

## **Sociable swine**

**Indirect genetic effects on growth rate  
and their effect on behaviour and production  
of pigs in different environments**

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# **Sociable swine**

**Indirect genetic effects on growth rate  
and their effect on behaviour and production  
of pigs in different environments**

Irene Camerlink

## **Thesis**

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## **Abstract**

Camerlink, I. (2014). Sociable swine: Indirect genetic effects on growth rate and their effect on behaviour and production of pigs in different environments. PhD thesis, Wageningen University, the Netherlands.

Social interactions between pigs can influence their health, welfare, and productivity. The effects of social interactions on individuals are partly genetic, and this genetic effect is known as an Indirect Genetic Effect. IGEs are thus the heritable effects of an individual on the trait values of its social partners, e.g. group mates. Previous research has identified IGE for production traits, which suggests that selection for IGE may contribute to selection response. However, validation through selection experiments is required.

The objectives of this thesis were a) to determine the consequences of selection for 'IGE on growth rate' (IGEG) for production traits and behaviour of pigs, and b) to study possible mechanisms underlying IGEG in pigs. First, the relationship between pig behaviour and growth rate was studied in several trials. This showed that oral manipulative behaviours directed at pen mates, such as tail- and ear biting and chewing, can reduce growth rate of the victims, whereas receiving social nosing may enhance growth rate. Second, a one-generation selection experiment was conducted in pigs. Sires ( $n = 24$ ) and dams ( $n = 64$ ) were selected to create a high vs. low contrast for IGEG in the offspring ( $n = 480$ ). The contrast was 14 g average daily gain (ADG). Offspring were studied in a 2×2 arrangement with IGEG (high vs. low) and housing conditions (conventional vs. enriched with straw bedding) to examine genotype × environment (G×E) interactions. Selection did not alter production traits, including ADG. Behaviour showed consistent changes, whereby high IGEG pigs showed less biting behaviour towards group mates and objects. High and low IGEG pigs did not differ in aggression or body lesions during 24-h regrouping with unfamiliar pigs. They did, however, differ in aggression towards their own group members when they were reunited after the temporary regrouping test. In combination with other tests and observations, this might indicate that high IGEG pigs are less fearful or less stress sensitive than low IGEG pigs. There were no G×E interactions, but enrichment had a positive effect on behaviour which was additive to that of selection. Despite the lack of response in ADG, genetic selection for IGEG and enriched housing conditions improved the behaviour and welfare of pigs.



No matter how long your life will last  
Or what its purpose may be (to yourself or to others)  
Each individual deserves to be treated with respect







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# **1**

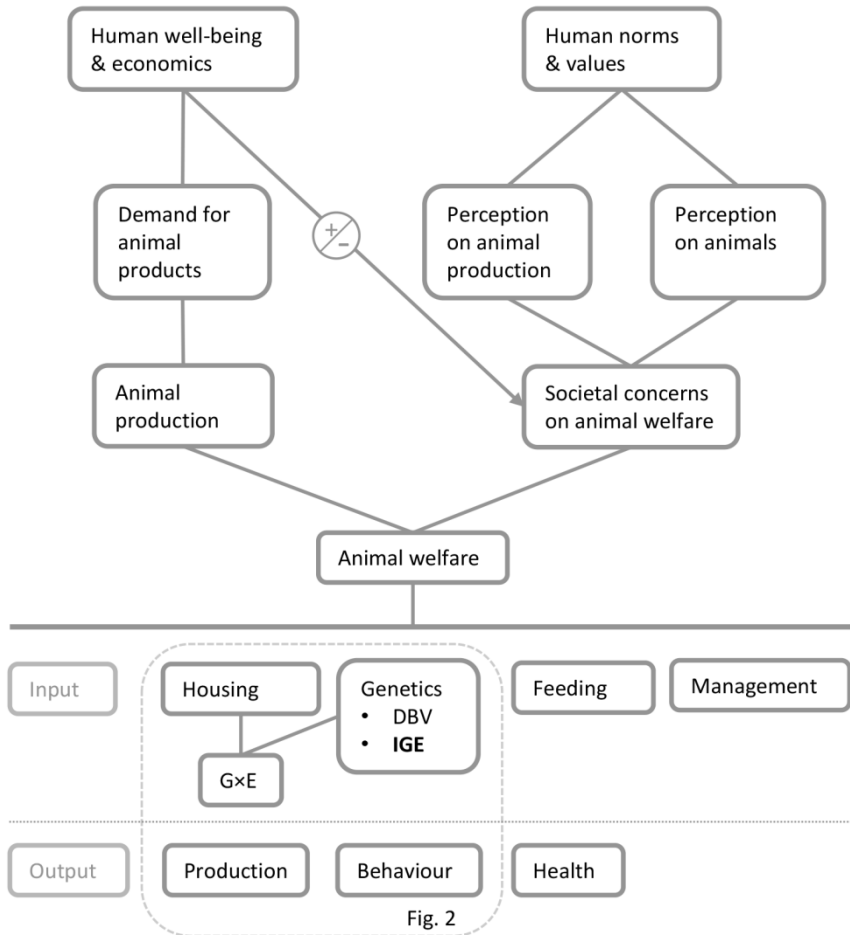
## **General introduction**

### 1.1 Introduction

Animal welfare is an important aspect of sustainable livestock production and is influenced by a number of factors. Figure 1 outlines how animal welfare relates to societal factors (above horizontal line), and factors that may determine animal welfare (below horizontal line). Within this framework, a multidisciplinary research program<sup>1</sup> was carried out to investigate opportunities to improve productivity and welfare of pigs through genetic selection on indirect genetic effects (IGE; Figure 1, marked in bold). Different biological aspects of indirect genetic effects were studied within this program: their genetic background (Duijvesteijn, 2014), their relationship with animal physiology and behaviour (this thesis; Reimert, 2014), and their dependence on the environment (this thesis). The success of animal welfare improvements, especially in intensive farming, may depend on the acceptance of society and the stakeholders (e.g. McGlone, 2001; De Bakker et al., 2012). The overall program therefore also investigated stakeholders' perception on animal production (Benard, 2014). This thesis specifically investigates the relationship between indirect genetic effects and production performance and behaviour of pigs which are kept in diverging housing conditions. As indirect genetic effects are the main topic of this thesis, this introductory chapter starts with the theoretical background on this topic. Thereafter follows a brief description of pig farming and pig behaviour, concluded by the objectives and the thesis outline.

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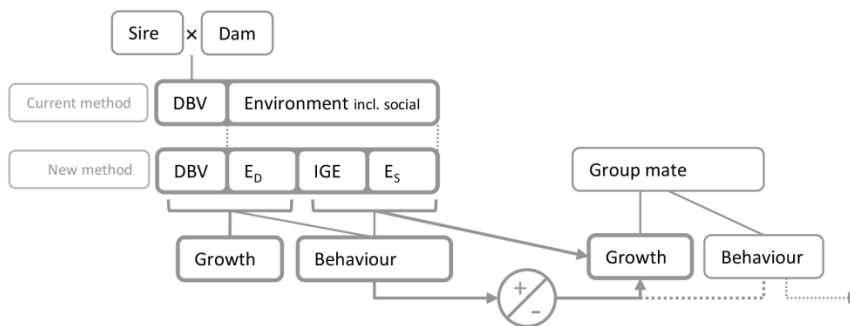
<sup>1</sup>The research project 'Seeking sociable swine? Incorporating social genetic effects into pig breeding programs to achieve balanced improvement in productivity and welfare', is a multidisciplinary sub-program of the program 'The Value of Animal Welfare', funded by the Dutch Ministry of Economic Affairs and the Netherlands Organisation for Scientific Research (NWO).



**Figure 1.** Schematic representation of factors involved in animal welfare. The dotted box refers to Figure 2 for detailed representation.

## 1.2 Indirect genetic effects (IGE)

Individuals may influence each other's health and welfare through social interactions. If, as a consequence, the performance is less than estimated based on genetic data, then this may result in a response to selection that is less than expected or even in opposite direction (e.g. Griffing, 1967; Goodnight, 1985; Agrawal et al., 2001). Current breeding value estimation hardly accounts for social interactions between group members. The classical model is applied whereby the phenotype of an individual is determined by the genes inherited from the parents and an error term (Lynch & Walsh, 1998) (Figure 2A). This error or environmental term may cause the phenotype of an individual to deviate from the predicted outcome and may in captive animals depend on housing, feed, diseases, and social interactions. If these social effects have a genetic component, they can be estimated through indirect genetic effects (Figure 2A).



**Figure 2A.** Schematic representation of new breeding method in which IGE are included in the breeding value estimation.

Indirect genetic effects (IGE), also referred to as associative-, competitive-, or social genetic effects or social breeding values, are the heritable effects of an individual on the trait values of its social partners (Griffing, 1967; Moore et al., 1997; Muir, 2005). For example, an animal may be highly aggressive and thereby reduce the health, welfare, and performance of the individual it interacts with, whereas its aggressiveness may be inherited. IGE do not necessarily represent one specific trait, such as aggressiveness, but rather reflect an overall effect on traits of others, which may vary from positive to negative.

IGE capture part of the heritable component of the (social) environment, that is hidden in current breeding value estimations (Figure 2A) (Griffing, 1967; Muir,

2005, Bijma et al., 2007b), and thereby may contribute to response to selection (Griffing 1967; Moore et al., 1997; Bijma et al., 2007a; Bijma and Wade, 2008). This can be approached through model 1 and 2, which were first described by Griffing (1967), and later amended by Muir (2005) and Bijma et al. (2007b). In model 1, the phenotype of an individual ( $P_i$ ) is the sum of its own genes and non-heritable effects ( $A_{D,i} + E_{D,i}$ ), and the genes and non-heritable effects of its social partners (remaining part of model 1). In model 2, the genetic contribution of an individual to the phenotype of its social partners is given by the total breeding value (TBV), which includes the own genes ( $A_{D,i}$  or DBV), as well as its own genetic effect on the performance of all of its social partners (remaining part of model 2).

$$\text{Model 1. } P_i = A_{D,i} + E_{D,i} + \sum_{j \neq i}^{n-1} (A_{S,j} + E_{S,j})$$

$$\text{Model 2. } TBV_i = A_{D,i} + (n - 1)A_{S,i}$$

In model 1 and 2,  $A_{D,i}$  is the direct breeding value (DBV) of individual  $i$ ,  $E_{D,i}$  is the corresponding non-heritable direct effect,  $A_{S,j}$  is the social breeding value (SBV) or indirect genetic effect (IGE) of group member  $j$  on individual  $i$ , and  $E_{S,j}$  is the corresponding non-heritable social effect. The  $n$  denotes the group size, which is reduced by 1 to account for the individual itself, thus  $n-1$  is the number of group mates of an individual.

These models have been explored for various issues, such as effects of (genetic) relatedness, i.e. kin and non-kin, and the dependence on group size (Ellen et al., 2007; Bijma, 2010; 2013; Alemu et al., 2014a). The application of these and related models provide clear evidence for the existence of IGE (Peeters et al., 2012; Alemu et al., 2014b; Nielsen et al., 2014).

IGE are estimated for all kinds of taxa, ranging from trees (interacting through competition for nutrients and sunlight), to laboratory animals and livestock (Bijma, 2011a). IGE can thereby occur within various contexts, as the character of the social interactions will depend on the species. In livestock, IGE are generally estimated based on production traits, i.e. the effect that an individual has on the production performance of others. For example, in pigs IGE are estimated for the effect that individuals have on growth rate of others (Arango et al., 2005; Chen et al., 2008; 2009; Bergsma et al., 2013). The term 'IGE' itself gives little information; it is the specification of the trait where IGE have been estimated for that adds the interpretation of the genetic effect. When IGE are estimated based on the effect

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that an individual has on the growth rate of others, such as the case in pigs, we refer to IGE as “IGE on growth rate”.

IGE have been explored statistically, but there is little evidence from practice to support the estimated effects, simply because selection experiments have hardly been carried out so far (reviewed by Rodenburg et al., 2010). The nature of the social interactions and the potential underlying mechanisms are therefore largely unknown. Hypotheses for underlying mechanisms in animals vary from behavioural interactions (Rodenburg et al., 2010), disease transmission (Lipschutz-Powell et al., 2012), or a general apathy which causes the animal to not affect group members (Rodenburg et al., 2010; Turner, 2011).

IGE have been mostly related to competition and aggressive behaviour (reviewed by Wilson, 2014). A clear indication that behaviour may underlie IGE stems from selection experiments in laying hens, where pecking behaviour is directly related to the death of group mates (Muir, 1996; Muir and Craig, 1998; Ellen et al., 2008). This pecking behaviour has a clear cause and effect. In other species the behavioural effects may be less prominent, and the relationship between IGE and behaviour is less clear. For example, some behaviours of pigs may affect the growth rate of the recipient (e.g. Wallgren and Lindalh, 1996; Sinisalo et al., 2012), but growth will at the same time also depend on many other social and non-social factors.

If behaviours indeed underlie the effects of IGE, than it would theoretically be possible to select animals that show behaviour which has a positive effect on the trait values of their group mates. This could be either through a reduction of harmful behaviour or through enhancement of positive behaviour. Via behaviour, IGE may contribute to animal welfare (Muir and Craig, 1998; Rodenburg et al., 2010).

**Box 1. Conclusion ‘IGE’.** IGE may contribute to response to selection and might offer ways to improve both production performance and animal welfare. These theories require empirical confirmation. This can be approached through selection experiments, which may validate the genetic estimates and give insight in the effects of selection on animal behaviour and physiology.

### 1.3 Sociable swine

IGE are especially relevant to intensive livestock farming as a) the demand for poultry and pork is expected to roughly double in 2030 compared to the year 2000



(FAO, 2011), and sustainable animal production could contribute to meeting these demands within the carrying capacity of our planet (Neeteson-van Nieuwenhoven et al., 2013); b) parameter estimates for IGE on production related traits indicate that response to selection may increase (laying hens: Peeters et al., 2012; pigs: Bergsma et al., 2013); and c) due to current farming systems many laying hens and pigs show aberrant behaviour which results in serious welfare issues that need to be addressed (e.g. Turner, 2011; Fraser et al., 2013; Manteca and Jones, 2013). Selection on IGE may potentially offer a solution to reduce welfare issues related to behaviour (e.g. Rodenburg et al., 2010). Studies in poultry yielded positive results with regard to selection on IGE for survival, leading to less mortality and thereby an increased egg production (Muir, 1996; Muir and Craig, 1998; Ellen et al., 2008). In pigs, IGE have been estimated for growth rate (IGEG), meaning that the IGE is the inherited effect that a pig has on the on the growth rate of its group mates. A pilot study with pigs selected and housed based on IGEG (Rodenburg et al., 2010), and a study with unselected pigs (Canario et al., 2012), both suggested that selection on IGEG may reduce aggression between pigs. These suggestions, however, need validation from a selection experiment of sufficient power. A selection experiment would give insight in the estimates for IGEG, and also offer the opportunity to obtain insight in the effects of this selection method on production, behaviour and welfare. Because of the potential of IGE to contribute production and welfare of pigs, and because of the questions surrounding IGEG in pigs, pigs were studied within the context of this thesis.

Pigs (*Sus scrofa*) are gregarious animals which in nature would life in small social groups and spend their day with foraging, rooting, and resting (D'Eath and Turner, 2009). A considerable part of the production pigs (estimated more than 1 billion by 2030; FAO, 2003) is kept in intensive farming systems. Here, pigs lack the possibility to forage or root, and thereby cannot fulfil their intrinsic need to carry out their basic natural activities (Van Putten, 1979; Studnitz et al., 2007). This often leads to aberrant harmful behaviour, such as oral manipulation, which may start already at early age and increases throughout the production cycle (e.g. Blackshaw, 1981; Zonderland et al., 2008).

