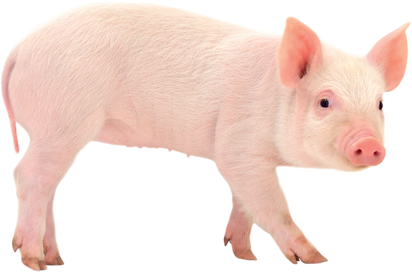
SHEILA AIKINS-WILSON

Analyses of tail length, skin lesions and active behaviour pattern of pigs in the context of genetics, feeding and genotype by feeding interactions



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submitted by

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Born in Saltpond, Ghana

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With the approval of the Faculty of Agricultural Sciences, Nutritional Science and
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Dedicated to my late parents

Mr. Joseph Aikins-Wilson and Madam Grace Esi Kosima Mensah

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LIST OF ABBREVIATIONS

ADG	Average daily gain
ADG_{CON}	Average daily gain- in control basal treatment
ADG_{HD}	Average daily gain- in herbal treatment
AIC	Akaike’s Information Criterion
AVPR1B	Arginine Vasopressin Receptor Gene
BCON	Body contact
BIC	Bayesian Information Criteria
BITE	Ear or tail biting
BT	Backtest
BW	Birth weight
CFC	Continuous Function Chart
CLE	Common litter effects
cm	Centimetre
CON	Control basal diet
CV	Coefficient of variation
DMI	Dry matter intake
DMU	Dynamic model updating
DMUV6	Dynamic model updating version 6
EC	European Commission
EBV	Estimated Breeding Value
EFSA	European Food Safety Authority
EXPLORE	Explorative behaviour
EU	European Union
FIGHT	Fighting

g	Gram
G x E	Genotype by Environment interactions
h^2	Direct heritability
h^2_d	Direct heritability
h^2_m	Maternal heritability
HD	Herbal diet (basal diet plus a supplement with chicory herbs)
HPA	Hypothalamic-pituitary-adrenocortical
HR	High Resisting
IFIGHT	Initiating fights
IGE	Indirect genetic effect
IR	Intermediate Resisting
kg	kilogram (s)
LIN	Linear model
LRT	Likelihood ratio test
LR	Low Resisting
LS	Lesion Score
LS_{CON}	Lesion score - in control basal treatment
LS_{HD}	Lesion score - in herbal treatment
lsmeans	Least squares means
NR3C1	Glucocorticoid receptor gene
PWW	Post weaning weight
PWW_{CON}	Post weaning weight- in control basal treatment
PWW_{HD}	Post weaning weight- in herbal treatment
RACT	Remaining activities
RBV-LS	Relative breeding values for skin lesions

REML	Restricted maximum likelihood
REST	Resting time
RFIGHT	Refusing of fights
SD	Standard Deviation
SE	Standard Error
SRUC	Scotland's Rural College
SINS	Swine inflammation and necrosis syndrome
TH	Threshold model
T-LEN	Tail Length
T-LES	Tail Lesions
WW	Weaning Weight

SUMMARY

A major unsolved welfare issue in pigs is aggressive and tail biting behaviour. This behaviour is induced by environmental, genetic, and nutritional factors. Genetic components as well as genotype by environment interactions have been identified to affect primary and functional trait responses to biting in pigs. Furthermore, one key trigger for tail biting is the length of the tail. The persistence of tail biting in commercial farm conditions has resulted in the majority of large pig enterprises considering docking of the tails of all piglets as a preventative measure, which does not correspond with legal animal welfare guidelines. Nevertheless, the future is to keep pigs with naturally long tails, implying improvements in animal breeding and behaviour. It remains unclear why some pigs are not victims of this aggressive behaviour in farm houses. Furthermore, it is imperative to identify the exact causes of abnormal behaviour, especially from a genetics perspective. Aggressive behaviour and tail biting in pigs can be mitigated by the use of breeding strategies and the modification of the production environment. This study focuses on the traits tail length, skin lesions and active behaviour pattern of pigs in the context of genetics, feeding and genotype by feeding interactions in pigs. Due to the lack of investigations in the literature addressing genetic parameters for tail characteristics and its effect on growth traits, **Chapter 2** is the first comprehensive report on genetic parameters for tail length (T-LEN). The chapter reported on T-LEN and growth traits: birth weight (BW), weaning weight (WW), post-weaning weight (PWW), and average daily gain (ADG) from 9,348 piglets from the University of Gießen research station. In addition, 4,943 binary observations from 1,648 pigs for tail lesions (T-LES) as indicators for tail necrosis, tail abnormalities, or tail biting were included in this analysis. T-LES were recorded at 30 ± 7 days after entry for rearing (T-Les-1), at 50 ± 7 days after entry for rearing (end of the rearing period, T-LES-2), and 130 ± 20 days after entry for rearing (end of fattening period, T-LES-3). Heritability estimate for T-LEN was 0.42 (± 0.03), indicating the potential for genetic selection on short tails. The maternal genetic heritability for T-LEN (0.05 ± 0.04), indicating the influence of uterine characteristics on morphological traits. The negative correlation between direct and maternal effects for T-LEN of – 0.35 (± 0.13), as well as the antagonistic relationships between T-LEN with the growth traits BW, WW, PWW, and ADG, complicate selection strategies and breeding goal definitions. The heritability for T-LES when considering the three repeated measurements was 0.23 (± 0.04) from the linear (repeatability of 0.30) and 0.21 (± 0.06; repeatability of 0.29) from the threshold model. The breeding value correlations between T-LES-3 and breeding values from the repeatability models were quite large (0.74 to 0.90), suggesting tail lesion recording at the end of the rearing period.

Nutrition plays a major role in pig behaviour such as the favourable feeding effects of the chicory herbal diet to reduce aggressiveness and simultaneously improve growth performance. For this reason, the aim of **Chapter 3** was to assess the feeding effect of the chicory herbal diet on production traits and lesions scores, and to study possible boar-diet and genotype by diet interactions in post weaning pigs. A cross-classified research design was implemented, focussing on an equal number of boar offspring in both feeding groups. Findings in chapter 3 indicate that the dietary treatment had no significant effect ($P > 0.05$) on growth traits (PWW and ADG). However, the dietary treatment significantly ($P < 0.05$) influenced the behaviour of the pigs, with a lower and favourable lesion score for the pigs allocated to herbal diet (HD; basal diet plus a supplement with chicory herbs). Results from the study indicate the importance of genotype by feeding interactions for pig breeding, suggesting specific boars for different feeding environments.

Chapter 4 provides an insight into the behavioural adaptation of individual piglets in the weaning stage kept in two different dietary environments. The backtest score (BT) behavioural tests was performed on piglets and classified as high-resisting (HR), low-resisting (LR) or intermediate-resisting (IR). Piglets were grouped based on the BT as well as the relative breeding value for skin lesions (RBV-LS) estimated for the sires. Video recordings of individual piglets were obtained and analysed on day one and at five weeks after weaning. Each animal was video monitored for 300 minutes for eight different behaviour traits. The aggressive behaviours traits and general activities decreased five weeks post weaning compared to the first day of weaning. Pigs classified as HR piglets were more aggressive than the LR and IR contemporaries, with significantly higher least squares means (lsmeans) for fight, ear or tail bite and exploration. The level of aggressiveness observed in the two dietary environments suggest that the herbal diet contributed to calm pig behaviour. Backtest scores as well as breeding values from a victim perspective (lesion scores) can be used as indicator traits for selection against aggressiveness.

Chapter 5 captured the results from the data and observations used for the analysis from **chapters 2, 3** and **4.** This chapter focussed on a general discussion based on the results from the previous chapters and presents conclusions drawn from the analyses. Recommendations were also given based on the findings, considering concerns and suggestions. In this regard, the heritability estimate for T-LEN suggested the possibility for breeding pigs with short tails. However, the maternal genetic influence on T-LEN as well as the correlations between T-LEN and traits of economic importance have to be taken into account when defining overall breeding goals. The importance of genotype by feeding interactions was detected, indicating re-rankings of sires in different feeding environments, and the favourable effect of herbal diet on pig behaviour.

ZUSAMMENFASSUNG

Aggressives Verhalten und Schwanzbeißen sind ein großes ungelöstes Tierschutzproblem in der Schweinehaltung. Dieses Verhalten kann durch die Umwelt, die Genetik, sowie durch ernährungsbedingte Faktoren ausgelöst werden. Genetische Komponenten, sowie Wechselwirkungen zwischen Genotyp und Umwelt, beeinflussen die primären und funktionellen Reaktionen auf das Beißen bei Schweinen. Ein wichtiger Auslöser für das Schwanzbeißen ist die Länge des Schwanzes. Da das Schwanzbeißen unter kommerziellen Haltungsbedingungen häufig auftritt, werden in den meisten Schweinebetrieben die Schwänze aller Ferkel als Präventivmaßnahme kupiert. Diese Vorgehensweise entspricht aber nicht den gesetzlichen Tierschutzrichtlinien. Zukünftig ist die Haltung von Schweinen mit natürlich langen Schwänzen gewünscht, was aber eine Verbesserung der Verhaltensmerkmale, auch über tierzüchterische Methoden, impliziert. Unklar ist u.a., warum einige Schweine keine Opfer von aggressiven Verhaltensweisen sind.Weiterhin müssen die genauen Ursachen des abnormen aktiven Verhaltens, insbesondere aus genetischer Sicht, ermittelt werden. Aggressives Verhalten und Schwanzbeißen bei Schweinen kann durch passende Zuchtstrategien und die Veränderung der Produktionsumgebung reduziert werden. Die hier durchgeführte Untersuchung betrachtet die Merkmale Schwanzlänge, Hautläsionen und Verhalten von Schweinen im Zusammenhang mit Genetik, Fütterung und Wechselwirkungen zwischen Genotyp und Fütterung bei Schweinen. Aufgrund fehlender Publikationen zu genetischen Parametern von „Schwanzmerkmalen“ und deren Auswirkungen auf Wachstumsmerkmale ist **Kapitel 2** eine erste umfassende Untersuchung in Bezug zu genetischen (Ko)Varianzkomponenten für das Merkmal Schwanzlänge (T-LEN). In diesem Kapitel wird der Zusammenhang zwischen T-LEN und Wachstumsmerkmalen, wie b Geburtsgewicht (BW), Absetzgewicht (WW), Gewicht nach dem Absetzen (PWW) und durchschnittliche Tageszunahmen (ADG) an 9.348 Ferkeln der universitären Forschungsstation der Justus-Liebig-Universität Gießen phänotypisch und genetisch analysiert. Zusätzlich wurden 4.943

binäre Beobachtungen an 1.648 Schweinen hinsichtlich Schwanzläsionen (T-LES) einbezogen. Die Schwanzläsionen gelten als Indikator für Schwanznekrosen, Schwanzanomalien und Schwanzbeißen. Die Erfassung von T-LES erfolgte 30 ± 7 Tage (T-LES-1), 50 ± 7 Tage (Ende der Aufzuchtperiode, T-LES-2) und 130 ± 20 Tage nach Einstallung in die Aufzucht (Ende der Mastperiode, T-LES-3). Die geschätzte moderate Heritabilität für T-LEN von 0,42 (± 0,03) eröffnet die Möglichkeit auf kurze Schwänze zu züchten. Die maternale genetische Heritabilität für T-LEN (0,05 ± 0,04) deutet auf den Einfluss von Uterusmerkmalen auf morphologische Merkmale der Nachkommen hin. Die negative Korrelation zwischen direkten und mütterlichen Effekten für T-LEN von -0,35 (± 0,13) sowie die antagonistischen Beziehungen zwischen T-LEN und den Wachstumsmerkmalen BW, WW, PWW und ADG erschweren aber mögliche Selektionsstrategien und Zuchtzieldefinitionen unter Berücksichtigung der Schwanzlänge. Die Heritabilität für T-LES unter Berücksichtigung von drei wiederholten Messungen innerhalb Tier betrug 0,23 (± 0,04) im linearen Modell (Wiederholbarkeit von 0,30) und 0,21 (± 0,06; Wiederholbarkeit von 0,29) im Schwellenwertmodell. Die Korrelationen zwischen dem Zuchtwert T-LES-3 und den Zuchtwerten aus den Wiederholbarkeitsmodellen waren recht hoch sowohl in linearen als auch in Schwellenwertmodellen (0,74 bis 0,90). Daher scheint ein einmaliger der Erfassungszeitpunkt von Läsionen am Ende der Mast als ausreichend.

Die Ernährung mit den dazu verwendeten Futterkomponenten hat einen wichtigen Einfluss auf das Verhalten von Schweinen. Beispielsweise kann der Zusatz von Kräutern im Futter die Aggressivität verringern und verbessert gleichzeitig die Wachstumsleistung. Aus diesem Grund war das Ziel in **Kapitel 3**, den Fütterungseffekt von Kräutern (Zugabe von Chicorée) auf die Produktionsmerkmale und Läsionen zu bestimmen und mögliche Wechselwirkungen zwischen Eber (Vater) und Futter sowie Genotyp und Futter bei Absatzferkeln zu untersuchen. Dazu wurde ein kreuzklassifiziertes Forschungsdesign mit gleichmäßiger Verteilung von genetischen Gruppen auf beide Fütterungssysteme (Chicoréezugabe versus Kontrollgruppe) implementiert.

implementiert. Die Ergebnisse in Kapitel 3 zeigen, dass die Fütterung keinen signifikanten Einfluss ($P > 0{,}05$) auf die Wachstumsmerkmale (PWW und ADG) hatte. Die Fütterung hatte jedoch einen signifikanten Einfluss ($P < 0{,}05$) auf das Verhalten der Schweine. Hierbei konnte für die Schweine mit Kräuterzusatz im Futter (Grundfutter plus Zusatz von Chicorée) eine niedrigere und somit günstigere Verletzungsrate beobachtet werden. Die Ergebnisse der Studie zeigen die Bedeutung der Wechselwirkungen zwischen Genotyp und Fütterung in der Schweinezucht. Für verschiedene Fütterungsumwelten werden bestimmte Väter (Eber) favorisiert, die sich aber in der Rangierung in den jeweiligen Umwelten nach geschätzten Zuchtwerten unterscheiden.

Kapitel 4 adressiert die Beziehungen zwischen frühen Verhaltensmerkmalen von Ferkeln mit späteren Verhaltensmerkmalen in der Mast in den zwei verschiedenen Fütterungsumwelten (Chicoréezugabe versus Kontrollgruppe). Mittels Backtest (BT) wurden die Ferkel als sehr widerstandsfähig (HR), wenig widerstandsfähig (LR) oder mittelstark widerstandsfähig (IR) eingestuft. Die Ferkel wurden basierend auf dem BT-Ergebnis sowie des für die Väter geschätzten relativen Zuchtwerts für Hautverletzungen (RBV-LS) in Gruppen eingeteilt. Am ersten Tag und 5 Wochen nach dem Absetzen wurde das Verhalten einzelner Ferkel per Video aufgezeichnet und ausgewertet. Zu jedem Tier standen Videoaufnahmen über eine Dauer von 300 Minuten zur Verfügung. Bei der Auswertung wurden 8 verschiedene Verhaltensmerkmale einbezogen. Die aggressiven Verhaltensweisen wie Beißverhalten und die allgemeinen Aktivitäten nahmen generell fünf Wochen nach dem Absetzen im Vergleich zum ersten Tag des Absetzens ab. Schweine, die als HR-Ferkel eingestuft wurden, waren aggressiver als ihre LR- und IR-Zeitgenossen. Diese Schweine hatten signifikant höhere LS-Mittelwerte (lsmeans) für Kämpfen, Beißen von Ohren und Schwanz sowie für das Erkundungsverhalten. Das in den beiden Fütterungsumwelten verglichene Aggressionsniveau deutet darauf hin, dass die pflanzliche Ernährung mit Chicoréezugabe zu einem ruhigen Verhalten der Schweine führt. Weiter zeigte sich, dass die Backtest-Einstufung sowie die Zuchtwerte aus der

Opferperspektive (Läsionswerte) als Indikatormerkmale für die Selektion gegen Aggressivität verwendet werden können.

In **Kapitel 5** sind die Ergebnisse aus den Kapiteln 2, 3 und 4 zusammengefasst. In diesem Kapitel wird auf Grundlage der Ergebnisse aus den vorangegangenen Kapiteln umfassend diskutiert und es werden Schlussfolgerungen und Empfehlungen auf Basis der vorliegenden Analyseergebnisse abgeleitet. Die geschätzte moderate Heritabilität für T-LEN deutet darauf hin, dass die Zucht von Schweinen mit kurzen Schwänzen auf Basis quantitativ-genetischer Modellemöglich ist. Der maternal genetische Einfluss auf T-LEN sowie die Korrelationen zwischen T-LEN und Merkmalen von wirtschaftlicher Bedeutung (Merkmale der Wachstumsleistung) müssen allerdings bei der Festlegung allgemeiner Zuchtziele berücksichtigt werden. Die Bedeutung von Wechselwirkungen zwischen Genotyp und Fütterung wurde für Verhaltensmerkamle nachgewiesen. Somit sollten gezielt Vatertiere (Eber) für bestimmte Fütterungsumwelten selektiert werden.

CHAPTER 1

GENERAL INTRODUCTION

1.1. Behaviour in animals

Animal behaviour is a complex phenomenon influenced by genetics, hormones, biological mechanisms known as internal factors and external factors such as environmental cues and social interactions (Ellen et al., 2008; Breed and Moore, 2012; Garland et al., 2016; Camerlink et al., 2018). Behaviour is the most immediate and effective way for individuals and populations respond to environmental challenges (Kappeler et al., 2013). Animals can react differently when confronted with unfamiliar conspecifics with behaviours such as nervousness, adventurous (Clark and Ehlinger, 1987; Wilson et al., 1994), aggression (Benus et al. 1992), fearful (Greenberg and Mettke-Hofmann, 2001) or curious (Winkler and Leisler, 1999; Canario et al., 2020). These behaviours provide fundamental understanding and information about husbandry conditions, feed, production efficiency, health and general welfare of animals (Liu et al., 2022). In an attempt to understand the aggressive behaviour in farm animals, the ontogeny, adaptation, phylogeny and the causation; the four questions asked by Tinbergen (1963) cited by Olsson and Keeling, (2005) has been very relevant in the development of scientific strategies to improve animal welfare and reducing aggressive behaviours. In modern behavioural science, new technologies such as the use of sensors to monitor animal behaviours and computer imaging have been developed to detect normal and abnormal behaviours (feeding, maternal, milking, aggressive and reproductive behaviour) in farm animals which is essential in improving production efficiency and animal welfare (Oczak et al., 2013; Desire et al., 2016; Rivera-Chacon et al., 2022). For example, the use of sensors in feeding behaviour to establish interactions between pen mates and social structure within a group (Ragab et al., 2019) and video images to identify aggressive animals (Desire et al., 2016).

Abnormal behaviour in farm animals is a welfare issue because of its negative consequences on production. The most notable abnormal behaviour in farm animals are ear and tail biting in pigs (D’Eath, et al., 2014), feather pecking and cannibalism in poultry (Riber and Forkman, 2007; Rudkin, 2022), wool-biting behaviour of sheep (Huang and Takeda, 2017) and agonistic behaviour in cattle (Pinheiro Machado et al., 2020). All these behaviours are heritable (Peden et al., 2018). In cattle for instance, temperament heritability have been reported to range between 0.10 ± 0.10 and 0.61 ± 0.17 without any significant correlations between behaviour and production traits suggesting that genetic improvement of behaviour can be done through genetic selection (Titterington et al., 2022). Cannibalistic feather pecking and aggressive behaviour in poultry and in pigs were found to be heritable with heritability ranging from 0.07 to 0.65 for feather pecking and 0.09 to 0.32 for tail biting in pigs (Craig and Muir, 1993; Kjaer and Sørensen, 1997; Breuer et al., 2005). Sows behaviour towards its piglets was estimated to be highly heritable (0.90) trait (Grandinson et al., 2003). Understanding the behaviour of animals, the strength of selection on behaviour, its genetic basis, and the genetic correlations between it and other traits is important to improve animal behaviour and welfare.

1.2. Behaviour in pigs

Animal behaviour have been grouped into five categories namely exploration, avoidance of novelty, willingness to take risks, sociability and agonistic behaviour (Réale et al., 2007). In pigs (*Sus scrofa*), the most evident behavioural changes are exploration, sociability and agonistic behaviour (Forkman et al., 1995; Jensen et al., 1995; Clouard et al., 2022). Behaviours in pigs such as nursing, resting, excretory, feeding and drinking have been classified as normal behaviours whiles as piglets savaging, anxiety, belly-nosing, tail biting and aggressiveness are classified as abnormal behaviour (Edwards, 2006; Allwin and Swaminathan, 2016; Clouard et al., 2022). Wood-Gush and Vestergaard (1993) defined exploratory behaviour of pigs as extrinsic and intrinsic exploration. In both extrinsic and intrinsic exploratory behaviour, the animal engages in novel situations which is found both in the wild and in modern husbandry systems. In extrinsic exploration behaviour the animal seeks information such as food, whiles intrinsic exploration is directed toward stimuli such as inspects a particular object (inspective exploration) and performs behaviour to make a change in its environment (inquisitive exploration). Highly exploring pigs are more interactive with the environment and their conspecifics. However, in intensive husbandry systems where movement is restricted, the urgency of the pig to perform exploration and foraging behaviour leads to redirected oral manipulation resulting in tail biting and aggressive behaviour (Fraser et al., 1991). In a study by Kavlak and Uimari (2019), estimated heritability of feeding behaviour varied between 0.17–0.47 and study concluded that feeding behaviour traits could be valuable in the breeding programme for animal welfare.

Pigs are known to be sociable animals in stable social groups established on a linear hierarchy based on dominant-subordinate relationships between group members (Ewbank, 1976). This relationship is formed through aggressive behaviours mostly observed during mixing in the weaning phase (Marques et al., 2012; Fels et al., 2012; Lau et al., 2015; Schrey et al., 2019). Aggressive behaviour includes different forms such as territorial aggression, dominance-related aggression and maternal aggression (Chang et al., 2012: Fels et al., 2012; Desire et al., 2016). The aggressive behaviours in pigs have received extensive research attention by exploring social personality traits and individual coping strategies in behaviour and physiology (Melotti et al., 2011; Ellen et al., 2014; Finkemeier et al., 2018; Canario et al., 2020). However, these authors used different concepts and terminology to explain individual differences making it difficult to compare studies. Moreover, the studies are mostly on adult pigs and little is known about the development of early social styles. According to Martínez-Miró et al. (2016) and Clark et al. (2014), early life experiences have been found to have long-term effects on an individual's phenotype and, in some cases, on that of its offspring. For instance, in sheep, tail docking has been found to have effects on an individual's development and behaviour (Champagne, 2013). Hessing et al. (1994) measured the behaviour of pigs at an early stage by placing the pig on its back and behavioural responses which may range from vigorous struggling and screaming to immobility recorded. The backtest responses were used as a representation from different coping styles to environmental challenges, which were grouped as active and passive (aggressive and non-aggressive behaviours, respectively) in the way as the proactive-reactive coping model described by Koolhaas et al. (1999). A correlation between the different reactions in the backtest and different behaviours in later life was observed (Hessing et al., 1994; van Erp-van der Kooij et al., 2003; Turner et al., 2008). In the same way, certain features have been associated with personality traits (Miranda-de la Lama et al., 2019). For instance, lighter weight pigs are found to be more biters, while the bigger pigs are more aggressive (Hessing et al., 1994; Rizvi et al., 2000; Van Erp-Van Der Kooij et al., 2003; Edwards, 2006; Turner et al., 2008; Palander et al., 2013). The avert, affiliative, aggressive; and less aggressive ewe differ in their body length, body weight and/or thorax circumference while aggressive and non-aggressive or affiliative animals showed contrasted cortisol levels (Miranda-de la Lama et al., 2019).

1.3. Tail biting in pigs

Tail biting is any form of oral manipulation or biting behaviour resulting in lesions of the tail (Van Putten, 1969; Schrøder-Petersen and Simonsen, 2001). It is a serious animal welfare and economic problem causing undesired injuries and pathological problems (Sihvo et al., 2012; Munsterhjelm et al., 2013), affecting the production and rejection of end products (Kritas and Morrison, 2007; Sinisalo et al., 2012; Boumans et al., 2018). Tail biting is multi factorial triggered by many factors such as environment, housing, nutrition, sex ratio, temperature fluctuations, inadequate ventilation, general health problems, as well as internal factors such as genetics and age playing a role in the occurrence of this behaviour (Schroder-Petersen and Simonsen, 2001; EFSA, 2007). Many of these factors have been considered in several studies aimed at eliminating aggressive behaviour and tail biting in pigs, but they have not been successful. The origin of tail biting is not known (Fraser, 1987; EFSA, 2007), but the major underlying cause of tail biting and aggressive behaviour is reported to be in environments where foraging behaviour is limited. For instance, a study by Rizvi et al. (2000) mentioned that, aggressive behaviour in sows was associated with the lack of foraging activities and access to feed. Even in the wild, where foraging behaviour is not restricted and pigs have unlimited access to explore, aggression behaviour was still observed among pigs (Allwin and Swaminathan, 2016). It is, however, unclear whether tail biting is induced by environmental, genetic, nutritional, and motivational influences for oral manipulation. In animal population, individuality can be expressed through behaviour which is consistent across time. However, in the expression of aggressive behaviour, many questions are asked regarding why some pigs are not victims of aggressive behaviour in farm houses (Keeling et al., 2004; Beattie et al., 2005). In view of this, a study by Brunberg et al. (2013a) found differences between neutrals, performers (pigs not bitten or involved in biting), and receiver biters in terms of their gene expressions, which could contribute towards understanding pig behaviour.

Three different behavioural types of tail biting have been described by Taylor et al. (2010): that is two-stage, sudden-forceful and obsessive behaviour. The stage two type of behaviour consists of a pre-injury stage and an injury stage (Fraser, 1987). In the pre-injury stage, pigs chew on the tail of other pigs without causing visible wounds or distress. At the injury stage, the wounds gets worse and bleeds more (Fraser, 1987), resulting in an outbreak of tail biting since pigs are attracted to blood (Fraser et al., 1991; Sandnabba, 1997). Taylor et al. (2010), further explained that the obsessive type of tail biters focus on biting usually characterised by forceful biting of inmate tails. The sudden-forceful type of tail biting is less frequent, acute, rapid and usually characterized by the removal of the tip of the tail or portions of the skin and flesh of the pig. All these behaviours have different motivational bases with different underlying problems, which are often unpredictable (Taylor et al., 2010; D'Eath, et al., 2014). It is, therefore, important to identify factors that are common in pigs that perform tail-biting behaviour, and that might be used in a predictive way to identify such animals (Beattie et al., 2005). Selection of pig genotypes that have a lower risk of being victims of tail biting offers an opportunity to change the predisposition of pigs to become victims of tail biting. To help in the selection process, Breuer et al. (2005), reported heritability for tail biting ranging between 0.09 to 0.32 and heritability of 0.06 for being a victim of tail biting (Canario and Flatres-Grall, 2018).

1.4. Aggressive behaviour in pigs

Aggression occur on several occasions, such as weaning piglets, transport to other farms or the slaughterhouse, and group conformation of sows during gestation. Piglets are often separated from the sow when they are 3 or 4 weeks old to produce a high number of litters per sow and year (Fels et al., 2012). Piglets from different litters are sorted by weight, sex, and mixed into new groups. This regrouping of piglets leads to agonistic behaviour with high rates of aggression aimed at establishing a social hierarchy within a group (Ewbank and Bryant, 1972; Estevez et al., 2007; Fels et al., 2012; Rizvi et al., 2000). According to Desire et al. (2016), some dominant individuals can establish social rank with minimal aggression, possibly via behavioural cues, or short, decisive fights. Hoy and Bauer (2005), observed that mixing acquainted sows reduces the level of aggressive interactions in contrast to mixing unacquainted pigs. However, mixing is done to achieve homogenous animals in terms of age and weight and the whole dynamics of a group is affected when regrouping (at weaning or when moving to the fattening house). Limited resources such as feed, water, or space to rest also lead to aggressive behaviour. However, establishment of dominance relationships through agonistic relationship occurs both in the absence of resources or in the presence of adequate resources (Camerlink et al., 2019).

Several methods have been used to minimise aggressive behaviour e.g. in sow using odour masking, tranquillising, the use of partial physical barriers, provision of enrichment material like straw objects (Beattie et al., 2001; Van de Weerd et al., 2006). However, Luescher et al. (1987) found that none of the methods used significantly reduced the amount of fighting. Until clarification of social ranking in the new environment, aggressiveness among pigs causes various behavioural reactions, escalating to damaging fights in addition to tail biting with associated skin lesions (Turner et al., 2009; Camerlink et al., 2016, Wurtz et al., 2017). These behaviours are seen to be part of natural exploratory behaviours (Wood-Gush and Vestergaard, 1993; Day et al., 1996; Van de Weerd et al., 2006; Taylor et al., 2010). It therefore becomes a welfare issue when aggression is severe or persist for a long time causing serious problems in animal welfare as well as in growth performance (D'Eath et al., 2014; Valros and Heinonen, 2015).

