profit maximisation for breeders, and differs depending on breeding goal, country, breed, species, environmental factors etc. Various studies use different approaches for the estimation of optimised/customised relative economic weights, such as objective, profit-oriented approaches (Amer et al., 1996; Fuerst-Waltl et al., 2010b), or alternative, non-objective methods, like choice experiments (e.g. von Rohr et al., 1999; Teegen et al., 2008; Martin-Collado et al., 2015; Roessler et al., 2012).

The latter was the objective of **Chapter 2**. Results showed that the applied discrete choice experiment (DCE) is suitable to derive environmental-specific relative economic weights (REW) for a limited number of traits or trait complexes. The use of external information, e.g. the production system and the farmers' educational level, confirmed heterogeneous farmers' trait preferences. These results are in accordance with studies by Martin-Collado et al. (2015), Ahlmann et al. (2014) and Slagboom et al. (2016 a,b). Organic farm managers placed a high weight on the fitness trait complex compared to conventional farm manager. This might be due to the need for robust cows; in addition, higher milk yields are most likely not to be achieved due to feeding restrictions. The same holds true for the marginal willingness to pay. Comparable results were found by Ahlman et al. (2014) for Swedish dairy farmers. Contrasting results were shown by Slagboom et al. (2016 a) for farmers in Denmark. The researchers explained the higher priority of production traits for organic farm manager with the need to improve problematic traits.

The farmers' responses to structured questionnaires make the DCE a bottom-up approach. In comparison to profit-oriented approaches, like the herd model (Amer et al., 1996; Fuerst-Waltl et al., 2010b), the discrete choice approach is not strictly economically driven, but it can model farmers' preferences very flexibly and straightforwardly. It is based on utility theory instead of the concept of profit maximisation, like the herd model or direct costing and profit functions (Brascamp et al., 1985; Nielsen and Amer, 2007). This makes the DCE a target-oriented method to judge the importance of specific traits for farmers. New traits in particular, such as the sucking behaviour of Brown Swiss calves (Dreher et al., 2019), can be evaluated, even if they have not yet been monetarily evaluated. Furthermore, environment-specific REW can be derived, which can be used to develop environment-specific total merit indices (see Chapter 3). The stated advantages of the DCE over strictly profit-oriented approaches might help breeding organisations in their decision-making processes. The application of those questionnaires on a regular basis can be used for the assessment of current total merit indices of breeding programmes. Results can then be used for the adjustment of current total merit indices or to answer questions like whether to include new traits or trait complexes in existing breeding schemes.

The results of Chapter 2 indicate, by comparing the DCE-derived REW and the currently used REW for the German Brown Swiss population, that they agree to a large extent. This might be due to recent adjustments of the total merit index for Brown Swiss (Fuerst-Waltl et al., 2016). In this study, farmers responded positively to the new trait sucking behaviour of the calf and desire its

inclusion in the total merit index. This would result in reduced REW for the milk traits complex. As a final assessment, a combination of discrete choice studies on a regular basis and purely profit-oriented approaches would be best to optimise existing breeding schemes and total merit indices.

Several studies investigated consumers' and farmers' preferences for specific attributes in pig breeding, using both, objective and non-objective methods. A study by Krupová et al. (2016) reviewed different methods to calculate economic weights for breeding traits in pigs. Serenius et al. (2007) used an objective, bio-economic approach to estimate economic values for sow efficiency and meat quality in pigs. Estimated economic values were high for the total number of piglets born, feed conversion ratio and lean meat. Additionally, meat quality should be considered in the production trait index to avoid its decline. Wallenbeck et al. (2016) used online-questionnaires to study farmers' preferences for pig breeding goals in organic and conventional pig breeding goals. They found that, regarding estimated desired genetic gain, organic farmers favoured health traits. Conventional farmers, on the other hand, favoured growth traits. Another study investigated the preferences for animal welfare in pig production. Denver et al. (2017) applied choice methods to determine consumers' preferences for pig welfare. Results indicated that consumers won't pay for improved animal welfare beyond a certain level. Roessler et al. (2008) used choice experiment to investigate preferences of smallholder farmers for specific pig breeding traits in Vietnam. Heterogeneous preferences were found for the resource-driven and demand-driven production systems. The variety of studies shows the need for the different methods to take available information, e.g. production environments, farmers' preferences and profit of production, into account for the optimisation of breeding schemes.