Current pig production is such that a sow gives birth to approximately 14 piglets, and weans around 12 piglets per litter (Rutherford et al., 2013). Due to the confined housing and the restraint of the sow, social cues may be missed and this may contribute to the onset of (mal)adapted and aggressive behaviour (Schouten, 1986; Oostindjer et al., 2011a; reviewed by Baxter et al., 2013). For example, during social conflict threat and withdrawal may not be properly expressed due to lack of

## 1 General introduction

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space, resulting in the development of more fierce aggressive strategies (Lammers and Schouten, 1985). The period that piglets spend with the sow is mostly referred to as farrowing phase or lactation period. In the EU, piglets are weaned, i.e. separated from their mother, at approximately four weeks of age. After weaning they enter the nursery phase, in which they are housed with other, often unfamiliar, piglets in a barren confined enclosure, i.e. pen, of  $\sim 0.4 \text{ m}^2$  per pig. After approximately four weeks at the nursery they have grown too big for the enclosures and move to other pens. Because of pen size and management strategies (such as grouping pigs on equal sex or weight) pigs are relocated into new groups whereby they again encounter unfamiliar pigs. This encounter with unfamiliar pigs results in intensive fights (e.g. Tan et al., 1991; Stookey and Gonyou, 1994; O'Connell et al., 2005), with the accumulation of injuries in the form of skin lesions (e.g. Turner et al., 2006; Stukenborg et al., 2011; Rydhmer et al., 2013). The aggression during regrouping is considered a severe welfare problem (e.g. Erhard et al., 1997; Turner, 2011; Rydhmer et al., 2013), especially when the intensity of fights increases due to increased weight and strength (Jensen, 1994; Turner et al., 2006). Management strategies, such as socializing pigs, may reduce aggression (e.g. D'Eath, 2005; Hessel et al., 2006; Rydhmer et al., 2013), but might not yet be applicable to each farm management. When pigs are regrouped, they start sorting out dominance relationships. Dominance relationships may be settled already after several hours, but may also take weeks before it has reached relative stability (Meese and Ewbank, 1973; Ewbank, 1976). For the remaining production cycle, which is approximately till 24 weeks of age, depending on slaughter weight, the group remains together. The period between the nursery phase and slaughter is often referred to as the finishing or fattening period. During the course of this period, aberrant behaviour may increase in frequency and severity, resulting in severe welfare problems (e.g. Schröder-Petersen and Simonsen, 2001; Kittawornrat and Zimmerman, 2011). Because group composition changes several times, but remains rather stable during the finishing phase, IGE estimates for growth rate are based on the growth rate in this phase of the production cycle.

Pigs have a broad behavioural repertoire, and when investigating IGEg, several behaviours may be relevant. As mentioned above, aggression is likely to occur in pig farming. Although the aggression around regrouping may result in severe (skin) injuries and stress (e.g. De Groot et al., 2001; Turner et al., 2006; Coutellier et al., 2007), the effects on growth rate are often minimal if present (McGlone et al., 1987; Marchant-Forde and Marchant-Forde, 2005; Rydhmer et al., 2013; but see Tan et al., 1991 and Ekkel et al., 1995 for substantial effects on growth). Oral

manipulation on the other hand, and in particular tail biting, may considerably affect health, welfare, and production performance of the recipient (Wallgren and Lindalh, 1996; Schrøder-Petersen and Simonsen, 2001; Sinisalo et al., 2012). Oral manipulative behaviour in pigs is the repeated chewing and biting on body parts of other pigs, whereby tails and ears are clearly most attractive to bite on. From the origin, oral manipulation is more a redirected foraging behaviour than a social behaviour. The impact of tail biting on growth rate makes tail biting a potential behaviour underlying IGE on growth rate, even though it might not be a social behaviour. When pigs are kept in organic or free-ranging systems, tail biting may still occur (Olsen, 2001; Walker and Bilkei, 2006), which indicates that improved housing conditions are not sufficient to eliminate all harmful behaviour, and solutions may need to come from breeding.

Welfare of pigs is thus impaired due to amongst others behavioural (mal)adaptations as a consequence of the housing conditions and management procedures. All animals may suffer from these circumstances, but not all animals respond by developing aberrant behavior which may be harmful to group mates. The deviations in behavioural response may partly depend on personality, which may be reflected in coping styles (Koolhaas, 1999; 2008). Briefly, coping styles refer to the extremes of any behavioural response and are classified as either reactive (passive) or pro-active (active) (Koolhaas, 1999; 2008). Animals of diverging coping styles show consistent differences in behaviour and physiology, especially when facing stressors (e.g. Koolhaas et al., 2011). In pigs, coping styles have been studied amongst others through the backtest (e.g. Hessing et al., 1993; Bolhuis et al., 2005a; Spake et al., 2012). The response in the backtest has been related to growth (Van Erp-van der Kooij et al., 2003; Cassady 2007; Spake et al., 2012), and a heritability of 0.53 has been estimated for the amount of struggling in the backtest (Velie et al., 2009). This suggests a link between behaviour and growth in pigs with a heritable component, and therefore piglets' coping style might relate to IGE.

**Box 2. Conclusion 'Sociable swine'.** Intensive pig farming is characterised by high production performance but faces many welfare issues as a consequence of a barren and confined housing environment and management procedures. Pigs in intensive systems may develop behaviours that negatively affect the performance of their group mates. IGE for growth rate have been estimated in pigs, but require validation.

### 1.4 Genotype by environment interactions

When studying genetics, it is important to bear in mind the possible dependence of the phenotypic expression of a genotype on the environment. For example, pigs of genotype A may perform best in moderate climates, whereas genotype B performs best in warm climates (Bloemhof et al., 2008). Genotype by environment (G×E) interactions thereby may affect genetic gain (Mulder and Bijma, 2005). G×E exist for several production traits in pigs (Schinckel et al., 1999). The environment may thereby represent, with pig studies as examples, different climates (Bloemhof et al., 2008), a test-environment versus commercial practice (Merks, 1989), diverging production systems (Wallenbeck et al., 2009), or adaptations to housing conditions (Guy et al., 2002a). The stability of the production performance across environments may reflect a certain robustness of the genotype (e.g. Visser et al., 2003; Knap, 2005). Thus, health and production performance of pigs may depend on the environment, whereby one environment may be better or less suitable for the health and performance of an animal with a certain genotype. Pigs of different genotype may behave differently (e.g. Breuer et al., 2003), and change their behaviour according to the environment. G×E interactions for pig behaviour have been found for maternal behaviour in sows (Baxter et al., 2011), but to our knowledge not for finishing pigs (Hill et al., 1998; Guy et al., 2002b).

If IGEg would contribute to pig breeding, it is important to know whether the effects of genetic selection are consistent across environments, and would apply to a larger range of environments or to a specific (suboptimal) environment. In Europe, changes in housing conditions are currently going on, or expected to come in the near future, to comply with higher animal welfare standards (EC Directive 2001/93/EC, 2001; Bracke et al., 2006; Elzen et al., 2011). An example of this is the enrichment of the conventional barren pens with substrate such as straw. Straw has often been mentioned as the most effective way to reduce oral manipulation, and is thereby suggested as a method to improve welfare (e.g. Fraser et al., 1991; Tuytens, 2005; Bracke et al., 2006). By studying G×E interactions it is possible to determine the potential contribution of genetic selection to productivity and behaviour for pigs kept in the current conventional conditions (barren) as well as in improved housing conditions.

**Box 3. Conclusion G×E interactions.** Genotype by environment (G×E) interactions may provide insight in the expression and consistency of IGE across environments. A G×E experimental set-up may clarify the impact of selection on IGE and improved housing conditions.

### 1.5 Objectives

The overall aim of the project was to study the opportunities to improve social interactions among pigs by incorporating indirect genetic effects in the breeding program and by investigating the implications of this selection method for behaviour and welfare (Van Arendonk et al., 2009).

With this thesis I aimed to investigate the relationship between pig behaviour and growth, the effect of selection for 'indirect genetic effects on growth rate' on the behaviour and production performance of pigs, and the impact of genotype by environment interactions with regard to IGE.

It was hypothesized that oral manipulation and aggression would affect growth rate of pigs, and that these behaviours would underlie the effects of IGE on growth rate. Pigs selected for a positive effect on the growth rate of their group mates were therefore hypothesized to show less of this harmful behaviour and because of that show an increased growth rate.

### 1.6 Thesis outline

This thesis is divided into two sections. The first section considers explorative studies on interactions between pigs and what the possible consequences of these interactions are for growth rate independent of genetics. The second section presents the work on indirect genetic effects in relationship to production and behaviour. The interrelation of the topics is outlined in Figure 2B, whereby also the chapter numbers are indicated. The register at the end of this thesis (page 213) enables to easily look up information on specific words or terms and includes illustrations of often mentioned behaviours.

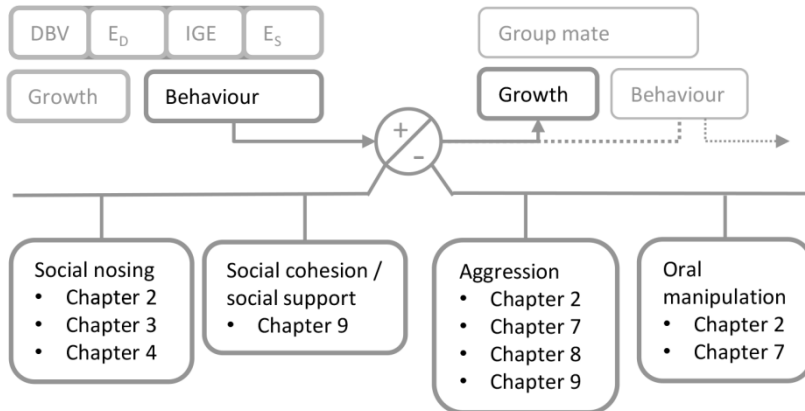
Chapter 2 describes the effect of pig behaviour on the growth rate of pigs, in particular for the recipients of behaviour. From this study it was noted that social nosing, which is gentle tactile contact of the snout of one pig with the snout or body of another pig, increased growth rate in the recipient. Social nosing was further explored in chapter 3 and 4. The relationship between growth and behaviour of piglets in a backtest was explored in chapter 5.

Chapter 6 to 9 are based on a one-generation selection experiment in which 480 pigs, that were selected for either high or low IGE on growth rate, were housed in barren and enriched pens. These pigs were studied from birth till slaughter for their behaviour and physiology. Chapter 6 discusses the effect of selection and housing conditions on the production performance. Chapter 7 outlines the effects of selection on the full behavioural repertoire. From the behaviours, aggression was

## 1 General introduction

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further explored in chapter 8. In chapter 9, aggression and social nosing join together in the assessment of spatial integration during social conflict. Here, we emphasized the importance of taking an integral approach when assessing animals or their welfare. The synthesis of this thesis discusses all previous chapters and in additions discusses whether pig welfare can indeed be improved through selection on indirect genetic effects and enriched housing.



**Figure 2B.** Behaviours that might potentially relate to the effects of IGE are indicated with reference to the thesis chapters in which these are discussed.

# **Part I**

**Pig behaviour**





# 2

## **Relationship between growth rate and oral manipulation, social nosing, and aggression in finishing pigs**

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### **Abstract**

Pigs may affect each other's health, welfare and productivity through their behaviour. The effect of a pig on the growth rate of its pen mates is partly heritable and is referred to as its social genetic effect. Social genetic effects, also known as indirect genetic effects, have been found in a number of livestock breeds, in natural and laboratory populations, and in plant breeding and forestry, and have become an important research topic in recent years. In pigs, social genetic effects are hypothesized to be related to behaviour. The mechanism behind social genetic effects for growth, as well as the relationship between behaviours and growth itself, is largely unknown. To gain insight in the mechanism behind social genetic effects, we investigated the relationship between behaviours and growth rate in pigs. On a commercial pig farm, 398 finishing pigs in 50 pens (eight pigs / pen) were observed at 12 w of age using 2-min instantaneous scan sampling for 6 h during daytime. For 324 observed pigs, growth rate during the finishing period was known. The relationship between behaviours and growth rate during the finishing period was analysed with behaviour as explanatory variable in a mixed model. Results show that time spent giving behaviours, like oral manipulation, social nosing, aggression and belly nosing, was not related to own growth rate. Receiving behaviours, however, did relate to growth. Pigs that received more oral manipulation, observed as tail biting, ear biting and paw biting, grew less well ( $P < 0.05$ ). Growth rate was  $43 \pm 17$  g/d lower in pigs that received oral manipulation during more than 2% of the observations as compared to pigs that did not receive oral manipulation. Pigs that received social nosing, a gentle touch or sniff at any part of the body, had a higher growth rate ( $P < 0.05$ ): growth rate differed  $29 (\pm 17)$  g/d between pigs that received social nosing during more than 2% of observations as compared to not receiving social nosing at all. Receiving aggression and belly nosing, a forceful rubbing of the belly, did not influence growth rate. In conclusion, receiving oral manipulation and social nosing related to growth rate. This suggests that pigs selected for positive social genetic effects for growth may potentially show behavioural changes. Effects of selection for social genetic effects on behaviour and growth will be studied in future research.

Key words: Indirect genetic effects, swine, tail biting, affiliative behaviour, average daily gain.

### 2.1 Introduction

Pigs, being social group-living animals, may affect each other's health, welfare and growth rate through their social behaviour. The effect of a pig on the growth rate of its pen mates is partly heritable and is referred to as its social genetic effect (Bergsma, 2011; Chen et al., 2007; Muir, 2005). Social genetic effects, also known as indirect genetic effects (Moore et al., 1997; Wolf et al., 1998), have been found in a number of livestock (reviewed in Bijma, 2011a), in natural and laboratory populations (e.g. Wilson et al. 2008), and in plant breeding and forestry (e.g. Cappa and Cantet, 2008), and have become an important research topic in recent years. In pigs, social genetic effects for growth, i.e. the inherited effects an individual has on the growth of its group members, are hypothesized to be related to behaviour (Rodenburg et al., 2010). If social genetic effects are indeed related to behaviour, then genetic selection for social genetic effects for growth would offer a method to indirectly select on behaviour. This would be complementary to direct selection against specific undesired behaviours like aggression (Turner, 2011), without the need for large scale behavioural phenotyping. Social behaviours of pigs, however, are rarely studied in relation to growth of their group members. To gain insight in the mechanisms underlying social genetic effects for growth, it is first important to understand the effect of behaviours on growth rate in pigs.

Pigs in nature show an organized social structure with formation of groups (Stolba and Wood-Gush, 1989). Pigs kept in intensive housing systems show behavioural changes due to the inability to express their natural behaviour (Hughes and Duncan, 1988). Especially in barren and confined housing, with a lack of suitable substrates for foraging and rooting behaviours, pigs may show oral manipulation of their pen mates, such as tail biting (Van Putten, 1979). Tail biting may reflect stress and poor welfare of the biters (Van Putten, 1979) and can have negative consequences for health, welfare and growth rate of the receivers (Gonyou, 1993). A few studies have reported a growth reduction due to severe tail biting wounds (England and Spurr, 1967; Sinisalo et al., 2012; Wallgren and Lindalh, 1996). Management practices like grouping unfamiliar pigs can cause excessive aggression (Ewbank and Meese, 1971). A growth reduction due to social stress related to grouping unfamiliar pigs has been reported (Hyun et al., 1998; Stookey and Gonyou, 1994). Under stable social conditions, pigs do not engage much in injurious mutual fighting, but series of head knocks and bites may occur (Bolhuis et al., 2005b). Both tail biting and aggression are moderately heritable in finishing pigs, with  $h^2 = 0.05 - 0.27$  for tail biting in Landrace pigs (Breuer et al., 2005) and

## 2 Relationship between growth rate and behaviour

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$h^2 = 0.08 - 0.43$  for post-mixing aggression (Turner et al., 2009). Positive behaviours between pigs, such as play and social grooming, are less well studied (Boissy et al., 2007), and their effects on health and growth are, to the best of our knowledge, unknown.