Individual variation and the level of aggressive behaviour depends on differences in body weight, individual aggressiveness and temperament, sex, different space or group sizes (Hoy and Bauer, 2005; Gil et al., 2019). Aggressive behaviour is also mediated by endocrine factors associated to sex, making male animals more aggressive than females (Gil et al., 2019). The degree of familiarity among pigs determines the intensity of aggressiveness and biting. Aggression can be either acute, occurring immediately following regrouping, or chronic, occurring when the animals are socially subordinate or isolated, or as a result of repeated social regrouping (Coutellier et al., 2007). In a study by Algers et al. (1990), it was observed that heavier pigs in a group are more confident, fight more with each other, and win more fights than the lighter pigs. In addition, aggressions are more intense as animals are more similar in body weight. Another study by Ewbank and Bryant (1972) noted that a decrease in the area available per pig leads to an increase in agonistic interactions.

Aggressive behaviour in farm animals is a heritable trait that can be selected against in animal breeding (Peden et al., 2018). In poultry for instance, the heritability of feather pecking was estimated to range between 0.07 to 0.65 (Craig and Muir, 1993; Kjaer and Sørensen, 1997). In pigs heritability for aggressive behaviour ranges between 0.27 to 0.90 (Grandinson et al., 2003; Breuer et al., 2005).

1.5. Causes and underlying mechanisms for tail biting and aggressive behaviour in pigs

1.5.1. Tail lengths

The tail of animals has various physiological functions, which varies from one animal to the other. In cattle, it is used as a means of communication, self-stimulation or used to avoid flies during fly seasons (Kiley-Worthington, 1976). It has also been seen as a means of covering the vulva with females having longer tails than males (Nannoni et al., 2014). However, in pigs longer tails trigger tail biting (Thodberg et al., 2018). Tail length like any other body part is an inherited trait comprising mono- or oligogenic as well as polygenic components reflecting a mixture of qualitative Mendelian and quantitative additive genetic effects (Xu et al., 2016; Oberpenning et al., 2022). Heritability of 0.60 ± 0.08 for tail length have been reported in sheep indicating the potential for genetic selection on short tails (Oberpenning et al., 2022). However, the shortening of tail is caused by mutations in the T-box domain of the Brachyury-gene (Yoo et al., 2017).

To prevent tail biting, most piglets in intensive husbandry systems are tail docked which is an animal welfare problem since it causes trauma and pain to the animal (Sutherland et al., 2011). In a study by Thodberg et al., (2018), tail biting significantly reduced when tails were docked. The study also found out that tail lesions reduced in short docked pigs than in long docked pigs. Apart from tail biting, failure to dock also results in low market value of pigs thereby losing profitability of the farmer. It was therefore concluded by Spoolder et al. (2011) that tail length could be used as an indicator for tail biting outbreaks and assessing welfare in pigs.

Scientific studies addressing the genetic variation of tail length in pigs, considering the direct genetic as well as the maternal genetic perspective to our knowledge, have not yet been published. Estimation of heritability for tail lengths and other aggressive behavioural traits and their correlations with each other are therefore essential for successful selection in a genetic improvement programme. Therefore, the first part of this thesis estimated the genetic (co)variance components for tail length and its correlation with growth parameters.

Figure 1.1: Measuring of tail length in pigs.

(Photo source: Justus-Liebig-Universität Gießen research station "*Oberer Hardthof*")

1.5.2. Skin lesions in pigs

Piglets are occasionally mixed into new groups during their productive life to facilitate management. This new groups are often characterised by aggressive interactions resulting in skin lesions on the body of piglets (Turner et al., 2009). To evaluate the relationship between skin lesion scores and aggressive behaviour categories, positive relationship between skin lesions and aggressive behavioural interactions in group-housed pigs was estimated by several authors (Turner et al., 2008 and 2009; Desire et al., 2016; Liu et al., 2022). This was made known through the counting of lesion score and the location of the lesions. For example, skin lesion located at the anterior part of the pig are positively correlated to active aggressive behaviour, while the fresh skin lesion counts on the caudal part of the pigs body are positively correlated to receiving aggression (Turner et al., 2008; Desire et al., 2015).

Skin lesion can be the major reason for the outbreak of tail biting in a pig group (Sandnabba, 1997; Statham et al., 2009). At the individual level, the skin lesions of a pig can increase attacks from other pigs in the pen through the continuous bleeding and the attraction of blood by pigs (Fraser et al., 1991; Sandnabba, 1997). Studies in mice and humans show that bleeding and the sight of blood as a result of biting are odour mediated which makes the animals sniff and escalate to more aggressive behaviours (Sandnabba, 1997; Coccaro et al., 2014). Pigs also have a genetic predisposition to deliver and receive aggression (Turner et al., 2008, 2009). Several approaches used by different authors in analysing behavioural models does not explicitly model the effect of the delivery of aggression by one individual on the count of lesions produced on the skin of the animal delivering aggression and of its group mates (Angarita et al., 2019). Therefore, in analysing behavioural models, the direct effect, which is the effect of the animal's genotype on its own phenotype and the social genetic effect, which is the effect of the animal's genotype on its group mates should be fitted in the models to have an accurate estimate for behaviour studies (Bergsma et al., 2008; Ellen et al., 2008; Canario et al., 2012; Alemu et al., 2014; Angarita et al., 2019). Furthermore, the use of location of a lesion to determine the type of aggressiveness as well as the time of occurrence needs to be considered.

1.5.3. Effect of health on pigs behaviour

The health status of pigs influences its behaviour by being a victim or a bitter. Several diseases have been reported to be associated with aggressive behaviour and tail biting. For example, lung lesions (Kritas and Morrison, 2007; Bučková et al., 2022), locomotor disorder (Munsterhjelm et al., 2013; Bučková et al., 2022) and respiratory disease (Munsterhjelm et al., 2019; Bučková et al., 2022). Lesions in pigs as a result of biting increase the risk of infection which in turn increases the concentration of serum haptoglobin, a major porcine acute phase protein (Chen et al., 2003). A rise in acute phase protein and inflammatory cytokine levels affects the general behaviour in pigs (Munsterhjelm et al., 2019). According to Bučková et al. (2022), locomotor disorder and respiratory variable occurrence increased at the same time with the occurrence of tail lesions in finishers pigs along with the occurrence of scouring increasing with a rise in ear lesions. Another study observed a positive correlation between tail biting and rectal prolapse respiratory disease (Moinard et al., 2003).

The mechanisms by which poor health works to increase the risk of a tail-biting outbreak is not known (Munsterhjelm et al., 2019). However, the sick pig becomes a victim by withdrawal from social activities. This makes them vulnerable to biting which may have a major effect on the rest of the pigs in the pen making them bitters e.g. severe pecking in poultry on sick and less active flocks (Riber and Forkman, 2007). On the contrary, poor health may increase irritation, emotional liability and short temperament thereby increasing the tendency of a pig to become a tail biter (Munsterhjelm et al., 2019).

1.5.4. Social interactions among pigs

In social behaviour, the expression of behaviour by an individual depends on the behaviour of the conspecific with which it interacts (Bijma et al., 2007; Ellen et al., 2008; Camerlink et al., 2018). In animals, social interactions also known as indirect genetic effect (IGE) are heritable effects that come from genes of interacting conspecifics contributing to social environment that affects the phenotypic values of other animals (Bailey et al., 2018; Snyder-Mackler et al., 2020; Clouard et al., 2022). This interaction can be either positive or negative influencing evolutionary processes (Runcie et al., 2013). An example of IGE is the maternal genetic effects on offspring phenotype, behavioural phenotypes such as sexual cannibalism, conspicuous sexual signalling, altruism, and aggression behaviours manipulating interacting partners (Bailey et al., 2018; Regan et al., 2020). Social interactions have been observed in feed intake, growth rate and aggressive behaviour in pigs (Bergsma et al., 2008; Canario et al., 2012). IGE contributed more than 65% and 72% of heritable variation in purebreds and crossbreds in laying hens, where the survival probability of an individual depends on the genotype of its cage mates (Peeters et al., 2012). Positive social interactions are essential for the health and well-being of domestic animals (Rault, 2018). Positive social interactions are mostly formed between closely related animals, and bonds between non-relatives are possible which are beneficial in increasing fitness and survival (Camerlink et al., 2018). In farm animals, maternal contact as well as social nosing helps in the development of positive social behaviour (Lee et al., 2022). However, negative social interactions have received more research because of their negative impact on animal welfare (Rault, 2018). Negative social interaction arises as a result of regrouping unfamiliar animals resulting in aggressive behaviour. Both negative and positive social interactions are affected by age, sex, personality, cognitive ability, affective state, and previous experience.

According to Bergsma et al. (2008), IGE played a role in growth, contributing 71% and 70% heritable variance in growth rate and feed intake respectively in pigs. IGE role in nosing is described as a contact behaviour to improve individual recognition in pigs behaviour (Wilson et al., 2009; Camerlink et al., 2018). Pig with high IGE perform less aggressive behaviour and establish dominance relationships with other pigs. IGE therefore have potential to alter evolutionary responses to selection and play a role in behavioural evolution in species with highly complex social interactions. Selection for IGE can reduce aggressive behaviours (Camerlink et al., 2013). Modelling genes expressed in social partners in the genetic estimation of behaviour is beneficial because it influences on behavioural traits (Bailey et al., 2018; Regan et al., 2020).

1.5.5. Genetic effects on pigs behaviour

1.5.5.1. Genes and hormones affecting pigs behaviour

The relationship between genes and behaviour have been expressed in science with associated form of heritable genetic variation influenced by different timeframes, ranging from organismal development, physiology and evolution (Robinson et al., 2008; Kappeler et al., 2013). Genes do not directly influence behaviour however, individual genes encode molecular products that build and govern the functioning of the brain through which behaviour is expressed (Robinson et al., 2008; Kappeler et al., 2013). The strength of the influence of genes on a particular behaviour is quantified by its heritability. Glucocorticoid receptor gene (NR3C1) and Arginine vasopressin receptor gene (AVPR1B) have been identified to be associated with aggressive behaviour (Muráni et al., 2010; Liu et al., 2021). According to Liu et al. (2021), glucocorticoids plays a major role in animal personality such as locomotor activity. Behaviour is a complex heritable trait affected by numerous interacting genes whose expression depends on the genetic make-up of the individual and the environment (Breuer et al., 2003; Baye et al., 2011). For example, the differences between neutrals, performers and receivers biters in terms of their genes expressions have been studied, contributing towards understanding pig behaviour (Keeling et al., 2004; Beattie et al., 2005; Brunberg et al., 2013a). Brunberg et al. (2013b) discovered differences in 19 genes in tail biters and receiver pigs which were associated with production traits (e.g. pyruvate dehydrogenase kinase, isozyme 4) compared to pigs not involved in tail biting. In cattle, gene associations with behavioural traits were found on all chromosomes except for chromosome 13, with associated SNPs reported on all chromosomes except 5, 13, 17, 18 and 23 (Titterington et al., 2022).

Hormones plays an important role in regulating animal behaviour (Nelson 1995). Behaviour is sensitive and react to a small changes in hormone and neurotransmitter levels (Capuron et al., 2002; Munsterhjelm et al., 2019). Numerous hormones, such as estrogen, testosterone, progesterone, adrenocorticotropic hormone, prolactin, oxytocin, and arginine vasopressin, affect behaviours in animals (Breed and Moore, 2012; Vaeroy et al., 2019). Adrenocorticotropic hormone, arginine vasopressin and oxytocin, the neuropeptides regulating the stress response and the hypothalamic-pituitary-adrenal (HPA) axis activity, are known to modulate aggressive behaviour (Vaeroy et al., 2019). In females for example, prolactin secreted by the anterior pituitary and oxytocin release during parturition facilitate maternal behaviour and social bonding (von Borell et al., 2007; Garland et al., 2016). The NR3C1 plays an important role in controlling HPA activity, which directly affects aggressive behaviour (Muráni et al., 2010; Liu et al., 2021). According to McMahon et al. (2022), exploratory behaviour and HPA are positively correlated. Stress influence behaviour in pigs and adjusting to stress affects behaviour and physiological responses including endocrine changes in the HPA axis. The HPA axis is important in the development and genetic susceptibility of aggressive behaviour in humans and animals. HPA influence the release of cortisol secretion via pituitary release of the adrenocorticotropic hormone (ACTH) thus releasing corticosteroids and aldosterone hormones (von Borell, 2001; Camerlink et al., 2018). Increased or decreased activation of the HPA axis is associated with aggressive behaviour (Vaeroy et al., 2019). In the proactive-reactive coping model described by Koolhaas et al. (1999), low HPA axis reactivity was associated with proactive pigs with increased concentration of catecholamines and reproductive hormones whiles reactive coping pigs have increased HPA axis reactivity.

1.5.5.2. Breeds effect on pigs behaviour

In animal behaviour, some breeds are more prone to aggressive behaviour and tail biting (Fraser and Broom, 1990). Differences between Landrace and Large White pigs in how they perform aggressiveness and tail biting have been reported by Breuer et al. (2005). Tail biting was found to be 0.05 ± 0.02, $P < 0.05$ heritable in Landrace but 0.00 ± 0.00, $P < 0.05$ not heritable in Large White pigs (Breuer et al., 2005). Duroc pigs were found to be more active, performing more biting, nosing and exploratory behaviours than Landrace and Large White pigs (Breuer et al., 2003). In the same way, Duroc sows were reported to be more aggressive towards piglets than Landrace sows, and crossbreds more aggressive than purebred Landrace and Duroc sows (Knap and Merks, 1987). Landrace pigs were more passive and performed less biting behaviours than the other breeds (Breuer et al., 2003). Selection for increased leanness and growth rate increase the incidence of tail biting (Breuer et al., 2005). Finnish Landrace sows perform more aggression towards their piglets than Finnish Yorkshire sows (Vangen et al., 2005). According to Bozkurt et al. (2006), aggressiveness may be due to the late and early maturing breeds present in a group. The early maturing breeds grows faster and reached bigger body size than the others and perform more aggressive behaviours. Evidence for breed differences can therefore be seen in the differences in the expression of aggressive, foraging and exploratory behaviours which are associated with the development of tail biting in pigs. However, there is a dearth of knowledge about the genetics and breed influences in the performance of aggressive behaviour.

1.5.6. Environmental effect on pigs behaviour

1.5.6.1. Husbandry practises

Several studies on economically feasible husbandry practises such as introduction of substrate, housing conditions are well documented because of the economic and health impact of tail biting and aggressive behaviour on animal welfare (Rhim, 2012). According to literature, intensive production systems characterised by slatted floors with no substrate increase behaviours such as ear and tail biting compared to environment with substrate such as straw (Beattie et al., 2001). Enrichment objects such as chains and straw, hay or roughage or a change in the diet (increase fibre content) have been noted to reduce aggressive behaviours in pigs (Zonderland et al., 2003; Schütz et al., 2020). However, there is conflicting data and little conclusive evidence that provision of toys such as chains, chewing sticks and balls can reduce the risk of tail biting (Hill et al., 1998; EFSA, 2007).

Significant effect of high stocking densities have been reported to increase the frequency of aggression, behavioural problems and reduce performance in sheep, poultry and in pigs (Thomas et al., 2011; Mayes et al., 2022; van der Eijk et al., 2022; Zeng et al., 2022). Therefore reducing stocking densities would decrease aggressive and behavioural problems in farm animals. Aggressive behaviour develops irrespective of whether or not pigs have access to a substrate or a playing ball. Nonetheless, provision of these materials helps to reduce aggressive behaviour in pigs.

1.5.6.2. Diet effect on pigs behaviour

Nutrition played a major role in tail, ear biting social behaviour in pigs (Beattie et al., 2005; Jensen and Pedersen, 2010; Holling et al., 2017). Tail biting and aggressiveness have been observed to be related to foraging behaviours, natural exploration, rooting and chewing (Moinard et al., 2003; Van de Weerd et al., 2006). There are speculative theories suggesting that animals make forage decisions based on metabolic deficiencies in their internal state and past nutritional experience (Kyriazakis et al., 1993 cited by Day et al., 1996). Thus, tail biting is a possible consequence of nutrient deficiencies in pigs.

According to Geers et al. (1985), access to feeds and high consumption by farm animals correlates with low tail biting events in farms. Pigs that indulge in tail biting have been observed to be lighter and thinner than their cohorts and this is suggested to be associated with nutritional inadequacies and reduced feed intake due to low social rank within the group with limited access to feed (Rizvi et al., 2000; Edwards, 2006; Palander et al., 2013). In a study by Jericho and Church (1972) and Jensen et al., (1993) feeding diets with low dietary protein levels may increase the occurrence of damaging behaviours such as ear and tail biting. Competition for feed, inadequate dietary sodium, deficiency of dietary essential amino acids, and a sudden change in diet composition increases tail biting and aggressive behaviour in pigs (EFSA, 2007). Effects of dietary tryptophan concentration on aggressive behaviour and stress in pigs have been reported by Castilha et al. (2016) and Gomes et al. (2018). Pigs fed low-protein diets without amino acid supplementation are more attracted to blood (Fraser et al., 1991; Sandnabba, 1997) and when wounds develop they bite more. Favourable effects of fibre levels in the feeding ration on pig behaviour have been reported to reduce aggressiveness and simultaneously improve growth performance (Brouns et al., 1994; Braund et al., 1998; Kallabis and Kaufmann, 2012).

The herbaceous plant chicory (*Cichorium intybus L.*) has been used as a fibre component in pigs and small ruminant diets, without compromising performance traits and improving nutrient digestibility, immune function and meat quality (Ivarsson et al., 2011; Yan et al., 2012; Cheng et al., 2017; Nwafor et al., 2017; Liu et al., 2018). The chicory plant has anthelmintic functions in the animal digestive tracts of animals reducing about 70% worm population that can cause infection in livestock (Peña-Espinoza et al., 2016). In human medicine, chicory is believed to have stimulated the appetite by increasing gastric secretions in the stomach, prevent slow digestion and abdominal fullness thereby increasing growth traits (Ahmed et al., 2003;

European Medicines Agency, 2012; Hitova and Melzig, 2014). Chapter three of this thesis therefore estimated the effect of chicory diet assumed to have a positive influence on the behaviour and growth of piglets.

1.5.7. Effect of genotypes by environment interactions on pigs behaviour

Genotype by environment interaction (G × E) refers to the differences in response of genotypes to different environments or situations in which genetic effects connected to a phenotype are dependent upon variability in the environment (Falconer and Mackay, 1996). When two genotypes rank differently in different environments, (e.g. differences in nutritional characteristics) it is referred to as crossover or re-ranking of estimated breeding value (EBV). However, scaling or non-crossover effect occurs if the interaction between genotypes vary between environments without causing a change in their ranking (Hamilton et al., 2003; Baye et al., 2011). Genetic selection strategies are used in pigs breeding programmes in improving productivity and animal behaviour. Pigs' behaviour are affected by their genetic constitution and the extent to which these behaviours are expressed may differ when the environment is altered (Bolnick et al., 2011; Langenhof and Komdeur, 2018). The combined interaction between genotype and environmental factors has been studied to have greater effects than their independent effects on primary and functional trait responses in pigs (Schiavon et al., 2019). The interactions between genotype and the environment might influence the effect of selection on behaviour and performance traits unless breeding programmes are structured to address different categories of environment. Furthermore, genetic information determines behaviour and the differences between individual animals may explain why some animals shows certain behaviours when the environment varies from generation to generation. Tail biting and aggressive behaviour have been seen to have seasonal effect. Scientific report from EFSA (2007) also saw an increase in tail biting during the autumn season and that hazards for tail biting are heat stress, cold stress and high airspeed. Another report by Bozkurt et al. (2006) also observed increased activities in the spring than in the winter seasons.

In behaviour science, domestication of animals have quantitatively modified behaviour by altering response thresholds (Teletchea, 2019). These behavioural changes may be brought about through artificial selection, or accidentally due to correlations between behaviour and production-relevant traits. Li et al. (2017) reported that genotype by environment interactions reduced heritability and overall genetic gain. It is therefore important to estimate genetic parameters under the conditions in which the piglets are kept to improve behaviour traits. However, few studies assessing the interaction between genotype and environment in pig behaviour have been conducted (Hill et al., 1998). Accordingly, this study estimated genetic parameters from two alternative dietary environments and from 14 different sire lines to determine the influence of genotype and environment has on pig behaviour.

1.6. Consequences of tail biting and aggressive behaviour

1.6.1. Diseases, Profitability and Food safety

Aggressive behaviour and tail biting encounters often results in pain, skin injuries and can additionally cause immune-suppressive effects (Tuchscherer and Manteuffel, 2000). It also increases the risk of infection, reduces immune competence, and increases the risk of disease spread, carcass abscesses, respiratory organ inflammation and lung pathologies (Kritas and Morrison, 2007; Munsterhjelm et al., 2013). Aggressive behaviour results in stress which have an impact on productivity by influencing their reproductive physiology. This have a great impact on the farmers incomes and the pig industry due to reduced weight gain, medication and labour costs (Zonderland et al., 2011; Sinisalo et al., 2012; Peden et al., 2021).

A high number of carcass condemnation rate (61 to 67%) and poor meat quality as a result of tail biting lesions have been observed in most abattoirs (Schroder-Petersen and Simonsen, 2001; Kritas and Morrison, 2007). Significant positive correlation has been reported between carcass condemnation and the severity of tail lesion (Souza et al., 2021). Injured tails at slaughter are more than 4% resulting in financial losses for the farmer (keeling et al., 2004). In agreement with keeling et al. (2004), Peden et al. (2021), recorded more than 50% economic loss in carcass value was due to tail biting. According to Souza et al. (2021) for example, Brazil recorded more than 0.1% carcasses condemned due to cannibalism. Apart from carcass loss, tail biting and aggressiveness have a negative impact on weight gain. About 25% of weight loss in pigs are attributed to tail biting and aggressive behaviour (Zonderland et al., 2011). Severely bitten pigs as well as those that are involved in biting have been observed to be significantly lighter at slaughter than those not bitten (Edwards, 2006; Palander et al., 2013). Increased numbers of dead animals after ascending abscesses can pose a considerable financial problem to the farmer and increased costs for carcass handling at the slaughterhouse. Tail biting has a great impact on animal growth throughout the life of the animal until slaughter.

1.6.2. Animal welfare

The improvement of animal welfare has gained political and societal importance which has resulted in the establishment of “Actionplan on the Protection and Welfare of Animals” (Kluge, 2018). In Germany, animal welfare is part of the State goal in the German constitution and regulated in the Animal Welfare Act under which farmers are to obliged and comply with the applicable regulations in order to promote the welfare of their animals. However, with this several interventions and advocacy programmes put in place to improve animal welfare problems, there has been little translation of these advocated techniques and building designs into practice (Peden et al., 2018). Major welfare issues in weaning pigs are risks associated with weaning, space allowance, type of flooring, enrichment material, air quality, health status, diet tooth clipping, tail docking and castration in males (EFSA, 2022).

Pigs are generally kept in groups and their social behaviour has an impact on animal welfare in both positive and negative ways. Animal welfare depends greatly on their ability to maintain homeostasis by responding, both behaviourally and physiologically, to challenges in their environment. Aggressive behaviour and tail biting have welfare implications for both the biter and the injured pig, since the inadequacies in their environment make them feel discomfort and unable to cope with their environment (EFSA, 2007; Valros et al., 2015; Thodberg et al., 2018). In Europe, the persistence of tail biting behaviour in commercial farm conditions has resulted in the majority of large pig enterprises to consider docking of the tails of all piglets as a preventative measure which defies animal welfare and ethical issues since it causes pain to the animal (Hunter et al., 2001; Moinard et al., 2003; Edwards, 2006; Sutherland et al., 2011). However, tail docking does not address the main underlying causes of tail biting (Nannoni et al., 2014). Thus, alternative preventive methods need to be investigated to reduce this problem on farms.

1.7. Prevention of tail biting

In any farm business management, maximising profit is an important goal to the farmer. Biting prevention is part of the farm animal health and welfare plan, which the farmer prepares together with the contracted veterinarian. Together they have to ensure that enough and appropriate enrichment material is provided and that husbandry, management and climate conditions are optimal (European Commission, 2008).

1.7.1. Genetic improvement of animal behaviour and tail lengths

Genetics is important in understanding the fundamentals underlying coping behaviour, in the field of coping and animal personality (van Oers et al., 2005). It is comprehensible that the focus of researches concerning pigs are for reproductive and early pig survival traits but not for animal behaviour. Few researches done on tail biting are basically about external factors but little has been done to understand the genetic influence on pig development and tail-biting (Breuer et al., 2003). Understanding the relationships between genes and social behaviour is difficult. Furthermore, no methods of experimental genetics have been developed for animals (Robinson et al., 2008). It is therefore not surprising that the use of genetic selection to reduce aggressive behaviour in pigs is under-studied and not fully utilised. Only a few studies have attempted to estimate the genetic influence on the behaviour of pigs with varying heritability estimate for behaviours.

Studies on tail biting, aggressive and animal behaviour have been shown to have genetic influence and are moderately heritable traits (Ogawa et al., 2004; Veroude et al., 2016). Tail biting and aggressive behaviour can be genetically selected against through the use of breeding programmes and modification of the production environment (Turner, 2011; Rohrer et al., 2013; Ellen et al., 2014; Peden et al., 2018). For example, heritabilities ranging from 0.05 to 0.27 have been reported by Breuer et al. (2005) in pigs for tail biting. Aggressive behaviour of sows towards piglets was found to be heritable with heritability ranging from 0.40 to 0.90 (Knap and Merks, 1987; Grandinson et al., 2003). Fighting and bullying behaviour were found to be inheritable traits (h^2 = 0.09 to 0.26) which were strongly correlated (rg > 0.88; Agha et al., 2022). Despite the differences in behaviour between closely related species, they also share similar behavioural traits as a result of common ancestry. However, selection of social behaviours are done by behavioural observation which are time consuming, making breeding based on behavioural observations not feasible in practice (Stafford, 2010; Ellen et al., 2014). Another alternative solution is the use of IGE to improve animal behaviour.

In a study by Ragab et al. (2019), feeding behaviour variables was used to measure the interaction between pen mates to improve the performance of pigs. Behaviours such as skin lesions an indicator of aggression as well as the location of skin lesions to differentiate the types of aggressive interactions have been used to select against aggressive behaviour. Turner et al. (2008) estimated significant genetic correlations between lesion scores and pig behaviour traits indicating the potentials for indirect selection based on skin lesion to reduce pig aggressiveness. IGE have been used to reduce aggressive behaviour in mice and in poultry (Rodenburg et al., 2008; Wilson et al., 2009). In a study by Canario et al. (2012), pigs with high IGE pigs showed reciprocal fighting and fewer lesions after regrouping. Camerlink et al. (2018), high IGE pigs showed considerably less aggression with familiar and unfamiliar pigs because of their high individual recognition developed through nosing and ability to establish dominance relationships than low IGE pigs. Heritable component in IGE, selection on these interactions is therefore possible to improve productivity and aggressive behaviours (Bijma et al., 2007).

1.7.2. Tail docking in pigs

Tail docking is done by amputating part of the tail mostly performed by farmers within the first few days of birth without any pain medication (Zonderland et al., 2008; Sutherland et al., 2011). Tail docking is performed using either clippers or a cauterising tail docking iron. This may cause thermal skin burns as well as tail necrosis which is associated with exposure to electric heating pads such as the once used docking (García et al., 2019). Simonsen et al. (1991) reported that tails are docked between 1.5 cm and 2.5 cm from the base of the tail between the vertebrae. However, according to Herskin et al. (2015) pigs with 75% of the tail removed had a higher occurrence of neuroma tissue when compared to pigs 50% or 25% of the tail was removed. Tail docking has several benefits such as reduction of aggressive behaviour, cleanliness, improvement in the ease of milking and the reduction of transmission of diseases (Leptospirosis in cow) to workers (Vallée et al., 2018). In pigs, tail docking is a common procedure performed for decades to reduce tail biting (Sutherland et al., 2011). Interestingly, this tail docking does not eliminate tail biting but rather reduce its incidence (D’Eath et al., 2014). Tail docking causes pain and stress to the pigs. In sheep, this pain and stress have been found to have long-term effects on an individual phenotype and, in some cases, on that of its offspring (Clark et al., 2014). Champagne, (2013), for example, found the effect of tail docking has on an animal development and behaviour. Subsequently, tail docking limits the communication between pigs and also the redirecting biting behaviour to other body parts such as ears and legs (Thodberg et al. 2018). Additionally, the capital involved in veterinary services and medication to provide pain relief, in accordance with the EU pig Directive when performed on piglets after 7 days of birth have a huge margin on farmers' income (EFSA, 2007). Tarazona et al. (2019), reported no significant effect on animal health as well as production performance in tail docking and recommended it to be eliminated. It is therefore important to consider the effects tail docking have on the welfare of pigs and thus an alternative preventive method is needed to investigate this problem on farms.