Genotype by environment interactions for varying environments (Chapter 3 and 4)

Besides the optimisation of current breeding schemes by revising economic weights or including new traits to address certain difficulties, the effect of the environment on animal breeding becomes a big issue. This is because of the globalisation of animal breeding and the variation of production systems and environments and need to be considered. These environmental challenges are not only due to changes on the market, e.g. international breeding cooperatives (e.g. EuroGenomics, Interbull, PIC). Climate and resource management, the role of the animal in food production,

relating animal welfare and consumers' demands lead to a variation in production systems and environments as well.

Thus, GxE are a source of variance in quantitative traits and need to be accounted for. Otherwise, they can lead to a reduced response to selection and, therefore, an inefficiency of the underlying breeding programme. Two types of GxE are of interest for animal breeding. Firstly, GxE can induce a different scaling of genotypes performances in varying environments without a reranking; secondly, it can lead to a reranking of genotypes. The latter indicates that the performance of the best animal in one environment may be impairing in the other environment.

GxE can occur between environments that can be easily defined in categories, for example organic and conventional farming systems (Nauta et al., 2006; Simianer et al., 2007; Pfeiffer et al., 2016) or geographical regions and the altitude level of the farm (Williams et al., 2012; Koenig et al., 2005). Other environments are better described by continuous variables, for example a temperature humidity index or the milk energy yield of dairy cows (Hayes et al., 2016; Calus et al., 2002; Streit et al., 2012). The definition of environments under investigation is crucial for the choice of approaches to account for GxE. Hayes et al. (2016) presented two common approaches to account for GxE, depending on the environmental descriptor used. Multitrait models consider a genotype's performance for a trait in varying environments as different but potentially correlated traits. The genetic correlation between the traits can be used as an indicator for the degree of reranking between the environments under study. For strongly varying environments a $r_g<0.8$ can occur, indicating the demand for separate breeding programmes for the traits and environments under investigation (Boelling et al., 2003; Robertson, 1959; Mulder et al., 2006). If the environment can be described best by a continuous variable, reaction norm models are the appropriate choice. Thereby, the response to environmental changes are modelled as a curve with an intercept and a slope for each genotype using random regression (Hayes et al., 2016).

Chapter 3 investigated GxE in Brown Swiss cattle in southern Germany for several common production and functional traits between varying production systems and farm altitude levels using bivariate sire models. Genetic correlations, estimated with a bivariate sire model on trait level, were high and indicated no severe GxE. Thus, no need for an adjustment of the existing breeding programme seems necessary. The study of GxE between organic and conventional production systems is of particular interest due to future circumstances, e.g. the optimal use of resources with

regard to climate change, political frameworks and consumers call for alternative production conditions. The results of Chapter 3 are in accordance with various studies investigating GxE for several traits between categorical environments (e.g. Nauta et al., 2006; Sundberg et al., 2010; Simianer et al., 2007; Pfeiffer et al., 2016). In general, genetic correlations for production traits, like milk yield, are above 0.8 between varying environments in the same country or area (Kearney et al., 2004; Simianer et al., 2007; Sundberg et al., 2010; Pfeiffer et al., 2016). This is different for functional traits. Genetic correlations for longevity, maternal calving ease and maternal stillbirth between different countries of the Interbull project are on average below 0.6 (Mark, 2004).