As hypothesized, the effect of behaviours on growth rate may underlie the estimated social genetic effects for growth in pigs. Knowledge on the possible relationships between negative, as well as positive, behaviours and growth rate is of great importance to validate this hypothesis. Besides the few studies on oral manipulation and aggression, however, evidence for a relationship between behaviours and growth rate in pigs is lacking. The objective of this study, therefore, was to investigate whether and how behaviours (given and received) are related with growth rate in finishing pigs. Hereto, growth data of finishing pigs were combined with behavioural observations.

### 2.2 Material and Methods

#### Animals and housing

Over four batches, behaviours of 398 crossbred finishing pigs from different genetic lines were observed. Batches were separated by a period of three weeks. Piglets were born and kept at an experimental commercial farm (IPG Beilen, The Netherlands). All piglets were tail docked and male piglets were castrated. At 26 days of age, piglets were weaned and placed in nursery groups of approximately 30 individuals of the same sex (female or castrated male) and a similar weight. Five weeks thereafter, pigs were moved to 50 finishing pens, distributed over seven compartments in the same farm building. Each nursery group was split into four finishing groups, to limit aggression due to grouping of unfamiliar pigs. Each finishing pen housed ~eight pigs of the same sex. Pens had half slatted floors with a space allowance of 1.0 m<sup>2</sup> per pig, and contained a metal chain with a galvanized polyurethane ball (75 mm diameter) placed on pig eye-height. Pen design did not allow pigs to interact with neighbouring pigs. Dry pelleted commercial feed was offered *ad libitum* from a single space feeder. Water was continuously available from a single nipple drinker per pen. Lights were on from 7:00 till 17:30 h. The experimental facilities were under supervision of The Institutional Animal Care and Use Committee of the University of Groningen, The Netherlands, which approved all protocols on the farm.

### **Behavioural observations**

Behaviours of individual pigs were recorded at 12 weeks of age, three weeks after start of the finishing period. A distinction was made between given and received behaviours (Table 1). Each pig was identified by a number which was spray marked on the back. Behaviour was scored during live observations using 2-min instantaneous scan sampling. Six hours of observation were carried out during the active period of the day, between 8:00 and 17:00 h, with a break from 11:30 to 13:30 h. This procedure resulted in 180 behavioural scans per pig (during 6 h every 2 min one scan). The Observer 5.0 software package (Noldus Information Technology B.V., Wageningen, The Netherlands) installed on a hand-held computer was used for behaviour recordings. Observations took place on two consecutive days. On the first day, half of the pens were observed at odd hours and the other half at even hours. On the second day this was reversed. Observations were performed by a single observer.

### **Growth data and breeding value estimates**

Data on growth rate from the start of the finishing period (eight weeks of age) till slaughter (26 weeks of age, app. 110 kg live weight) were provided by the Institute for Pig Genetics BV. Growth rate was expressed in grams per day (g/d). Due to 12 missing ear tags and 62 missing growth records, 74 animals were excluded from the analyses on growth rate. Estimated breeding values for direct and social genetic effects, based on realized growth rate during the finishing period, were also provided by the Institute for Pig Genetics BV. Average estimated direct breeding value (DBV) for the studied animals was +2.24 (SE 1.56) and average estimated social breeding value (SBV), i.e. the estimated social genetic effect for growth, was -0.56 (SE 0.06). DBV and SBV were negatively correlated with  $r = -0.41$  ( $P < 0.001$ ).

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**Table 1.** Ethogram of recorded behaviours.

Behaviour	Description
Social nosing	Gently touching or sniffing any part of a pen mate
Oral manipulation	Nibbling (belly), sucking or chewing part of the body of a pen mate, including tail biting, ear biting and paw biting.
Aggression	Pushing, biting or giving head knocks to a pen mate
Belly nosing	Rubbing belly of a pen mate with up and down snout movements
Mounting	Standing on hind legs while having front legs on other pig's body
Disturbing	Disturbing resting pig by other behaviour than manipulation or nosing, e.g. by stepping on sleeping pig. Irrespective of reaction of resting pig.
Receiving social nosing	
Receiving oral manipulation	
Receiving aggression	
Receiving belly nosing	
Mounting received	
Lying <sup>1</sup>	Lying inactive
Sitting <sup>1</sup>	Sitting or kneeling
Eating or drinking <sup>1</sup>	Eating or drinking
Play <sup>1</sup>	Running around the pen, sometimes with gently nudging of pen mates
Other active <sup>1</sup>	Any other behaviour not listed

<sup>1</sup>Behaviours scored only when shown without any of the behaviours (given or received) listed above.

### **Analysis**

The 180 behaviour samples per pig were summed and expressed as a proportion of the total observation time. Data were analysed using SAS version 9.2 (SAS Institute Inc. 2002-2008). Residuals were checked for normality.

The relationship between behaviours and growth rate during the finishing period was analysed with growth rate as dependent variable, using a mixed model including batch, genetic line and sex as fixed class effects. The effect of a behaviour was estimated by including the proportion of time spent on this behaviour as a fixed continuous explanatory variable in the mixed model. To find the best fit for

the regression curve, behaviours were included in the model both linearly and quadratically. Random effects were compartment and, pen nested within batch, compartment and sex. Effects of the interaction between sex and behaviour on growth rate were tested but omitted from the final model as they were not significant.

The relationship between time spent on a behaviour and growth rate might reflect pre-existing differences in body weight at start of the finishing period, rather than an effect of behaviour on growth rate. To investigate possible confounding between weight at start of the finishing period, behaviour and growth rate, weight at start of the finishing period was included as a covariate in the model. Weight at start of the finishing period did not affect the relationship between behaviours and growth and was therefore excluded from further analysis.

To facilitate interpretation of results, the proportion of time spent on behaviours that significantly affected growth rate was also expressed in categories (0%, 0-1%, 1-2% and >2%), and effects were re-estimated. Hereto, the same model was applied with time spent on a behaviour included as a fixed class effect.

The relationship between behaviours and estimated SBVs was tested in a mixed model with estimated SBV as dependent variable. Fixed effects were behaviour (continuous), batch, genetic line and sex, and random effects were compartment and, pen nested within batch, compartment and sex.

All data are reported as means  $\pm$  SEM.

### 2.3 Results

Growth rate during the finishing period was not affected by time spent on giving social nosing, oral manipulation, aggression or disturbing other pigs (Table 2). Mounting was only observed seven times out of all observations and was therefore excluded from further analysis. There was no relationship between giving belly nosing and growth rate. The occurrence of belly nosing varied largely, especially between pens. From the 82 pigs that were observed to perform belly nosing, 46 pigs originated from 10 pens only. These 46 pigs performed 74% of all observed belly nosing. Belly nosing did not significantly influence growth within these 10 pens, nor were differences in growth between these 10 pens and the other pens caused by belly nosing. None of the given behaviours were significantly influenced by sex differences.

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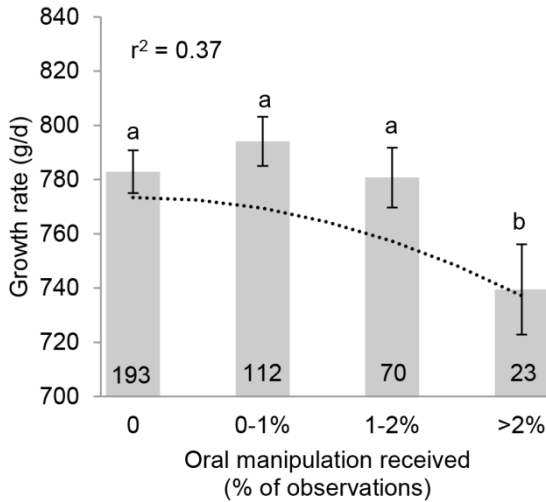
**Table 2.** Descriptive statistics. Mean represents occurrence of behaviour as percentage of observation time.

Behaviour	Mean % (SEM)	Range	Effect on growth ( <i>P</i> value)
Social nosing	0.98 (0.06)	0 - 7.8	0.21
Oral manipulation	0.61 (0.04)	0 - 5.0	0.25
Aggression	0.18 (0.02)	0 - 2.8	0.39
Belly nosing	0.47 (0.07)	0 - 13.9	0.43
Disturbing	0.17 (0.02)	0 - 2.2	0.26
Receiving social nosing	0.70 (0.04)	0 - 4.4	0.03*
Receiving oral manipulation	0.54 (0.04)	0 - 6.7	0.01*
Receiving aggression	0.13 (0.02)	0 - 1.7	0.25
Receiving belly nosing	0.40 (0.05)	0 - 8.3	0.99
Lying	72.6 (0.6)	35.0 - 99.4	0.81
Sitting	2.4 (0.12)	0 - 16.1	0.75
Eating or drinking	7.5 (0.19)	0 - 19.4	0.13
Play	0.08 (0.01)	0 - 1.7	0.90
Other active	13.1 (0.36)	0.6 - 35.6	0.36

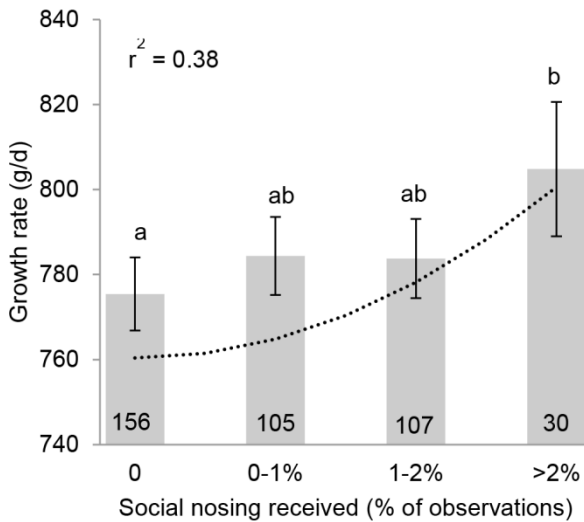
\*Significant by  $P < 0.05$ .

Growth rate was lower in pigs that received more oral manipulation ( $F_{1,261} = 6.19$ ,  $P = 0.01$ ,  $b = -13.2$  g/d per % oral manipulation received). Individual pigs varied largely in how often they were the victims of oral manipulation (Table 2). Pigs that received oral manipulation more than 2% of the observations grew on average  $43 \pm 17$  g/d less during the finishing period than pigs that did not receive oral manipulation (Figure 1). This corresponds to a weight difference of approximately 4 kg at the end of the finishing period. The categorical representation suggests that the relationship between received oral manipulation and growth rate follows a quadratic regression rather than a linear line. When received oral manipulation was included in the model as a quadratic continuous explanatory variable,  $R^2$  remained 0.37 while significance increased to  $P = 0.002$ . Thus, received oral manipulation, both as linear and quadratic explanatory variable, showed a negative relationship with growth rate. Weight at start of the finishing period had no effect on received oral manipulation ( $P = 0.86$ ).





**Figure 1.** Growth rate (g/d) in LSMeans  $\pm$  SEM per category of oral manipulation received, presented with number of animals per category. The dotted line represents the quadratic regression line. <sup>a,b</sup> Means lacking a common letter differ by  $P < 0.05$ .



**Figure 2.** Growth rate (g/d) in LSMeans  $\pm$  SEM per category of social nosing received, presented with number of animals per category. The dotted line represents the quadratic regression line. <sup>a,b</sup> Means lacking a common letter differ by  $P < 0.10$ .

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Pigs that received more social nosing had a higher growth rate ( $F_{1, 261} = 4.68$ ,  $P = 0.03$ ,  $b = 11.8$  g/d per % nosing received). Receiving social nosing during more than 2% of observations increased growth by  $29 (\pm 17)$  g/d as compared to not receiving social nosing at all (Figure 2). Including receiving social nosing as a quadratic continuous explanatory variable in the model slightly improved the fitted curve, with an increase in  $R^2$  from 0.37 to 0.38 and increase of significance to  $P = 0.02$ . Thus, received social nosing, both as linear and quadratic explanatory variable, showed a positive relationship with growth rate. Weight at start of the finishing period had no effect on receiving social nosing ( $P = 0.37$ ). Receiving social nosing and receiving oral manipulation were positively, albeit weakly, correlated ( $r = 0.24$ ,  $P < 0.001$ ).

Received aggression and received belly nosing were not associated with growth rate during the finishing period. Sex did not significantly influence any of the received behaviours.

Other observed behaviours showed no significant relationship with growth rate. These were, lying, sitting, eating, play and other active behaviours (Table 2). Thus, from all behaviours observed, receiving oral manipulation and receiving social nosing showed a significant relationship with growth rate of finishing pigs.

Estimated SBV, i.e. the estimated social genetic effect of an individual on growth rate of its pen mates during the finishing phase, did not show a significant relationship with any of the behaviours.

### 2.4 Discussion

This study has investigated the relationship between (social) behaviours and growth rate of pigs. Receiving oral manipulation was associated with a reduced growth rate, whereas receiving social nosing was associated with an increased growth rate during the finishing period.

#### Oral manipulation and growth

Oral manipulation consisted of tail biting, ear biting, paw biting and other nibbling of pen mates. Though no distinction was made between the different forms of oral manipulation, tail biting seemed to occur most. Pigs that were more frequently the recipient of oral manipulation had a lower growth rate. Other studies reported a growth reduction in pigs that were severely tail bitten (England and Spurr, 1967; Sinisalo et al., 2012; Wallgren and Lindal, 1996). Receiving tail bites has a negative

effect on health (Schrøder-Petersen and Simonsen, 2001). Via open wounds on the tail, infections can spread throughout the body and cause infections to organs (Schrøder-Petersen and Simonsen, 2001). This also holds for mild tail biting wounds (Smith and Penny, 1998). Also when no tail damage is visible, however, pigs may already receive tail bites (Zonderland et al., 2011). In the present study, pigs were not observed for ear or tail biting wounds. It can therefore not be said whether the lower growth rate in pigs that received tail biting was due to infections caused by tail biting wounds.

Oral manipulation may also negatively affect growth rate because it causes stress to the receiver. It has been demonstrated that stress may negatively affect growth rate in pigs (Hyun et al., 1998). More specifically, stress due to oral manipulation was reflected in increased salivary cortisol levels (Munsterhjelm, 2009; Smulders et al., 2006), which are associated with lower growth rate (Smulders et al., 2006).

On the other hand, the reduced growth rate of pigs that were frequently orally manipulated could also reflect another, underlying problem, rather than being the result of the manipulation itself. For instance, animals that are not healthy, and therefore have a reduced growth rate, may be more vulnerable to receive oral manipulation. Animals that are ill show less activity (Hart, 1988), lie down more often and may show a reduced reaction to being tail bitten (Kritas and Morrison, 2004). It has been suggested indeed, that receiving oral manipulation might also be a consequence of poor health (Munsterhjelm et al., 2010). Weight at the start of the finishing period, three weeks before behavioural observations, did however, not significantly affect the amount of received oral manipulation. Although it is difficult to distinguish between cause and effect in the relationship between oral manipulation and growth, it is clear that oral manipulation may have negative consequences for health, welfare and productivity.

### **Aggression, belly nosing and disturbing other pigs**

Excessive aggression causes stress, exhaustion and skin lesions, and can reduce growth rate (Stookey and Gonyou, 1994). In reciprocal fighting growth rate might therefore be related to both given and received aggression. Though in stable situations aggression occurs much less, aggression at three weeks after regrouping may be indicative for received aggression during regrouping (Turner et al., 2009). Aggression hardly occurred in the present study, likely because observations were done in a stable situation, three weeks after entering the finishing facilities, and because grouping of unfamiliar pigs was avoided.

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Belly nosing is usually observed most frequently in the first weeks after weaning, where it was reported to occur 2.4% of the actual time on average (Li and Gonyou, 2002). In the first weeks after weaning, belly nosing may reduce growth rate of pigs that perform belly nosing, while it may be received more often by heavier pigs (Straw and Bartlett, 2001). This suggests that both giving as well as receiving belly nosing may be related to growth rate. Growth rate in the present study, however, showed no relationship with either given or received belly nosing. This might be due to its low occurrence, because behavioural observations were done eight weeks after weaning.