1.7.3. Environmental and Managerial practises

Pigs are exploratory animals spending most of their time foraging and exploring their surroundings. Inability to fulfil this exploratory behaviour leads to tail biting (Fraser et al., 1991; EFSA, 2007; Allwin and Swaminathan, 2016). In a study by Rizvi et al. (2000), vulva biting was associated with frustration due to lack of foraging activity. In order to meet the exploratory and foraging needs of pigs, environmental enrichment such as provision of straw are known to provide bedding and rooting material and remedy tail biting in pigs (EFSA, 2007; Swiss Federal Council, 2008; Camerlink et al., 2015). Different opinions on enrichment's materials such as the amount and frequency in which this material should be provided and hygiene etc. have been discussed in several studies (Hill et al., 1998). However, provision of straw is the most commonly used enrichment material used in most European countries (European Commission, 2008). Provision of iron chains, pieces of wood, ropes, salt blocks, playing balls are also used to reduce this damaging behaviour (Hill et al., 1998; EFSA, 2007; Camerlink et al., 2015). Another preventive method is to decrease in stocking density during production (Zeng et al., 2022). According to the working practises recommended by the European Union legislation, pig should be provided with adequate opportunities to escape and hide from other pigs (European Commission, 2008). It should be noted that, tail biting is multi-factorial which implies that different factors come together to affect this behaviour. Therefore, an independent prevention method such as enrichment materials may not be the only preventive method to apply to reduce or eliminate tail biting and does not influence the effects of other factors on tail biting.

Managerial practises such as cleaning of pens, ventilation of pen houses, decreasing stocking density and enrichment provision thereby improving the health pigs would directly reduce tail biting and aggressive behaviour in pigs. In situations where the cause of tail biting has been identified, managerial practise in removing the biter and bitten pigs for medical treatment have been recommended (Hunter et al., 2001; Sutherland et al., 2011). Observing early warning signs of tail biting such as increased activity in the pen, tail postures, video images etc. help reduce the outbreak of tail biting (D'Eath et al., 2014).

1.7.4. Legislation

According to Council Directive 2008/120/EC, docking of part of the tail is allowed. Tail docking must not be performed routinely, but only when there is evidence of injury to the ears or tails of other pigs. Before performing this procedure, other measures must be taken to prevent tail biting and other aggressive behaviour, taking into account the environment and stocking density. For this reason, inappropriate environmental conditions or housing systems must be modified. According to EFSA (2007) and Harley et al. (2012), 80% to 100% of piglets on farms in Germany, France, the Netherlands, Denmark, Spain, Ireland, and Belgium are docked to reduce tail biting. It is likely that this percentage of docked piglets has not decreased to date. In 2016, the European Union also issued Recommendation (EU) 2016/336 which is to provide guidance on the application of Directive 2008/120/EC and sets minimum requirements for the protection of pigs in relation to measures to reduce the need for tail docking. In this context, the farmer is required to conduct a risk assessment of the occurrence of tail biting based on animal and non-animal indicators ("Risk Assessment"). In addition, member states are to establish criteria for compliance with the requirements set out in the legislation and make them publicly available on a website. A first step towards implementing the recommendations was taken in Germany, with the adoption of the "Aktionsplan Kupierverzicht" (Kluge, 2018). Tail biting outbreaks are still sporadic and unpredictable and therefore it is very difficult to study them in a research setting (Edwards, 2006). Even in situations where the cause of tail biting has been identified, interventions to reduce the occurrence are either expensive or difficult to implement, considering the current production systems. It remains very difficult for farmers to implement working practices recommended by EU legislation, such as reducing stocking density during the production period and providing continuous straw. Nevertheless, the future is to keep pigs with naturally long tails, thus, implying improvements and alternative preventive methods in animal behaviour.

1.8. Objectives of study

The main objective of this study was to reduce tail biting and aggressive behaviour in pigs through breeding programmes and modification of the production environment. This was achieved by examining the genetics architecture of tail length, skin lesions and active behaviour patterns of pigs in the context of genetics, feeding and genotype by feeding interactions in pigs. In chapter 2, the objective is to improve animal welfare using genetic trait improvement selection scheme to breed naturally short tail pigs. Thus estimating genetic (co)variance components for the traits tail length, tail abnormalities including tail lesions and growth traits via quantitative genetic modelling approaches with and without consideration of maternal genetic effects.

Chapter 3 evaluated the favourable effects of chicory (*Cichorium intybus L*) on pigs' behaviour and performance traits. A cross-classified research was designed to estimate the effects of the herbal diet on skin lesions and growth traits in post weaning pigs. Piglets from 14 genetic sire lines that differed in genetic merit for skin lesions, post weaning weight and average daily gain were investigated in two alternative dietary environments, to determine the influence genetics and environment have as well as associated re-rankings of animals, not only on piglet behaviour per se but also on its influence on growth trait.

Chapter 4 focuses on pigs' behaviour enhancing the fundamental understanding of early piglet behaviour through the backtest score to provide insights on the relationship between early and late behaviour to improve animal welfare. Finally, the study aimed to investigate the effects of feeding, sire line and breeding values for skin lesions on abnormal behaviour patterns monitored via video images of pigs during the post weaning period.

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CHAPTER 2

GENETIC PARAMETERS FOR TAIL CHARACTERISTICS: MATERNAL AND DIRECT GENETIC PARAMETERS FOR TAIL LENGTH, TAIL LESIONS AND GROWTH TRAITS IN PIGS

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ABSTRACT

Tail length and tail lesions are the major triggers for tail biting in pigs. Against this background, 2 datasets were analyzed to estimate genetic parameters for tail characteristics and growth traits. Dataset 1 considered measurements for trait tail length (T-LEN) and for the growth traits birth weight (BW), weaning weight (WW), postweaning weight (PWW), and average daily gain (ADG) from 9,348 piglets. Piglets were born in the period from 2015 to 2018 and kept on the University of Gießen research station. Dataset 2 included 4,943 binary observations from 1,648 pigs from the birth years 2016 to 2019 for tail lesions (T-LES) as indicators for tail necrosis, tail abnormalities, or tail biting. T-LES were recorded at 30 ± 7 d after entry for rearing (T-Les-1), at 50 ± 7 d after entry for rearing (end of the rearing period, T-LES-2), and 130 ± 20 d after entry for rearing (end of fattening period, T-LES-3). Genetic statistical model evaluation for dataset 1 based on Akaike's information criterion and likelihood ration tests suggested multiple-trait animal models considering covariances between direct and maternal genetic effects. The direct heritability for T-LEN was 0.42 (±0.03), indicating the potential for genetic selection on short tails. The maternal genetic heritability for T-LEN was 0.05 (±0.04), indicating the influence of uterine characteristics on morphological traits. The negative correlation between direct and maternal effects for T-LEN of –0.35 (±0.13), as well as the antagonistic relationships (i.e., positive direct genetic correlations in the range from 0.03 to 0.40) between T-LEN with the growth traits BW, WW, PWW, and ADG, complicate selection strategies and breeding goal definitions. The correlations between direct effects for T-LEN and maternal effects for breeding goal traits, and vice versa, were positive but associated with a quite large SE. The heritability for T-LES when considering the 3 repeated measurements was 0.23 ± 0.04 from the linear (repeatability of 0.30) and 0.21 ± 0.06 (repeatability of 0.29) from the threshold model. The breeding value correlations between T-LES-3 with breeding values from the repeatability models were quite large (0.74 to 0.90), suggesting tail lesion recording at the end of the rearing period. To understand all genetic mechanisms in detail, ongoing studies are focusing on

association analyses between T-LEN and T-LES, and the identification of tail biting from an actor's perspective.

Key words: growth traits, genetic parameters, maternal effects, tail length, tail lesions

INTRODUCTION

Tail biting is a serious multifactorial animal welfare issue, causing injuries, pathological problems and economic losses (D'Eath et al., 2014). One key trigger for tail biting is the length of the tail (Thodberg et al., 2018). To minimize tail biting, tail docking is a common management practice over decades, but is not in line with legal animal welfare guidelines as defined in the EU Directive 2008/120/EG (European Commission, 2008).

The genetic architecture of tail length across species comprises mono- or oligogenic as well as polygenic components (Xu et al., 2016), reflecting a mixture of qualitative Mendelian and quantitative additive genetic effects. In some animal species (e.g. in Manx cats) deformities and impairments of the embryo due to mutations in the T-gene were associated with a drastic shortening of tails (Buckingham et al., 2013a). Studies on tail length in sheep showed a Gaussian distribution for tail length, and an infinitesimal model of inheritance (Scobie and O'Connell, 2002). Quantitative genetic studies in sheep breeds estimated heritabilities for tail length in the range from 0.39 to 0.77 (James et al., 1991). Apart from sheep, quantitative genetic parameter estimates for tail length are available in different non-livestock species, for example in Toque Macaques (Cheverud and Dittus, 1992) and in mice (Kramer et al., 1998). Heritabilities were 0.67 and 0.46, respectively. Short tails also occur in pigs. However, to the best of our knowledge, there is a substantial lack of scientific studies addressing the genetic variation of tail length in pigs, considering the direct genetic as well as the maternal genetic perspective.

Tail abnormalities and the responsible genetic mechanisms may differ from the early birth stage of young piglets (tail abnormality = trait of the individual) compared with trait observations later in life (tail abnormalities or tail lesions (TLES) due to tail biting of contemporaries), suggesting analyses of a longitudinal data structure for tail traits with piglet aging. A new syndrome as detected and described by Reiner et al. (2019) and Reiner and Lechner (2019) is defined as “swine inflammation and necrosis syndrome (SINS)”. SINS contributes to signs of clinical inflammation and dead tissue in the acral regions but is independent from tail biting. T-LES due to SINS can appear in suckling piglets within the first days of life. First SINS indicators are inflammatory changes, continuing with tail necrosis, especially at the base and tip of the tail. In a German research experiment, more than 50% of all litters showed signs of SINS (Reiner and Lechner, 2019).

Mono- and oligogenetic impact on tail length was associated with pleiotropic effects on tail conformation traits including lethal factors. The T-gene was identified as a major gene influencing tail length but causing serious pleiotropic effects (Herrmann et al., 1990). Thus, the reported mutations in the T- gene induced early embryonic death in mice, altered spine structures in cats and cattle (Buckingham et al., 2013b; Kromik et al., 2015) and increased embryonic mortality in dogs and sheep (DeForest and Basrur, 1979; Hytönen et al., 2009). To our knowledge, quantitative genetic analyses focusing on genetic relationships between tail lengths with growth traits (e.g., estimates of genetic correlations), are not available. Consequently, the aim of the present study was to infer genetic (co)variance components for the traits tail length, tail abnormalities including T-LES and growth traits via quantitative genetic modelling approaches with and without consideration of maternal genetic effects.

MATERIAL AND METHODS

Animal care and proceedings used in this study were in accordance with guidelines and principles of the statutes of the Justus Liebig University, Giessen, for safeguarding good scientific practice. Data included only traits from the conventional performance tests (existing database) and visual observations for T-LES. Therefore, no additional statement of institutional animal care and use committee is required.

Animals and traits

Two datasets were available for the present study. Dataset 1 was used to infer genetic (co)variance components between tail length (T-LEN) and growth traits. Dataset 1 only included pigs from the University of Gießen research station "Oberer Hardthof". Tails of these piglets were docked after measuring T-LEN. Dataset 2 included longitudinal measurements for T-LES from pigs kept on the performance test station of the respective breeding organization from the federal state of Hesse, Germany. Dataset 2 was used to estimate genetic parameters and to calculate breeding value correlations for T-LES from different ages. For such a research objective, the whole piglet raising and pig fattening period considered animals with their naturally long tails (no application of routinely tail docking). Apart from the German Landrace pigs with an average genetic relationship of 0.01, there was no genetic connectedness between animals from dataset 1 and dataset 2, suggesting separate dataset analyses.

Dataset 1. Dataset 1 considered the traits for T-LEN and growth traits from the breeds Piétrain, German Landrace, Duroc, German Edelschwein, and rotational crosses kept on the University of Gießen research station "Oberer Hardthof". After editing, the data consisted of 9,348 records for T-LEN at birth, 12,112 records for birth weight (BW), 10,319 records for weaning weight (WW), 1,483 records for post-weaning weight (PWW), and 10,312 records for average daily gain (ADG) from piglets born in the period from 2015 to 2018. The piglets were offspring from

337 dams (on average 32.13 offspring per dam) and 206 sires (on average 58.80 offspring per sire) with complete pedigree information for four generations. Pedigree completeness and genetic structures was analyzed using the CFC software package (Sargolzaei et al., 2006).

On the “Oberer Hardhof” research stations, pigs were housed in modern and intensive management systems, with slatted floor pens and air-conditioning. Within the first 24 hr after birth, piglets were tattooed (ear numbers) for easy identification, and they received iron injections. In the context of this first management action, individual BW of piglets was recorded, and their tails were measured. Tail length comprised the distance (in cm) from the tail root to the tip of the tail. Afterward, as routinely done in conventional pig production systems, tails were docked. WW was recorded at the average age of 24 d (SD: 4 d), and PWW at the average age of 63 d (SD: 6 d). ADG was calculated considering BW and WW with the respective ages. Descriptive statistics for the pig traits from dataset 1 are given in Table 2.1.

Dataset 2. Dataset 2 included 4,943 observations from 1,648 pigs for T-LES as indicators for tail necrosis, tail abnormalities, or tail biting. Scoring for T-LES considered 3 categories: 1 = completely healthy tail without any abnormalities, 2 = partly tail losses with mild lesions, 3 = complete tail losses with severe lesions. In the next step of data preparation, T-LES observations were transformed into a binary T-LES data structure, with a score = 0 for the completely healthy tails without any abnormalities and a score = 1 for the remaining cases (i.e., combining the animals from categories 2 and 3). The scores 2 and 3 were merged into 1 category due to the small fraction of pigs showing complete tail losses with severe lesions. Tail scoring was performed at the following 3 different time points: T-LES-1: 30 ± 7 d after entry for rearing; T-LES-2: 50 ± 7 d after entry for rearing (end of rearing period); T-LES-3: 130 ± 20 d after entry for rearing (end of fattening period). Trait recoding on the performance test station was always done by the same trained person. The 1,648 recorded pigs were offspring from mating of German Landrace sows with Piétrain boars (1,441 pigs) and with German Landrace boars (207 pigs). The pigs were offspring from 39 sires (on average 42.25 offspring per sire) and from 54 dams (on average 30.52 offspring per dam). Recorded pigs were from the birth years 2016 to 2019. Pigs with trait records could be traced back to at least four generations. The pedigree dataset comprised 5,462 pigs with genetic relationships to the animals with records. The data distribution for the originally T-LES scores as well as for binary T-LES at the different recording dates is given in Table 2.2.

Table 2.1: Descriptive statistics for T-LEN, BW, WW, PWW and ADG.

Trait	Mean age (d)	No. of observations	Mean	SD	Min	Max	CV (in %)
T-LEN (cm)	0	9348	8.87	1.21	0[1]	16.80	13.61
BW (kg)	0	12,112	1.45	0.40	0.26	2.95	27.59
WW (kg)	24	10,329	7.16	1.61	1.32	13.60	22.49
PWW (kg)	63	1,483	24.66	7.76	4.7	49.00	31.47
ADG (kg)	24	10,285	0.23	0.06	0.01	0.50	26.09

[1] Piglets with complete tail losses at birth.

Table 2.2: Distribution of the original scorings for T-LES from different ages and incidences after transformation into a binary trait distribution.

Trait (date)[1]	Original scoring 1 = healthy	 2 = mild lesions	 3 = severe lesions	Binary trait definition 0 = healthy	 1 = diseased	 Incidence, in %	Total no. of obs.
T-LES- 1	1,289	603	60	1,289	663	33.97	1,952
T-LES- 2	1,001	640	19	1,001	659	39.69	1,660
T-LES- 3	926	403	2	926	405	30.43	1,331
T-LES	3,216	1,646	81	3,216	1,727	34.94	4,943

[1] T-LES-1, 30 ± 7 d after entry for rearing; T-LES-2, 50 ± 7 d after entry for rearing (end of rearing period); T-LES-3, 130 ± 20 d after entry for rearing (end of fattening period); T-LES, repeated measurements for T-LES as used for the repeatability model.

Statistical analyses

Dataset 1. First, to identify the most appropriate model, single-trait analyses were performed considering 5 different models. The evaluated models in matrix notation were defined as follows:

$$\text{Model 1: } y = Xb + Z_a a + e \qquad [1]$$

$$\text{Model 2: } y = Xb + Z_a a + Z_m m + e \text{ with } \mathrm{Cov}(a, m) = 0 \qquad [2]$$

$$\text{Model 3: } y = Xb + Z_a a + Z_m m + e \text{ with } \mathrm{Cov}(a, m) = A\sigma_{am} \qquad [3]$$

$$\text{Model 4: } y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with } \mathrm{Cov}(a, m) = 0 \qquad [4]$$

$$\text{Model 5: } y = Xb + Z_a a + Z_m m + Z_c c + e \text{ with } \mathrm{Cov}(a, m) = A\sigma_{am} \qquad [5]$$

where **y** was the observation vector for T-LEN, BW, WW, PWW or ADG; **b** is a vector for fixed effects (sex, breed, year-month at recording, litter size, litter number, age of dam at farrowing, age of pig at trait recording), **a** is a vector for random direct additive genetic effects, **m** is a vector for random maternal genetic effects, **c** is a vector for random maternal permanent environmental effects, and **e** is a vector for random residual effects; **X,** Z_a, Z_m, and Z_c were incidence matrices relating the records to fixed, additive direct genetic, maternal genetic and permanent environmental effects, respectively.

The (co)variance structure for random effects in model 5 was (and correspondingly reduced in the remaining models with a smaller number of random effects):

$$\mathrm{var}\begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_c\sigma_c^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

where **A** was the numerator relationship matrix between animals; σ_{am} was the covariance between direct additive and maternal genetic effects; I_c and I_n were identity matrices for permanent environmental effects considering c sows and residual effects considering n records, respectively. The direct heritability (h_d^2), maternal heritability (h_m^2), maternal permanent environmental effect (c^2) and direct-maternal genetic correlation (r_{am}) were calculated as follows: $h_d^2 = \frac{\sigma_a^2}{\sigma_p^2}$, $h_m^2 = \frac{\sigma_m^2}{\sigma_p^2}$, $c^2 = \frac{\sigma_c^2}{\sigma_p^2}$ and $r_{am} = \frac{\sigma_{am}}{\sqrt{\sigma_a^2 \times \sigma_m^2}}$, where, σ_a^2, σ_m^2, σ_c^2 and σ_p^2 were direct genetic, maternal genetic, maternal permanent environmental and phenotypic variances, respectively, and σ_{am} was the direct-maternal genetic covariance.

Single-trait model evaluation based on the Akaike's information criterion (**AIC**; Akaike, 1973) and on a likelihood ratio test (**LRT**) The LRT was performed as follows:

$$\mathrm{LRT} = -2(\mathrm{LogL}_{\mathrm{reduced\ model}} - \mathrm{LogL}_{\mathrm{full\ model}}),$$

where $\mathrm{LogL}_{\mathrm{reduced\ model}}$ was the log likelihood from models 1, 2, 3 or 4, and $\mathrm{LogL}_{\mathrm{full\ model}}$ was the log likelihood from the most complete model 5. Differences in LogL between models were tested at $P < 0.05$ with values following a chi-square distribution. Degrees of freedom were equal to the differences in the number of (co)variance components fitted for the 2 models. Model evaluation criteria -2LogL, AIC and the LRT are given in Table 2.3.

The LRT for the full model 5 did not significantly differ from the remaining models. Hence, we used model 5 for the ongoing multiple-trait analyses, aiming at the estimation of all possible direct and maternal genetic (co)variance components. Model 5 considering all 5 traits simultaneously is:

$$\begin{bmatrix} y_1 \\ \vdots \\ y_5 \end{bmatrix} = \begin{bmatrix} X_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & X_5 \end{bmatrix} \begin{bmatrix} b_1 \\ \vdots \\ b_5 \end{bmatrix} + \begin{bmatrix} Z_{a1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & Z_{a5} \end{bmatrix} \begin{bmatrix} a_1 \\ \vdots \\ a_5 \end{bmatrix} + \begin{bmatrix} Z_{m1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & Z_{m5} \end{bmatrix} \begin{bmatrix} m_1 \\ \vdots \\ m_5 \end{bmatrix} + \begin{bmatrix} Z_{c1} & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & Z_{c5} \end{bmatrix} \begin{bmatrix} c_1 \\ \vdots \\ c_5 \end{bmatrix} + \begin{bmatrix} e_1 \\ \vdots \\ e_5 \end{bmatrix}$$

For multi-trait analysis, the (co)variance structure for random effects was:

$$\mathrm{var}\begin{bmatrix} a_1 \\ \vdots \\ a_5 \\ m_1 \\ \vdots \\ m_5 \\ c_1 \\ \vdots \\ c_5 \\ e_1 \\ \vdots \\ e_5 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a1} & \cdots & A\sigma_{a1,m5} & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots & & & \\ A\sigma_{m5,a1} & \cdots & A\sigma^2_{m5} & 0 & \cdots & 0 & & & \\ 0 & \cdots & 0 & I_c\sigma^2_{c1} & \cdots & I_c\sigma_{c1,c5} & \vdots & \ddots & \vdots \\ & & & \vdots & \ddots & \vdots & & & \\ & & & I_c\sigma_{c5,c1} & \cdots & I_c\sigma^2_{c5} & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & 0 & \cdots & 0 & I_n\sigma^2_{e1} & \cdots & I_n\sigma_{e1,e5} \\ & & & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & 0 & 0 & \cdots & 0 & I_n\sigma_{e5,e1} & \cdots & I_n\sigma^2_{e5} \end{bmatrix},$$

where, σ^2_{ai} and σ^2_{mi} were direct and maternal genetic variances, respectively, for trait *i* (*i* = 1 to 5); $\sigma_{ai,mj}$ was the covariance between direct genetic effect for traits *i* and maternal genetic effect for trait *j* (*j* = 1 to 5); σ^2_{ci} was the maternal permanent environmental variance for the *i*th trait; $\sigma_{ci,cj}$ was the maternal environmental covariance between trait *i* and *j*; and σ^2_{ei} and $\sigma_{ei,ej}$ were residual variances and covariances, respectively; **A** was the numerator relationship matrix among animals; I_c and I_n were identity matrices for maternal permanent environmental effects considering *c* sows and residual effects considering n records, respectively.

In the multi-trait analysis, genetic correlations between direct genetic effect for trait *i* and maternal genetic effect for trait *j*, or vice versa, were calculated using the following formula:

$$r_{ai,mj} = \frac{\sigma_{ai,mj}}{\sqrt{\sigma^2_{ai} \times \sigma^2_{mj}}},$$

where $\sigma_{ai,mj}$ was the covariance between direct genetic effects for trait *i* and maternal genetic effects for trait *j*; σ^2_{ai} and σ^2_{mj} was the direct genetic variance for trait *i* and the maternal genetic variance for trait *j*, respectively.

Genetic (co)variance components were estimated via REML, and using the REMLF90 software package (Misztal et al., 2002).

Table 2.3: Model evaluation of the 5 single-trait animal models (as described in the text) considering -2 Log likelihood values (-2LOGL), Akaike information criterion (AIC) and likelihood ratio tests (LRT, as described in the Materials and Methods).

Trait	Model	No. of parameters	-2LogL	AIC	LRT
T-LEN	Model 1	2	1,607.91	1,611.91	24,031.73*
	Model 2	3	**-22,422.30**	**-22,416.30**	1.5208 ns
	Model 3	4	-22,423.72	-22,415.72	0.0978 ns
	Model 4	4	-22,423.92	-22,415.92	-0.1016 ns
	Model 5	5	-22,423.82	-22,413.82	
BW	Model 1	2	1,060.90	1,064.90	24,054.55*
	Model 2	3	-22,993.71	-22,987.71	-0.0516 ns
	Model 3	4	**-22,993.63**	**-22,985.63**	0.0253 ns
	Model 4	4	-22,993.50	-22,985.50	0.155 ns
	Model 5	5	-22,993.66	-22,983.66	
WW	Model 1	2	4,200.11	4,204.11	24,032.09*
	Model 2	3	**-19,831.53**	**-19,825.53**	0.4459 ns
	Model 3	4	-19,831.85	-19,823.85	0.1326 ns
	Model 4	4	-19,831.96	-19,823.96	0.0228 ns
	Model 5	5	-19,831.98	-19,821.98	
PWW	Model 1	2	589.73	593.73	24,031.13*
	Model 2	3	**-23,441.56**	**-23,435.56**	-0.1594 ns
	Model 3	4	-23,441.55	-23,433.55	-0.1498 ns
	Model 4	4	-23,441.49	-23,433.49	-0.0943 ns
	Model 5	5	-23,441.40	-23,431.40	
ADG	Model 1	2	-31,078.03	-31,074.03	24102.14*
	Model 2	3	-55,161.59	-55,155.59	18.5799*
	Model 3	4	-55,164.52	-55,156.52	15.6477*
	Model 4	4	**-55,179.31**	**-55,171.31**	0.8562 ns
	Model 5	5	-55,180.17	-55,170.17	

[1] Values from the best model are highlighted in bold. * = $P \leq 0.05$; ns, non significant, $P > 0.05$.

Dataset 2. Single-trait animal models were applied to estimate genetic parameters for binary T-LES-1, T-LES-2 and T-LES-3 in consecutive runs. In a further model for repeated measurements, T-LES-1, T-LES-2 and T-LES-3 were considered simultaneously. All analyses were performed using generalized linear mixed models with an identity link function (i.e., depicting a typical linear model (**LIN**)) and with a logit link function (i.e., to account properly for the binary trait structure in threshold models(**TH**). The repeatability model 6 is as follows:

$$\mathrm{y_{ijklmn}} \mid \text{link funciton}(\mathrm{y_{ijklmn}}) = \mu + \mathrm{RFB_i} + \mathrm{PS_j} + \mathrm{IA_k} + \mathrm{a_l} + \mathrm{Group_m} + \mathrm{pe_n} + \mathrm{e_{ijklmn}} \quad [6]$$

where $\mathrm{y_{ijklmn}}$ = observations for T-LES; $\mathrm{RFB_i}$ is the fixed effect for rearing and/or fattening bay; $\mathrm{PS_j}$ is the fixed effect for piglet supplier; $\mathrm{IA_k}$ is the fixed effect for initial tail assessment at entry for rearing; $\mathrm{a_l}$ is the random additive-genetic animal effect; $\mathrm{Group_m}$ is the random group effect for either crossbreeds or German Landrace pigs; $\mathrm{pe_n}$ is the random permanent environment effect in the repeatability models, and $\mathrm{e_{ijklmn}}$ is the random residual effect for the LIN applications. For the TH with the logit link function, the residual was fixed to $\pi 2/3$ (Southey et al., 2003).

Genetic analyses were performed using the REML algorithm, and applying the software package DMUV6 (Madsen and Jensen, 2013).

RESULTS

Genetic parameters for tail length and growth traits

Variance components and variance ratios for T-LEN, BW, WW, PWW and ADG from the multiple-trait model 5 are given in Table 2.4. Interestingly, among all traits, the largest direct heritability with 0.42 (± 0.03) was estimated for T-LEN. The direct heritability for PWW was moderate with 0.22 (± 0.04), but smaller for BW (0.07 ± 0.01), WW (0.12 ± 0.03) and ADG (0.15 ± 0.04). The maternal heritabilities for all traits were small and in a narrow range from 0.05 (± 0.02) for T-LEN to 0.10 (± 0.03) for BW. The maternal permanent environmental effect reflecting the common litter environment contributed to <5% of the phenotypic variations. Pronounced negative and antagonistic relationships were estimated between direct and maternal genetic effects in the range from -0.35 (± 0.13) for T-LEN to -0.90 (± 0.19) for PWW. Estimated direct heritabilities, maternal heritabilities, and correlations between direct and maternal genetic effects for T-LEN from the different single-trait animal models 1 to 5 reflect the results from the multiple-trait model (Supplementary Table 2.1 A). Also alternative single-trait animal models 1 to 5 with BW as covariate confirmed the quite large direct heritability estimates, which were in a range from 0.36 (± 0.01) to 0.46 (± 0.03) (Supplementary Table 2.1 B). The alternative single-trait animal models with BW as covariate generally contributed to slightly smaller residual and additive-genetic variances.