The advantages of the applied multitrait approach are the flexibility in modelling the variance-covariance structure and the use of the results for straightforward conclusions for adaptions of breeding programmes (Mulder, 2007). Furthermore, the approach is capable of handling various types of data structures. The data used in Chapter 3 was slightly off-balance regarding the number of phenotyped animals, farms and sires between the investigated environments. Even though this might have affected the detection of GxE effects, this data structure depicts reality most accurately. In animal breeding, the multitrait approach is widely used because GxE can easily be estimated using relationship information, e.g. genetic information between sires' daughters performing in varying environments, and genetic correlations between environments provide indications for optimizing breeding programmes.

In addition to the investigation of GxE effects at a trait level, putative GxE effects for the production system environments at an index level were estimated in Chapter 3. Sires' EBV for organic and conventional production systems were estimated and environment-specific relative economic weights, approximated by factors from routine applications, were used to create total merit indices. Estimated rank correlations indicated no severe reranking of sires at an index level. Differences in performance can be the result of GxE, the underlying breeding goals or genetic variances and correlations between traits. To study GxE for multiple traits in two environments at an index level, Mulder (2007) introduced an alternative approach to the applied method presented in Chapter 3. He presented the genetic correlation between breeding goals (r_H), combining economic values of environments under investigation and the full genetic variance-covariance matrix between the traits in those environments. Studying differences between organic and conventional production systems and possible GxE effects, breeding goals for both environments are divergent, but usually not contrary. For this kind of breeding goals, effects of economic values

are smaller and the correlation between the breeding gaols is mostly driven by the genetic correlation (Mulder, 2007). The results of Chapter 3 suggested no separate breeding programmes for Brown Swiss cattle for the investigated environments. Nevertheless, the provision of an organic TMI (LfL, 2018) for this breed is beneficial for breeders. The environment-specific TMI allows a selection of animals best suited for the production environment and therefore a maximization of genetic gain in the population, especially for organic production systems' preferred functional traits.

The previously used multitrait approach is not suitable for multiple environments, because of convergence, and estimation problems (Strandberg, 2006). In consequence of the classification of two specific production environments, the data set used in Chapter 3 was slightly unbalanced. Accordingly, to estimate GxE effects for common production and functional traits, the adaption of the environmental descriptor and the application of reaction norm models were focused on in **Chapter 4**. Following several studies, a continuously scaled descriptor (milk energy yield; MEY), capturing a large range of herd environments, was used (Calus et al., 2002; Strandberg et al., 2009; Streit et al., 2012). The results of chapter 4 showed no GxE for the investigated functional traits but for the production trait fat yield. This might be due to the modelling of the environmental descriptor MEY which was calculated using the derivates of the production traits milk, fat and energy yield (Nostitz and Mielke, 1995; Streit et al., 2012). As a result, this descriptor might be more suitable to detect possible GxE effects for the investigated production traits compared to the functional traits. The same was found and discussed by Streit et al. (2012), who studied GxE for several production traits in German Holstein cattle, using MEY or somatic cell score as environmental descriptors. The findings for functional traits contrast with the results of Kolmodin et al. (2002) and Loberg et al. (2015). Heritabilities for functional traits are low and the influence of the environment is greater. Hence, the impact of GxE on the phenotypic expression of such traits might be more probable.

The estimated slope variances of the study in Chapter 4, describing the environmental sensitivity of the investigated genotypes, indicated no GxE either. This might be due to several reasons: individuals under investigation seem to be quite robust, meaning they are not very sensitive to environmental changes. In addition, the variance of considered environments might be small in the terms of very homogenous herd production levels across production environments. Furthermore,

Spearman rank correlations between the estimated breeding values for the sires and investigated traits were calculated, indicating a severe reranking of genotypes.