Disturbing other pigs can cause restlessness in the pen, which may lead to stress and loss of energy. Disturbing other pigs, however, was observed infrequently in this study.

### **Social nosing and growth**

A positive relationship was found between receiving social nosing and growth rate. Social nosing amongst commercially housed pigs is often classified as harmful social behaviour (Beattie et al. 1996; Breuer et al., 2003; Van de Weerd et al., 2005), partly because oral manipulation is often preceded by nosing the body of the receiver (Schrøder-Petersen et al., 2004). Beattie et al. (2005) reported a positive correlation between nosing pig and tail biting of  $r = 0.31$ , which is slightly higher than the  $r = 0.24$  of the present study. The weak correlation, together with the positive relationship between social nosing and growth, indicates that not all social nosing may be related to oral manipulation.

We can only speculate about the reason for a positive effect of receiving social nosing on growth. Receiving social nosing might enhance growth through physiological reactions to positive social contact. Positive social contact, such as touch or allogrooming, is known to activate the brain's reward system, and stimulates the release of the neuropeptide oxytocin (Pellis and Pellis, 2010; Rault, 2012). Oxytocin has been found to reduce stress and to increase growth rate, possibly through its effect on parasympathetic-vagal activity (Uvnäs-Moberg 1998; Uvnäs-Moberg et al., 1998). In pigs, simulation of grooming behaviour has been demonstrated to provoke relaxation behaviour in the receiver, and long term grooming simulation increased parasympathetic activity (Hansen, 2000). Although it has been suggested that pigs do not show allogrooming (Špinká, 2009), others have reported that free-ranging pigs do engage in mutual grooming behaviour, also at eight weeks of age (Gonyou, 2001; Meynhardt, 1980). If social nosing, via touch

or allogrooming, alters positive social contact or reduces stress, this may have small but significant effects on growth.

On the other hand, the positive relationship between receiving social nosing and growth could be due to a third, unobserved, factor, such as social status. Dominant animals have predominance over feed stocks, but may also receive more social grooming, as has been shown in primates (e.g. Di Bitetti, 1997) and indicated in pigs (Ewbank and Meese, 1971), which could both potentially increase growth rate. If social nosing can be regarded as a positive social behaviour, our results underpin the importance of offering a positive social environment to pigs, which is often ignored in research on welfare in domestic animals. The positive effect of social nosing on growth may be an opening in following research on social genetic effects in pigs.

Animal welfare research has focused mainly on aspects that harm animal welfare (Boissy et al., 2007). Because of that, we previously may have overlooked subtle differences within certain behaviours that may have a different effect on welfare and growth. Our results suggest that social nosing is an example of such a behaviour. A possible solution to disentangle positive social behaviour from behaviour that is potentially harmful, might be a distinction between body regions. Van de Weerd et al. (2005) distinguished between “nose or chew tail, ear, hock or anal area or genitals of pen mates” as pig manipulation and “sniffing, touching body of another pig with snout” as nose pig, which they later describe as social contact (Van der Weerd et al., 2006). Though they do not mention why this distinction was made, their results show that pig manipulation follows a different frequency pattern over time than ‘nose pig’, which suggests different behavioural categories. If a distinction between body regions would have been applied in the current study, part of the observed social nosing might have been attributed to oral manipulation. With subtle differences in seemingly similar behaviours, a kind of specification may be necessary to distinguish positive from negative effects.

### **Social genetic effects and pig behaviour**

It has been hypothesized that social genetic effects are a consequence of behavioural interactions between animals. This hypothesis can be true only when behaviour has a genetic basis and affects the growth rate of pen mates. A genetic basis has been reported for several behaviours in pigs, such as tail biting (Breuer et al., 2005; Turner, 2011). Here, we showed that a relationship between behaviour and growth indeed exists in pigs, which contributes to the hypothesis that social genetic effects are a result of behavioural interactions. Our results suggest that

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especially oral manipulation may underlie social genetic effects, due to its genetic basis and significant effect on growth. The estimated SBVs for growth, however, did not relate to any of the behaviours. The lack of evidence for a relationship between SBVs and behaviours might be because pigs in this study showed only small differences in SBV, because they were not divergently selected for SBV.

In conclusion, receiving oral manipulation was associated with a reduced growth rate, whereas receiving social nosing was associated with an increased growth rate. The latter result shows that positive social behaviours are also of importance and should receive more research attention. The relationships found between behaviour and growth, suggest that selection on social genetic effects for growth might potentially lead indirectly to pigs that show less oral manipulation and show more social nosing. Consequences of selection for social genetic effects in pigs will be studied in future research.

### 2.5 Acknowledgements

This study is part of the project 'Seeking sociable swine? Incorporating social genetic effects into pig breeding programs to achieve balanced improvement in productivity and welfare' which is financially supported by the program 'The Value of Animal Welfare' of the Netherlands Organization for Scientific Research (NWO). We would like to thank TOPIGS and the Institute for Pig Genetics BV (IPG) for providing data. Special thanks to René Heijting from IPG Beilen for the assistance at the animal facilities.

# 3

## **The pig's nose and its role in dominance relationships and harmful behaviour**

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#### **Abstract**

Affiliative behaviour may have an essential role in many behavioural processes. Gently nosing between group members occurs in almost all social behavioural processes of pigs (*Sus scrofa*), but the reasons for its performance are unclear. We examined whether nosing between pigs was related to dominance relationships or harmful behaviours such as manipulation of the tail using 80 crossbred pigs. Both males and females, housed in straw pens, were studied at 8 weeks of age (10 pigs / pen). Dominance ranks were determined by a feed competition test. The behaviour of 64 focal pigs was observed for 2 h in total. Pigs nosed their pen mates on average  $36 \pm 3$  times within 2 h, and nosing behaviour mainly consisted of nose-to-nose contact, nosing the head and nosing the body, rather than nosing the ear, groin, tail or ano-genital region. These gentle pig-directed nosing behaviours, i.e. gently touching another individual with the snout, was here defined as social nosing. Dominance relationships did not influence the amount of nosing given or received. Social nosing was largely unrelated to harmful behaviour. Nosing the tail correlated with tail biting ( $r_s = 0.37$ ), but only 0.3 percent of social nosing was followed by this behaviour. Pigs which delivered much nosing did not receive less aggression, and nor did they receive a heightened amount of nosing in return. We suggest that pigs may nose each other for social recognition, as affiliative behaviour, to gain olfactory signals, or to satisfy an intrinsic need to nose. In conclusion, social nosing in pigs was largely unrelated to harmful behaviours, was not related to dominance relationships and should remain largely unaffected by efforts to minimise harmful behaviours in farming systems.

Key words: Allogrooming, swine, dominance hierarchy, tail biting, snout contact



### 3.1 Introduction

It is often unclear why animals expend energy on performing certain social behaviours whose benefit to the performer is not obvious. Social behaviours without clear positive or negative effects on the individual or its conspecifics are much less studied and understood than behaviours that clearly affect animal fitness or welfare, which is especially the case in farm animals (Boissy et al., 2007; Yeates and Main, 2008).

Touch and nose contact have an essential role in communication, recognition, social grooming and the maintenance of dominance relationships (Newberry and Wood-Gush, 1986; Spruijt et al., 1992). Touch has been shown to be important for physical and mental health and development in humans and in other mammals (McDonald-Culp, 1997). Touch may stimulate the release of oxytocin in both the actor and the receiver, and may generate a positive affective state (Uvnäs-Moberg, 1998; Odendaal and Meintjes, 2003). Gentle touch between animals is most evident when engaged in social grooming, which has been well studied in primates, but to a lesser extent in other species (Spruijt et al., 1992). Social grooming may serve a number of functions associated with improving body hygiene, reducing tension and improving social bonding (Spruijt et al., 1992). Affiliative behaviours like touch and nose contact may contribute to group cohesion, which may minimise the occurrence of aggressive behaviour (Marler, 1976; Lehmann et al., 2007). Subtle touch or nose contact may therefore also have an essential role in other, more prominent, social behaviours.

In fundamental studies, affiliative behaviours and touch are generally considered to have a positive impact on the receiver (Feldman et al., 2003; Odendaal and Meintjes, 2003). In more applied studies related to farm animals, touch between animals is often viewed in the context of harmful behaviours, such as tail biting in pigs (Breuer et al., 2003; Van de Weerd et al., 2005). In pigs, the relationship between gentle pig-directed nosing and damaging forms of nosing and oral manipulation are not well understood, although a study on indoor commercially kept pigs showed that there is a positive correlation between pig-directed nosing and tail biting (Beattie et al., 2005). Efforts continue to minimise the expression of harmful oro-nasal behaviours in pigs, amongst others by extensive research on the causes and consequences of tail biting, and the development of strategies to reduce it (reviewed by Schrøder-Petersen and Simonsen, 2001). If minimising such behaviours also has correlated effects on the expression of nosing behaviour, this may have implications for the attainment of the benefits associated with non-damaging forms of pig-directed nosing which need to be understood.

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In a previous study we found that immature pigs, *Sus scrofa*, that received much nosing had a higher growth rate (Camerlink et al., 2012a). In primates, dominant animals are the primary recipients of social grooming (Schino, 2001). It remained unclear from our earlier study whether the apparently beneficial effect of receiving nosing on growth was also due to dominance in which a dominant individual may be expected to receive a large amount of nosing and to obtain preferential access to feed and to grow most rapidly (Ewbank and Meese, 1971). The purpose of the current study was therefore to examine how nosing behaviour is embedded in the behavioural repertoire of pigs and specifically to examine whether the receipt of nosing is influenced by dominance relationships and whether this behaviour is correlated with harmful oro-nasal manipulation.

### 3.2 Material and Methods

#### Animals and housing

A total of 80 crossbred pigs ((Large White × Landrace) × Pietrain; 39 entire males and 41 females) of approximately 8 weeks of age ( $39.5 \pm 6.4$  kg) were studied at the SRUC pig unit (Roslin, UK). To facilitate behavioural observations, half of the pigs were studied for 5 days in the first week of the trial (batch 1) and the other half was studied directly thereafter in the second week of the trial (batch 2). Four pens of 20 pigs (formed 3 weeks earlier at the start of the finisher phase) were each split into two at the start of each batch, two days before the behavioural observations, to create a total of eight mixed sex groups of 10 pigs. Pigs originated from 12 different litters, and final pens were composed of on average of 2 pigs from 5 different litters. One male was excluded due to poor health after the start of the trial, leading to  $n = 79$ . Pens measured  $1.8 \times 5.3$  m ( $0.95$  m<sup>2</sup> / pig), had a solid floor with a light dusting of straw and were cleaned and provided with approximately 4.5 kg fresh straw daily between 8.30 and 10.00 am. Each pen contained a dry pellet feeder with space for two pigs, and a separate nipple drinker. Pigs received a spray marked number on their back for recognition which was refreshed before tests and observations. Pigs were individually weighed at 4 weeks (weaning), 8 weeks (start of trial) and 9 weeks of age (end of trial). The work was subjected to an ethical appraisal by the Animal Experiments Committee at SRUC.

#### **Feed competition test**

A feed competition test was performed to determine the dominance hierarchy and was modified from the description by Thodberg et al. (1999). Access to feed was denied from the afternoon of the day prior to the test and pens were then tested in random order on the test day itself from 12.00 to 14.00 h. To conduct the test, the observer entered the pen and ensured that all pigs were standing and were paying attention to the observer. One kilogram of dry pelleted feed was then placed in the middle of the pen after which the observer exited the pen and recorded each feed-related aggressive interaction and the identity of the initiator and receiver. When the feed had been consumed, the pig that had initiated the most attacks (but at least 3) was removed from the pen. A new sample of feed, 200 g less in weight than in the previous round, was placed in the middle of the pen and the process repeated. This procedure continued until the position of all pigs in the hierarchy had been determined. Where no pig initiated 3 or more attacks the procedure was repeated without removal of a pig. Repetition of the procedure without removal of a pig was allowed on a maximum of two consecutive occasions. The test was ended on the third occasion if no pig attacked at least 3 times, which usually occurred when there were ~3 pigs left in the pen. Pigs were ranked within their pen using first the order of removal, and thereafter the number of attacks delivered and then order of initiating an attack. Pigs with zero attacks shared the lowest rank. Animals with rank 1 – 5 were classified as relatively dominant pigs, and those with rank 6 – 10 were classified as relatively subordinate pigs for further analysis. This resulted in 39 dominant pigs (17 females and 22 males) and 40 subordinate pigs (24 females and 16 males).

#### **Live behavioural observations**

Continuous live observations were performed on 64 pigs to record the occurrence of different forms of nosing behaviour, together with aggression and potentially injurious oro-nasal manipulation (an ethogram is provided in Table 1). Focal pigs were selected based on the feed competition test, whereby the 2 most dominant and 2 most subordinate pigs of each sex were chosen from each pen. Each pig was observed for 120 min (2 h), composed of 12 blocks of 10 minutes distributed during the active period of the day (08:00–16:30 h). Observation blocks were spread over five consecutive days and balanced for day and time. Two pigs were observed simultaneously within each observation block. For all behaviours given by a focal pig, the receiver was noted.

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**Table 1.** Ethogram.

Behaviour	Description
Nose-to-nose contact	Snout touches the snout of another pen mate
Nosing head	Touching, gently rubbing or licking the head of a pen mate with the snout, including licking and nibbling hairs or eyelashes
Nosing ear	Touching, gently rubbing or licking the ear of a pen mate with the snout without taking it into the mouth
Nosing body	Touching, gently rubbing or licking the body, or nibbling hairs of a pen mate with the snout. Except for ears, head, tail and belly.
Nosing groin	Touch or non-aggressive push with the snout in the groin of a pen mate
Ano-genital nosing	Touching, gently rubbing or licking on the ano-genital region of a pen mate with the snout
Nosing tail	Touching the tail of a pen mate with the snout without taking it into the mouth
Nudge	Single gentle push or up and down snout movement on body of pen mate, excluding the belly
Tail biting	Taking the tail of a pen mate into the mouth or nibbling, sucking or chewing the tail
Ear biting	Taking the ear of a pen mate into the mouth or nibbling, sucking or chewing the ear
Belly nosing	Repetitive up and down snout movement on the belly of a pen mate
Manipulation other	Chewing part of the body of a pen mate except tail and ear
Head knock	A rapid thrust upwards or sideways with the head against any part of the body of a pen mate
Bite	Aggressive bite at any part of the body of a pen mate
Fight	Mutual ramming or pushing, with or without aggressive biting
Mounting	Standing on hind legs while having front legs on other pig's body
Play	Running around the pen with rapid changes in direction. Not associated with delivery or receipt of aggression but sometimes with gentle nudging of pen mates
Exploration pen	Nosing, sniffing, touching, rooting or scraping pen surface or bedding
Other non-social	All other behaviours whereby no interaction between pen mates occurred

#### **Statistical analyses**

Statistical analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC, U.S.A.). For the focal pigs the frequency of behaviours directed at others during the 2 h observation period was known. For each focal and non-focal pig, the frequency of behaviours received over a total period of 8 h was known (calculated from 2 h of observations per focal pig x 8 focal pigs / 2 as two focal pigs were observed simultaneously). Residuals of the frequency of behaviours given and received were checked for their approximation to a normal distribution. Behaviours that were not normally distributed were square root transformed and analysed in a Generalized Linear Mixed Model (Mixed Procedure). If square root transformation did not lead to a normal distribution, the data were transformed to binary data (0: no occurrence, 1: > 0 occurrence) and analysed accordingly (GLIMMIX Procedure). All models included dominance group (dominant or subordinate), sex and observation week as fixed effects and pen, nested within observation week, as a random factor. Weight showed no statistically significant effect on behaviour and was omitted from the final analyses. Growth was analysed as a dependent variable with nosing behaviour as a fixed effect in the model. Relationships between behaviours with a Gaussian distribution were calculated by Pearson correlations and otherwise by Spearman rank correlations. Data are presented as untransformed means  $\pm$  SEM. Sequential analyses were performed as described in Van den Berg et al. (1999). Transition matrices were constructed for dominant and submissive pigs separately by placing the current behaviour in rows and the succeeding behaviour in columns. Diagonals were set to structural zeroes (de Vries et al., 1993). From the transition matrices, adjusted residuals were calculated using MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands). Adjusted residuals follow a Z-distribution and, therefore, behavioural transitions with a value above 1.96 ( $P < 0.05$ ) were considered to occur more often than expected by chance. Results in Figure 1 were presented in a first-order Markov chain where behavioural transitions of  $Z > 2.58$  ( $P < 0.01$ ) were connected with thin arrows and transitions of  $Z > 3.29$  ( $P < 0.001$ ) were connected with thick arrows (Metz et al., 1983).