Table 2.4: Estimates of (co)variance components and variance ratios from the multiple-trait animal model application.

	Variance components and genetic parameters[1]								
Traits	σ_p^2	σ_e^2	σ_a^2	σ_m^2	σ_c^2	σ_{am}	r_{am}	h_d^2	h_m^2	c^2
T-LEN	1.57	0.79	0.66	0.07	0.05	-0.08	-0.35	0.42	0.05	0.03
BW	0.13	0.11	0.01	0.01	0.00	0.01	-0.49	0.07	0.10	0.02
WW	2.39	1.84	0.29	0.17	0.09	-0.10	-0.44	0.12	0.07	0.04
PWW	21.95	14.60	4.82	1.85	0.69	-2.67	-0.90	0.22	0.08	0.03
ADG[1]	3.24	2.37	0.50	0.21	0.17	-0.17	-0.54	0.15	0.07	0.05

[1] σ_p^2, phenotypic variance, σ_e^2, residual variance, σ_a^2, direct genetic variance, σ_m^2, maternal genetic variance, σ_c^2, permanent environmental variance, σ_{am}, covariance between direct and maternal genetic effects, $r_{am,}$ correlation between direct and maternal genetic effects, h_d^2, direct heritability, $h_{m,}^2$ maternal heritability, c^2, common litter environment.

[2] (co)variance components: multiplication of given values with 10^3.

Standard errors for h_d^2 and h_m^2 ranged from 0.01 to 0.04; standard errors for r_{am} ranged from 0.11 to 0.19.

Genetic correlations among tail length and growth traits

Estimates of genetic covariances and genetic correlations among traits considering direct and maternal genetic effects are given in Table 2.5. The genetic correlation for direct genetic effects between T-LEN with BW was moderate (0.40 ± 0.03). Both traits T-LEN and BW were recorded on the same date. Further genes and environmental effects might influence the remaining growth traits recorded with pig aging. Hence, the direct genetic correlations with T-LEN altered, and were close to zero in the range from 0.02 ± 0.01 (PWW) to 0.03 ± 0.01 (WW and ADG). The correlations between the direct genetic effects for T-LEN with the maternal genetic effects for the breeding goal traits BW, WW and ADG were quite large in the range from 0.55 ± 0.21 (ADG) to 0.73 ± 0.26 (WW), but close to zero with the maternal genetic effect for PWW (0.13 ± 0.19). Accordingly, positive but weak correlations were estimated between maternal genetic effects for T-LEN with direct genetic effects for all other breeding goal traits in the range from 0.10 ± 0.10 (ADG) to 0.27 ± 0.16 (PWW). The correlations between maternal genetic effects for T-LEN with maternal genetic effects for BW, WW, PWW, and ADG were in a narrow range and close to zero, i.e., 0.09 (± 0.06), 0.08 (± 0.06), 0.09 (± 0.06), and 0.06 (± 0.09), respectively. From an antagonistic across-trait perspective, and with a focus on direct-maternal genetic associations, negative correlations were estimated among BW, WW, PWW, and ADG.

Table 2.5: Genetic covariances (above the diagonal) and genetic correlations (below the diagonal) for direct genetic (A), maternal genetic (M) and direct-maternal genetic associations.

		A					**M**				
	Traits	T-LEN	BW	WW	PWW	ADG	T-LEN	BW	WW	PWW	ADG
A	T-LEN		0.66 (0.02)	0.03 (0.04)	0.01 (0.05)	0.04 (0.04)		0.08 (0.07)	0.06 (0.05)	0.25 (0.07)	0.03 (0.06)
	BW	0.40 (0.03)		0.01 (0.10)	0.00 (0.12)	0.06 (0.09)	0.14 (0.14)		-0.01 (0.14)	-0.01 (0.21)	-0.01 (0.14)
	WW	0.03 (0.01)	0.27 (0.02)		0.29 (0.07)	0.34 (0.05)	0.11 (0.10)	-0.05 (0.06)		-0.10 (0.18)	-0.09 (0.12)
	PWW	0.02 (0.01)	0.08 (0.05)	0.29 (0.05)		4.82 (0.34)	0.27 (0.16)	-0.09 (0.10)	-0.04 (0.10)		-2.67 (0.47)
	ADG	0.03 (0.01)	0.04 (0.01)	0.96 (0.11)	0.07 (0.04)		0.10 (0.10)	-0.01 (0.07)	-0.00 (0.08)	-0.01 (0.06)	
M	T-LEN		0.51 (0.08)	0.37 (0.08)	0.15 (0.13)	0.40 (0.07)		0.07 (0.13)	0.01 (0.17)	0.07 (0.24)	0.03 (0.17)
	BW	0.65 (0.21)		-0.29 (0.11)	-0.18 (0.12)	-0.16 (0.09)	0.09 (0.06)		0.01 (0.11)	0.02 (0.17)	0.00 (0.08)
	WW	0.73 (0.26)	-0.37 (0.24)		-0.14 (0.15)	-0.41 (0.10)	0.08 (0.06)	0.32 (0.07)		0.17 (0.18)	0.13 (0.12)
	PWW	0.03 (0.19)	-0.07 (0.16)	-0.12 (0.17)		0.05 (0.14)	0.09 (0.06)	0.02 (0.05)	0.23 (0.06)		1.85 (0.18)
	ADG	0.55 (0.20)	-0.25 (0.19)	-0.56 (0.36)	0.05 (0.19)		0.06 (0.09)	0.08 (0.10)	0.91 (0.18)	0.11 (0.11)	

[1] Standard errors of correlation estimates in parentheses.

Genetic parameters for tail lesions at different ages

For T-LES-1, TLES-2, and T-LES-3, heritabilities and corresponding SE were larger from linear than from TH (Table 2.6). Nevertheless, heritabilities from the TH were estimated on the underlying liability scale and from LIN on the observed scale. According to the theory of TH (Dempster and Lerner, 1950), heritabilities in either liability or observed scales may differ, especially in the case of low disease incidences.

In repeatability models, heritabilities from both modelling approaches were very similar (0.23 ± 0.04 for LIN and 0.21 ± 0.06 for TH), and SE were smaller than from the single-trait models. All estimated variance components were larger than the TH. The largest additive genetic variance for T-LES with 1.65 was estimated with the threshold repeatability model. Accordingly, the group variances were larger than the TH for all T-LES definitions. Especially, the fixation of the residual variances (value $\pi^2/3$, Southey et al., 2003) contributed to the smaller heritabilities for T-LES from the TH.

Breeding value correlations for T-LES at different ages

Breeding value correlations between T-LES from different ages (Figure 2.1) indicate that T-LES or tail abnormalities during rearing are genetically different traits. The lowest breeding value correlation was 0.13 between T-LES-3 from the TH with T-LES-1 from the LIN. Generally, correlations between breeding values from the early diagnosis date (T-LES-1) with breeding values from the latest diagnosis date (T-LES-3) were quite low, for threshold as well as for LIN applications. For the same trait definitions, correlations between breeding values from linear and TH were throughout larger than 0.90, i.e., 0.92 for T-LES-1, 0.94 for T-LES-2, 0.98 for T-LES-3, and 0.90 when considering the repeated measurement data structure. The breeding values correlations from both repeatability models (LIN and TH) with T-LES from both early diagnosis dates were quite large in the range from 0.68 to 0.90, but only moderate with breeding values for T-LES-3 (0.31 to 0.32).

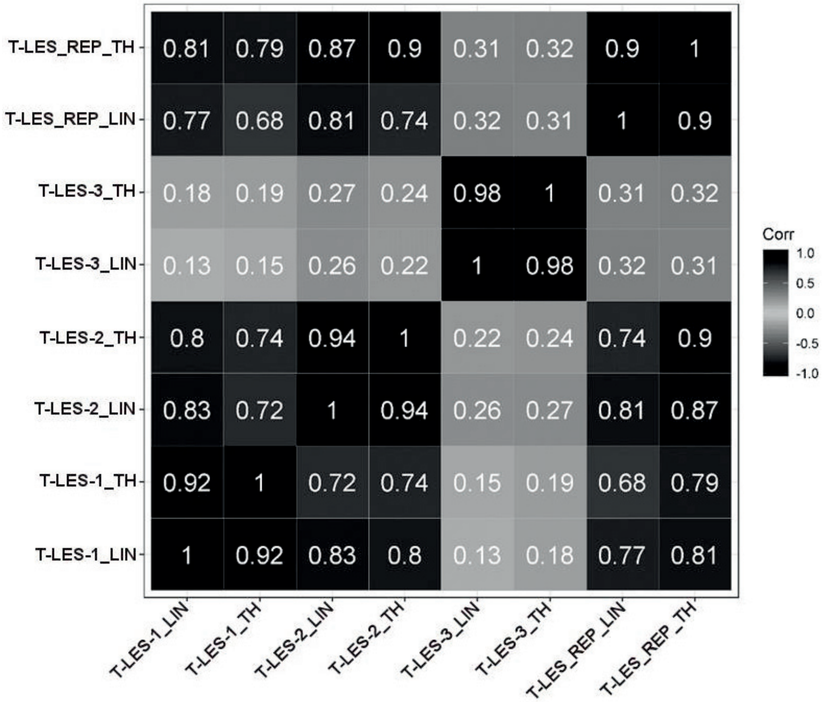
Table 2.6: Genetic parameters[1] for T-LES from different age and LIN and TH applications considering single trait or repeated measurements.

Trait	**Model**	***h²* ± SE**	σ^2_a	σ^2_{group}	σ^2_e
T-LES-1	LIN/single trait	0.18 ± 0.14	0.041	0.088	0.102
T-LES-1	TH/single trait	0.01 ± 0.07	0.062	4.105	3.290
T-LES-2	LIN/single trait	0.46 ± 0.15	0.112	0.059	0.073
T-LES-2	TH/single trait	0.11 ± 0.06	0.714	2.455	3.290
T-Les-3	LIN/single trait	0.39 ± 0.19	0.084	0.048	0.083
T-LES-3	TH/single trait	0.10 ± 0.09	0.587	2.257	3.290
T-LES	LIN/repeatability	0.23 ± 0.04	0.044	0.026	0.120
T-LES	TH/repeatability	0.21 ± 0.06	1.646	2.898	3.290

[1] h^2, heritability (for linear models on the observed scale and for threshold models on the underlying liability scale), σ^2_a, additive genetic variance, σ^2_{group}, variance for the genetic group effect, σ^2_e**,** residual variance.

[2] T-LES-1, 30 ± 7 d after entry for rearing; T-LES-2, 50 ± 7 d after entry for rearing (end of rearing period); T-LES-3, 130 ± 20 d after entry for rearing (end of fattening period); T-LES, repeated measurements for T-LES as used for the repeatability model.

[3] The repeatability from the LIN was 0.30, and from the TH 0.29.



	T-LES-1_LIN	T-LES-1_TH	T-LES-2_LIN	T-LES-2_TH	T-LES-3_LIN	T-LES-3_TH	T-LES_REP_LIN	T-LES_REP_TH
T-LES_REP_TH	0.81	0.79	0.87	0.9	0.31	0.32	0.9	1
T-LES_REP_LIN	0.77	0.68	0.81	0.74	0.32	0.31	1	0.9
T-LES-3_TH	0.18	0.19	0.27	0.24	0.98	1	0.31	0.32
T-LES-3_LIN	0.13	0.15	0.26	0.22	1	0.98	0.32	0.31
T-LES-2_TH	0.8	0.74	0.94	1	0.22	0.24	0.74	0.9
T-LES-2_LIN	0.83	0.72	1	0.94	0.26	0.27	0.81	0.87
T-LES-1_TH	0.92	1	0.72	0.74	0.15	0.19	0.68	0.79
T-LES-1_LIN	1	0.92	0.83	0.8	0.13	0.18	0.77	0.81

Figure 2.1: Breeding value correlations between T-LES considering pigs with more than 6 offspring from different ages. T-LES-1: 30 ± 7 d after entry for rearing; T-LES-2: 50 ± 7 d after entry for rearing (end of rearing period); T-LES-3: 130 ± 20 d after entry for rearing (end of fattening period); T-LES: repeated measurements for T-LES as used for the repeatability model; *_LIN = linear model applications; *_TH = threshold model applications.

DISCUSSION

Genetic parameters for tail length and breeding goal traits

The direct heritability for T-LEN with 0.42 was quite large and significantly larger than for the breeding goal traits from the present study reflecting piglets' weights and growth. The substantial genetic variation for T-LEN indicates that selection on short tails may reduce tail length in the pig populations within a few generations. Successful breeding on short tails was reported for several sheep breeds, which was possible in short time due to the large direct heritabilities ranging from 0.40 to 0.80 (Scobie and O'Connell, 2002). Regarding interpretations, it should be kept in mind that several breeds were considered simultaneously in the present study for the estimation of genetic parameters. From the strict theoretical background, a heritability is a population parameter. Nevertheless, several multi-breed studies have been conducted, but mostly based on genomic data enabling connectedness among breeds through the genomic relationship matrix (Yin et al., 2019). Additionally, we run breed-specific analyses, but the complex models did not properly converge. When including all breeds together, we had quite stable estimates from different models 1 to 5 (Supplementary Table 2.1). To account for the breed impact, we included breed as a fixed effect in the statistical model 1. Accordingly, Lo et al. (1992) defined a statistical model with a fixed breed effect, and estimated heritabilities for growth, backfat thickness, carcass, and meat quality traits in a mixed population including Landrace, Duroc, and their reciprocal crosses. Meyer et al. (1993) estimated genetic parameters in a multi-breed beef cattle population. In their pedigree-based modelling approach, they did not include any effect reflecting the breed or genetic compositions. Birth weight is a trait of increasing importance in pig breeding, because BW is strongly associated with piglet vitality, survival, growth performance and weight gain (Gondret et al., 2005; Muns et al., 2013; Klein et al., 2019). The direct heritabilities for BW from single trait models 2 to 5 were in a narrow range from 0.05 to 0.09, confirming the direct heritability from the multiple-trait model (0.09) and heritability estimates from previous studies (Arango et al., 2006; Tomiyama et al., 2010, Alves et al., 2018). Dufrasne et al. (2013) reported a larger BW heritability of 0.25, but the recording date was time-lagged with at least 4 days after birth. Accordingly, Edwards et al. (2006) reported increasing body weight heritabilities in piglets with aging. The direct body weight heritabilities from the present study gradually increased with age up to 0.22 for PWW. Accordingly, Alves et al. (2018) found an increase of direct heritability estimates with age due to the decreasing maternal influence. Substantial differences in direct heritabilities for BW from single-trait (0.51) and multiple-trait model applications (0.05) were identified by Banville et al. (2015) in Chinese–European Tai Zumu pigs. A tendency for slightly smaller heritabilities for growth traits from multiple-trait model applications was also found in the present study.

The maternal genetic effect was considered in models 2, 3, 4 and 5. Ignoring the maternal genetic component contributed to biased genetic evaluations and lowered response to selection (Näsholm and Danell, 1994; Solanes et al. 2004). For all traits in our study, we estimated similar direct heritabilities from the single-trait models 2 to 5 and from the multiple-trait model, but the direct heritability increased for all traits when ignoring the maternal genetic impact in model 1. This is exemplarily shown in Supplementary Table 2.1 for TL. From a statistical model perspective, it seems to be imperative to separate the maternal component into a maternal genetic and a maternal permanent environmental effect, and to consider a covariance structure between direct genetic and maternal genetic effects. Also from a physiological perspective, the impact of uterus characteristics on morphological and growth traits in offspring suggests consideration of maternal genetic effects. In pigs and other species, uterus size was related with improved nutrient transport from the mother to the fetus, initiating larger body size of offspring (Fowden et al., 2006). Yuan et al. (2015) reported associations between uterine characteristics with the efficiency of placental transports of nutrients, with further impact on piglet BW. Maternal genetic influence through uterine nutrition status and supply levels, uterus capacity and milk production was detected for piglet weights and weight gains (Kaufmann et al., 2000; Alves et al., 2018). In a long-term selection experiment in pigs (Freking et al., 2007), increasing uterus capacity was associated with offspring performance and fertility traits. Matheson et al. (2018) defined the percentage of piglets with delayed growth as a maternal uterus indicator trait and estimated negative genetic correlations with BW.

Interestingly, the maternal genetic component explained 5% of the phenotypic variation for T-LEN, indicating uterine influence on tail characteristics. Consequently, we assume uterine impact on piglet conformation traits including vertebrae characteristics (e.g., the number of dorsal vertebras). In this regard, Haverkamp et al. (2015) proved associations between the number of dorsal vertebras and tail length in a Merino sheep population. In mice, Cowley et al. (1989) proved the impact of the maternal uterine genotype on growth parameters, body size and tail length in offspring.

Among all traits, and with regard to the single-trait model 5 and the multiple-trait modelling approach, the largest maternal heritability was estimated for BW (0.10). Maternal heritabilities for BW in the range from 0.02 to 0.15 were reported by Kaufmann et al. (2000), Tomiyama et al. (2010), and Alves et al. (2018). As expected from a physiological perspective, maternal heritabilities for weight traits slightly decreased with aging (i.e., the maternal heritabilities for WW and PWW). The gradual decline of maternal heritabilities with aging was explored by Yin and König (2018), considering a dense longitudinal body weight data structure and random regression methodology. In contrast, Zhang et al. (2000) estimated a quite low direct heritability (0.03) but a larger maternal heritability (0.11) for piglet weights at the age of 28 days Zhang et al. (2000) explained the larger maternal heritability with the strong impact of sow milk productivity and sow behavior. Nevertheless, with ongoing piglet aging from weeks 8 to 22, also Zhang et al. (2000) reported a substantial decline of the maternal genetic impact.

The estimates for the direct heritability of 0.12 and for the maternal heritability of 0.07 for WW from model 5 are very close to estimates as reported by Damgaard et al. (2003) and Tomiyama et al. (2010). Hermesch (2001), Kaufmann et al. (2000), and Alves et al. (2018) estimated slightly lower WW heritabilities. The direct heritability for PWW with 0.22 and the maternal heritability with 0.08 was very similar when comparing to estimates from Tomiyama et al. (2010) for weight gain at 60 days. Direct and maternal heritabilities for ADG (0.15 and 0.07, respectively) reflect genetic parameter estimates for weight gain in the period from birth to the weaning date (Banville et al., 2015). Larger direct and maternal genetic heritabilities for daily gains were reported for Chinese pig populations (Zhang et al., 2016), Landrace pigs in the United States (Jiao et al., 2014) and Yorkshire in the United States (Lopez et al., 2018).

The negative correlations between direct and maternal effects for weights and growth traits are in agreement with estimates in other species, e.g., in dairy cattle (Johanson et al., 2011), beef cattle (Chud et al., 2014), and sheep (Boujenane et al., 2015). Explanations addressed the antagonistic relationships between milk yield of the dam (maternal impact) in the suckling period and the direct genetic impact on growth. However, the mechanisms explaining the negative correlations between direct and maternal genetic effects for T-LEN are unclear, suggesting molecular, morphological, and physiological investigations.

Genetic correlations between tail length and growth traits

The direct genetic correlation between T-LEN and BW was positive (0.40), indicating that larger piglets have longer tails. Addressing tail biting, the heavy and large pigs from the same group displayed dominant behavior and were stronger involved in biting activities than the smaller group contemporaries (Andersen et al., 2011). Accordingly, Edwards (2006), Taylor et al. (2010), and Palander et al. (2013) associated tail biting with pig weights or pig growth. Hence, from a tail-biting perspective, the selection on lighter piglets contributes to shorter tails (as identified in the present study) and to fewer cases for tail necrosis. However, the positive genetic correlations between BW with other breeding goal traits reflecting piglet survival and piglet vitality (Klein et al., 2018) suggest selection on increasing individual piglet size.

Furthermore, in the present study, we estimated positive (but weak) direct genetic correlations between BW and the other growth traits, as reported previously (Kerr and Cameron 1995; Kaufmann et al., 2000). The direct genetic correlation was largest (0.27) between BW and WW, but declined to 0.08 when correlating BW with PWW. The changing genetic correlations between BW with growth traits record later in life suggest consideration of repeated weight records during aging in body weight indices. The genetic correlation between BW and ADG was weak (0.04), but quite large between WW and ADG (0.96). Differences in body weight trait (co)variance components with aging indicate that different genes are switched on or off along the growth trajectory, as outlined by Schaeffer (2004) when introducing random regression models for animal breeding. Also within parity or lactations, body weight heritabilities and correlations among body weights from different measuring dates altered substantially (Yin and König, 2018).

To our knowledge, this is the first study addressing correlations between direct genetic effects for T-LEN with maternal genetic effects for growth traits, between maternal genetic effects for T-LEN with maternal-genetic effects for growth traits, and between maternal genetic effects for T-LEN with direct genetic effects for growth traits. All correlations with T-LEN when considering maternal effects of either T-LEN or of the growth traits were positive. Hence, from a practical breeding perspective, breeding on improved maternal abilities for body weights and growth traits contributes to longer tails in pig populations, and vice versa. Overall, the antagonistic (positive) correlations between T-LEN with all direct and maternal genetic components of body weight traits suggest the development of breeding goals or selection indices considering direct measurements for T-LEN. Especially in organic pig production, tail docking is under very critical focus, implying to raise long-tail pigs. The newly developed selection indices for organic pig production emphasizing larger BWs with an associated positive impact on piglet vitality (Klein et al., 2018) are counterproductive from a T-LEN breeding perspective. Direct-maternal and maternal-direct genetic correlations among the growth traits BW, WW, and PWW were negative, reflecting the antagonistic relationships between direct and maternal genetic effects within the same traits. Hence, also from a time-lagged body weight recording perspective, unfavorable direct-maternal genetic associations complicate breeding goal definitions and hamper selection efficiency. Direct-maternal associations close to zero among body weights from different ages were reported by Herring et al. (2010).

Genetic parameters for T-LES

Heritabilities for T-LES in the present study were in a broad range from 0.01 to 0.39, depending on the recording date and the genetic-statistical modelling approach. Heritabilities from the LIN were throughout larger than from the TH. Varona et al. (1999) made comprehensive evaluations and comparisons with regard to linear and TH applications. In the case of a typical binary data structure, they identified TH superiority accompanied with larger heritabilities. Larger heritabilities from threshold than from LIN are in line with the theory for the analysis of categorical data (Dempster and Lerner, 1950). Not only for the T-LES in the present study but also for piglet skin lesions (König von Borstel et al., 2018), the LIN heritabilities were larger than the heritabilities from the TH. The tail and skin lesions recording in both studies based on a scoring system comprising several classes. Afterward, for TH applications, data were transformed into a binary structure. It may be more appropriate to consider TH allowing more than 2 classes for such kind of data, but the frequencies for score 3 (severe T-LES) were extremely low. On the other hand, Pashmi et al. (2009) suggested transforming nonlinear health indicators into a binary data structure. According to the moderate heritabilities for T-LES from both repeatability models, T-LES may be proper indicator traits for genetic selection on pig behavior. Nevertheless, the ultimate goal is to reduce tail biting not from a victim, but instead from an actor's perspective. Identification of biting pigs implies comprehensive video analyses (which are very difficult to analyze), or a combination of modern video techniques with complex machine learning algorithms (D’Eath et al., 2018). As an alternative, several recent studies suggested to focus on recordings of tail or skin lesions (Gentz et al., 2019), which might be a suitable database for genetic group selection or models with social interactions (Heidaritabar et al. 2019). Accordingly, Turner et al. (2008) estimated quite large genetic correlations between lesion scores and pig behavior traits, indicating that selection on lesion scores indirectly reduces pig aggressiveness. Furthermore, T-LES can be the major reason for the outbreak of tail biting in a pig group (Statham et al., 2009).

When considering T-LES as indicators for genetic selection on reduced tail biting, the optimal recording period has to be determined. Due to the stable heritabilities from linear repeatability and threshold repeatability models accompanied with smallest SE, we suggest to analyze a longitudinal data structure. On the other hand, from a practical perspective, trait recording implies tremendous efforts on logistics and on labor, suggesting only 1 observation per pig during aging. Based on the breeding value correlations from the present study, we suggest tail lesion scoring at an age of 50 d, i.e., at the end of the rearing period. Accordingly, other quantitative genetic studies focusing on skin lesion analyses suggested trait recording before moving the pigs to the finishing barn (König von Borstel et al., 2018). Genetic analyses of lesions from this period contributed to the best genetic differentiation (i.e., the largest additive genetic variances).

In conclusion, the moderate additive genetic variances and direct heritabilities for T-LEN indicate the possibilities for successful genetic selection on short tails in pigs. Such a breeding approach may be the most sustainable solution to improve pig welfare considering both aspects: tail biting and tail docking. Nevertheless, we also identified a small maternal genetic effect on T-LEN and antagonistic associations between direct and maternal genetic effects, which complicates the definition of breeding goals and selection strategies. As a further constraint from a practical perspective, breeding on short tails is genetically related to a decrease in body weights at different ages, especially with BW. T-LES from repeatability models had moderate heritabilities and could be used as indicators for pig behavior. When aiming at single-trait genetic evaluations, T-LES should be recorded at the end of the rearing period. In an ongoing study, to fully understand all trait associations genetically, we suggest the estimation of covariances between tail lengths with T-LES. For datasets 1 and 2 in the present study, pedigree genetic relationships larger than zero only were identified for German Landrace. Hence, we will focus on pig genotyping and on inferring genetic covariances between tail length and T-LES considering genomic relationships and multi-breed genomic approaches as suggested and evaluated by Yin et al. (2019) and VanvanHossou et al. (2020). A second ongoing research objective should consider tail biting traits from an actor's (biting) perspective.

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Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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APPENDIX

Supplementary Table 2.1

Estimates of (co)variance components and variance ratios for tail length from different single trait animal models (as explained in the methods). **A**: without birth weight as covariate, **B**: with birth weight as covariate.

A

	Variance components and genetic parameters[12]									
Model	σ_p^2	σ_e^2	σ_a^2	σ_m^2	σ_c^2	σ_{am}	r_{am}	h_d^2	h_m^2	c^2
1	2.85	1.39	1.45	-	-	-	-	0.51	-	-
2	2.37	1.12	1.10	0.15	-	-	-	0.46	0.06	-
3	2.02	1.21	0.68	0.12	-	-0.05	-0.18	0.34	0.06	-
4	2.01	1.14	0.71	0.08	0.08	-	-	0.35	0.04	0.04
5	1.88	0.93	0.78	0.09	0.07	-0.08	-0.28	0.41	0.05	0.04

B

	Variance components and genetic parameters[12]									
Model	σ_p^2	σ_e^2	σ_a^2	σ_m^2	σ_c^2	σ_{am}	r_{am}	h_d^2	h_m^2	c^2
1	1.99	0.95	0.94	-	-	-	-	0.50	-	-
2	1.94	0.91	0.88	0.15	-	-	-	0.45	0.09	-
3	1.65	0.86	0.59	0.19	-	-0.11	-0.33	0.36	0.12	-
4	1.68	0.68	0.66	0.22	0.11	-	-	0.39	0.13	0.07
5	1.78	0.66	0.71	0.26	0.14	-0.13	-0.32	0.40	0.14	0.08

[1] σ_p^2 = phenotypic variance, σ_e^2 = residual variance, σ_a^2 = direct genetic variance, σ_m^2 = maternal genetic variance, σ_c^2 = permanent environmental variance, σ_{am} = covariance between direct and maternal genetic effects, r_{am} = correlation between direct and maternal genetic effects, h_d^2 = direct heritability, h_m^2 = maternal heritability, c^2 = common litter environment

[2] Standard errors for h_d^2 and h_m^2 were in the narrow range from 0.01 to 0.03; Standard errors for r_{am} were in the range from 0.09 to 0.15.

CHAPTER 3

EFFECTS OF HERBAL DIET, DIET X BOAR LINE AND DIET X GENOTYPE INTERACTIONS ON SKIN LESIONS AND ON GROWTH PERFORMANCE IN POST-WEANING PIGS USING A CROSS-CLASSIFIED EXPERIMENT

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HIGHLIGHTS

The highlight of the present study is the analysis of genotype by diet interactions in the context of skin lesions in pigs. This is a novel study, indicating the importance of collaborative work including both disciplines animal breeding and animal nutrition.