The investigation of genotype by environment interactions is a key issue in cattle breeding, hence breeding programmes and structures, production environments and management systems are varying more than in pig breeding. This is a consequence of the international use of genetics and the divergent management systems. In general, studies investigating GxE in pigs are rare. Commonly, GxE between nucleus and commercial environments are investigated because these environments are strongly divergent. Nucleus breeding programmes are characterised by small purebred herds, bred under controlled conditions, e.g. feeding regime, production climate, number of animals and hygiene level (Mulder, 2007). In contrast, production or commercial environments are used for the piglet production. This is achieved by crossbreeding various purebred breeds, for instance Duroc sires with excellent meat quality and sows with a high reproduction rate and good mothering abilities (e.g. German Landrace). Several studies estimated genetic correlations between these production systems and found a wide range of estimates, from 0.3 up to unity (Merks, 1988; Cameron, 1993). Findings suggest a distinction between GxE effects and "non-unity genetic correlations between purebred and crossbred performance". The latter can, hence, lower the correlation between environments under investigation (Mulder, 2007). A study by Brandt et al. (2009) investigated GxE for growth and carcass traits in various pig breeds between organic and conventional production systems. They concluded that no separate breeding programmes for the breeds and environments under investigation are needed. Linear reaction norms were estimated by Knap and Su (2008). The total litter size at birth as a function of routine herd-year-season effects were estimated for two PIC lines and their crosses, spread over various environments (America, Europe, Asia, Australia). Their results indicated that for the reaction norm approach a great amount of data and a wide range of environments is necessary to produce reliable results.

The findings of this thesis underline the need of a revision of existing breeding programmes in pigs and Brown Swiss cattle on a regular basis. Various external influences, like economical, political, ethical and environmental changes, lead to possibly necessary modifications of breeding schemes for livestock. The analysis of the usage of **new traits** for the improvement of animal productivity, health and the economic optimisation of production systems is of great interest. The data recording for mothering ability traits in pigs under the field is closest to practical conditions. The results indicate that, if phenotyping strategies are most objective and repeatable, behaviour traits are

heritable and of use for the improvement of breeding schemes. A direct transmission of the collected on-farm data to the breeding organisation simplifies quantitative analyses processes and quick results can motivate the involved parties to investigate new traits and to cooperate. The inclusion of such traits can help to improve the mothering ability of sows in the future.

To involve breeders' preferences for specific attributes or traits of their breed, the **discrete choice experiment** seem to be a straightforward approach. The design of the choice sets is crucial, and traits considered need to be known by or well explained to the farmers. However, the participation in the survey is very intuitive and farmers as well as breeding organisations can benefit from the results. Moreover, operational characteristics of farms or farmers can be included to estimate environmental-specific relative economic weights for the queried traits. Furthermore, in contrast to strictly economic approaches, the preferences for new and not yet monetarily evaluated traits or trait complexes is possible, thus the interest of participants for common and new traits can be evaluated on a regular basis. Results of the DCE might lead to the revision of existing breeding programmes regarding included traits and environment-specific economic weighting factors of such in Brown Swiss cattle.

In addition, the investigation of **GxE** for several production and functional traits in varying environments in Brown Swiss cattle seem to be crucial regarding future circumstances. Both approaches applied in this thesis showed that currently separate breeding programmes for the studied environments and traits do not seem necessary, neither on trait nor on index level. The multitrait approach enables an analysis of possible GxE effects for two classified environments, e.g. organic and conventional production systems. The bivariate sire model can handle unbalanced data sets (close to practical data conditions), is flexible in modelling the variance-covariance structure, and the results can be used for straightforward conclusions for adaptations of breeding programmes. Random regression norm models can be applied if the environmental descriptor is a continuous variable, like the described milk energy yield. Reasonable estimates can be achieved, if the data structure is suitable and the amount of data and variability is sufficient. Due to the difficulty of finding appropriate environmental descriptors for GxE, the reaction norm approach has not been implemented in practical animal breeding so far (Mulder, 2007).

Even though no severe GxE were found for the investigated traits and environments in the German Brown Swiss cattle population, further analyses using single herd-test-day-records and other,

promising environmental descriptors might be of interest to investigate possible GxE in German Brown Swiss cattle. Even though this breed seems to be quite robust to environmental changes, differences in performance are known. Currently, the environmental-specific organic total merit index (LfL, 2018) takes this into account. It allows breeders to select animals best suited for their production environment and, therefore, maximise the genetic and economic merit based on farmers' preferences.

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