## 3.3 Results

### Nosing behaviour

Nosing between pigs consisted mainly of nose-to-nose contact, nosing the body and nosing the head rather than nosing the ears, groin, tail or ano-genital region (Table 2). These gentle pig-directed behaviours were here defined as social nosing. All interactions between pigs, with the exception of aggressive behaviours, were either preceded or followed by significant associations with nosing a certain body region (Figure 1A, B). Females received slightly more nosing from males than from females; 54% versus 46% of total nosing received respectively ( $F_{1,70} = 5.17$ ,  $P < 0.05$ ). Males performed more aggression (males:  $16.0 \pm 1.4$ ; females:  $9.9 \pm 1.4$  occurrences in 2 h;  $F_{1,54} = 9.96$ ,  $P < 0.01$ ) and mounting (males:  $0.68 \pm 0.1$ ; females:  $0.09 \pm 0.1$  occurrences in 2 h;  $F_{1,54} = 8.79$ ,  $P < 0.01$ ) than females and tended to receive more social nosing overall ( $F_{1,69} = 2.80$ ,  $P = 0.10$ ), but did not perform more social nosing. Pigs did not show a preference to nose litter mates that they had known from birth as compared to a pig that they had known for four weeks ( $F_{1,54} = 1.64$ ,  $P = 0.21$ ). Weight at the start of the trial did not significantly influence the amount of nosing given or received (given  $F_{1,54} = 0.20$ ,  $P = 0.56$ ; received  $F_{1,69} = 0.00$ ,  $P = 0.99$ ). Growth rate between weaning at 4 weeks and the start of the experiment at 8 weeks, or during the one week period of the experiment itself, showed no relationship with the amount of nosing received (week 4 – 8:  $F_{1,32} = 0.13$ ,  $P = 0.72$ ; week 8 – 9:  $F_{1,33} = 0.00$ ,  $P = 0.95$ ).

### Social nosing and dominance relationships

Pigs that were classified as dominant showed more aggressive behaviour during the continuous observations and tended to tail bite more, but dominance group did not influence the amount of nosing given or received (Table 2). The sequential analyses showed that social nosing was more often associated with mounting in dominant pigs than in subordinate pigs (Figure 1A and B). Dominance group had no influence on the number of pen mates that a pig nosed ( $P = 0.84$ ). Pigs nosed on average 8.1 out of their 9 pen mates, but directed  $26.7 \pm 0.8$  percent of their nosing towards a single pig (with the exception of eight pigs that nosed two to three pigs equally often). This preferred pig differed by on average  $3.5 \pm 0.3$  rank positions above or below the actor, and contact was largely unilateral (Figure 2). Within a pen, some pigs were preferred by several of the focal pigs (Figure 2). Those that gave much social nosing did not benefit by receiving less aggression ( $r_p = -0.08$ ,  $n = 64$ ,  $P = 0.50$ ) and nor were they the recipients of a large amount of nosing in return ( $r_p = 0.04$ ,  $n = 64$ ,  $P = 0.77$ ).

**Table 2.** Mean frequency and SEM for behaviours of dominant and subordinate pigs. Note that  $n = 64$  for behaviours given and  $n = 80$  for behaviours received.

Behaviour	Dominant	Subordinate	P
Nosing received	32.0 ± 2.0	28.6 ± 1.7	0.30
Nosing given	36.4 ± 3.2	38.7 ± 4.1	0.65
Nose-to-nose contact	12.1 ± 1.0	13.1 ± 1.2	0.55
Nosing head	6.2 ± 0.8	7.5 ± 1.1	0.46
Nosing ear‡	1.1 ± 0.2	1.8 ± 0.3	0.11
Nosing body‡	11.9 ± 1.3	13.4 ± 2.0	0.58
Nosing groin§	0.5 ± 0.1	0.5 ± 0.2	0.66
Nosing ano-genital‡	1.0 ± 0.3	1.1 ± 0.3	0.82
Nosing tail‡	0.9 ± 0.2	0.7 ± 0.2	0.69
Nudge‡	2.2 ± 0.5	1.5 ± 0.5	0.25
Aggression received	10.8 ± 1.0	10.2 ± 1.1	0.76
Aggression given	15.6 ± 1.6	10.3 ± 1.2	<0.05
Fight	3.2 ± 0.6	3.1 ± 0.7	0.51
Head knock	7.1 ± 0.7	5.0 ± 0.7	<0.1
Bite‡	5.2 ± 0.8	2.4 ± 0.4	<0.01
Oro-nasal manipulation received‡	1.6 ± 0.3	1.0 ± 0.2	<0.1
Oro-nasal manipulation given‡	1.8 ± 0.4	1.6 ± 0.4	0.85
Tail biting§	0.4 ± 0.2	0.1 ± 0.1	<0.1
Ear biting§	0.3 ± 0.1	0.2 ± 0.1	0.60
Belly nosing§	0.9 ± 0.3	1.1 ± 0.5	0.59
Other manipulation§	0.3 ± 0.1	0.2 ± 0.1	0.52
Mounting§	0.9 ± 0.4	0.5 ± 0.2	0.73
Play‡	2.2 ± 0.5	2.7 ± 0.6	0.71
Pen exploration	26.3 ± 2.3	29.1 ± 2.2	0.32
Other non-social	28.6 ± 2.1	27.0 ± 1.5	0.55

‡ Square root transformed for statistical analysis. Raw means ± SEM are presented.

§ Transformed to binary distribution for statistical analysis. Raw means ± SEM are presented.

### 3 Social nosing and dominance

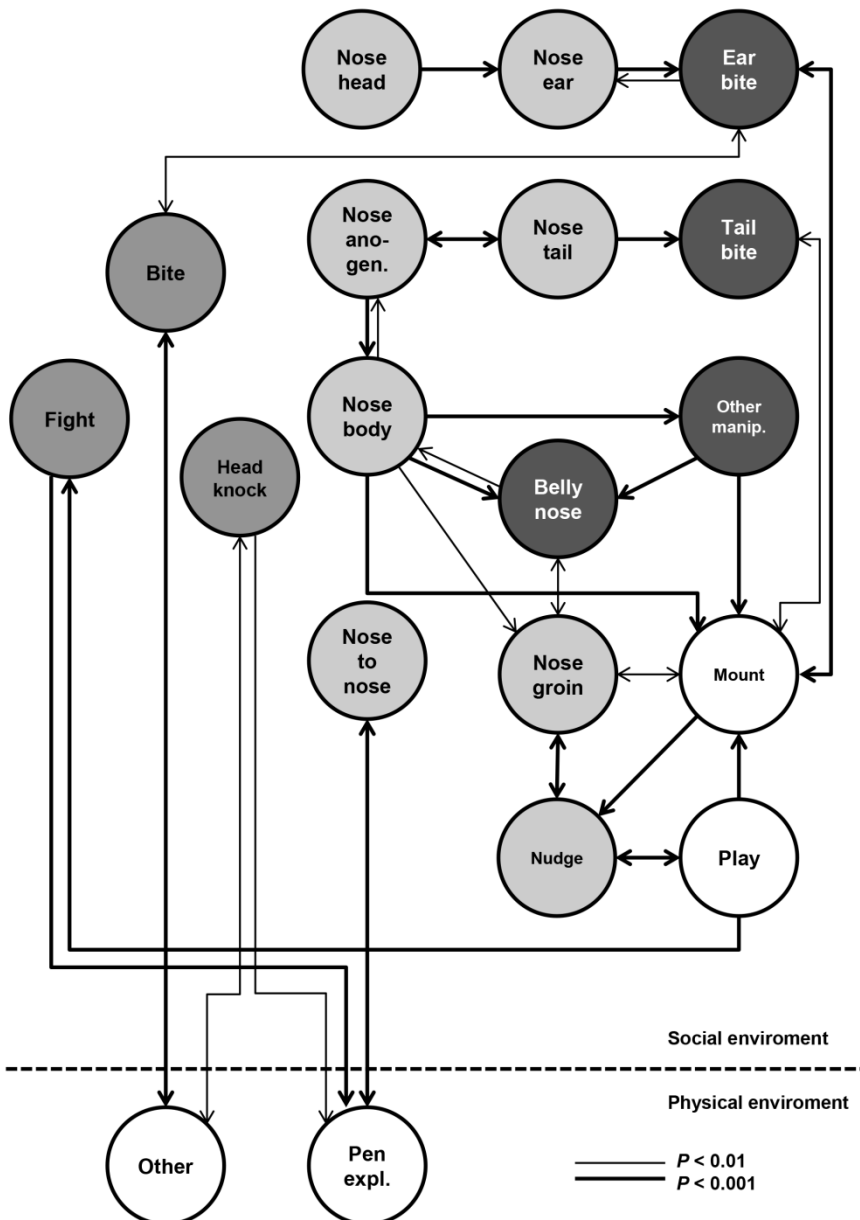


Figure 1A. Markov chain of significant behavioural transitions of dominant pigs.



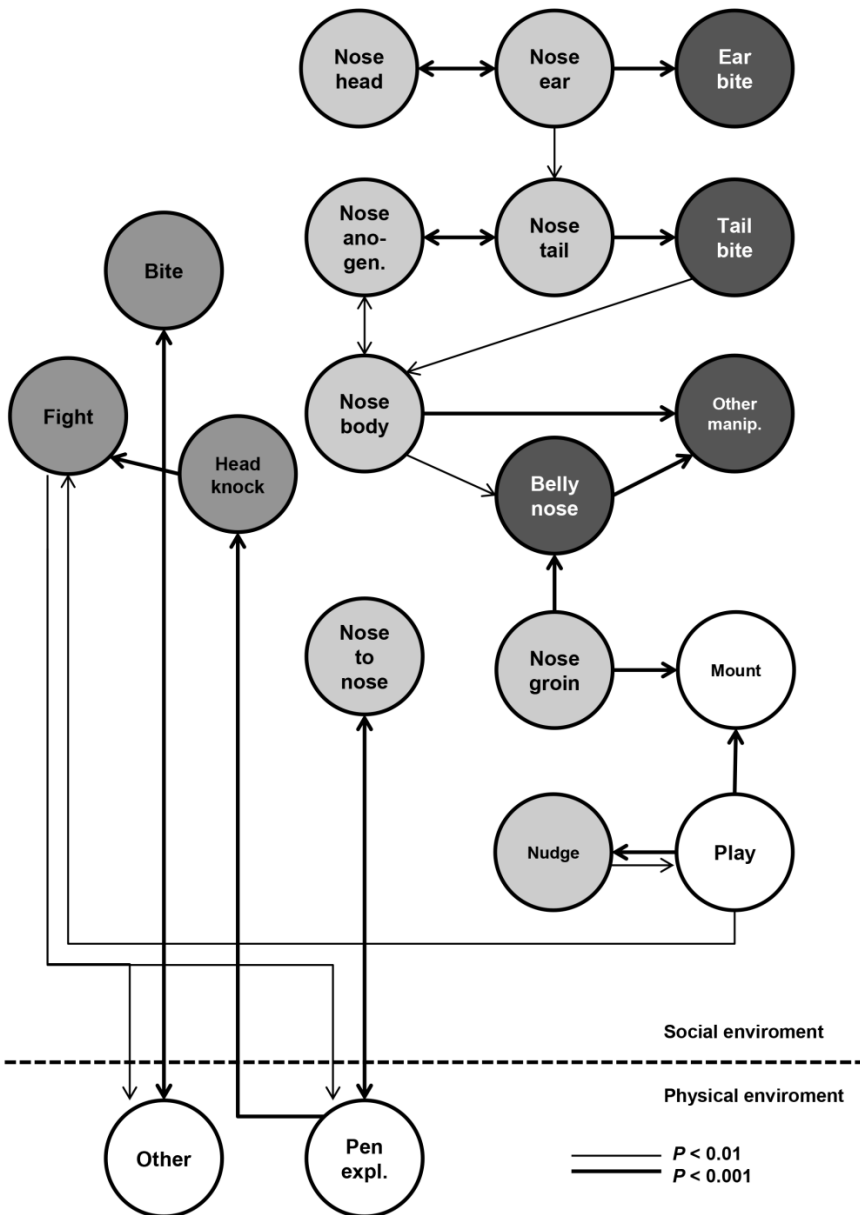
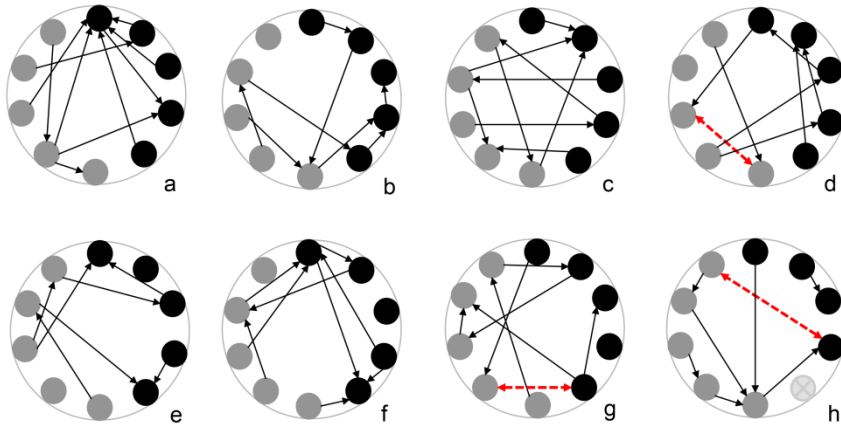


Figure 1B. Markov chain of significant behavioural transitions of subordinate pigs.

### 3 Social nosing and dominance



**Figure 2.** Within pen network of social nosing behaviour for each of the 8 pens. Black circles indicate dominant pigs and grey circles indicate subordinate pigs. Arrows point to which pig received social nosing most often from a focal pig ( $n = 64$ ), with red arrows for a mutual preference to nose each other.

**Table 3.** Spearman rank correlations between social nosing behaviours and related behaviours,  $n = 64$ . 'Activity' is the sum of all active behaviours except social nosing.

	Nosing by body part						
	Nose	Head	Body	Tail	Ear	Groin	Nudge
Tail bite	0.25*	ns	0.24†	0.37**	ns	0.25*	0.26*
Ear bite	ns	0.26*	ns	ns	0.48*	ns	0.24†
Belly nose	ns	ns	0.40**	ns	ns	0.46***	0.40**
Play	0.33**	0.49***	0.27*	ns	ns	0.39**	0.59***
Pen expl	0.66***	0.68***	0.56***	0.36**	0.35**	0.42***	0.32*
Activity	0.59***	0.59***	0.53***	0.33**	0.29*	0.47***	0.49***

† =  $P < 0.10$ ; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

#### **Social nosing and oro-nasal manipulation**

Only 2.5 percent of social nosing was followed by potentially injurious oro-nasal behaviour, of which 0.3 percent was attributed to tail biting, 0.4 percent to ear biting, 1.3 percent to belly nosing and 0.4 percent to other forms of oro-nasal manipulation such as biting the foot. Nosing the tail correlated with tail biting and nosing an ear correlated with ear biting, but nosing other parts of the body was unrelated to such damaging forms of interaction (Table 3). The performance of tail biting, ear biting and belly nosing were not correlated with each other, indicating that these behaviours were performed by different pigs in this population. In contrast to harmful behaviour, nose-to-nose contact, nosing the head, body and groin, and nudging were related to play behaviour. Pigs that were more active in general, however, showed more nosing on all body parts, but social nosing showed the strongest positive correlation with pen exploration (Table 3). Two pigs showed extreme frequencies of social nosing (104 and 109 times within 2 h), mainly consisting of nosing the head and body of the recipient, but were only seen to perform oro-nasal manipulation on 2.5 occasions and received aggression 4.5 times. Both pigs were females of average weight and had the lowest rank in their group.