ABSTRACT

The aims of the present study were to assess the effect of an herbal diet (HD; basal diet plus a supplement with chicory herbs) on production traits and lesions scores in post-weaning pigs, and to study possible boar x diet and genotype x diet interactions considering the two feeding groups HD and control (CON). In this regard, a cross-classified research design was implemented, aiming on an equal number of boar offspring in both groups HD and CON. Grouping of piglets (993 crossbred piglets from 14 different Piétrain boars sire to German Landrace or German Edelschwein sows) was done after weaning, and the feeding experiment was conducted in post-weaning period up to the pig age of nine weeks. Studied traits included the post-weaning weight (PWW) at the age of nine week 9, average daily gain (ADG) considering the period from weaning until week 9 and a skin lesion score (LS) at week 9. Herbal diet effects and sire x diet effects were inferred via linear models for Gaussian distributed PWW and ADG, and via generalized linear mixed models with a logit link function for categorical LS. Possible genotype x diet interactions were proved in multiple-trait models via Gibbs sampling, by defining same traits recorded either in CON and HD as different traits, i.e., post-weaning weight control (PWW_{CON}) and post-weaning weight herbal diet (PWW_{HD}), average daily gain control (ADG_{CON}) and average daily gain herbal diet (ADG_{HD}), and lesion score control (LS_{CON}) and lesion score herbal diet (LS_{HD}). The dietary treatment had no significant effect ($P > 0.05$) on PWW and ADG. The dietary treatment significantly ($P < 0.05$) influenced the behaviour of the pigs with a lower and favourable LS score for the pigs allocated to HD. Significant sire x diet interactions were identified for LS, PWW and ADG. Pearson correlations between estimates for sire effects from both diets CON and HD (i.e., the sire x diet effect) were 0.84 for PWW, 0.71 for ADG and 0.56 for LS. Genetic correlations smaller than 0.80 between PWW_{CON} and PWW_{HD}, ADG_{CON} and ADG_{HD}, and LS_{CON} and LS_{HD} indicate genotype x diet interactions, especially for the functional and low heritability LS. Hence, re-rankings of sires according to their estimated breeding values (EBV) were observed in both environments CON and HD, displaying smaller genetic and EBV variations for LS in the HD group. The HD dietary supplement contributed to fewer skin lesions, probably due to the favourable effect on pig behaviour, but a more pronounced genetic differentiation seems to be possible in the more challenging CON environment. Generally, the results from the present study indicate the importance of genotype x feeding interactions for pig breeding, suggesting specific boars for different feeding environments.

Keywords: herbal diet, skin lesion, growth parameters, genotype by environment interactions

INTRODUCTION

In the EU, the 'routinely' use of tail docking is not allowed according to the EU Council Directive 2008/120/EC from December 2008, which focuses on restrictions of non-curative invasions. However, the directive allows tail docking if 'there is evidence that injuries to other pigs' ears or tails have occurred'. Consequently, about 95% of the pigs in European countries, such as Germany, Denmark, France and others, have docked tails (D'Eath et al., 2014; EFSA, 2007). Nevertheless, the future is to keep pigs with naturally long tails, implying improvements in animal behaviour. Aggressive behaviour in pigs was observed at different growth stages, especially during the weaning phase (Lau et al., 2015; Schrey et al., 2019). At weaning, major stressors associated with aggressive behaviours include the removal of piglets from the sow, their transfer into a new environment and mixing with unfamiliar pigs, as well as the change from a liquid to a solid diet (Lecce et al., 1979; Campbell et al., 2013). Until clarification of social ranking in the new environment, aggressiveness among pigs causes various behavioural reactions, escalating to damaging fights in addition to tail biting with associated skin lesions (Wurtz et al., 2017; Camerlink et al., 2016, 2014; Turner et al., 2009). Several approaches have been initiated to mitigate aggressive behaviour and tail biting through genetic selection, and through modifications of the production environment (Turner, 2011; Rohrer et al., 2013; Ellen et al., 2014). Aikins-Wilson et al. (2021) evaluated prospective breeding strategies in pigs, and identified genetic associations between tail length with tail biting and incidences for skin lesions.

Nutrition played a major role in tail and ear biting, i.e., stimulated foraging, exploratory and social behaviour in pigs (Holling et al., 2017; Jensen and Pedersen, 2010; Beattie et al., 2005). In this regard, feeding diets with low dietary protein levels contributed to an increase of ear and tail biting (e.g. Jensen et al. 1993; Fraser et al. 1991). Some other studies pointed out the favourable effects of fibre levels in the feeding ration on pig behaviour (Kallabis and Kaufmann, 2012; Braund et al., 1998; Brouns et al., 1994). Cheng et al. (2017) and Yan et al. (2012) concluded that the inclusion of herbs and their extracts in swine diets improves growth performance, nutrient digestibility, immune function and meat quality. In this regard, the herbaceous plant chicory (*Cichorium intybus L.*) has been used as a fibre component in pigs and small ruminant diets, without compromising performance traits and improving nutrient digestibility, immune function and meat quality (Liu et al., 2018; Cheng et al., 2017; Nwafor et al., 2017; Yan et al., 2012; Ivarsson et al., 2011). In addition, active ingredients such as proteins, metabolic energy, vitamins, minerals and bioactive compounds in plant-based diets improved digestion, metabolism and increased overall vitality (Saeed et al., 2017). The nutrition company Dr. Schaette, Saluvet GmbH (personal communication, 2018) indicated the favourable feeding effects of the herbal diet “Kräuterkraft Aufzucht & Verdauung” which consists of 30% chicory root to reduce aggressiveness and simultaneously improving growth performance. However, such hypotheses indicating favourable feeding effects of the herbal diet on pig behaviour and performance traits are mostly based on visual inspections and lacking scientific evidence. Furthermore, the genetic component as well as genotype x diet interactions affected primary and functional trait responses in pigs (Schiavon et al., 2019). Genotype by environment interactions with associated re-rankings of animals in different production environments were mainly due to differences in nutritional characteristics (Hamilton et al., 2003). Augspurger et al. (2002) carried out a feeding experiment in pigs and concluded that different genotypes have different nutrient requirements for growth performances, and differed with regard to feed intake and feed efficiency. Accordingly, Fabian et al. (2002) evaluated growth parameters and reported significant interaction effects for amino acid contents in the diets in different genetic Duroc lines. A selection focus on boar lines was suggested to improve production efficiency and profitability in pig farming systems (Elbert et al., 2020; Vázquez-Gómez et al., 2020; De Cuyper et al., 2019). Especially in rotational crossbreeding systems (i.e., in crisscross designs) with intra-herd replacements of sows, the genetics of dam lines is less variable than the genetics of end products due to the utilization of bars from worldwide operating breeding companies. Elbert et al. (2020), Vermeulen et al. (2016) and Bidanel and Ducos (1996) studied the growth trajectory in pigs and found strong effects of the boar on birth weight up to weights gains in the fattening period, without evaluating possible genotype by nutrition interactions.

Consequently, the objective of the present study was to implement a cross-classified research design to infer the effects of the herbal diet and of diet x genotype interactions on skin lesions and growth traits in post-weaning pigs. In this context, also quantitative-genetic models were defined for the estimation of variance components and variance ratios in different feeding systems, and for the proof of possible diet x genotype interactions through genetic correlation estimates.

Materials and Methods

Animals, housing and feeding

The present study considered 993 crossbred pigs from 77 German Landrace x German Edelschwein dams sired by 14 different Piétrain boars, kept at the teaching and research station "Oberer Hardthof" of the Justus Liebig University in Giessen, Germany. From birth onwards, piglets suckled their mother and additionally received a supplementary diet until weaning at 24 ± 2 days of age. At weaning, piglets were allocated to either a basal diet (**CON**) or herbal diet (**HD**) group. The feed ration in the CON dietary treatment included wheat, soybeans and barley as concentrates plus minerals and vitamins. The HD treatment was the basal diet plus a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”. The composition of the supplementary feed “Kräuterkraft Aufzucht & Verdauung” in the HD diet consisted of 30% chicory (*Cichorium intybus L.*), root, carbonic acid algae lime (*Lithothamnion calcareum*), alumroot (*Heuchera americana*), 5% yarrow herb (*Achillea millefolium*), fenugreek seeds (*Trigonella foenum-graecum*), nettle herb (*Urtica dioica*), malt sprouts, sugar beet molasses, yeast and seaweed (*Ascophyllum nodosum*) flour. Piglets in both groups CON and HD were fed a two-phase diet after weaning: Phase 1 (starter diet) was fed for 6 days, followed by phase 2 (growing diet) until they are sold for fattening. Piglets were fed ad libitum with a sensor feeding system that supplied diets at appropriate time intervals. Samples of all feed mixtures were collected and analyzed in an accredited laboratory (Landesbetrieb Hessisches Landeslabor, Kassel). Ingredient composition and analysed nutrient content of the experimental diets are presented in Table 3.1.

Piglets were allocated to the dietary treatment considering a similar number of offspring per boar in each treatment to ensure the same genetic background in both groups CON and HD. Accordingly, 534 and 459 piglets were considered for CON and HD, respectively. Maximal 15 piglets were allocated to 8 pens per treatment, implying a floor space of at least 0.36 m^2 per piglet. Temperatures were regulated electronically, to ensure a constant climatic production environment from 29°C at the beginning of the rearing period to 21°C at the end of the experiment. Each pen was equipped with two automated nipple drinkers at different heights and a one-meter trough.

Table 3.1: Ingredient composition of the experimental diets[1].

Stage	Starter diet		Growing diet	
Treatment	CON	HD	CON	HD
Dry matter (%)	89.8	89.9	88.6	89.4
Metabolic energy (MJ/kg)	14.4	14.4	14.1	13.0
Ingredient, % of DMI				
Insoluble ash	5.2	5.6	8.0	7.9
Crude Protein	18.2	18.8	16.6	17.1
Crude fiber	3.1	3.3	2.4	4.9
Crude fat	6.0	6.3	3.3	3.3
Calcium	0.75	0.60	1.06	1.57
Copper	0.01	0.01	0.01	0.02
Total phosphorus	0.56	0.55	0.52	0.62
Magnesium	0.15	0.14	0.15	0.16
Sodium	0.18	0.16	0.21	0.33
Zinc	0.02	0.01	0.02	0.01
Lysine	1.25	1.31	0.98	1.22
Methionine	0.41	0.39	0.35	0.40
Cystin	0.26	0.28	0.30	0.28
Threonine	0.80	0.79	0.67	0.71

[1] CON: basal diet with no additives; HD: basal diet with a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”.

Animal traits

Individual piglet weights were determined at weaning at an age of four weeks (weaning weight; WW) and post-weaning age at the age of nine week 9 (postweaning weight; PWW). Average daily gain (ADG) in g per day (g/day) was calculated for the period from weaning to the age at nine weeks considering the measurements for WW and PWW. The same pigs were scored for skin lesions at the weaning and at the post-weaning weight date from one trained classifier. In this regard, lesion scores (LS) were assigned based on the protocol described by Pluske and Williams (1996) and Bünger et al. (2015). Accordingly, a lesion implied a single or continuous scratch, and scores were assigned as follows: score 1 = no lesion or less than 5 slight skin lesions; score 2 = mild lesion with more than 5 mild lesions including hair loss, redness, irritation, scratches or small abrasions; score 3 = severe lesion, bleeding and loss of tissue. The descriptive statistics for the traits PWW, ADG and LS is given in Table 3.2. The pedigree dataset for all animals with phenotypic records for PWW, ADG and LS was traced back to five generations.

Table 3.2: Descriptive statistics for post weaning weight (PWW), average daily gain (ADG) and lesion score (LS) recorded at the post-weaning date.

Trait	Group[1]	Mean	SD	CV (%)	Min	Median	Max
PWW (kg)	CON	18.94	4.60	0.24	7.70	18.90	31.80
	HD	20.00	4.61	0.23	8.60	19.40	35.00
ADG (g)	CON	358.00	94.18	0.26	90.00	360.00	630.00
	HD	365.86	92.91	0.25	40.00	360.00	660.00
					Score 0 (in %)	Score 1 (in %)	Score 2 (in %)
LS	CON	1.22	0.71	0.59	17	44	39
	HD	1.22	0.69	0.56	15	48	37

[1] CON= basal diet with no additives; HD: basal diet with a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”.

Statistical Analyses

Models inferring fixed effects, random effects and sire x diet effects

Statistical analyses were performed to infer fixed and random effects on performance traits and skin lesions using the statistical software package R (R Core Team, 2020). The “lme4” package (Bates et al., 2015) was applied to fit the linear mixed model (model 1) for the Gaussian distributed traits ADG and PWW as follows:

$$y_{ijklmnopqr} = \mu + L_i + G_j + T_k + LN_l + SL_m + YS_n + b_1\,(WW_o) + b_2\big(age_p\big) + S_q + (S_q \times T_k) + e_{ijklmnopqr} \qquad [1]$$

where $y_{ijklmnopqr}$ was the observation for PWW or ADG; μ was the overall mean effect; L_i was the fixed effect of the i^{th} litter size group (five groups: 3-11, 12-15, 16-17, 18-19 or 20-24); G_j was the fixed effect of the j^{th} sex (male or female); T_k was the fixed effect of the k^{th} treatment (CON or HD); LN_l was the fixed effect of t^{th} litter number (l = 1 to 5); YS_n was the fixed effect for the n^{th} year-season at recording; SL_m was the fixed effect of the m^{th} lesion score at weaning (*m* = 0, 1, 2); $\mathrm{WW_o}$ was weaning weight as a covariate (linear regression); $\mathrm{age_p}$ was the age of the pig at the recording date as a covariate (linear regression); $\mathrm{b_1}$ and $\mathrm{b_2}$ were the regression coefficients of the trait on $\mathrm{WW_o}$ and $\mathrm{age_p}$, respectively; $\mathrm{S_q}$ was the random effect of the q^{th} sire family (q = 1-14); $\mathrm{S_q \times T_k}$ was the effect of the interaction between sire and treatment, and $\mathrm{e_{ijklmnopqr}}$ was the random residual effect.

Generalized linear mixed models with a logit link function from the "ordinal" package in R (Christensen, 2019) were applied to analyse the categorical trait LS from the post-weaning weight date. The respective model 2 was:

$$\mathrm{logit}\left(\mathrm{P}(\mathrm{y_{ijklmnopqr}} \le \mathrm{c})\right) = \log\frac{\mathrm{P}(\mathrm{y_{ijklmnopqr}} \le \mathrm{c})}{1 - \mathrm{P}(\mathrm{y_{ijklmnopqr}} \le \mathrm{c})}$$

$$= \mu_\mathrm{c} + \mathrm{L_i} + \mathrm{G_j} + \mathrm{T_k} + \mathrm{LN_l} + \mathrm{SL_m} + \mathrm{YS_n} + \mathrm{b_1}\,(\mathrm{WW_o})$$

$$+ \mathrm{b_2}(\mathrm{age_p}) + \mathrm{S_q} + (\mathrm{S_q} \times \mathrm{T_k}) \qquad [2]$$

where $\mathrm{y_{ijklmnopqr}}$ was the observation for LS with three categories; $\mathrm{P}(\mathrm{y_{ijklmnopqrs}} \le \mathrm{c})$ was the cumulative probability of y less than or equal to a specific category *c* = 1 and 2, because $\mathrm{P}(\mathrm{y_{ijklmnopqrs}} \le 3) = 1$ and $1 - \mathrm{P}(\mathrm{y_{ijklmnopqrs}} \le 3) = 0$, with a maximum of *c* = 3; μ_c was the baseline value of the transformed cumulative probability for category c; $\mathrm{S_q \times T_k}$ was the interaction between sire and treatment. The remaining effects were the same as defined for model 1.

For both models 1 and 2, pairwise comparisons of least squares means were made using the Tukey test. Least square means with corresponding standard errors were considered statistically significant at a confidence level of 95% ($P \le 0.05$). Spearman rank correlations were calculated between sire effect estimates for PWW, ADG and LS in the production environments CON and HD.

Models for genetic analyses

(Co)variance components were estimated using a Bayesian approach via Gibbs sampling. In this regard, we used the programs GIBBS3F90 and THRGIBBS3F90 from the BLUPF90 software package (Misztal et al., 2002). In genetic analyses, each trait recorded in the two different dietary treatment groups CON or HD were considered as two different traits in consecutive runs, e.g., PWW_{CON} and $\text{PWW}_{\text{HD,}}$ ADG_{CON} and ADG_{HD}, and LS_{CON} and LS_{HD}. The bivariate animal model 3 was defined as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a_1} & 0 \\ 0 & Z_{a_2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c_1} & 0 \\ 0 & Z_{c_2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \tag{3}$$

where y_i were the observation vectors for the same trait (PWW, ADG or LS) recorded in the ith dietary treatment (i = 1 and 2 for CON and HD, respectively); b_i were the vectors of fixed effects including sex, litter size, litter number, age of dam at farrowing and lesion score at weaning as categorical effects, and age at recording and weaning weight as covariables with the corresponding incidence matrix X_i; a_i were the vectors of random additive genetic effects with incidence matrices Z_{a_i}, and c_i were the vectors of random common litter environmental effects with incidence matrices Z_{c_i}, and e_i were the vectors of random residual effects. The (co)variance structure for random effects in bivariate analyses was:

$$\text{var}\begin{bmatrix} a_1 \\ a_2 \\ c_1 \\ c_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} A\sigma^2_{a_1} & A\sigma_{a_{12}} & 0 & 0 & 0 & 0 \\ A\sigma_{a_{12}} & A\sigma^2_{a_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & I\sigma^2_{c_1} & I\sigma_{c_{12}} & 0 & 0 \\ 0 & 0 & I\sigma_{c_{12}} & I\sigma^2_{c_2} & 0 & 0 \\ 0 & 0 & 0 & 0 & I\sigma^2_{e_1} & 0 \\ 0 & 0 & 0 & 0 & 0 & I\sigma^2_{e_1} \end{bmatrix}$$

where $\sigma^2_{a_i}$ and $\sigma^2_{c_i}$ were the additive genetic and the common litter environmental variances, respectively, for the same traits in the ith dietary treatment (i = 1 and 2 for CON and HD, respectively); $\sigma_{a_{12}}$ and $\sigma_{c_{12}}$ were the additive genetic and common litter environmental covariances, respectively, between the same traits in CON and HD; $\sigma^2_{e_1}$ and $\sigma^2_{e_2}$ were the residual variances for the same traits in the respective treatment; A was the numerator relationship matrix among animals, and I were identity matrices for common litter environmental and residual effects. Heritability (h^2_i) and common litter environmental variance in relation to the phenotypic variance (c^2_i) for the trait in the *i*th treatment group were calculated as $h^2_i = \sigma^2_{a_i}/(\sigma^2_{a_i} + \sigma^2_{c_i} + \sigma^2_{e_i})$, and $c^2_i = \sigma^2_{c_i}/(\sigma^2_{a_i} + \sigma^2_{c_i} + \sigma^2_{e_i})$, respectively. The genetic correlation (r_a) and common litter environment correlation (r_c) between the same trait in CON and HD were calculated as $r_a = \sigma_{a_{12}}/\sqrt{\sigma^2_{a_1} \times \sigma^2_{a_2}}$ and $r_c = \sigma_{c_{12}}/\sqrt{\sigma^2_{c_1} \times \sigma^2_{c_2}}$, respectively. The same pig cannot be recorded in the same environment CON and HD. Consequently, there is no residual covariance between PWW_{con} and PWW_{HD}, between ADG_{con} and ADG_{HD}, and between LS_{con} and $LS_{HD.}$ Nevertheless, as implemented in the BLUPF90 software package (Misztal et al., 2002), we calculated an overall “total correlation” between same traits from different treatments considering the (co)variance components for additive genetic and common litter environmental effects as

$r_t = \frac{(\sigma_{a_{12}}+\sigma_{c_{12}})}{\sqrt{(\sigma^2_{a_1}+\sigma^2_{c_1}+\sigma^2_{e_1})\times(\sigma^2_{a_2}+\sigma^2_{c_2}+\sigma^2_{e_2})}}$, where $\sigma_{a_{12}}$ and $\sigma_{c_{12}}$ were the additive genetic and common litter environmental covariances between the same trait in CON and HD, respectively, and $\sigma^2_{a_i}$, $\sigma^2_{c_i}$ and $\sigma^2_{e_i}$ were the additive genetic, common litter environmental and residual variances for the ith dietary treatment.

In total, 200,000 Gibbs samples were generated, and 50,000 samples were discarded as a burn-in period. Afterward, a sampling interval of 100 cycles was considered to calculate posterior means and posterior standard deviations of (co)variance components. Statistics for post-Gibbs analyses were performed using the POSTGIBBSF90 program (Misztal et al., 2002). The length of the burn-in period and the number of iterations was determined based on the analyses of genetic covarinces according to the method by Raftery and Lewis (1992), as implemented in the BOA software package (Smith, 2005).

RESULTS

Fixed effects, random effects and sire x diet effects

Least squares means for ADG, PWW and LS with respective standard errors from model 1 for the effect levels are presented in Table 3.3. The season effect was significant ($P < 0.001$) for PWW, ADG and LS, indicating lower ADG and PWW for piglets born in spring and summer 2018 than for piglets born in winter from the same year. Age had a significant effect ($P < 0.001$) on ADG and PWW with least squares means of 5.51 g and 0.41 kg, respectively, (Table 3.3). The dietary treatment had no significant ($P > 0.05$) effect on PWW and ADG. Least squares means for PWW and ADG for animals from CON were larger than for animals from HD, but differences were not significant ($P > 0.05$).

The sex effect was not significant ($P > 0.05$) for LS at the post-weaning weight date. However, least squares means for LS were lower (= favourable) for female than for male piglets. Significant differences ($P < 0.05$) were observed between LS recorded in winter, spring and summer 2018. Least squares means for LS were highest in 2018-summer (1.55 ± 0.29), followed by spring (2018-spring: 0.54 ± 0.28, 2019-spring: 0.80 ± 0.29). The trend for higher LS in the summer season was observed for each recording year. It was also observed that piglets with severe and mild lesions sores at the weaning date had increased least squares means for LS (1.54 and 0.83, respectively) at the end of the experiment at the post-weaning weight date. The dietary treatment significantly ($P < 0.05$) affected LS, indicating higher least squares means for LS for pigs allocated to the CON group (0.79) than for pigs from the HD group. Pearson rank correlations between estimates for sire effects of same traits from both dietary groups CON and HD (i.e., the sire x diet effect) were 0.84 for PWW, 0.71 for ADG and 0.56 for LS.

Table 3.3: Least square means and corresponding standard errors (in parenthesis) for levels of fixed effects on post weaning weight (PWW, in kg), average daily gain (ADG, in g) and lesion score (LS).

Effect	ADG	PWW	LS
Sex			
Male	402.00 (17.70)	21.20 (0.60)	0.72 (0.16)
Female	404.00 (17.80)	21.40 (0.60)	0.45 (0.17)
Year-Season			
2018-winter	431.00^{ab} (31.10)	22.40^{ab} (1.06)	-0.17^{a} (0.48)
2018-spring	379.00^{ab} (27.00)	20.70^{ab} (0.94)	0.54^{a} (0.28)
2018-summer	354.00^{ab} (48.50)	19.40^{ab} (1.66)	1.55^{b} (0.29)
2018-autumn	375.00^{a} (24.30)	20.80^{ab} (0.87)	0.60^{ab} (0.36)
2019-winter	452.00^{b} (23.20)	22.90^{a} (0.89)	0.23^{ab} (0.40)
2019-spring	426.00^{ab} (23.20)	21.50^{b} (0.83)	0.80^{ab} (0.29)
Age of animal	5.51*** (2.24)	0.41*** (0.08)	0.03 (0.06)
Litter number			
1	396.00^{ab} (18.70)	20.90^{ab} (0.64)	
2	385.00^{a} (18.70)	20.60^{a} (0.64)	
3	399.00^{ab} (18.90)	21.10^{ab} (0.64)	
4	421.00^{b} (19.90)	21.90^{b} (0.68)	
5-7	414.00^{ab} (19.00)	21.80^{b} (0.64)	
Litter size			
≥12	434.00^{a} (21.30)	22.30^{a} (0.72)	0.56 (0.34)
13 - 15	400.00^{ab} (19.80)	21.50^{ab} (0.67)	0.43 (0.25)
16 - 17	389.00^{b} (18.20)	20.80^{b} (0.62)	0.65 (0.20)
18 - 19	397.00^{ab} (19.30)	21.00^{ab} (0.66)	1.04 (0.25)
≥20	395.00^{ab} (18.40)	20.90^{b} (0.62)	0.27 (0.17)
Weaning weight	18.42*** (2.44)	1.62*** (0.08)	0.30*** (0.07)
LS-W[1]			
0	405.00 (18.90)	21.40 (0.64)	-0.59^{a} (0.21)
1	400.00 (17.90)	21.20 (0.61)	0.83^{b} (0.14)
2	404.00 (17.90)	21.30 (0.61)	1.54^{c} (0.27)
Group[2]			
CON	408.00 (17.80)	21.50 (0.60)	0.79^{a} (0.17)
HD	398.00 (17.80)	21.10 (0.60)	0.39^{b} (0.16)

[1] LS-W = lesion score recorded at weaning

[2] CON= basal diet with no additives; HD: basal diet with a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”.

Within each effect, least square means with different letters differ significantly ($P \leq 0.01$). For regression coefficients, *** and ** represent significant at $P \leq 0.001$ and $P \leq 0.01$, respectively.

Variance components and heritabilities in different dietary treatments

Variance components and corresponding variance ratios (heritabilities and the fraction of the common litter environment) for PWW, ADG and LS estimated in both groups CON and HD, are given in Table 3.4. Additive genetic variances for PWW were larger in the HD (2.94 ± 2.00) compared to CON group (2.27 ± 1.52). Accordingly, the estimated heritability for PWW in HD was slightly larger in CON than in HD (0.35 ± 0.16 vs 0.33 ± 0.14, respectively). Similarly, a higher heritability was estimated for ADG in HD (0.34 ± 0.19) in comparison to CON (0.29 ± 0.14). In contrast, the heritability for LS was larger in CON than in HD (0.25 ± 0.14 vs 0.14 ± 0.12, respectively). The common litter environmental variance as a proportion of the phenotypic variance ranged from 0.07 ± 0.05 for LS in HD to 0.16 ± 0.08 for PWW in HD.

Table 3.4: Posterior means (respective posterior SD in parentheses) of genetic parameters[1] for post weaning weight (PWW), average daily gain (ADG) and lesion score (LS) in both dietary groups.

Trait	**Group**[2]	σ^2_p	σ^2_a	σ^2_c	σ^2_e	h^2	c^2
PWW	CON	8.11 (0.81)	2.77 (1.52)	0.98 (0.51)	4.35 (0.84)	0.33 (0.14)	0.12 (0.06)
	HD	8.19 (0.87)	2.94 (2.00)	1.33 (0.75)	3.92 (1.08)	0.35 (0.16)	0.16 (0.08)
ADG	CON	6589.8 (629.08)	1967.7 (1103.4)	672.87 (358.25)	3949.2 (638.20)	0.29 (0.14)	0.10 (0.05)
	HD	6433.5 (679.16)	2250.5 (1533.8)	922.46 (552.85)	3260.6 (840.97)	0.34 (0.19)	0.14 (0.08)
LS	CON	0.50 (0.06)	0.13 (0.08)	0.06 (0.03)	0.31 (0.05)	0.25 (0.14)	0.12 (0.06)
	HD	0.42 (0.04)	0.06 (0.05)	0.03 (0.02)	0.33 (0.04)	0.14 (0.12)	0.07 (0.05)

[1] σ^2_p = phenotypic variance, σ^2_e = residual variance, σ^2_a = direct genetic variance, σ^2_c = permanent environmental variance, c^2 = common litter environment, h^2= direct heritability

[2] CON = basal diet with no additives; HD = basal diet with a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”.

Correlations between the same traits in different dietary treatments

The overall total correlations between the same traits in CON and HD were 0.36 ± 0.15 for PW, 0.33 ± 0.14 for ADG, and 0.10 ± 0.13 for LS (Table 3.5). Genetic correlations were 0.70 ± 0.20 between PWW_{CON} and PWW_{HD}, and 0.72 ± 0.22 between ADG_{CON} and ADG_{HD}, indicating genotype x diet interactions for both production traits. The small genetic correlation of 0.15 ± 0.25 between LS_{CON} and LS_{HD} indicates clear genotype x diet interactions. Correlations between common litter environmental effects were larger than the genetic correlations in same traits, i.e., 0.74 ± 0.23 for PWW, 0.74 ± 0.24 for ADG and 0.60 ± 0.27 for LS.

Table 3.5: Overall total, genetic and common litter environmental covariances and correlations (respective posterior SD in parentheses) between the same traits (post weaning weight (PWW), average daily gain (ADG), lesion score (LS) recorded in CON and HD groups[1].

Traits		**Overall total**	**Genetic**	**Common litter**
PWW	Covariance	3.11 (1.45)	5.12 (0.21)	0.87 (0.55)
	Correlation	0.36 (0.15)	0.70 (0.40)	0.74 (0.33)
ADG	Covariance	2190.8 (1062.5)	1591.3 (1219.9)	599.52 (391.68)
	Correlation	0.33 (0.14)	0.72 (0.30)	0.74 (0.34)
LS	Covariance	0.05 (0.06)	0.02 (0.06)	0.03 (0.02)
	Correlation	0.10 (0.13)	0.15 (0.25)	0.60 (0.37)

[1] CON = basal diet with no additives; HD = basal diet with a mixture of 0.2% "Kräuterkraft Aufzucht & Verdauung".

Changes in estimated breeding values (EBV) of the 14 boars with offspring in CON and HD are presented in Fig. 3.1. For PWW, we only observed slight re-rankings of boars across the dietary groups. For instance, the sire 5 with an EBV of +0.63 kg was ranked on the third position in CON, but a decrease of 0.28 kg implied rank 5 in in the HD environment. Similar results were observed for ADG, indicating that the same 5 sires were top-ranked in both treatment groups. In contrast, a considerable re-ranking of sires was observed according to their EBV for LS, displaying a shrinkage of EBV variations in the HD environment. The estimates of common litter environmental effects for 14 randomly selected dams in both groups CON and HD are presented in Fig. 3.1. Similar to the EBV of sires, only minor re-rankings were observed for the moderate heritability traits PWW and ADG. In contrast, for the functional trait LS, stronger dam re-rankings and a decline of effect variations in the HD group, were observed. However, the re-rankings and the variation shrinkage in the HD group were more obvious for the additive genetic component, i.e., for the sire EBVs.

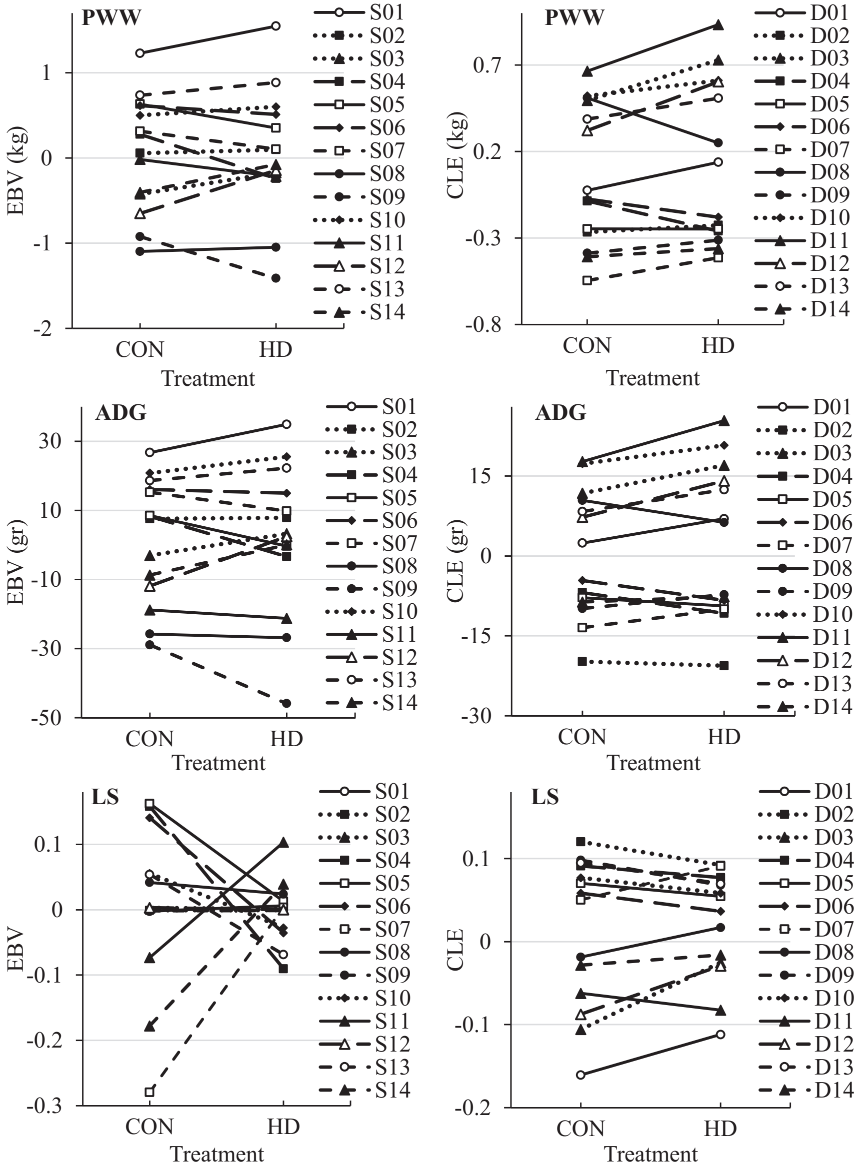

Figure 3.1: Estimated breeding values (EBV) for the 14 sires (left) and common litter effects (CLE) for 14 randomly selected dams (right) for post weaning weight (PWW), average daily gain (ADG) and lesion score (LS) in CON (basal diet with no additives) and HD (basal diet with a mixture of 0.2% “Kräuterkraft Aufzucht & Verdauung”).

DISCUSSION

Herbal diet supplement effects on growth performance

Reports from the European Medicines Agency (2012) indicate that supplies with chicory roots prevent slow digestion, abdominal fullness and temporary loss of appetite in humans. Liu et al. (2011) and Velasco et al. (2010) also observed improvements in feed intake and body weight traits in broilers when adding chicory roots to the feed ration. However, in our trial, piglets from the CON group had 0.40 kg higher PWW and 10 g/day higher ADG compared to piglets from the HD group. In a pig feeding experiment including a group receiving an herbal diet, Presto et al. (2019) supported the results obtained from the present study. Similarly, Déru et al. (2020) identified better growth performances for pigs receiving a conventional diet compared to a "high fiber diet" group. In a pig feeding experiment conducted by Sevillano et al. (2018), the effect of the diet (i.e., cereal alternative ingredients versus a corn-soybean diet) on growth parameters was non-significant. According to Lebret et al. (2018) and Liao et al. (2015), lysine supplements stimulated protein synthesis, but a lysine and methionine deficiency was associated with limited growth. Nevertheless, in the present study, the percentages of lysine and methionine in the HD diet during the second phase of the dietary treatment were quite high, but ADG was lower than in the CON group. Ginane et al. (2015), Nyachoti et al. (2004) and de Haer et al. (1993) explained that lower ADG also depends on the physiological state of piglets and of growing pigs. Another possible explanation addresses the lower energy content of the HD treatment compared to the CON treatment (13.0 MJ/kg vs 14.1 MJ/kg). In this regard, several studies mentioned the lower energy content of diets enriched with fiber, with detrimental impact on growth parameters and feed efficiency (Cho et al., 2012; Li et al., 2012; Kallabis and Kaufmann 2012). Martino et al. (2014) observed a negative effect of organic feeding characterized by higher roughage content on body weight traits in pigs, similarly to the results from the present study. However, in contrast, Zhao et al. (2016) associated supplementation of fermented herbs with improved growth performance and improved nutrient digestibility in weaning and post-weaning pigs. Wallenbeck et al. (2014) suggested only a small amount of crude fiber in the diet of growing pigs, to avoid negative effects on the digestive capacity.

Herbal diet supplement effect on lesion scores

Associations have been reported between weights of pigs and aggressiveness, with lighter pigs being more aggressive (Palander et al., 2013; Turner et al., 2008; Edwards, 2006; Van Erp-Van Der Kooij et al., 2003; Hessing et al., 1994) as identified in the present study. Although piglets in the HD group had more lesions at the weaning date indicating aggressiveness and increased activity in the pen, the same pigs had a smaller and favourable LS at the end of the experiment. Hence, their improved calmness could be due to the higher crude fibre (4.9% vs 2.4%) and crude protein (17.1% vs 16.6%) contents in the HD compared to the CON ration. The low LS in the HD group reflect the observations by Bernardino et al. (2016) and Kallabis and Kaufmann (2012), i.e., the favourable effects of diets enriched with fibre on social animal behaviour, on feeding behaviour and on overall calmness. In our feeding experiment, we made the observation in the HD group that pigs tend to spend more time to digest roughage, implying reduced time for foraging and improved wellbeing. Presto et al. (2019) and Carlson et al. (1999) observed limited abnormal behaviour pattern such as nosing with other pigs and aggressiveness with group contemporaries when fed chicory, the active ingredient in the HD treatment. The chicory roots might stimulate calmness, and accordingly reduced fighting and aggressive behaviour in the HD group, as proved by a fewer number of skin lesions in the HD than in the CON group. In addition, chicory herbs have medicinal properties to treat various ailments including diabetes and played a role in wound healing (Häkkinen et al., 2021; Saeed et al., 2017; Street et al., 2013), possibly explaining the lower and favourable LS in the HD group.

In the present study, the prevalence of skin lesions significantly ($P < 0.001$) increased with increasing body weight in the CON group. Camerlink et al. (2014) reported positive phenotypic correlations between skin lesions and body weight, and they assumed untypical behaviour in extremely heavy pigs. In contrast, other researches (Turner et al., 2008, Edwards, 2006; Beattie et al., 2005; Schrøder-Petersen and Simonsen, 2001) associated aggressive behaviour and tail biting in pigs with small body sizes, but they did not study the relationship with skin lesions.

Genetic parameters in different diet groups and diet x genotype interactions

The genetic statistical model selection based on the Akaike information criterion (AIC; Akaike (1973), and the finally defined model 3 additionally considering the litter environmental effect displayed lower AIC than a model only including the random additive genetic effect. However, some of the genetic parameters were associated with quite large posterior SD, suggesting a larger sample size for this pig experiment. Accordingly, Gourdine et al. (2019) reported large posterior SD for genetic parameters in a backcross (Large White x Creole) pig population comprising 1,298 piglets. Especially when fitting multiple-trait models for the proof of possible genotype by environment interactions (i.e., models without residual covariances), the accuracy of genetic parameter estimates strongly depended on the sample size (Falconer and Mackay, 1996).

The moderate heritabilities for PWW and ADG were expected and reflect estimates in other pig populations at a similar age (e.g. Zhang et al., 2016; Alves et al. 2018; Gourdine et al., 2019). Alves et al. (2018) estimated a direct heritabilities of 0.33 for PWW in Yorkshire and of 0.27 in Landrace pigs. Zhang et al. (2016) reported a heritability of 0.34 for ADG in a Landrace pig population in China, and Lopez et al. (2017) a heritability of 0.52 in a Landrace population located in Korea. For PWW and ADG, variance components and variance ratios were very similar in both dietary groups HD and CON. Genetic variances and heritabilities for PWW and

ADG were only slightly larger in HD than in CON, reflecting a minor effect on feeding characteristics on genetic parameter estimates or on gene activities. Stronger alterations of genetic variances in dependency of dietary characteristics were observed for LS. The smaller genetic variance for LS in the HD group indicate intra-family similarity, and consequently, the similarity might contribute to narrowed genetic differentiation in the HD environment. The smaller variation of boar EBVs for LS in the HD group is a further indicator in this regard. For low heritability functional traits, Schierenbeck et al. (2011) suggested a "challenging test environment" to improve genetic differentiation. In contrast, for moderate heritability production traits, König et al. (2005) suggested to keep and to select animals in environments reflecting superior nutritional value, so that such an environment supports the fully expression of the true genetic potential. Nevertheless, from a practical breeding scheme perspective, the increased genetic variance, heritability and EBV range for LS simplify selection strategies on behaviour in the challenging CON environment. In such context, Velie et al. (2009) and Rohrer et al. (2013) favoured consideration of environmental stressors to optimize pig selection.

Interestingly, the common litter environmental effect explained about 12% of the phenotypic variation for the studied traits. In pig populations, families of full- and half-sibs share non-genetic litter-specific environmental conditions such as uterus capacity and nutrition during the suckling period. Thus, piglets sharing the same environment in early life develop similar body weight characteristics and social skills in adulthood (Kaufmann et al., 2008; Canario et al., 2017). Similarly, Canario et al. (2017) explained that social experience in early life strongly influences behaviour patterns and social interactions of piglets in adulthood. Such physiological background may explain that the common litter environmental correlations between PWW_{CON} and PWW_{HD}, between ADG_{CON} and ADG_{HD} and between LS_{CON} and LS_{HD} were larger than the respective genetic correlation.

In several studies (e.g., König et al., 2005), a genetic correlation smaller than 0.80 between same traits recorded in different environments was considered as an indicator for genotype by environment interactions. Accordingly, genotype x diet interactions were proved in the present study for all traits PWW, ADG and LS. Especially for LS, the genetic correlation was extremely small (0.15). Accordingly, obvious and very significant sire x diet interactions were identified for LS. The correlations between estimates for boar effects in the HD and in the CON group were largest for PWW. For the moderate heritability growth rate, Hermesch et al. (1999) disproved any genotype x feeding regime interactions, because the genetic correlation was close to one.

Nevertheless, in analogy to the results from the present study for PWW and ADG, Hermesch (2004) identified re-rankings of sires in relation to feeding levels. Very obvious genotype by environment interactions were reported by Godinho et al. (2018) when stratifying the environment according to feed content characteristics. Li and Hermesch (2016) utilized mean performance levels of pigs as environmental descriptor in reaction norm models. In this regard, they identified significant genotype by environment interactions. Accordingly, Chiba et al. (2002) carried out a feeding experiment and identified variations of sire responses with environmental alterations. Hence, they suggested genotype dependent optimization of feeding strategies. Contrarily, Schiavon et al. (2019) and Sundrum et al. (2011) disproved breed or genotype x diet interactions. Fabian et al. (2002) proved feed by genotype interactions for the traits feed efficiency and weight gain in Duroc pigs. The major feed component contributing to significant interactions was the lysine content. As an explanation for genotype x feeding interactions, Elbert et al. (2020) addressed the specific “genetic make-up” of each sire. In summary, for production traits in pigs, most of the conducted research studies proved genotype x feeding interactions (Quander-Stoll et al., 2021; Hofer et al., 2018; Agroscope, 2017;

Hamilton et al., 2003). Therefore, selection of appropriate boars implies consideration of the environmental particularities, especially the feeding strategies in different production systems.

CONCLUSION

The present study highlighted the importance of a specific diet, diet x sire and diet x genotype effects on performance traits and on skin lesions in pigs. The results showed that piglets allocated to the HD group had smaller LS, indicating the favourable effects of an herbal diet on skin lesions. In addition, the herbal treatment (chicory) did not have any negative effects on growth performances. The significant interactions between sire and treatment detected for ADG, PWW and LS indicate specific sire trait responses, depending on the dietary characteristics. Furthermore, via multiple-trait models, genetic correlations smaller than 0.80 between PWW_{CON} and $PWW_{HD,}$ ADG_{CON} and ADG_{HD}, and LS_{CON} and LS_{HD} indicate genotype x diet interactions, especially for the functional and low heritability LS. Hence, re-rankings of sires according to their EBVs were observed in both environments CON and LD, displaying smaller genetic and EBV variations for LS in the HD group. The HD dietary supplement contributed to fewer skin lesions, probably due to the favourable effect on pig behaviour, but a more pronounced genetic differentiation seems to be possible in the more challenging CON environment.

Declaration of Competing Interest

We declare that we have no conflicts of interest.

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CHAPTER 4

ASSESSING THE EFFECTS OF PIGLET BEHAVIOUR, DIET SUPPLEMENTATION, AND LESION SCORE BREEDING VALUES OF SIRES ON BEHAVIOUR PATTERN IN WEANED PIGS

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HIGHLIGHTS

- A herbal diet supplement implying a diet enriched with crude fibre, protein and chicory, was associated with less aggressive pig behaviour in the post-weaning period.
- Early piglet behaviour was related with respective behaviour pattern in the post-weaning period.
- Correlations between breeding values for lesion scores (victim perspective) with video behaviour pattern reflecting the actor perspective were only weak to moderate.
- Video images can be used to monitor active pig behaviour in the post-weaning period, but it is very challenging to include a large number of pigs due to the time consuming complexity.

ABSTRACT

The aim of the present study was to study effects of feeding in terms of herbal diet supplement (HD; basal diet plus a supplement with chicory herbs), of early piglet backtest scores and of relative breeding values for skin lesions (RBV-LS) on behaviour pattern of weaned pigs during the post-weaning period. In this regard, we implemented a balanced research design, allowing a semi-randomized allocation of pigs in groups with a very similar number of observations for all sub-cells of diet by backtest score by RBV-LS class combinations. With regard to backtest scores, piglets were classified as high-resisting (HR), low-resisting (LR) or intermediate-resisting (IR). RBV-LS were estimated for the sires based on skin lesions from 993 offspring. The sires were categorized into 2 groups with RBV-LS > 100 (favourable genetic value indicating only a few or no lesions) or RBV-LS ≤ 100 (indicating a large number or severe lesions). Video images were analysed one day after weaning and 5 weeks later, and considered 300 min per monitoring date for the 8 different possible behaviour traits resting time (REST), body contact (BCON), initiating fights (IFIGHT), fighting (FIGHT), refusing of fights (RFIGHT), ear or tail biting (BITE), explorative behaviour (EXPLORE) and remaining activities (RACT). Finally, 104 pigs with complete observations over the total video monitoring time at both recording dates, and with complete observations for the explanatory variables sire RBV-LS, backtest score and feeding group, were considered for ongoing association studies. The 104 pigs were crosses from matings of Piétrain boars with German Landrace or German Edelschwein sows. The 104 pigs were offspring of 9 different boars (sire lines). Effects of feeding, backtest score and RBV-LS class on video behaviours were inferred via mixed model analyses, implying 8 different runs for the 8 video behaviour traits. Least squares means (lsmeans) significantly ($P < 0.05$) differed between HD and the control feeding group (CON) for FIGHT and BITE, with longer durations of aggressive behaviour for CON pigs. Vice versa, lsmeans for REST indicating calm behaviour were larger for the HD group. Pigs classified as

HR piglets were more aggressive than the LR and IR contemporaries, with significantly higher lsmeans for FIGHT, BITE and EXPLORE. The pigs allocated to the sire RBV-LS > 100 group had significantly ($P < 0.05$) longer durations for REST and RFIGHT. Vice versa, pigs allocated to the sire RBV-LS ≤ 100 groups spent more with aggressive behaviour in terms of BITE and FIGHT. Consequently, boar RBV-LS were favourably correlated with REST, IFIGHT and RACT. In conclusion, the early piglet backtest scores as well as breeding values from a victim perspective (lesion scores) can be used as indicator traits for selection against aggressiveness. Nevertheless, results from the present study are first indications and breeding value correlations are approximations in this regard, which should be validated in ongoing studies based on larger datasets via real genetic correlation estimates between actor and victim traits, and considering social interactions and interactions between all fixed effects simultaneously.

Keywords: Video behaviour traits, piglet backtest, skin lesions, herbal diet, breeding value associations

INTRODUCTION

Aggressiveness of pigs including biting is part of natural dominance behaviour (e.g., Taylor et al., 2010). However, tail biting in pigs is a severe abnormal behaviour with multi-factorial origin and wide ranging consequences, addressing economic aspects and animal welfare. Even though tail biting is mainly observed in intensive production systems (e.g., Thodberg et al., 2018), it also appears in outdoor herds (Walker and Bilkei, 2006) and under organic conditions (Hansson et al., 2000), but in lower prevalence. The routinely use of tail docking in piglets, an effective procedure to reduce tail biting in all pig production systems, is banned in the EU according to the EU Council Directive 2008/120/EC from December 2008. Consequently, it is imperative to evaluate alternative methods addressing feeding and breeding strategies.

The impact of feeding includes various aspects, e.g., food quality or type of food presentation. In this regard, the natural need of rooting and chewing was identified as an important factor to reduce tail biting (Sonoda et al., 2013), which cannot be compensated when feeding a liquid diet (Temple et al., 2012). Aikins-Wilson et al. (2022) reported a lower prevalence for lesion scores in piglets fed herbal diet with higher crude fibre and crude protein contents compared to the control group fed a basal diet. In contrast, Hunter et al. (2001) found higher levels of tail injuries in pigs fed pelleted when compared to pigs receiving meal or liquid feed. Fraser et al. (1991) and Fraser (1987) found that food diets with inadequate protein or mineral content attract pigs to blood. Diets enriched with herbs implied less aggressiveness and fewer tail and skin lesions (Jensen et al., 1993; Kallabis and Kaufmann, 2012). In addition, endotoxins generated in case of high-density energy feeding rations caused ear and tail necrosis with acute itchiness (Jaeger, 2013). Due to this unpleasant side effect, affected pigs may be attracted to or even tolerate biting attempts by pen mates.

With regard to breed effects, Westin (2003) reported differences in the propensity to bite (Landrace > Yorkshire > Hampshire) as well as in the propensity to be bitten (Yorkshire > Landrace > Hampshire). Accordingly, Sinisalo et al. (2012) identified Yorkshire pigs as victims more often than Landrace pigs. In other studies (Lund and Simonsen 2000; Guy et al., 2002), the breed effect on tail biting was non-significant. Aikins-Wilson et al. (2021) outlined the possibilities to use skin lesion scores to select against aggressive pigs. Oppositely, based on comprehensive video analyses for pig behaviour combined with data for skin lesions, Liu et al. (2022) highlighted the effects of standoff and being bullied on lesions rather than the possible cause of unilateral active aggressive behaviour. Regarding feeding by genotype interactions, Aikins-Wilson et al. (2022) identified significant sire by diet interactions (herbal diet vs. basal diet) on lesion scores, and they suggested specific boars for different feeding environments.

However, from an actor or biting perspective, there is a lack of knowledge addressing interactions between feeding with breed, sire line or genotype effects.

Effects of the pigs' personality and coping style to aversive stressors, evaluated through associations between behavioural tests before weaning with biting behaviours later in life, are unclear (Prunier et al., 2019). First hints in this regard were outlined in some previous studies (Hessing et al., 1993; D'Eath and Burn, 2002; Melotti et al., 2011). Turner et al. (2008) and Hessing et al. (1993) performed behaviour backtests in piglets (according to the protocol by Zebunke et al., 2015). Abnormal piglet behaviour was associated with aggressiveness later in life, suggesting the use of early backtest scores as indicator traits in pig selection schemes. Prunier et al. (2019) addressed the complexity of this topic including the aspects and the interplay of coping style, personality and biting behaviour, and they indicated the challenges of behaviour trait recording. Several electronic techniques, such as location detectors (D'Eath et al., 2014), activity measurement devices (Dawkins et al., 2009) and 3D-cameras (Scotland's Rural College (SRUC), 2022), have been used to detect abnormalities in pig tail postures automatically. Changes in tail postures and in behaviour pattern can be used as early warning indicators for tail biting outbreaks. Specifically, Zupan et al. (2012) used heart-rate belts to detect differences in heart rates between pigs performing tail biting, pigs that were victims and pigs that were not involved in tail biting at all. Such automatic techniques are efficient to identify biters, but costly. D'Eath et al. (2014) favoured the analysis of comprehensive video images or a combination of modern video technique with machine learning algorithms to identify biters, but they also indicated the time consuming aspects in monitoring video images. Consequently, taking into account all above-mentioned challenges, the aim of the present study was to infer the effects of early piglet behaviour, feeding, boar line and breeding values for skin lesions (indicator trait for a bitten pig) on abnormal behaviour pattern monitored via video images of pigs during the post-weaning period.

MATERIALS and METHODS

Research design, feeding and housing conditions

The experiment was conducted at the research farm Oberer Hardthof of the Institute of Animal Breeding and Genetics, University of Giessen, Germany, over a period of 12 months from March 2018 to February 2019. The piglets with later observations after weaning for video behaviour images used in this experiment were a sub-sample from 993 piglets as considered in the study by Aikins-Wilson et al. (2022) for the estimation of breeding values for lesion scores. The piglets were offspring from matings of Piétrain boars with German Landrace or German Edelschwein sows. The piglets were weaned 28 days after birth. At weaning, 112 piglets were semi-randomly allocated to two different feeding groups either receiving a basal diet (CON, $N = 56$ pigs) or an herbal diet (HD, $N = 56$ pigs). The semi-randomly grouping approach aimed on an equal number of offspring per boar (= sire line) and of an equal distribution of piglet behaviour scores in both feeding groups. In this regard, we used the stratify R function (Reddy and Khan, 2021) from the R-software package. The 112 selected pigs were offspring of 9 different boars (sire lines), implying 13 pigs per sire line. In the post-weaning phase, a sample of 104 pigs could be used for video image analyses.

The feed ration in both groups after weaning is the same as described in the previous skin lesion study (Aikins-Wilson et al., 2022). Hence, in the CON group, pigs received a standard diet based on wheat, soybeans and barley as concentrates plus minerals and vitamins. The HD treatment was the standard diet plus a mixture of 0.2% "Kräuterkraft Aufzucht & Verdauung". The composition of the supplementary feed "Kräuterkraft Aufzucht & Verdauung" in the HD diet consisted of 30% chicory (*Cichorium intybus*) root, carbonic acid algae lime (*Lithothamnion calcareum*), alumroot (*Heuchera americana*), 5% yarrow herb (*Achillea millefolium*), fenugreek seeds (*Trigonella foenum-graecum*), nettle herb (*Urtica dioica*), malt sprouts, sugar beet molasses, yeast and seaweed (*Ascophyllum nodosum*) flour. During the experiment in the post-weaning period, the pigs were kept on a partially slatted floor (0.38 m^2 per animal) and the pig: feeding place ratio was 1.5:1. Each of the eight fattening compartments comprised 14 pigs. The fattening compartments were separated among each other through solid pen walls. The pigs had ad libitum access to dry food and water.

Animal traits

Behaviour test of piglets and lesion scoring after weaning

At birth and at the age of 7 days, a backtest score (BTS) was performed on the 954 piglets using procedures as described by Hessing et al. (1993). During the backtest, the piglets were lifted from their pen on a mat lying on a table. The experimenter turned the piglets on their back by fixing the piglets legs for 60 s with both hands. Based on the number of escape attempts (struggling with at least the hind legs), the piglets were classified into high-resisting (HR = more than 2 escape attempts, indicating aggressiveness), low-resisting (LR = less than 2 escape attempts, indicating calm pigs) or intermediate-resisting (IR= exactly 2 escape attempts, indicating intermediate aggressiveness) groups.

Skin lesions were determined by one trained person at day 1 after weaning and 5 weeks later following the protocol by Pluske and Williams (1996). The lesion score (LS) was assigned as follows: LS 1= no lesion or less than 5 slight skin lesions; LS 2= mild lesion with more than 5 mild lesions including hair loss, redness, irritation, scratches or small abrasions; LS 3= severe lesion, bleeding and loss of tissue. The LS phenotypes were used for the estimation of LS breeding values in our previous study by Aikins-Wilson et al. (2022). Hence, the nine Piétrain sires had LS breeding values based on all phenotyped offspring and related animals ($N = 993$) as considered for lesion scoring. The LS breeding values were standardized to obtain relative breeding values for LS (mean= 100; SD= 12). The relative LS breeding values (RBV-LS) of the nine sires ranged from 81 (indicating a large number of lesions) to 133 (indicating only a few or no lesions). According to the threshold for the RBV-LS of 100, the 9 sires were allocated to two groups (5 sires with RBV-LS > 100, and 4 sires with RBV-LS ≤ 100).

Behaviour video images of rearing pigs

Behaviour of the 112 pigs after weaning was monitored at two dates using a 24-time lapse video camera. Cameras were placed above the pen and connected with a laptop. The first video monitoring date over a period of 5 hours was one day after weaning, and the second video monitoring date also considering the period of 5 hours was 5 weeks after weaning. The recording time was scheduled between the morning and the evening feeding times from 10:00 am to 3 pm. We also made video observations 2 and 4 days after these two recording dates, and we calculated the accuracy of prediction (r) with repeated records compared with single records (according to Mrode 2005) as follows:

$$r = \sqrt{\frac{1}{t + \frac{(1+t)}{n}}}$$

with t = repeatability and n = the number of repeated measures per pig. For a repeatability of 0.11, the extra gain in prediction accuracy from 2 to 4 measurements in relation to the prediction accuracy from a single measurement was moderate (+ 39%). However, due to the complexness in statistical modelling approaches (see more details in the statistical modelling section), we considered the two measurements, i.e., from the weaning date and 5 weeks later in the ongoing analyses.