#### **3.4 Discussion**

Nosing between pigs mainly consisted of nose-to-nose contact, nosing the head and nosing the body, rather than nosing the ear, groin, tail or ano-genital region, and was defined as social nosing. Almost all interactions between pigs were either preceded or followed by significant associations with nosing a certain body region. Social nosing was largely unrelated to dominance relationships and harmful oro-nasal behaviour.

#### **Social nosing and dominance relationships**

Pigs did not base their social nosing behaviour on dominance relationships which is in agreement with observations that social grooming is not based on dominance relationships in cattle, even though both cattle and the pigs in the present study directed behaviour preferentially towards certain recipients (Sato et al., 1993; Val-Laillet et al., 2009). This is in contrast to primates in which social grooming is performed mostly by subordinate animals especially after the receipt of aggression, and is possibly a way of placating a dominant individual (Spruijt et al., 1992; Kutsukake and Clutton-Brock, 2006). Pigs do form dominance relationships (Ewbank, 1976), and it has also been reported that they engage in social grooming (Meynhardt, 1980). In the current study, pigs that were the recipients of aggression

### 3 Social nosing and dominance

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did not perform a heightened level of social nosing and, in the sequential analysis social nosing was not significantly associated with aggression. This suggests, together with the lack of a relationship with dominance, that the function of social nosing in pigs may be different to the social grooming behaviour in primates. If pigs do not nose according to dominance relationships, do not nose in expectation of a similar level of reciprocation and, at the individual level, do not benefit from the receipt of reduced aggression as a result of nosing, then it is appropriate to ask what benefit is derived from the performance of social nosing.

#### **Olfactory cues and recognition**

One obvious explanation for why pigs may nose is that they obtain important information from their environment by olfactory cues. Like most mammals, pigs mainly use olfactory cues to recognize other individuals (Kristensen et al., 2001; Ferguson et al., 2002). Recognition, and the ability to differentiate between familiar and unfamiliar individuals, is essential for the maintenance of dominance relationships (Ferguson et al., 2002). This also holds for pigs (Stookey and Gonyou, 1998; Mendl et al., 2002). Pigs also obtain chemical signals from their physical and social environment (Vieuille-Thomas and Signoret, 1992). In particular, non-volatile chemosensory cues such as pheromones, which are detected by the vomeronasal system, are obtained through direct physical contact (Brennan and Zufall, 2006). This may explain why pigs were so frequently involved in physical nose-to-body and nose-to-nose contact. Through these chemical signals, animals may gain specific information on conspecifics, like their health and reproductive state (Brennan and Kendrick, 2006). Social nosing in pigs may therefore serve for recognition of individuals and to facilitate communication, thereby enabling the maintenance of dominance relationships and olfactory learning (Brennan and Zufall, 2006).

#### **An intrinsic need to nose**

It has often been emphasized how important it is for pigs to occupy their nose (Graves, 1984; Van Putten, 1979). In a semi-natural environment, pigs spend around half of the daylight period foraging with the nose for feed (Stolba and Wood-Gush, 1989). In commercial pig production which is often characterized by high stocking densities and a stimulus-poor environment, this intrinsic need to nose or forage may lead to behavioural problems like tail biting (Van Putten, 1979; Moinard et al., 2003). Even in the absence of injurious oro-nasal behaviour, the social nosing observed may in part occur without an obvious function beyond fulfilling an intrinsic need to nose. Social nosing may therefore contribute to meeting a behavioural need that is over and above any role related to recognition.

#### **Social nosing in relation to oro-nasal manipulation**

Related to pigs' intrinsic need to nose is the occurrence of oro-nasal manipulation such as tail and ear biting. In the current study there was a correlation between nosing the tail and tail biting, and between nosing an ear and ear biting. These correlations are higher than those reported between overall social nosing and tail biting (Beattie et al., 2005:  $r = 0.31$ ). In studies on tail biting, social nosing is sometimes regarded as a precursor to harmful behaviour (Breuer et al., 2003; Van de Weerd et al., 2005). The behavioural patterns studied here show that only 2.5 percent of all social nosing is related to harmful oro-nasal behaviour and that labeling social nosing as harmful is unjustified in the majority of cases. Pigs had access to straw in the current study which may have helped to minimize the occurrence of harmful oro-nasal behaviour. Behaviours such as tail biting are more common in environments which do not offer manipulable substrates (Moinard et al., 2003), and under such conditions the relationship between harmful behaviours and social nosing may be different to that reported here. In the current setting, however, social nosing seemed largely unrelated to oro-nasal manipulation with the exception of nosing the targeted body part. Efforts to reduce the occurrence of harmful oro-nasal manipulation may therefore reduce the occurrence of nosing to the tail and ears, but are unlikely to affect the occurrence of nosing to other parts of the body.

#### **Affiliative behaviour**

Affiliative behaviour in the form of touch and social grooming may offer another explanation why pigs would invest effort in social nosing as these behaviours are believed to lead to benefits such as removal of ectoparasites, tension reduction and improved social bonding (Spruijt et al., 1992). The ethogram applied in this study intentionally did not include social grooming as this behaviour is composed of actions that also occur in other contexts (e.g. nibbling also occurs during oro-nasal manipulation), and is therefore difficult to classify objectively. Social grooming in pigs has been described as 'systematically touching the skin surface of another pig with the rooting disk, thereby removing alien objects and dirt with the snout' (Hansen, 2000; translation by author). Although it has been suggested that pigs do not engage in social grooming (Špinková, 2009), there are studies that report social grooming between familiar pairs of sows and younger pigs and it has been seen to benefit the removal of ectoparasites in wild boar (Meynhardt, 1980; Ruitkamp, 1985; Gonyou, 2001). However, it has been suggested that pigs show less social grooming under intensive housing conditions (Ruitkamp, 1985). Two pigs in the

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present study were observed to spend a considerable amount of time on social grooming when the definition of social grooming provided by Hansen (2000) was applied. They gently nosed the body and head of pen mates, thereby nibbling the hairs and making soft rubbing movements on the skin with their snout. The fact that only two out of the 64 pigs could be marked as social groomers suggests that most social nosing was not related to grooming that might be expected to lead to the removal of parasites, but that affiliative behaviour through gentle touch may have derived other benefits. Receiving a gentle touch may lead to a decline in heart rate and stimulate the release of oxytocin in both the performer and receiver (Drescher et al., 1980; Uvnäs-Moberg, 1998; Odendaal and Meintjes, 2003). Oxytocin contributes to many physical processes and may therefore have benefits ranging from a feeling of well-being, to improved growth and social recognition (Uvnäs-Moberg, 1998; Ferguson et al., 2002). In pigs, gentle touch may increase parasympathetic activity (Hansen, 2000) and administration of oxytocin may affect pigs' stress-coping abilities (Rault, 2011). Therefore, through affiliative behaviours such as social grooming or gentle touch with the nose, pigs might obtain intrinsic benefits which make them perform this behaviour more often than would otherwise be necessary.

#### **Preferential associations**

Pigs seemed to nose without reference to dominance rank, sex or status as littermates. Pigs nosed 8 out of their 9 pen mates, but finally directed 27 percent of their nosing bouts to one pig, though this contact was largely unilateral. It was observed that some pigs within a pen were preferred by several of their pen mates. The reason why these pigs were so attractive to nose for other pigs, independent of dominance, remains unclear. During the behavioural observations it was often noted that a pig would nose the body of several pen mates before choosing a lying location. Indoor-housed pigs have preferred lying areas (Turner et al., 2003) and within a pen pigs may form preferential associations with pen mates regarding lying in close proximity (Durrell et al., 2004; Stookey and Gonyou, 1998). This could suggest that pigs have preferred nosing partners, but could also reflect a preferred lying location. Social nosing may be more likely to occur between pigs that rest in close proximity or, regarding the unilaterality of the contact, pigs that for example rest close to the feeder might receive more (unilateral) nosing due to their position at a location which is often visited by all pen mates.

#### **Benefits of social nosing**

In previous research it was found that pigs that received much nosing had a high growth rate (Camerlink et al., 2012a), although no effect on growth was apparent in the current study, possibly as it was measured over a short time period. As discussed here, social nosing may stimulate the release of oxytocin, reduce tension by physical reactions to gentle touch, and may contribute to the maintenance of preferred associations. Thus, except for the relationship between nosing the ears and tail and the performance of harmful oro-nasal manipulation, social nosing is mainly involved in social processes that are likely to be beneficial to the individual or to group cohesion.

#### **3.5 Conclusion**

Pigs engaged frequently in social nosing behaviour in a manner that was not related to dominance relationships and was largely unrelated to harmful oro-nasal manipulation. Pigs may nose each other for recognition, as affiliative behaviour, or to satisfy an intrinsic need to nose which is thwarted by a stimulus-poor indoor environment. Efforts to minimise harmful forms of oro-nasal manipulation are unlikely to significantly affect the expression of the majority of social nosing behaviour or to compromise the benefits derived from its expression.

#### **3.6 Acknowledgements**

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# 4

## **Intranasally administered oxytocin in relationship to social nosing behaviour in domestic pigs**

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### **Abstract**

Oxytocin relates to positive social behaviour, and intranasal administration of oxytocin has been shown to reinforce these behaviours. Social nosing has been suggested as a positive social behaviour in pigs (*Sus scrofa*), and more insight in the specific expression of this behaviour might contribute to the current search for positive indicators of animal welfare. Our objective was to investigate whether oxytocin alters social nosing in pigs, and whether all social nosing is influenced or only snout contact. Sixty-four female pigs of 13 wk of age were subjected to intranasal administration of oxytocin (24 IU dose) and saline (placebo) on consecutive days. Forty minutes after administration, pigs (kept in groups of six) were observed for the frequency of social nosing upon return in the home pen after being temporarily separated of group mates. Social nosing was observed as nose-to-nose contact and gentle nose-to-body contact. Results indicated no influence of oxytocin on the frequency of nose-to-nose contact (oxytocin  $2.1 \pm 0.2$ ; saline  $2.6 \pm 0.3$ ;  $P = 0.55$ ), or nosing-to-body contact (oxytocin  $5.5 \pm 0.5$ ; saline  $5.9 \pm 0.6$ ;  $P = 0.90$ ). Pigs did more often nose the body of pen mates when they were, presumably, in a positive emotional state, regardless of oxytocin or saline. The relationship between social nosing and oxytocin, either exogenous or endogenous, may merit further research.

Keywords. Social nosing, oxytocin, behaviour, nose contact, welfare

### 4.1 Introduction

Animal welfare research has been largely focussed on situations where animal welfare is most at stake, such as harmful behaviours (Boissy et al., 2007; Yeats and Main, 2008). The insights in harmful behaviours may contribute to solutions to improve animal welfare, but only shed light upon part of the behavioural repertoire which animals may express and the emotions they may experience. Recently, positive behaviours and emotions are increasingly addressed, amongst others as indicators of positive welfare in farm animals (reviewed by Boissy et al., 2007; Yeats and Main, 2008). The boundary between 'neutral' behaviour and positive behaviour, however, is often vague. For example, play is interpreted as positive behaviour and indicator of good welfare (reviewed by Boissy et al., 2007; Held and Špinka, 2011), but has many overlaps with agonistic behaviours (Held and Špinka, 2011). Similarly, social nosing in pigs, which is a gentle tactile contact with the snout, can be a positive social behaviour (Meynhardt, 1980; Blackshaw and Hagelsø, 1990; Hansen, 2000; Camerlink and Turner, 2012), but it can easily turn into oral manipulation such as tail biting, which is harmful to the recipient (Schrøder-Petersen et al., 2004; Beattie et al., 2005). Insight in these behaviours may enable interpretation of the underlying emotional states (Held and Špinka, 2011), which may contribute to the assessment of welfare (Rutherford et al., 2012). Positive social behaviour is related to oxytocin, and vice versa. Oxytocin, either endogenous released or exogenous administered, may elicit (mostly positive) social behaviour, whereas positive social behaviour usually triggers the release of oxytocin (reviewed by e.g. Uvnäs-Moberg, 1998; Churchland and Winkielman, 2012). The relationship between oxytocin and social behaviour has been extensively studied, and a vast amount of reviews have been published covering the role of oxytocin in various social contexts (e.g. Uvnäs-Moberg, 1998; Insel, 2010; MacDonald and MacDonald, 2010; IsHak, 2011; Churchland and Winkielman, 2012). Oxytocin has been associated with, amongst others, maternal care (Champagne et al., 2001; Francis et al., 2001), social recognition (Ferguson et al., 2002), and feelings of empathy and trust (De Dreu, 2012). Intranasal administration of oxytocin is a frequently applied method to study the role of this neuropeptide in the brain and the subsequent changes in social cognition and behaviour (e.g. Insel, 2010; Churchland and Winkielman, 2012; Graustella and MacLeod, 2012). Social nosing may serve in pigs, amongst others, detection of olfactory cues, recognition of conspecifics (Kristensen et al., 2001), and social grooming (Meynhardt, 1980). Each of these functions may be enhanced by oxytocin (olfactory: Yu et al., 1996; recognition: Ferguson et al., 2002; Bielsky and Young, 2004; Winslow and Insel, 2004; and grooming: e.g. Spruijt et al., 1992; Francis et al.,

2001; Dunbar, 2010). Snout contact, i.e. nose-to-nose contact, may be of particular interest for its interactive character and role in social bonds (pigs: Petersen et al., 1980; Blackshaw and Hægelsø, 1990). Snout contact requires close proximity between the animals involved, whereby both are aware of each other and have a certain acceptance or mutual willingness to involve into social contact. This approach behaviour and social bonding can relate to oxytocin (Lim and Young, 2006; Ross and Young, 2009). Nosing other body parts also serves to investigate the other, and may in part be rather explorative than social (Schrøder-Petersen et al., 2004; Beattie et al., 2005). Snout contact may thus give a better reflection of close social contact than nosing of other body parts.

Here, we subjected pigs to intranasal administration of oxytocin with the hypothesis that this would provoke social nosing behaviour. In this study, a distinction was made between snout contact, i.e. nose-to-nose contact, and nosing of other body parts, to gain insight in the type of nosing behaviour that might be altered by oxytocin administration. Our objective was to investigate whether intranasally administered oxytocin influences social nosing behaviour in pigs, and whether this relates to all social nosing or specifically to snout contact.

### 4.2 Material and methods

This study was part of an experiment on emotional contagion in pigs (Reimert et al., submitted), and the current trial has been based on that experiment. The study was approved by the Animal Care and Use Committee of Wageningen University.

#### Animals and housing

Young female pigs (Pietrain × (Great Yorkshire×Dutch Landrace)) were located at the experimental farm of Wageningen University, the Netherlands, over two batches of 48 pigs each ( $n = 96$ ). Pigs were 9 weeks of age when they arrived, and 13 weeks of age when the behavioural observations started. Pigs were housed with 6 per pen. From each pen, 4 pigs were selected as focal pigs, resulting in a sample size of 64 animals, originating from 16 pens in total. Each pen offered 0.85 m<sup>2</sup> per pig, and had a bedding of wood shavings (68 l) and straw (~1.5 kg). Pens were cleaned daily, after which approximately 500 g of fresh bedding was supplemented. Standard pelleted feed was provided *ad libitum* from a single space feeder and water was available *ad libitum*. Lights were on from 07:00 – 19:00 h, as well as a radio to get pigs acquainted to noise from the environment. Each pig was individually recognizable by a spray marked number on her back.