104 pigs had complete video images with two repeated observations for all behaviour traits. These 104 pigs were considered for the ongoing analyses. The trait categorization of the video images considered the behaviour trait definitions according to Statham et al. (2009) as outlined in Table 4.1. Hence, the 8 analysed behaviour traits included resting time (REST), body contact (BCON), initiating fights (IFIGHT), fighting (FIGHT), refusing of fights (RFIGHT), ear or tail

biting (BITE), explorative behaviour (EXPLORE) and remaining activities (RACT). Identification of specific behaviours and changes of behaviour pattern when analysing the video images based on protocols by Samarakone and Gonyou (2009). Due to the low frequencies of ear and tail biting, BITE considered both traits simultaneously. The time per behaviour trait category and piglet was measured in minutes. A total monitoring time of 5 hours implied 300 minutes for 8 different possible behaviour traits per recoding date and pig. The total recording time for the 104 pigs and both recording dates as used for video image analyses comprised 62,400 minutes. All videos were analysed by the same trained observer. Eight pigs considered in the original research experiment, videos were difficult to follow, i.e., due to ambiguous animal identification over the full 5 hours recording period. These 8 pigs were excluded from the ongoing analyses.

Table 4.1: Description of the recorded behavioural traits based on video images

Behavioural trait	Abbre-viation	Description
Resting time	REST	Lying, sitting or standing
Body contact	BCON	Light touch to body of opponent with nose without force
Initiating fights	IFIGHT	First attempt to provoke a fight
Fighting	FIGHT	Head-to- head knocks, head- to-body knocks
Refusing fights	RFIGHT	Pig receives aggression, but does not react
Ear or tail biting	BITE	Any contact with the tail or ear of the pen mate
Explorative behaviour	EXPLORE	Occupation with the toy (metal chain), sniffing and chewing with the toy (metal chain), sniffing with the nose, touching the body of another pig with snout, belly-nosing, genital nosing
Remaining activities	RACT	Feeding, drinking, excretion, running with the head up, and all other general behaviours not listed above

The distribution of pigs used for video image analyses for all possible feeding by backtest score classes are given in Table 4.2. The applied chi-squared test for frequencies in the different feeding by backtest score sub-cells indicated non-significant differences (*P* = 0.15), supporting the randomized and balanced setup of the research design. With regard to all sub-cells of Table 4.2, 50% of pigs had a sire LS breeding value > 100, and 50% of pigs had a sire LS breeding values ≤ 100.

Table 4.2: Number of pigs for the different sub-classes of backtest response and feeding group (CON = control group, HD = supplement of an herbal diet). (The frequencies within the feeding group by backtest score groups did not differ significantly with *P* = 0.15).

	Feeding Group		
Backtest	CON	HD	Total
Low-resisting (LR)	16	24	40
Intermediate-resisting (IR)	12	16	28
High-resisting (HR)	22	14	36

Statistical analyses

The non-Gaussian behaviour traits REST, BCON, IFIGHT, FIGHT, RFIGHT, BITE, EXPLORE and RACT were transformed to achieve normality using Blom's method (see Solomon and Sawilowsky, 2009) as implemented in the function blom.r of the R-software package (R core Team, 2020). Mixed model analyses as implemented in the lme4 function from the lmerTest R-package (Bates et al., 2015) were applied to infer fixed and random effects on the video behaviour traits. The statistical model (1) was defined as follows:

$$y_{ijklmnopq} = \mu + sex_i + FG_j + BTS_k + SEAS_l + RBV - LS_m + b_1\,(W_n) + b_2\,(age_o) + pig_p + e_{ijklmnopq} \qquad [1]$$

where $y_{ijklmnopq}$ was the q^{th} video observation for REST, BCON, IFIGHT, FIGHT, RFIGHT, BITE, EXPLORE or RACT; μ was the overall mean; sex_i was the fixed effect of the ith sex (male or female); FG_j was the fixed effect of the j^{th} feeding group (HD or CON); BTS_k was the fixed effect of the k^{th} piglet backtest score (LR, IR or HR); $SEAS_l$ was the fixed effect for the l^{th} season (spring 2018, summer 2018, winter 2018, spring 2019) at recording; $RBV\text{-}LS_m$ was the fixed effect for the m^{th} RBV-LS class of the sire (below or above the average), W_n was weaning or post weaning weight as a covariate (linear regression); age_o was the age of the pig at the recording date as a covariate (linear regression); b_1 and b_2 were the regression coefficients of the trait on W_n and age_o, respectively; pig_p was the random permanent environmental effect of the p^{th} pig due to the repeated measurements; and $e_{ijklmnopq}$ was the random residual effect.

From the same model, and using the same R function, least squares means (lsmeans) for all levels of fixed effects were computed. Pair wise comparisons were adjusted for multiple comparisons by applying the Tukey-Kramer test. Differences between levels within fixed effects were considered as significant at $P < 0.05$.

We were also interested in estimating effects of the sires representing nine Piétrain sire lines on video behaviour traits. However, additional inclusion of the random sire effect into the statistical model (1) failed convergence due to the rather small phenotypic dataset. We attempted to circumvent this problem via a two-step method of analysis, and we used the solutions from model (1) to correct the phenotypic observations for fixed effects. Hence, the pre-corrected phenotype y* of a pig p standardized to a weight, *w* of 16 kg at an age of 40 days was:

$$y_p{}^* = y_p - sex_i - FG_j - BTS_k - SEAS_l - RBV - LS_m$$

In a second step, we run a reduced sire model (2) just considering the random sire effect on the pre-corrected phenotype of pig y*:

$$y *_{st} = \mu + sire_s + e_{st} \qquad [2]$$

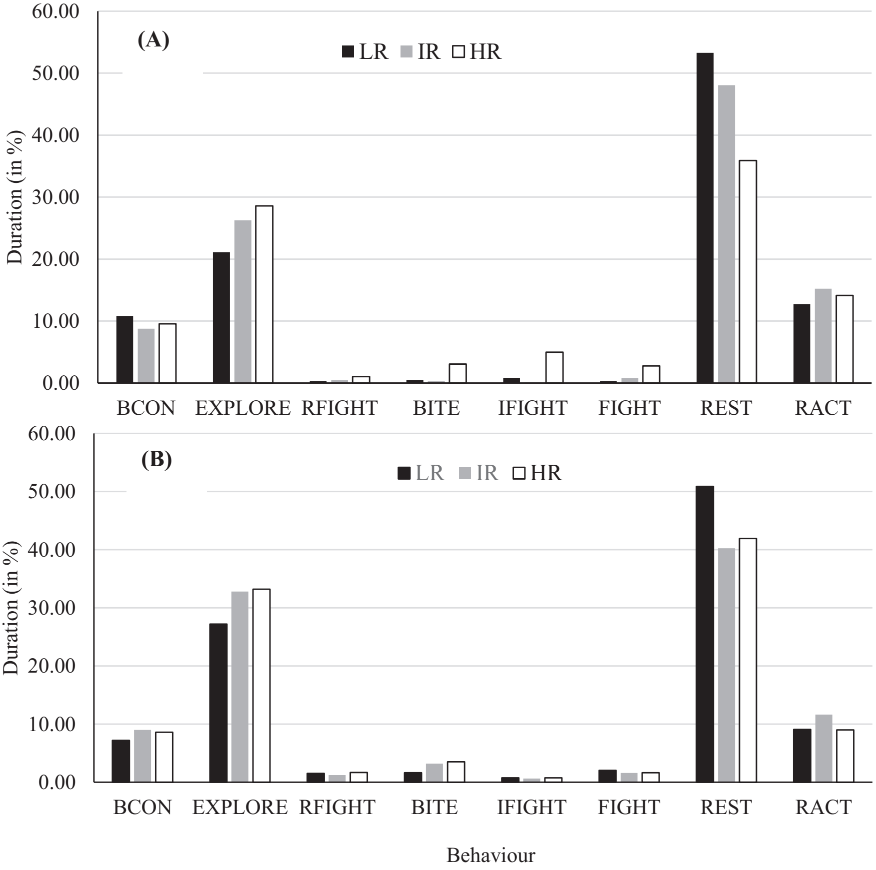
with $y *_{st}$ denoting the pre-corrected phenotype, sires denoting the random sire effect, and e_{st} denoting the random residual effect.

RESULTS

Phenotypic distribution of video behaviour pattern

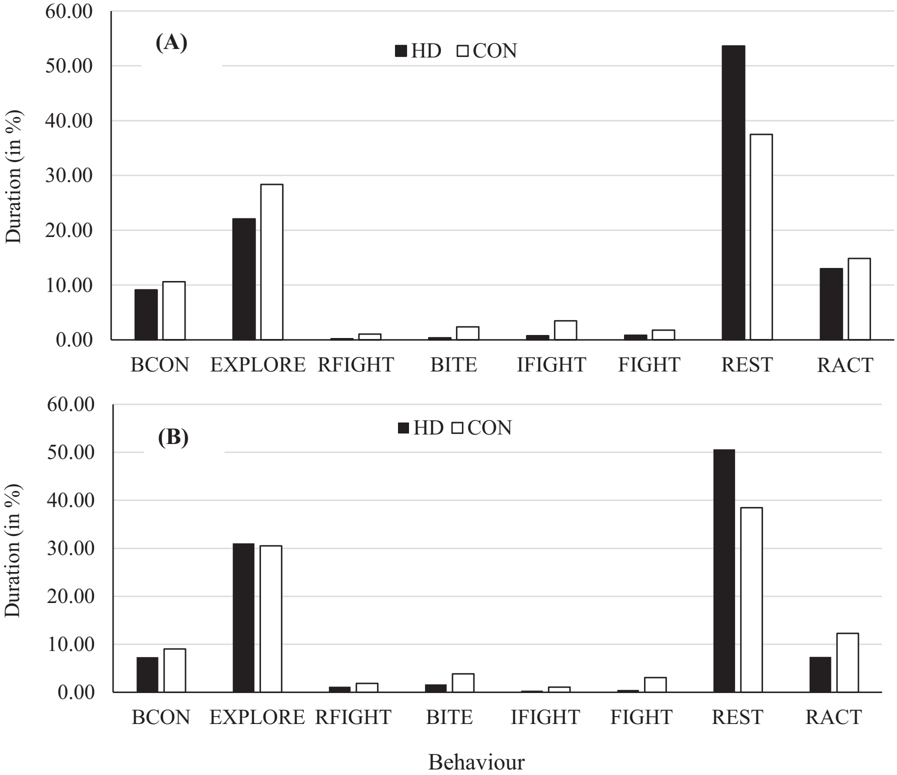
Figure 4.1 A shows the proportion of video behaviour patterns on day one after weaning for the different backtest scores, and Figure 4.1 B shows the respective phenotypic associations five weeks later. Phenotypically, there is a clear tendency for aggressive behaviour in the early post-weaning phase including IFIGHT, FIGHT and BITE for pigs classified as highly resistant HR piglets. Also, for EXPLORE, reflecting first contact behaviour with other pen contemporaries, the video duration was longer in HR than in LR or IR pigs. Consequently, pigs classified as IR or LR spent more time with normal behaviour reflecting calmness and without disturbing other pigs, i.e., as shown via higher duration percentages for REST. For feeding, drinking and excretion (as summarized in RACT), duration percentages were very similar for all three groups HR, IR and LR. The distribution of video behaviour scores displayed almost identical patterns when comparing both recording data directly after weaning and five weeks later. However, the differences between the three backtest groups for the behaviours indicating aggressiveness (BITE, IFIGHT, FIGHT) were negligible five weeks after weaning.

Figure 4.1: Duration of specific behaviours (in relation to the total time of 300 minutes) in the post-weaning period from video images within classes for piglet backtest scores (LR = low resisting piglets, IR = intermediate resisting piglets, HR = high resisting piglets) at the weaning date (**A**) and 5 weeks after weaning (**B**).



At both video recording dates at day one after weaning (Figure 4.2 A) and five weeks after weaning (Figure 4.2 B), pigs from the HD groups spent more time for REST than pigs from the CON group. Vice versa, in the CON group pigs, we identified slightly longer periods for the aggressiveness indicators IFIGHT, FIGHT and BITE. In addition, first signs for body contact with other pigs (BCON) implied more time in the CON than in the HD groups. The HD supplement also had an effect on EXPLORE at the weaning date, contributing to a lesser extent of sniffing with the nose, touching the body of another pig with the snout, belly-nosing or genital nosing.

Figure 4.2: Duration of specific behaviours (in relation to the total time of 300 minutes) in the post-weaning period from video images within feeding classes (CON = control group; HD = supplementation with a herbal diet) at the weaning date (**A**) and 5 weeks after weaning (**B**)



Significance of fixed effects and least squares means within fixed effect levels for video behaviour pattern

The lsmeans for levels of classical fixed effects including sex and year-season of recording are given in Table 4.3. The duration of responses for most of the video behaviour traits was very similar for male and female pigs, and differences were non-significant ($P > 0.05$). Only for BCON, behaviour for female pigs indicated stronger curiosity, with a significant ($P < 0.05$) longer duration of 31.60 minutes compared to 27.20 minutes for barrows.

Interestingly, during spring, pig behaviours indicating activity, aggressiveness and abnormality (FIGHT, BCON, BITE, EXPLORE), displayed significant longer durations compared to the other seasons. Consequently, the time spent on REST was smaller during spring. Regression coefficients for the age of the animal were negative for FIGHT, IFIGHT, BCON, BITE and EXPLORE, indicating a tendency for more calmness and longer duration of common behaviour (eating, lying, sitting) in older pigs. At the same ages, the heavier pigs were more aggressive, with longer duration for FIHGT, IFIGHT and BITE than younger pigs.

The lsmeans for video behaviour traits within fixed effect levels for the backtest score and the feeding group (Table 4.4) from the repeated measurement analyses (model 2) reflect the raw phenotypic means as depicted in Figures 4.1 and 4.2. In this regard, the HR pigs spent significantly less minutes ($P < 0.05$) for REST than the LR pigs. Consequently, durations for all behaviour pattern reflecting activity (IFIGHT, BCON, BITE, EXPLORE) were longer in HR than in LR pigs, with significant differences ($P < 0.05$) for the aggressiveness indicators FIGHT and BITE. The lsmeans for REST were higher in the HD than in the CON feeding group, indicating the significant effect of the herbal diet supplementation. The significantly longer duration for REST in the HD group was associated with less time spent on aggressive behaviour including FIGHT, IFIGHT and BITE. Especially for FIGHT, the lsmeans in the HD group were extremely low, with 0.08, and consequently, very sparely observed.

Table 4.3: Least squares means (in minutes) within levels of fixed effects and regression coefficients for the covariate “age of animal” and “weaning weight” with corresponding standard errors (in parenthesis) for video behaviour traits (significant differences at $P < 0.05$ for different levels within fixed effects are denoted with different superscripts).

	Behaviour trait[1]							
Fixed effect	REST	FIGHT	RFIGHT	IFIGHT	BCON	BITE	EXPLORE	RACT
Sex								
Male	140.00 (6.27)	4.59 (0.94)	1.11 (0.26)	6.02 (1.42)	27.20 (2.90)^{a}	3.06 (1.61)	76.30 (4.76)	43.70 (2.03)
Female	134.00 (6.79)	3.37 (1.02)	0.45 (0.31)	5.55 (1.54)	31.60 (3.15)^{b}	3.81 (1.75)	78.00 (5.17)	40.50 (2.21)
Season								
2018-spring	121.01 (12.37)^{b}	6.03 (1.85)^{b}	2.15 (1.02)	8.31 (2.80)	35.30 (5.71)^{b}	6.34 (3.17)^{b}	78.80 (9.39)	45.90 (4.01)
2018-summer	136.00 (11.73)^{a}	4.17 (1.77)^{a}	1.51 (0.97)	6.71 (2.67)	27.40 (5.45)^{a}	1.33 (3.02)^{a}	75.80 (8.95)	41.80 (3.82)
2019-winter	146.27 (7.94)^{a}	4.60 (1.20)^{a}	1.72 (0.65)	4.77 (1.81)	28.50 (3.69)^{a}	2.42 (2.05)^{a}	68.80 (6.06)	41.40 (2.59)
2019-spring	117.39 (9.28)^{b}	6.12 (1.39)^{b}	2.37 (0.76)	6.34 (2.11)	36.40 (4.30)^{b}	6.34 (2.39)^{b}	85.20 (7.06)	39.30 (3.01)
Age of animal	0.60 (2.49)	-0.36 (0.37)	0.24 (0.21)	-0.30 (0.56)	-0.43 (1.15)	-0.63 (0.64)	-1.41 (1.89)	0.90 (0.80)
Weaning weight	-3.50 (4.34)	0.85** (0.65)	-0.60 (0.36)	1.92 (0.98)	0.14 (2.01)	0.98 (1.11)	0 .47 (3.29)	-1.65 (1.41)

[1] Abbreviations of behaviour traits as defined in Table 4.1.

For regression coefficients, ** represent significant at $P \leq 0.05$.

Table 4.4: Least squares means (in minutes) and corresponding standard errors (in parenthesis) for video behaviour traits within levels of fixed effects (significant differences at $P < 0.05$ for different levels within fixed effects are denoted with different superscripts).

	Behaviour trait[1]							
Fixed effect	REST	FIGHT	RFIGHT	IFIGHT	BCON	BITE	EXPLORE	RACT
Backtest score[2]								
LR	157.06 (11.50)^{a}	3.39 (1.89)^{a}	4.96 (1.49)	1.64 (0.94)	22.72 (3.76)	5.82 (2.05)^{a}	81.59 (7.00)^{a}	26.91 (6.40)
IR	137.00 (17.50)^{b}	5.53 (2.54)^{a,b}	2.41 (2.27)	1.97 (1.41)	27.42 (5.72)	9.35 (3.12)^{b}	102.15 (7.64)^{b}	28.04 (8.96)
HR	136.62 (13.90)^{b}	8.34 (2.18)^{b}	2.75 (1.81)	2.88 (1.45)	26.31 (4.56)	10.73 (2.48)^{b}	104.28 (8.47)^{b}	25.81 (7.46)
RBV-LS-sire[3]								
High	156.00 (13.10)^{a}	5.08 (2.02)	1.17 (1.71)^{a}	1.96 (1.07)	26.63 (4.31)	5.74 (2.34)	90.21 (8.00)	26.55 (7.02)
Low	141.00 (10.60)^{b}	6.03 (1.96)	5.58 (1.38)^{b}	2.27 (0.85)	26.44 (3.47)	9.53 (1.89)	100.37 (6.46)	28.67 (6.61)
Feeding group[4]								
CON	130.00 (11.80)^{a}	11.02 (1.91)^{a}	3.78 (1.54)	3.20 (0.96)	27.61 (3.88)	10.89 (2.11)^{a}	90.7 (7.22)	31.82 (6.66)
HD	167.00 (11.30)^{b}	0.08 (1.94)^{b}	2.97 (1.47)	1.03 (0.09)	25.43 (3.70)	6.38 (2.01)^{b}	99.7 (6.87)	28.36 (6.41)

[1] Abbreviations of behaviour traits as defined in Table 4.1.

[2] LR = low-resisting; IR = intermediate-resisting; HR = high-resisting.

[3] High = Relative breeding value for sire lesion score (LS) > 100; Low = relative breeding value for sire lesion score (LS) ≤ 100.

[4] CON = basal diet without supplements; HD = basal diet supplemented with a mixture of herbs.

Effect of breeding values for lesion scores

With regard to RBV-LS of the sire (Table 4.4), we identified significant lsmeans differences ($P < 0.05$) for REST and for RFIGHT. The offspring of boars with RBV-LS above the threshold (indicating fewer skin lesions) spent more time for REST and RFIGHT compared to offspring of boars with RBV-LS below the threshold. Hence, the healthy genetic group (with regard to skin lesion) aimed on the activities reflecting calmness (lying, sitting, standing), and on avoiding fights. Same associations were identified when correlating the sire solutions (= estimated sire breeding values) from model (2) for the video behaviour traits with their breeding values for lesion scores (Table 4.5). The Piétrain boars with favourable RBV-LS had breeding values below the average for video behaviour traits indicating aggressiveness (FIGHT, BITE, IFIGHT) as indicated via negative breeding value correlations. In Table 4.4, we associated sire RBV-LS with phenotypic behaviour pattern of offspring, and high RBV-LS were associated with a short duration for RFIGHT. Oppositely, the sire breeding value correlations between RBV-LS and RFIGHT were positive with 0.20 (Table 4.5). Hence, the consideration of all related animals in the pedigree relationship might contribute to differences in phenotypic and genetic correlations, but opposite signs in this regard suggest more detailed investigations or analyses of additional data. Nevertheless, the breeding value correlation between RBV-LS and RFIGHT of 0.20 did not differ significantly from zero ($P > 0.05$). Breeding value correlations between RBV-LS with breeding values for REST and RACT were positive, genetically indicating fewer skin lesions for pigs spending more time with “usual” and calm behaviour (e.g., eating, drinking, lying, sitting and standing). The breeding value correlations among traits reflecting aggressiveness (FIGHT, IFIGHT, BITE) were positive, but these behaviours were negatively correlated with the traits indicating calmness (REST, RACT). The breeding value correlation between REST and RACT was positive with 0.56, being the largest correlation among all trait combinations. The breeding value for IFIGHT was negatively correlated with the breeding value for refusing fights (RFIGHT).

Table 4.5: Correlations between relative breeding values for skin lesion scores (RBV-LS)[1] with breeding values for video behaviour traits[2] and among breeding values for video behaviour traits of Piétrain boars. Correlations significantly differing from zero ($P < 0.05$) are highlighted in bold.

	Behaviour trait							
	REST	FIGHT	RFIGHT	IFIGHT	BCON	BITE	EXPLORE	RACT
RBV-LS	0.41	-0.33	0.20	-0.14	-0.09	-0.36	-0.19	0.37
REST		-0.44	0.10	-0.28	-0.10	-0.20	-0.14	0.56
FIGHT			-0.18	0.51	0.22	0.28	0.27	-0.35
RFIGHT				-0.34	-0.11	-0.15	-0.05	0.38
IFIGHT					0.40	0.45	0.26	-0.39
BCON						0.23	0.21	-0.17
BITE							0.32	-0.47
EXPORE								-0.11

[1] Standardized relative breeding values above 100 are favourable, indicating less skin lesions than the average.

[2] Abbreviations of behaviour traits as defined in Table 4.1. The breeding values are expressed in the unit of the traits (in minutes), indicating that larger breeding values are associated with longer duration for the respective trait

DISCUSSION

The effect of feed supplements on behaviour pattern in the post-weaning period

In the present study, the effects of the HD supplements on the video behaviour pattern were very similar on day one after weaning and five weeks after weaning. Czycholl et al. (2019) studied the test-retest reliability of behaviours of growing pigs on-farm, which is the consistency of behaviour patterns over time. Only for a few tests reflecting human-animal relationships and considering the first and second farm visits, the evaluation criteria indicated sufficient reliability. From a within-animal perspective, Botreau et al. (2013) indicated behaviour consistency with ageing for uniform environmental characteristics, which are difficult to realize under field conditions. In our present study based on a standardized research design on-station, major herd environment characteristics were very similar at both behaviour-monitoring dates, which might explain the almost identical behaviour pattern within the HD and with the CON group for the two monitoring dates, even for the large interval between measurements of five weeks. The HD supplement seems to have a prompt effect at feeding day two, indicating less fighting and biting, but longer durations for calm behaviour signs as reflected via lsmeans for REST and RACT. Very prompt effects when supplementing the feeding ratio with herbs in terms of fewer skin lesions were reported by Aikins-Wilson et al. (2022), or more aggressive behaviour for extremely strong feeding alterations, e.g., when switching from a liquid to a solid diet (Campbell et al., 2013). With regard to a solid feeding system, diets enriched with crude fibre contributed to less pig aggressiveness (Bernardino et al., 2016; Kallabis and Kaufmann, 2012), supporting the observations from the present study. Generally, an undersupply of specific feed ingredients seems to support abnormal behaviour, as shown by increased ear and tail biting in a feeding group with a reduced protein supply (Jensen et al., 1993; Fraser et al., 1991). With regard to the herbal supplement used in the present study, less aggressiveness in the HD compared to the CON group can be explained through the higher crude fibre (4.9% vs 2.4%) and crude protein content (17.1% vs 16.6%), plus the specific effects of the chicory herbs being a major component of the HD supplement. Pouille et al. (2022) reported favourable effects of chicory on different response variables (e.g., appetite regulation and health indicators) in a comprehensive mice study including metabolomics data and nutrigenomic analyses. In their review article, Street et al. (2013) addressed similar medical properties of the chicory ingredients from a plant perspective and for different species.

Associations between piglet behaviour and behaviour patterns in weaned pigs

The results from the present study indicate more aggressiveness after weaning (as indicated by through long duration for FIGHT, BITE, and IFIGHT) for piglets allocated to the HR group according to their backtest score. Hence, the active piglets with several escape attempts in the backtest also displayed activity at later ages including the abnormal activity pattern. Clouard et al. (2022) classified suckling piglets into three behaviour categories reflecting three different social styles, i.e., low-solicited inactive animals (inactive), active animals (active) and highly-solicited avoiders (avoiders). With regards to repeated classifications over time, the group allocation of the individuals was quite stable, indicating that an active piglet at an early age was an active pig during ageing. Furthermore, as identified in our present study, the effect of sex on behaviour was not significant. In the study by Clouard et al. (2022), the group contemporaries did not change over time, but the regrouping of piglets initiating a new social hierarchy within a group, was identified as a major effect on agonistic behaviours (Fels et al., 2012). In the present study, aiming for a well-balanced research design several effects (genetic line, backtest score, RBV-LS), piglets were mixed after weaning. However, the barn environment in the research station did not change, i.e., the rearing environment and the post-weaning environment were identical with regard to farm location and farm employees. Hillmann et al. (2003)

highlighted the environmental alterations from a feeding and husbandry perspective when evaluating behaviours in pigs. Studnitz et al. (2007) identified behaviour changes in pigs with ageing, e.g., a decrease in curiosity expressed by reduced sniffing and rooting, but changes in behaviour patterns were similar for all individuals. Hence, a pig with a longer duration for explorative behaviour than herd contemporaries at a young age also displayed longer duration than the contemporaries at later ages, but on generally lower levels. In the present study, the lsmeans for EXPLORE and further traits reflecting pig activity were very similar at both recording dates in post weaning period at day one after weaning and five weeks later. Consistent differences in behaviour patterns from a between-animal perspective suggest the implementation of selection strategies at early ages.

The present study associated resistant piglet behaviour with aggressiveness after weaning phenotypically. However, with regard to breeding and selection, it is imperative to estimate genetic correlations between early indicators and target traits, implying broadening the study to a larger sample size. The small sample size in the present study indicates first associations, but validations based on larger datasets are needed. Nevertheless, the analysis of video images remains a challenge in this regard. In simulations, König and Swalve (2006) showed that early indirect selection is justified for genetic correlations with the breeding goal trait for genetic correlations larger than 0.70. Apart from the genetic correlations, some other factors, including the costs and logistics of trait recording for the different traits at different ages, as well as generation intervals, should be taken into consideration when determining optimal selection strategies. From a logistic perspective, both trait recording schemes the piglet backtest as well as analysing video images, are extremely labour and time intensive. As an alternative, sensor technique can be used to measure behavioural changes automatically. The sensor outputs were valuable in discriminating general behaviour patterns in farm animals such as eating, sleeping or oestrus detection, but the differentiation within behaviour categories was quite difficult

(Jaeger et al., 2019). Enhanced camera techniques considering locomotor activities from 3D trajectories are more accurate and allow a clearer behaviour picture (Matthews et al., 2017), but identifying actors for tail biting implies the time consuming study of video images of a trained person. A promising approach to specify pig behaviour in detail is the combination of video data combined with innovative statistical predictions such as machine learning or semi-supervised neural network analyses (Wuttke et al., 2020). In the neural network or machine learning algorithms to predict later behaviour, trait responses from suckling piglets could also be included.

Associations between skin lesions and aggressive behaviour: Victim-actor perspective

Efficient prevention of an outbreak of aggressive behaviour, especially tail biting, implies the separation of biters from the group. The first signs of tail lesions were associated with exponentially increasing tail biting activities (Statham et al., 2009). However, as stated above, the identification of aggressive pigs implies time-consuming and difficult video analyses, or a combination of modern video techniques with complex statistical predictions such as machine learning algorithms (D'Eath et al., 2014). Hunter et al. (2001) stated that the identification of victims is much easier than the detection of biters. Prunier et al. (2019) indicated the broad variety of biting characteristics, which complicates harmonizing biting recording schemes. Consequently, from a genetic perspective, Gentz et al. (2019) and Aikins-Wilson et al. (2022) suggested selection strategies based on tail or skin lesions, especially in the context of group selection. However, to our knowledge, genetic correlation estimates between biting (actor) and being a victim, are not known. From a genetic-statistical perspective, it is a challenge to estimate genetic correlations between traits with small additive genetic variances or heritabilities. The heritability for active tail biting was only 0.05 (Breuer et al., 2005), and that of being a victim was only 0.06 (Canario and Flatres-Grall, 2018). In the present study, we correlated boar breeding values for a victim trait (RBV-LS) with breeding values for an actor trait (BITE), indicating less skin lesions when selecting against biting. However, the estimates are based on a small dataset for the actor trait, and breeding value correlations can differ substantially from true genetic correlations in cases of low breeding value accuracies (Calo et al., 1973). Nevertheless, results from some genomic studies confirm the breeding value correlation from the present study. Brunsberg et al. (2013) studied gene expressions in the brains of pigs, indicating a very similar patterns for biters and victims, but more differences in neutral pigs. Similarly, Wilson et al. (2012) identified same the SNP markers with significant effects on biter and victim traits, but other SNPs were associated with being neutral. Hence, such molecular findings plus our estimate for the breeding value correlation indicate the possibility for indirect selection of victim traits to reduce biting.

Nevertheless, from a genetic-statistical perspective, it remains very difficult to infer genetic covariance components between biter and victim traits, due to mutual relationships between cause and effect. In this regard, the social component, i.e., the effect of biting on herd contemporaries, has to be taken into account, suggesting the application of genetic evaluations with social interaction effects (e.g., Ellen et al., 2014; Heidaritaba et al., 2019). In such a context, Bijma et al. (2007) addressed the magnitude of covariances for residual effects between the individual of interest and the group members, which changed depending on the environmental characteristics. Canario and Flatres-Grall (2018) suggested direct selection against biting in cases of direct-social correlations close to zero, due to negligible effects on the "to be bitten risk" of group members. Furthermore, for behaviour traits in terms of "early learning behaviour" or competition among siblings (Drake et al., 2008), it is imperative to consider the maternal-genetic component, but enhanced statistical modelling complicates inferring genetic parameters and the convergence of statistical models.

CONCLUSION

The multi-factorial semi-randomized experiment indicated significant effects of feeding (herbal diet), piglet behaviour (backtest score) and sire breeding values for victim traits (RBV-LS) on behaviour traits of pigs monitored via video images in the post-weaning period. The HD supplement implying a diet enriched with crude fibre, protein, and chicory, was associated with less aggressive pig behaviour, i.e., lower duration for FIGHT, IFIGHT, and BITE compared to the CON group. The more active piglets indicated as highly resistant in the backtest showed more active and aggressive behaviour patterns than piglets classified as LR or IR. Pigs with sire RBV-LS below the average, indicating a higher lesion prevalence spent more time with explorative, fighting, and biting behaviour, but the differences between sire groups were not significant. The correlation between boar RBV-LS and breeding values for active biting was moderately negative. Consequently, selection according to favourable breeding values for skin lesions or early selection of IR or LR piglets might contribute to a reduction of aggressive behaviour in crossbred rearing pigs. The comprehensive video analyses from two monitoring dates indicated a strong overlap of behaviour signs (from a within-pig perspective) with ageing. Genetic-statistical modelling approaches considering, e.g., interactions among main fixed effects simultaneously, which base on larger datasets, are strongly suggested for ongoing validations of the present findings.

Declaration of Competing Interest

We declare that we have no conflicts of interest

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CHAPTER 5

GENERAL DISCUSSION

The main aim of this study was to improve animal welfare using genetic trait improvement selection scheme to breed naturally short tail pigs to prevent tail biting in pigs. Phenotypic data from tail lengths, skin lesions and growth parameters were computed to estimate genetic (co)variance components for tail lengths, skin lesions and their correlations with growth parameters. This information was used to genetically select pigs with short tails (see Chapter 2). In addition to the heritability estimates for tail length, lesions and growth traits, the effects of the herbal diet and diet by genotype interactions on skin lesions and growth traits in post-weaning pigs were analysed in chapter 3. To provide a better explanation for the aggressive behaviour, the third study investigated individual behaviour contributing to the development of aggressive behaviour and tail biting using phenotyping aggressive behaviour via video observation in Chapter 4.

5.1. Tail length and Growth traits

5.1.1. Genetic parameters for tail length and growth traits

The tail of an animal is responsible for various physiological functions. However, longer tails in pigs are reported to generate tail biting (Thodberg et al., 2018). Therefore, one major objective of this study is to naturally breed pigs with short tails. Tail shortening is caused by mutations in the T-box domain of the Brachyury-gene and a single copy of the gene will result in short tailed in animals (Wu et al., 2010; Buckingham et al., 2013; Yoo et al., 2017). Tail length in animals is an inherited trait (Hytönen et al., 2009; Greeff et al., 2015; Oberpenning et al., 2022). However, the mechanism of short tails in animals are mostly investigated using the mouse as a model animal and the principles applied to other species (Wu et al., 2010). Nevertheless, with variation between species, there has been successful breeding of short tail length in sheep with heritabilities ranging from 0.39 to 0.77 (Hümmelchen et al., 2022; Kalds et al., 2021; Scobie and O'Connell, 2002). Our first publication in which the Piétrain x German

Landrace or German Edelschwein pigs featured prominently found the possibilities for successful genetic selection on short tails in pigs. Moderate additive genetic variances and heritability for tail length ranging from 0.34 to 0.51 were estimated. Maternal heritability of 0.05 ± 0.02 was estimated indicating uterine influence on tail characteristics. The impact of the maternal uterine genotype on growth parameters, body size and tail length in offspring have been observed in animals (Cowley et al., 1989; Dandolu, et al., 2010; Lee et al., 2022). This maternal genetic effect on tail length and antagonistic associations between direct and maternal genetic effects identified may complicate the definition of breeding goals and selection strategies. The negative relationship between direct additive and maternal genes results are unclear, suggesting molecular, morphological, and physiological investigations. Similar observation was in line with studies in sheep estimating a negative relationship between direct additive and maternal genetic effects for tail length and body weight traits (Oberpenning et al., 2022). Accordingly, Greeff et al. (2015) reported a maternal permanent environmental effect on spine length and weight. However, comparing heritabilities of T-LEN in this study to other studies in pigs could not be established since this study is the first study on tail lengths in pigs. The growth traits are influenced by both direct additive and maternal genetic effects (Albuquerque and Meyer, 2001). Direct heritability values of 0.07 were estimated for BW and were similar to those from previous studies (Arango et al., 2006; Tomiyama et al., 2010; Alves et al., 2018). Direct heritability estimates for BW were generally low (Wang et al., 2016; Tribout et al., 1998). Despite its low heritability, it is an important trait with successful genetic improvement in pig breeding. On a phenotypic scale, BW is negatively related to pre-weaning mortality, sow productivity, piglet vitality, survival, growth performance and weight gain (Romero et al., 2022; Klein et al., 2018; Muns et al., 2013; Gondret et al., 2005). However, contradictory result was reported by Dufrasne et al. (2013) with a larger direct heritability of 0.25 at day 4 for BW.

Unlike BW, with higher direct and low maternal heritability, WW and PWW direct heritabilities increased with age indicating that direct heritability gradually increased with age (Yin and König, 2019; Estrada-León et al., 2014; Lopes et al., 2013). Our findings were in line with estimates from the literature (Arango et al., 2006; Tomiyama et al., 2010; Alves et al., 2018). The increasing direct heritability estimates for WW and PW with age were due to the decreasing maternal influence. Conversely, a low direct heritability of 0.03 and a larger maternal heritability of 0.11 was estimated by Zhang et al. (2000) for piglet weights at the age of 28 days. It was concluded that the large maternal heritability estimated was as a result of the strong impact of sow milk productivity and sow behaviour. Direct and maternal heritabilities for ADG (0.15 and 0.07, respectively) reflect genetic parameter estimates for weight gain in the period from birth to the weaning date (Banville et al., 2015). Negative correlations estimated between direct and maternal effects for growth traits were in agreement with studies in other species, e.g., in dairy cattle (Johanson et al., 2011), beef cattle (Chud et al., 2014) and sheep (Boujenane et al., 2015).

5.1.2. Genetic correlations between tail length and growth traits

Direct genetic correlations among growth traits were positive and of medium to high magnitude showing no genetic antagonism between them. A highly significant positive correlation (0.66, $P < 0.01$) was observed between T-LEN and BW. These findings correspond with studies of Jafari and Razzagzadeh (2016) in sheep with positive genetic and phenotypic correlation between growth rates and fat-tail dimensions (ranging from 0.18 to 0.76 for genetic and 0.13 to 0.22 for phenotypic). This indicates positive direct influence of the dams on BW and T-LEN of their offspring, implying that selection based on BW will produce larger piglets with longer tails. However, from animal welfare perspective, the heavy and large pigs from the same group displayed dominant behaviour and are strongly involved in aggressive activities than the smaller pigs in the group (Jensen and Yngvesson, 1998; Andersen et al., 2011). Therefore selection of lighter piglets contributes to shorter tails (as identified in the present study) and to fewer cases for tail biting and tail necrosis. Nevertheless, higher BW has a positive correlation with pig survivability and further development (Klein et al., 2018; Knol et al., 2022).

Positive direct genetic correlation was found between BW and WW suggesting that both traits are under the influence of similar genes and selection for higher BW will result in higher WW (Smith et al., 2007; Jankowiak et al., 2020). Conversely, a smaller genetic correlation (0.08) was estimated between BW and PWW. The direct genetic correlation between BW and ADG was weak (0.04) due to the fact that these traits tend to compensate for the high or low gain in corresponding trait. However, quite large direct genetic correlation was estimated between WW and ADG (0.96) which means improvement in one will result in improvement of another.

5.2. Tail lesion and skin lesions

5.2.1. Genetic parameters for tail lesion and skin lesions

In the quest to find solutions and detect tail biting and aggressive behaviour early in pigs, several traits such as tail and skin lesions have been proposed as indicators of aggressive behaviour in pigs (Kanis et al., 2004; Turner et al., 2010). Heritability for tail lesions (ranging from 0.74 to 0.90, $P < 0.05$) and skin lesion (ranging from 0.10 to 0.43, $P < 0.05$) have a significant heritable component. Positive correlation between aggressive behaviour and skin lesions are high suggesting the possibility of improving pigs' welfare through selective breeding (Desire et al., 2016; Wurtz et al., 2017; Peden et al., 2018; Liu et al., 2022). In this study, heritabilities for T-LES range from 0.01 to 0.39, depending on the recording date and the genetic-statistical modelling approach. Comparing our results to other studies was relatively difficult since data collection and scoring systems differ (Keeling et al., 2012). Nevertheless, results from this study was similar and within the range recorded in literature (Parois et al., 2015; Desire et al., 2016; Wurtz et al., 2017; König von Borstel et al., 2018).

Heritabilities from categorical data using the threshold model are mostly larger than from LIN model (Dempster and Lerner, 1950; Kizilkaya et al., 2014). On the contrary, our study recorded high heritability for T-LES from the LIN model. Similar findings were reported in the literature for skin lesions with larger heritabilities from the LIN model (König von Borstel et al., 2018). Both methods recorded moderate heritabilities for T-LES from both repeatability models, which is good trait for genetic selection enabling breeding against these traits.

5.2.2. Associations between skin lesions, aggressive behaviour and growth traits

Pig aggression causes injury in the form of skin lesions. These lesions can be selected against to reduce aggression observed at mixing both on a genetic and phenotypic level (Desire et al., 2016; Liu et al., 2022). To breed against aggressiveness, there is the need to understand how individual aggressiveness is related to other behaviour traits. For example, skin lesions on pigs can be an indication of an attack from another pig indicating that the pig that performed the most active aggressive behaviour may not be the one with the most severity of skin lesions in a pen. Another scenario can be that pigs whose lesions heal before lesion score counting may be incorrectly considered as not being previously bitten. This may be inaccurate to select pigs for reduced aggression based on the skin lesions at the individual pig level (Marques et al. 2012). Therefore, failure to distinguish between the main causes of lesions may lead to biased estimates of individual aggression. Positive genetic correlations between skin lesions and aggressive behaviour are well documented by several authors (Turner et al., 2008, 2009; Desire et al., 2016; Liu et al., 2022). Accordingly, Turner et al. (2008) estimated large genetic correlations between lesion scores and pig behaviour traits, indicating that selection on lesion scores indirectly reduces pig aggressiveness. All these studies however, failed to establish the relationship between the performer and the receiver of aggressive behaviour as well as the relationship between the severity of skin lesions on the body and active aggressive behaviour. This study provided evidence at the individual pig level estimating the relationship between performer and the receiver of aggressive behaviour. It was observed that aggressive behaviours (FIGHT, BITE and IFIGHT) are intense post-mixing recording more lesions 24 hours after mixing. This explains the high heritabilities reported for lesion as well as high heritability for aggression in the literature (Desire et al., 2016; Liu et al., 2021). These lesions may be as a reflection of the number of attacks received from another pig, but not being an initiator of aggressive interactions (König von Borstel et al., 2018). Lesions on the anterior part and the caudal part of the pig have been reported to be positively correlated to active aggressive behaviour and receiving aggression respectively (Turner et al., 2008; 2009; Desire et al., 2015). It was noted that offspring from sire with more relative breeding value for skin lesion (RBV-LS > 100) had significantly ($P < 0.05$) longer durations for REST and RFIGHT. Similar result was obtained by Desire et al. (2016) indicating that piglets with low anterior skin lesion 24-hours post weaning would result in the reduction in mean EBVs for behavioural traits relating to aggression.

In chapter two of this study, it was noted that direct selection for growth would increase tail length and subsequently increase aggressiveness. In line with our findings, significant positive correlation was observed between aggressive behaviour and growth traits (Kjaer and Mench, 2003; Rydhmer and Canario, 2022). A study by Camerlink et al. (2018) indicated that selection for high growth rate results in increased general activity but decrease the motivation to participate in social interactions. However, Turner et al. (2006) found the two traits to be genetically independent. Increased general activity often results in aggressive behaviour such as tail biting which have a positive genetic and phenotypic correlation value with lean tissue and a negative genetic correlation between tail biting and backfat thickness (Breuer et al., 2005;

EFSA, 2007) albeit the genetic basis remains unclear. However, Hermesch, (2018) reported that incidence of tail-biting victims had no genetic association with growth rate or backfat of growing pigs and selection strategies for higher lean meat growth do not lead to higher incidence of tail biting.

Bozkurt et al. (2006) reported a close relationship between high-energy diets and aggressive behaviour in beef cattle. In this study, piglets in the CON environment recorded significant minutes of FIGHT, IFIGHT, BITE and BCON compared to piglets in the HD environment. This can be associated with the high level of energy in the ration (14.1 MJ/day and 13.0 MJ/day for CON and HD treatments, respectively). In line with our findings, significant positive correlation was observed between daily feed intake and aggressive behaviour but no significant correlation between aggressiveness and weight gain (Palander et al., 2013; Li et al., 2016). This is an indication that, aggressive animals consume more feeds, and use the energy to perform fights but did not convert into body weight gain. Similar results have been reported in cattle with less aggressive animals phenotypically and genetically associated with growth rates as identified in the present study (Nkrumah et al., 2007; Reinhardt et al., 2009).

5.2.3. Behavioural parameters

Animals develop behavioural strategies to effectively respond to environmental challenge to ensure their survival and reproduction (Kappeler et al., 2013; Yamaguchi et al., 2018). A typical example is the foraging behaviour in livestock to optimize strategies to efficiently exploit food sources (Zampaligré and Schlecht, 2018; Whiteway et al., 2021; Schofield et al., 2022). However, differences that exist between individual animals and behavioural measurements often have high variance which is influenced by the experience of the animal being observed and the environmental conditions during observation (Bradbury and Vehrencamp, 2014).

Several behaviour test such as the human approach test, novel object test and the backtest to show the pigs fear of humans, exploratory behaviour and the aggressiveness of the pig respectively have been conducted (Scheffler et al., 2014; Juhas et al., 2019; Haigh et al., 2020). However, these tests showed the temperament in the pig but failed to indicate the aggressive potential. Therefore, personality profiles via the use of comprehensive video analyses predict some potential behaviours of the pig (Ellen et al., 2014; Whiteway et al., 2021).

This study combined genetic line, backtest score, relative breeding values for skin lesions of sires, and video behavioural measurements in two feeding environments to analyse behavioural patterns of piglets during the post-weaning period. Offspring of sires with few or no lesions and severe lesions were used to predict the expected phenotypic response in aggressive behaviour.

Pigs have the impetus to bite as results from this study show that the majority of piglets BITE, IFIGHT and FIGHT in the 24-hours period weaning with offspring of sires with less relative direct breeding value for skin lesion spending more time on these behaviours. Stukenborg et al. (2011) reported agonistic behaviour in the first 24 hours after mixing; however, other studies have reported agonistic behaviour lasting for several days (Larsen et al., 2018; Puppe et al., 1997). This could be related to hierarchy formation and relationship establishment within the group. Based on direct observations our study indicates that, BITE happens simultaneously, however, it was initially difficult to tell whether piglets were playing or fighting mainly on the fact that the other pigs stood still without any reaction. Keeling et al. (2004) and Larsen et al. (2018) suggested that, outbreak of tail biting usually occurs after increased activities in the pen and these activity levels could be an early detector of tail biting. A single pig that became a tail-biter is more active than its pen-mates in the days prior to an outbreak (Edward, 2006; Svendsen et al., 2006; Sonoda et al., 2013). This statement was in agreement with what was observed in this study as one particular docked piglet was very active and jumps from one pen to the other and from direct observation this piglet happens to bite the most. However, no outbreak of ear-tail biting or aggressive behaviour was observed in this study. In poultry, deliberate injury to other animals in groups which were less active have been observed (Riber and Forkman, 2007). Piglets that had several escape attempts during the backtest were more active and performed significantly ($P < 0.05$) more aggressive behaviour (FIGHT and BITE) at later ages. Stukenborg et al. (2011) observed that more aggressive growing pigs tended to also be more aggressive sows. However, for the influence of diet on behaviour, significant effect of the herbal diet supplementation contributed to the calm behaviour of the HR piglets in the HD group with longer duration for REST. The fibre content in the HD diet contributed to the longer duration for REST and forage as predicted by Rhim et al. (2015). In a study by König von Borstel et al. (2018) it was concluded that selection for less aggressive pigs are possible using the backtest as indicator trait.

5.3. Herbal diet supplement effects on growth performance and behaviour in post weaning

Chicory (*Cichorium intybus L.*) is a perennial deep-rooted herb with high nutrient values used for foraging in livestock (Nwafor et al., 2017; Liu et al., 2018; Niderkorn et al., 2019). There have been evidence that chicory in diet improves feed intake and body weight traits in livestock (Velasco et al., 2010; Liu et al., 2011; Niderkorn et al., 2019). Studies in different livestock species showed that improved body weight traits of animals feed on chicory diet (Velasco et al., 2010; Liu et al., 2011; Peña-Espinoza et al., 2016). The high growth rate was attributed to the high acceptable rate and better balance of nutrient supply (protein: energy) as well as a higher efficiency of metabolisable energy use (Komolong, 1994). However, contrary to the high growth rate associated with chicory diet, our study recorded a 0.40 kg increase in PWW and 10 g/day increase in ADG in piglets from the CON group compared to piglets from the HD group. One explanation for the low growth rate in HD piglets could be the high percentages of lysine and methionine in the HD diet during the second phase of the dietary treatment which is associated with limited growth (Lebret et al., 2018; Liao et al., 2015). Additionally, the lower energy content of diets which was seen in the case of the HD diet has a negative impact on growth (Li et al., 2012; Kallabis and Kaufmann, 2012). Nevertheless, our findings were comparable to a study by Presto et al. (2019).

Skin and tail lesions on piglets in both treatments were more during the first few days after weaning indicating aggressiveness and increased activity in the pen. It can be concluded that irrespective of the environment, aggressive behaviour is intense during the first three days of mixing. This confirms reports in the literature about the association between hierarchy formation within a group and aggressiveness (Fels et al., 2012; Schrey et al., 2019) as well as between weight and aggressiveness (Turner et al., 2008; Palander et al., 2013). Even though lighter piglets are associated with bites, piglets in the HD group with lighter weight gains had less lesion scores, were calm and had more REST at the end of the experiment. This would be as a result of the positive effect chicory diet had on the behaviour of piglets as well as the role it plays in wound healing (Saeed et al., 2017; Häkkinen et al., 2021). The higher crude fibre and crude protein contents in the HD reduce the time for BCON, IFIGHT, FIGHT, RFIGHT, BITE, and other aggressive behaviours. In this study, aggressive behaviours such as IFIGHT, FIGHT, RFIGHT and BITE resulting in more skin lesions were observed in the CON group. Skin lesions significantly ($P < 0.001$) increased with increasing body weight in the CON group. This result agrees with a study by Camerlink et al. (2014), where a positive phenotypic correlation was observed between skin lesions and body weight, thus bigger pigs were more aggressive. Another explanation could be that the favourable effects of chicory on appetite regulation and health indicators which is absent in the CON diet could have increased these behaviours (Pouille et al., 2022).

5.4. Genotype by Diet interactions

5.4.1. Genetic parameters in different diet groups

Genetic parameters and genetic correlations between different environmental conditions can be used to determine the presence of G x E interactions (Chen et al., 2021). When using phenotypic measurements obtained in different environments fitted in multiple-trait models, the accuracy of genetic parameter estimates is dependent on the sample size (Mulder, 2016; Titterington et al., 2022). The objective of this study was to estimate variance components and variance ratios in different feeding systems, and for the proof of possible diet by genotype interactions through genetic correlation estimates. Estimates for heritabilities were higher in HD than in CON, reflecting a minor effect on feeding characteristics on genetic parameter estimates or on gene activities. This may imply that, the feed in HD group was more favourable than in CON group, which led to higher genetic variances. Therefore, selection of animals in environments reflecting superior nutritional value means the environment supports the fully expression of the true genetic potential (König et al., 2005; Chen et al., 2021). In this case, selection for traits under study in the HD environment may increase the selection response due to the higher genetic variances and higher heritabilities. This would also lead to higher accuracies of EBVs. Our results were consistent with other reports for PWW and ADG (Zhang et al., 2016; Alves et al., 2018; Gourdine et al., 2019). Low genetic variance recorded for LS in the HD group indicated intra-family similarity, and consequently, the similarity might contribute to narrowed genetic differentiation in the HD environment. The high heritability of LS in the CON group suggest that this trait has a strong genetic component with not much environmental influence.

Genotype by environment interactions in livestock breeding programs is important in improving productivity and animal welfare (Wakchaure et al., 2016). Calus (2006) defined genotype as breeds, lines, strains, families and sires, while environment include factors such as time, location, nutrition, management and housing. In a study by Nirea and Meuwissen, (2017), it was noted that the accuracy of estimated breeding values decreased when G x E interactions are not accounted for in the genetic evaluation models. Re-ranking of genetic merit of progenies depends on environment and management in which performance is recorded. This interaction is important in selecting sires for improved performance which is not being observed in the performance in the offspring (Wakchaure et al., 2016).

Genotype by Environment interaction can be detected at the phenotypic level by estimating the genetic correlation of a trait between environments. Comparing the performance of the progeny of sires from two different dietary environments, diet by genotype were evaluated for PWW, ADG and LS. Genetic correlation between same traits recorded in different environments that are lower than 0.8 are considered as evidence of genotype by environment interactions (König et al., 2005; Zhang et al., 2019). In this regard, genetic correlation was small (0.15) for LS indicating a significant sire by diet interaction. The slightly high genetic correlation between estimates for sires effects in the HD and in the CON group was observed for PWW illustrating that there is only a very small contribution of the interaction. However, re-rankings of sires in relation to feeding levels were identified. This result was similar to reports by Hermesch (2004). On the contrary, genotype by environment interactions were reported by Godinho et al. (2018) in feed experiment. In this study, the major feed component contributing to significant interactions was the lysine content. As an explanation for genotype by feeding interactions, Elbert et al. (2020) addressed the specific "genetic make-up" of each sire. Therefore, selection of appropriate sires implies consideration of the environment involved.

5.4.2. Correlations between same traits recorded in different dietary treatments

Genotype by environment interactions influence the effect of selection on the performance of pigs (Wakchaure et al., 2016). Genetic parameters for the traits studied differ between the two dietary treatments. In this study, low genetic correlation between PWW_{CON} and PWW_{HD}, and between ADG_{CON} and ADG_{HD}, indicating genotype by diet interactions for both production traits. The low correlation is a good indicator that the two traits function independently. Small genetic correlation of 0.35 ± 0.20 between LS_{CON} and LS_{HD} indicates clear genotype by diet interactions. LS had high heritabilities and low genotype by environment interaction is a good indicator that the two traits performed independently in different environment. This study observed that correlations between common litter environmental effects between PWW_{CON} and PWW_{HD}, between ADG_{CON} and ADG_{HD} and between LS_{CON} and LS_{HD} were larger than the respective genetic correlation. This may be the similar weight and social interaction in the same environment which influences behaviour patterns and social interactions of piglets in adulthood (Kaufmann et al., 2008; Canario et al., 2017). For the growth trait ranking of sires were similar with the different environment for most sires. However, re-ranking of sires was observed according to their EBV for LS, displaying a shrinkage of EBV variations in the HD environment. This means that the genotypes act differently in each environment.

5.5. Conclusions and recommendations

The aim was to keep pigs with undocked tails which implies improvements in animal breeding. To the best of our knowledge, this study is the first to estimate genetic variances and direct heritabilities for tail length. We were therefore poised to provide the potential for reducing aggressive behaviour in pigs via selection against lesions and breeding for short tails, providing characteristics that this trait could be used for selection purposes. In summary, direct heritability for tail length was high indicating the possibility of breeding short-tailed pigs to improve pig welfare considering tail biting and tail docking. The heritability of lesion scores from this study shows that lesion scores are important indicator traits for genetic selection on pig behaviour to reduce aggression. Nonetheless, using lesion scores as indicators for genetic selection can be misleading as different recording periods are used and pigs whose lesions heal before recording may be incorrectly considered as not being previously bitten. Therefore, the optimal recording period needs to be determined. Our study suggested lesion scoring at the end of the rearing period contributes to the best genetic differentiation. Our study observed that the most active aggressive behaviour may not be the one with the most severe skin lesions indicating that this pig rather attacks other pigs in the group. Appropriate parameters have to be considered in order to detect tail biting at an early stage. The use of location of a lesion and time of occurrence can be useful in determining the type of aggressiveness. Accordingly, comparative studies with appropriate experimental design are mandatory for adequate decision-making regarding the relationship between the severity of skin lesions on the body and active aggressive behaviour to improve economic efficiency and animal welfare in the pig industry. Furthermore, the genetic estimation of behaviour is beneficial to model genes expressed in social partners as it influences behavioural traits. Implementation of these will contribute to accurate estimation of heritabilities in order to genetically improve pigs' behaviour.

Dietary supplementation with herbs had an effect on lesion scores, pig behaviour and growth traits. Genotype by diet interaction evaluated in this study indicated the presence of G x E interactions with high heritability for lesion scores, pig behaviour, growth traits and low genetic correlation between PWW and ADG in the two different environments. Re-rankings of sires in two dietary environments was observed highlighting the need to consider G x E interactions in pig production and the use of appropriate genotypes (sire) for efficient production. Implementation of these findings will provide insights that could be used to improve aggressive and tail biting in pigs. Furthermore, it will contribute to more accurate estimates of breeding values by considering G x E interactions in order to genetically improve the behaviour of sire-line pigs. In conclusion, our findings provided evidence that the chicory-supplemented diet does not negatively affect growth traits, instead improved the behaviour of pigs by calming and performing less aggressive behaviour due to the high fibre content in the diet. To minimise production costs through utilization of cost effective diet as well as minimizing the physical activity of the pigs, we therefore recommend the use of high fibre diet such as the chicory roots which can alter the behaviour of pigs.

A number of benchmarks have been recommended to improve pig behaviour such as improvement in the environment and genetic selection of less aggressive animals. Our findings indicated that behaviour is spontaneous. Therefore, studying tail biting and aggressive behaviour at the individual level and the use of automated data collection methods helps to identify the type of tail biting and subsequently the applying the appropriate measures to prevent the development of tail biting behaviour. Comprehensive research on other aspects of pigs behaviour such as stress physiology that contribute to the development of tail biting and aggressive behaviour and early detection of aggressive behaviour is useful in selecting against these behaviours. Despite interesting observations from this study, pigs performed more exploratory behaviours suggesting the need to provide environmental enrichments as recommended by the EU legislation.

Based on the findings of this study, we further recommend the following measures:

- Genetic selection of short tail pigs and identification of genetically less aggressive pigs for breeding programmes.
- The use of chicory forage as an alternative for fibre-rich feed to reduce the incidence of aggressive behaviour and contribution to improved general behaviour of pigs.
- Advanced research on genetic architecture of aggressive behaviours and the use of genomic information for accurate estimation of the variation underlying aggressive behaviours for long-term sustainability of pig industries.

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Erklärung gemäß der Promotionsordnung des Fachbereichs 09 vom 07. Juli 2004 § 17 (2)

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