### **Treatment with oxytocin and saline**

Pigs were subjected to intranasal administration of oxytocin and saline (placebo) on two consecutive test days. Pigs served as their own control, meaning that each pig would receive oxytocin at one test day and saline on the other day or vice versa. The treatment with oxytocin included a dose of 24 IU of oxytocin (VWR International BV, Amsterdam, the Netherlands). Hereto, 50 µg oxytocin was diluted in 0.5 ml of 0.9 % saline. The placebo was 0.5 ml of 0.9% saline. A Mucosal Atomizer Device (MAD 300, Vandeputte Medical Nederland BV, Nieuwegein, the Netherlands), i.e. nasal spray, connected to a 1 ml syringe, was applied to spray 0.25 ml of the treatment solution in each nostril (based on Rault et al., 2013a). Treatments were given 40 minutes before behavioural observations commenced.

### **Behavioural observations**

Behavioural observations on social nosing took part in a larger study on emotional contagion between pigs (Reimert et al., submitted). All pigs had a role within the larger study, whereby per pen three pig pairs were distinguished, which is described in Table 1. The 'naïve' pigs may have been influenced by the 'aroused' pigs through olfactory and auditory cues, and the experience of the aroused pigs (either positive or negative) was included in the statistical analyses. Behavioural observations were started immediately from the moment that all pigs had returned to the home pen. Per observation moment, one pig pair was continuously observed during 10 minutes. The frequency of giving social nosing was scored manually from live observations. A distinction was made between nose-to-nose contact and nose-to-body contact, whereby from each nosing behaviour the actor and receiver were noted. This resulted in four variables per pig, which are described in Table 2. The pens and treatments were randomly distributed over and within the four consecutive test days. Behavioural observations were performed by one observer, who was unaware of the treatments the pigs had received.

### **Data analysis**

Data were analysed with SAS 9.2 (SAS Inc.). The frequencies of social nosing were square root transformed to approximate normal distribution. The effect of treatment on social nosing was analysed in a mixed model including the frequencies of giving or receiving social nosing as response variables. The explanatory variables were class effects for treatment (oxytocin / saline), experience of the 'aroused' pigs in the test room (positive / negative), order of treatment (saline-oxytocin / oxytocin-saline), test order at the observation day (1 – 8), and batch. Type of participation in test room (naïve / control) had no significant

#### 4 Social nosing and oxytocin

effect on social nosing and was omitted from the model to allow inclusion of the variable describing the experience in the test room. No significant interactions were found between the variables. Pig (nested within pen and order of treatment), and pen were included as random effects. Values presented are (untransformed) means  $\pm$  SE.

**Table 1.** Experiences in the test room.

Pig pair	<i>n</i>	Experience in test room	Treatment
Aroused	32	Positive or negative experience. Positive: compartment filled with peat, straw and chocolate raisins. Negative: isolation in a compartment where previously they had experienced a nose sling	Excluded from observations on social nosing
Naive	32	For 4 minutes in a barren compartment (app. 3 m <sup>2</sup> ) while ‘aroused’ pigs were in adjacent compartment. Pigs had auditory and olfactory (no visual) cues from the adjacent compartments.	Oxytocin on one day, saline on other day
Control	32	For 4 minutes in a barren compartment (app. 3 m <sup>2</sup> ) without any happening.	Oxytocin on one day, saline on other day

**Table 2.** Ethogram.

Social nosing	Description
Nose contact given	Focal pig touches, or actively attempts to touch, with its snout the snout of another pig irrespective of the reaction of the recipient.
Nose contact received	Focal pig is touched on its snout by the snout of another pig, with or without active participation or seeking mutual contact.
Nosing body given	Focal pig gently touches the skin or hairs (e.g. eye lashes) of another pig with its snout. This may include gently rubbing and nibbling without harmful consequences for the receiver, i.e. the recipient should not respond with a sudden pain response or agonistic behaviour.
Nosing body received	Focal pig is gently touched, rubbed or nibbled on its skin or hairs by the snout of another pig, while the focal pig is not responding with agonistic behaviour or a pain response.

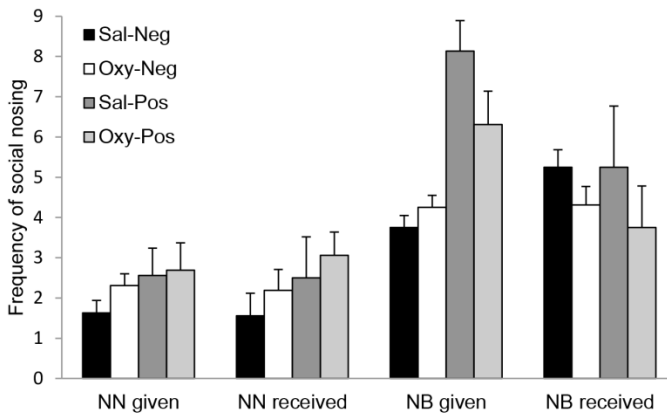
### 4.3 Results

The nosing behaviour of pigs, as reflected in nose-to-nose and nose-to-body contact, did not differ between oxytocin and saline (Table 3). There were no differences between the treatments for giving or receiving social nosing (Table 3). The nosing of the body of another pig occurred twice as much as snout contact.

**Table 3.** Frequency of nose contact (NC) and nosing body (NB) during 10 minutes, in pigs subjected to intranasal administration of saline or oxytocin.

	Saline			Oxytocin			<i>P</i> -value
	Mean ± SE	Min	Max	Mean ± SE	Min	Max	
NC given	2.56 ± 0.30	0	10	2.06 ± 0.21	0	6	0.55
NC received	2.38 ± 0.25	0	9	2.16 ± 0.19	0	6	0.96
NB given	5.88 ± 0.59	0	23	5.47 ± 0.47	0	16	0.90
NB received	5.33 ± 0.45	0	18	4.55 ± 0.39	0	16	0.14

The pigs that had in the test room been located near pigs that had a positive experience (aroused pigs), where nosing the body of their pen mates, among which the aroused pigs, more upon return in the home pen than pigs that had been located near pigs with a negative experience (Figure 1;  $P = 0.03$ ). This was irrespective of whether pigs had received oxytocin or saline, i.e. there was no interaction between the treatment and the experience in the test room (Figure 1;  $P > 0.10$ ).



**Figure 1.** Frequency of social nosing ( $n$  times within 10 minutes) for nose-to-nose (NN) and nose-to-body contact (NB), when pigs had received oxytocin (Oxy) or saline (Sal) and where located in a compartment adjacent pigs that experienced a positive (Pos) or negative treatment (Neg),  $n = 64$ .

### 4.4 Discussion

In the current trial, social nosing was not affected by intranasal administration of oxytocin. We hypothesized that administration of oxytocin would increase social nosing and in particular snout contact, i.e. nose-to-nose contact. In contrast to this expectation, the raw means suggested lower frequencies of social nosing when pigs received oxytocin as compared to when they received saline, but these differences were not significant.

Intranasal administration of oxytocin to pigs has, to our knowledge, only been investigated by Rault and coworkers (2011; 2013a; 2013b). These studies indicate that the method and dose of intranasally administered oxytocin used in this trial was expected to be effective in pigs. These studies, however, also yielded unexpected results. For example, neonatal pigs treated with oxytocin showed more aggressive behaviour (Rault et al., 2013a). The current study was part of a trial on emotional contagion (Reimert et al., submitted). During the time in the test room for emotional contagion, the pigs that had received oxytocin did not differ in their behaviour compared to pigs that had received saline. The ‘aroused’ pigs that underwent a positive or negative experience, however, showed changes in their behaviour when they were located near oxytocin treated pigs as compared to being near saline treated pigs (Reimert et al., submitted). This suggests that the administration of oxytocin was, at least in part, effective.

Upon return in the home pen, the pigs that had been located in the test room while the ‘aroused’ pig pair underwent a positive experience, were nosing the body of their pen mates, amongst which the ‘aroused’ pair, more often. This was irrespective of whether they had received oxytocin or saline. This suggests that the ‘naïve’ pigs were influenced in their behaviour by the auditory or olfactory signals from their pen mates in the adjacent compartment (Reimert et al., submitted; Döpjan et al., 2011). This effect of emotional contagion, which in this case presumes that the pigs were in a positive emotional state (Hatfield et al., 1994), lasted at least ten minutes after the pigs had returned to their home pen, whereby they were reunited with the positively ‘aroused’ pen mates. This finding also suggests that social nosing may increase when being in a positive emotional state, regardless of the intranasal administration of oxytocin.

Social nosing may in part be an expression of affiliative behaviour and social grooming (pigs: Meynhardt, 1980; Hansen, 2000; Camerlink and Turner, 2012). Affiliative behaviour and grooming are positively associated with oxytocin, at least in rodents and primates (Spruijt et al., 1992; Francis et al., 2001; Dunbar, 2010). Intranasal administration of oxytocin did not increase social nosing between pigs, which suggests that affiliative behaviour or social grooming were unaffected.



Pigs were observed from the moment upon arrival in the home pen, i.e. when they were reunited with familiar pen mates. Social nosing may have predominantly functioned to gain olfactory cues and to recognize conspecifics (Kristensen et al., 2001). Olfactory memory and social recognition may improve due to oxytocin (rats: Popik et al., 1992; mice: Ferguson et al., 2002). Pigs which had received oxytocin might have better recognized conspecifics, which could reduce the necessity to repeatedly gain social cues through social nosing. The current data did not reveal an effect of intranasally administered oxytocin on social nosing. However, the extensive body of literature that confirms in other species the influence of exogenous and endogenous oxytocin on the biological mechanism which relate to social nosing in pigs, it is reasonable that oxytocin may have a role in social nosing through other pathways.

### **4.5 Conclusions**

Intranasal administration of oxytocin did not influence the expression of nose-to-nose and nose-to-body contact in pigs, as compared to saline, a placebo treatment. Nose-to-body contact did increase when pigs were, presumably, in a positive emotional state. Social nosing in pigs may have several functions, and each of these functions has in other species been related to either endogenous or exogenous oxytocin. This implies that there may be a role for oxytocin in social nosing, but which could not be detected in the current trial. The relationship between social nosing and oxytocin may merit further research.

### **4.6 Acknowledgements**

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# 5

## **Struggling to survive: early life challenges in relation to the backtest in pigs**

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### **Abstract**

Intensively reared piglets may face many early life challenges. Early life challenges may alter behavior and personality, although conversely, some challenges may also be induced by (maladapted) behavior and personality. The objective of this study was to examine the relationship between piglets' early life circumstances and their behavioral response in a backtest, which may reflect their personality. Hereto, 992 piglets of 14 d of age were subjected to a backtest, in which they were 1 min restrained in supine position. The number of struggles in the backtest was assessed in relation to data on ADG, BW, BW relative to litter mates, teat order, litter size, and health. Piglets that had a lower ADG from birth till the test day were struggling more ( $b = -2.4$  g ADG/struggle;  $P = 0.03$ ). Also piglets with a lower BW at 14 d of age tended to respond more actively in the backtest ( $b = -0.03$  kg/struggle;  $P = 0.08$ ). The response to the backtest was unrelated to ADG from birth till weaning, birth weight, weaning weight, teat order, litter size, and health. ADG and BW were unrelated to the variation of backtest responses within the litter. The results suggest that smaller slower growing piglets actively fight against a challenge, either because piglets born with such a behavioral response were able to survive, or that piglets adapted their behavioral response to their physical condition. Despite the lack of a relationship with most of the early life conditions in the current study, it remains important to minimize challenges that might negatively affect animal health, welfare, and behavior.

Keywords. coping style, early life, health, growth, pig, stress

### 5.1 Introduction

Intensively reared piglets often grow up in a highly competitive social environment and face many early life challenges (Rutherford et al., 2013), such as painful interventions (Weary et al., 2006) and early weaning (Robert et al., 1999). These challenges may mostly affect smaller piglets, which may suffer from injuries and undernourishment (Milligan et al., 2001; Rutherford et al., 2013). A lack of a stable and nourishing early environment can greatly impact behavioral and physiological development (e.g. Anisman et al., 1998; Sih, 2011), and may alter personality (Carere et al., 2005; Biro and Stamps, 2008).

Personality, or coping style, may be reflected in the response to challenges, whereby the response can be more proactive or more reactive (Koolhaas et al., 1999). Proactive copers are more likely to show an active behavioral response and easily develop routines, whereas reactive copers may behave more explorative and flexible (Koolhaas et al., 1999; Carere et al., 2005). The possibility to shift between response styles, but also the diversity of coping styles within a group, may be beneficial to adapt to environmental challenges (Koolhaas et al., 2007; Dingemanse et al., 2010). For instance, in times of feed scarcity, animals may develop a more proactive response (Carere et al., 2005).

In piglets, the coping style may be reflected in the backtest (e.g. Hessing et al., 1993; Bolhuis et al., 2005a). The response of piglets in this restraint test previously showed an association with growth, whereby smaller piglets responded more actively (Velie et al., 2009; Spake et al., 2012). This suggests a possible relationship between early life circumstances and coping style in piglets. The objective of this study was to examine the relationship between piglets' early life circumstances, which were measured in terms of health, weight, growth, litter uniformity, litter size and teat order, and their response in a backtest.

### 5.2 Materials and methods

All procedures were approved by the Animal Care and Use Committee of Wageningen University and approval was then adopted by the Animal Care and Use Committee of the University of Groningen, as this committee was connected to the experimental farm.

#### **Animals and housing**

A total of 1153 piglets were life born out of 80 litters from in total 65 sows (Topigs-20, a Landrace × Large White cross), which were serviced by one out of 24 boars (Tempo, a synthetic line of Large White). Farrowing took place over five consecutive batches between August 2011 and September 2012 on the

experimental farm of TOPIGS BV, Beilen, The Netherlands. The trial was part of a larger study on indirect genetic effects for growth, whereby two contrasting groups of high and low social breeding value were formed (described in Camerlink et al., 2013). The genetic contrast did not affect any of the here described backtest parameters (Reimert et al., 2013a), and is not further discussed.

Sows were housed in conventional barren farrowing crates where the sow is locked between bars during the entire farrowing period. The temperature in the farrowing house was on average 25°C. Sows within a batch farrowed within 6 d of each other. Two sows were lost to follow-up due to a uterus prolapse, and their piglets were excluded from the trial.

Cross-fostering was applied only if a litter consisted of more than 14 piglets. Milk replacer was only provided when the sow had insufficient milk for the litter (20% CP, 20% crude fat, 1.7% Lys). Dry creep feed (15.2 ME MJ/kg, 21% CP, 8.5% crude fat, and 1.6% Lys) was provided from 7 d after birth until 3 wk of age, and then replaced by piglet pellets (10.6 ME MJ/kg, 15.5% CP, 5.5% crude fat, and 1.2% Lys) which were given until weaning at 4 wk of age. Piglets had continuously access to a nipple drinker. Before 5 d of age each piglet was given an anticoccidial agent (Baycox, Bayer, Belgium; 0.1 cc), an iron injection (Pig-Ironject, Dopharma B.V., the Netherlands; 0.5 cc), and antibiotics (Naxcel, Pfizer Limited, United Kingdom; 0.2 cc). All piglets kept intact tails and teeth. Male piglets were castrated under CO<sub>2</sub>/O<sub>2</sub> anesthesia around 5 d of age. In case of infection or disease piglets received Penject 30 (0.1 cc/kg body weight) during 3 d. Skin wounds were treated with an antimicrobial spray (Chlortetracycline). All treatments, including reason of treatment, were recorded. To enable recognition of piglets, piglets received a number on their back with black hair dye, which was redone before tests and observations. Due to tests and measurements, piglets were on average three times a week shortly handled. Piglets that were not viable or did not recover after treatment were euthanized.

### **Body weight and health**

Piglets were individually weighed at d 1 (day of birth), and around d 14 and 27. Besides absolute body weight (BW), a relative BW was determined to compare weights within litter as a measure of litter uniformity. Relative BW was calculated as the actual weight of the piglet minus the average weight within the litter. Average daily gain (ADG) in g / d was calculated by the weight gain over a period divided by the number of days, calculated from actual day of birth of each piglet.

Once a week, in addition to the daily routine checks, individual piglets were scored for vitality, body condition, and diarrhea. The vitality score indicated either no

vitality problems (score 1), vitality problems which did not require lifesaving treatment (score 2), or life threatening situations such as diseases and disorders that can cause death (score 3). Body condition score indicated overweight (backbone not palpable) (score 0), good condition (score 1), or lean (score 2). Diarrhea was weekly visually scored as absent or present for each piglet. For analyses, all weekly scores were averaged per individual into one score for each of the three variables.

### **Backtest**

A total of 992 piglets, of  $14 \pm 0.5$  d of age, were subjected to a backtest. The backtest was carried out according to the procedure of Hessing et al. (1993), and has in detail been described in Melotti et al. (2011). Briefly, piglets were held in a supine position for one minute to observe their behavioral response. The number of struggles (also referred to as escape attempts), the number of vocalizations, and latency times until the first struggle and vocalization were recorded. The backtest was carried out by two experimenters who were trained to handle the pig in the same manner, and by one observer who counted vocalizations and latencies.

The variation of coping styles within a group may be essential for the success of the population (Koolhaas et al., 2007). The variation in backtest response within a litter was approximated by a gliding scale from 0 to 100. Zero indicated that either 100% of the piglets within a litter did not struggle (all 0 struggles), or 100% of the piglets did struggle (all >0 struggles), reflecting little variation within a litter. One hundred reflected maximum variation within the litter, whereby 50% of the piglets did not struggle, and 50% of the piglets did struggle. The values between zero and hundred indicated the varying percentages of piglets that did or did not struggle.

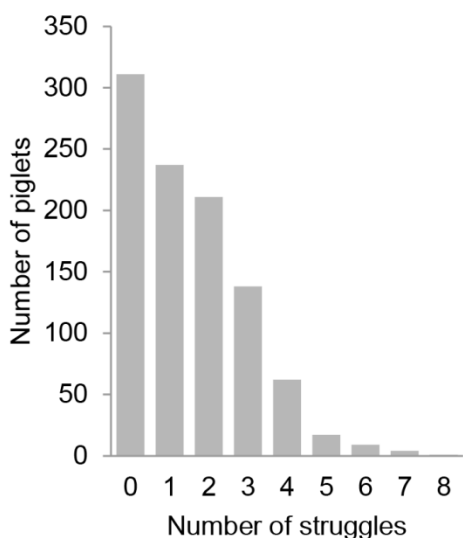
### **Teat order**

Teat order, i.e. the location of each piglet at the udder of the sow, was recorded at three different suckling bouts, divided over the second week of life. The location of each piglet on the udder was noted by recording the individual piglet number and the teat number. Anterior teats received number 1, and each following teat was incrementally numbered, up to a maximum of 9 teats on each teat line (based on Hemsworth et al., 1976 and Ruis et al., 2000). Dysfunctional teats were recorded, but not included in the numbering. It was noted on which side a sow was lying, and whether piglets were in the upper or lower row of teats.

### Statistical analyses

Data were analyzed with SAS 9.2 (SAS Inst. Inc., Cary, NC). Variables were checked for normality and, if required, square root or logarithmically transformed. Data are presented as untransformed means  $\pm$  SEM.

If an animal did not struggle or vocalize during the backtest, the latency times were set at maximum (60 s). The raw data of the number of struggles was skewed towards the left tail of the distribution (Fig. 1), but the residuals of the four backtest variables did approach normality (Shapiro-Wilk test). The residuals were obtained by testing the four backtest variables in a general linear model that contained batch as a fixed effect. The residuals of the four variables showed strong correlations ( $r_p$  0.51 – 0.75; all  $P < 0.001$ ). Therefore, in line with other studies, only the number of struggles was considered for further analysis (Van Erp-van der Kooij et al., 2003; Cassady, 2007).



**Figure 1.** Distribution of number of struggles of 989 piglets tested in the backtest.

Teat order was consistent across observations ( $r_p = 0.83 - 0.86$ ;  $P < 0.001$ ), and observations were therefore averaged per piglet. To enable equal comparison between sows with a different litter size, the teat order was expressed into categories. Hereto, the udder was divided into anterior, middle and rear by dividing the maximum number of piglets on a row of teats by three. Piglets were categorized into this teat order rank based on their average teat order.



The relationships between the number of struggles in the backtest and the piglet characteristics (BW, ADG, relative BW, vitality score, body condition score, antibiotic treatment, diarrhea, and teat order rank) was analyzed in two different ways.

The first model (model 1) was a mixed model (Proc MIXED) with 'number of struggles' as dependent variable, and the piglet characteristics entered singly as independent variables to test their effects on the backtest response of the piglets. Litter size, sex, and being cross-fostered were independent effects, and sow, nested within batch, was included as random effect. Interactions that were relevant to the research question were explored and, if significant, also tested in the second model.

The second model (model 2) was applied to enable extra examination of the relationship between backtest behavior and other pig characteristics while correcting for sex, litter size, cross-fostering and batch, which were likely to affect the piglet characteristics. The continuous variables (BW, ADG, relative BW, vitality, body condition, and diarrhea) were analyzed with Proc MIXED, whereas a generalized mixed model (Proc GLIMMIX) was used to analyze the antibiotics treatment (binary distribution, logit link) and teat order rank (multinomial distribution, glogit link). Piglet characteristics were entered as dependent variables, and the 'number of struggles', sex, litter size, being cross-fostered, and batch were included as fixed effects. The different weight and growth variables were singly included as fixed effects, but were not included in the models where BW or ADG were the dependent variable. Sow, nested within batch, was included as random effect. As the number of antibiotics treatments was low, the model had to be simplified by removing 'batch' from the fixed effects of that model.

All models were run once with the biological sow to determine the effect of genetics, and once with the nursing sow (although often the same as biological sow) to determine the relationship with the sows rearing capacity. Both options gave similar outcomes, and because biological sow had the best model fit, results were presented based on biological sow. The number of struggles was fitted both linearly and quadratic into the models to determine the best curve, but the linear fit gave the best model estimates.

The within-litter variation with regard to the backtest response was first analyzed on pen (litter) level to determine the effect of within-litter variability of backtest responses on (average) litter traits (GLM Procedure without random effect). Thereafter, within-litter variability, and its interaction with the number of struggles, was tested as fixed effect in model 2.

### 5.3 Results

The statistical model that enabled correction for weight (model 2, backtest as independent variable) resulted in similar significance values as in model 1, where backtest was the dependent variable. Reported P-values originate from model 2, unless otherwise specified.

#### General health and weight

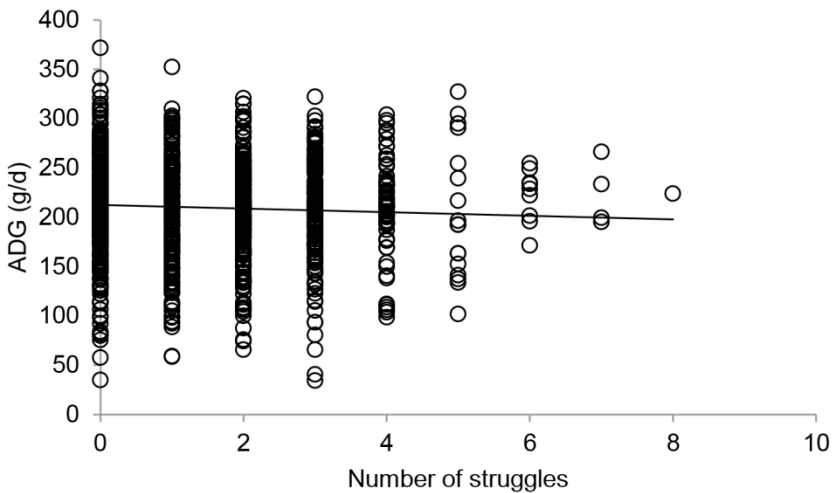
In total, 1153 piglets were live born of which 985 piglets were eventually weighed at weaning. The average number of live born piglets per sow was 15.1 (range 3 – 21). A total of 74 piglets (6.1 %) were cross-fostered. Most piglets had no vitality problems (mean score  $1.3 \pm 0.01$ ) and had a good body condition (mean score  $1.1 \pm 0.01$ ) (Table 1). This was also reflected in the low percentage of piglets with (visible) diarrhea, and the few antibiotics treatments (Table 1). The average birth weight was  $1.3 \pm 0.01$  kg (range 0.4 – 2.7 kg). From birth till weaning, piglets had an ADG of  $6.5 \pm 0.04$  g, leading up to an average weaning weight of  $7.9 \pm 0.05$  kg (range 2.4 – 12.9 kg). Body weight, relative BW (i.e. BW minus average litter weight), and ADG, all at any period during lactation, strongly affected the body condition score, the vitality score, and antibiotics treatment (all  $P < 0.001$ ), with smaller and slower growing piglets being thinner, less vital, and receiving more often antibiotics compared to heavier piglets. BW and ADG, at any time period, were not related to the occurrence of diarrhea.

**Table 1.** Descriptive statistics of health measurements,  $n = 1210$  (including stillborn).

Measurement	Piglets (%)
Vitality score	
Good	62.2
Impaired	23.3
Life-threatening	1.5
Body condition score	
Overweight	4.1
Good	66.6
Lean	16.3
Diarrhoea	9.4
Antibiotics treatment	3.6
Stillborn	4.7
Total mortality (excl. stillborn)	13.8

### Backtest

The number of struggles tended to relate to the BW measured at the day of the backtest ( $b = -0.03$  kg / struggle;  $t(986) = -1.74$ ;  $P = 0.08$ ), but not to BW at birth ( $P = 0.78$ ) or at weaning ( $P = 0.21$ ). Piglets that had a lower ADG between birth and the day of the backtest (d 14) showed a higher number of struggles ( $b = -2.4$  g ADG / struggle;  $t(984) = -2.14$ ;  $P = 0.03$ ; Fig. 2). This relationship was not apparent in the ADG from birth till weaning ( $P = 0.15$ ). The number of struggles was unrelated to the relative BW (relative BW d 1  $P = 0.56$ ; d 14  $P = 0.14$ ; and d 24  $P = 0.31$ ). The association between BW and the number of struggles may relate to the litter size, but litter size did not interact with number of struggles, nor did it influence performance.

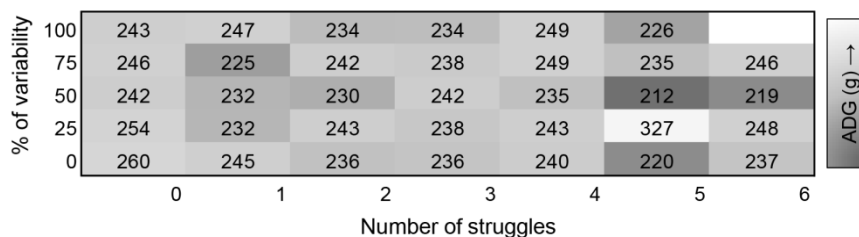


**Figure 2.** Average Daily Gain between d 1 – d 14 (ADG in g/d) in relation to the number of struggles during the backtest.

The number of struggles was unrelated to the litter size at d 14 ( $P = 0.24$ ), sex ( $P=0.20$ ), and cross-fostering ( $P = 0.15$ ), which were included in each model ( $P$ -values model 1). The number of struggles was unrelated to the health measurements, i.e. body condition ( $P = 0.93$ ), vitality ( $P = 0.36$ ), antibiotics treatment ( $P = 0.15$ ), and occurrence of diarrhea ( $P = 0.86$ ). The number of struggles in the backtest was influenced by both biological sow and actual nursing sow (as random effect both  $P<0.001$ ). The within litter variation of the backtest response or its interaction with the number of struggles did not relate to any of the

## 5 Struggling to survive

tested dependent variables (Fig. 3). In other words, BW, ADG and health did not depend on the variety of backtest responses within a litter.



**Figure 3.** Heat map of the ADG (g) of piglets from birth to weaning in relationship to the response of the backtest (number of struggles) and the within litter variation regarding the backtest response (0 – 100% variety in response).

### Teat order

The anterior teats were mostly occupied by heavier piglets, while the rear teats were occupied by lighter and slower growing piglets (for all BW and ADG  $P < 0.001$ ; model 2). This relationship was strongest for the relative birth weight, whereby piglets that occupied the anterior teats were at birth on average 80 g heavier than the litter average ( $P < 0.001$ ). Teat order class was unrelated to the number of struggles in the backtest ( $P = 0.55$ ) and to the variation of the number of struggles on litter level ( $P = 0.53$ ). There was no interaction between the number of struggles and the relative BW at birth for the location at the udder ( $P = 0.88$ ).

## 5.4 Discussion

Piglets that had a lower ADG from birth till the test day responded more actively during the backtest, and piglets with a lower BW at the test day (d 14) tended to respond more actively. This is in line with other studies that reported that piglets with a lower ADG during lactation and a low BW at d 21 of age showed a higher activity during the backtest, but also in these studies the associations were weak (Velie et al., 2009; Spake et al., 2012). Activity at a restraint in a weighing crate was also weakly negatively correlated with BW (Holl et al., 2010). These relationships suggest that piglets with a low ADG or BW show a more proactive coping response (Hessing et al., 1993; Bolhuis et al., 2005a). The link between the backtest and coping styles has been criticized because of the lack of correlation between the backtest and other behavioral tests (Jensen et al., 1995; Spake et al., 2012). However, different behavioral tests may reflect different personality dimensions, such as coping style, sociality, or fearfulness (Van Reenen et al., 2005; Koolhaas et

al., 2007), and the response in the backtest might reflect one of those dimensions (Van Erp-van der Kooij et al., 2002). This would most likely be the trait which is usually referred to as 'coping style' which has, apart from a divergence in responding actively versus passively to acute mild stress, behavioral flexibility as a main characteristic (e.g Bolhuis et al., 2004). In fact, the extremes with regard to backtest response at a young age have been found to differ in behavioral, physiological and neurobiological responses to acute and chronic stress up till adulthood (Geverink et al., 2003; Karman, 2003), with consequences for their production performance (Geverink et al., 2004).

The backtest response was not significantly related to the birth weight of the piglets, indicating that weight at birth was not determinative of the behavior. It is unknown whether the association between backtest response and ADG in the first two weeks of life reflects a causal relationship, and, if so, it is also hard to disentangle cause and effect. One option is that by d 14 piglets had adapted their behavioral response in the backtest to the postnatal situation. In order to cope with challenging situations, animals may adopt different behavioral styles (Bell, 2007). In other species it has been shown that animals that suffered from malnutrition, or had to compete more, may adopt a more proactive coping style or respond more aggressive (D'Eath and Lawrence, 2004; Carere et al., 2005), which might explain the effect that we observed in the current study. It should be noted, though, that animals that respond more actively or bold may, however, also have a higher ADG, as has been proven through a vast number of studies (Stamps, 2007; reviewed in Biro and Stamps, 2008). From an evolutionary perspective, the active response may coincide with increased risk taking in foraging, consequently acquiring more feed, and thereby resulting in a higher ADG, but also a higher predation risk (Stamps, 2007). The effect of an active coping strategy may also depend on environmental circumstances, such as availability of resources and stability of the environment (Benus et al., 1991). Also in pigs, in some studies an active backtest response has been associated with a high ADG (Van Erp-van der Kooij et al., 2003; Cassady, 2007). Ruis et al. (2000) also reported a higher ADG during lactation, which is in contrast with the present results and those of others (Schrama et al., 1997; Velie et al. 2009; Spake et al. 2012). Ruis et al. (2000) ascribed the higher ADG of piglets with an active backtest response to their successful competition for the anterior teats. Rank order at the teats did not relate to the backtest response in this study, however, nor did litter size influence or interact with the backtest response in its effect on ADG, even though litter size may have a marked effect on behavior and competitiveness (Mendl and Paul, 1990). Also the variation of activity responses within the litter was in this study unrelated

to BW, ADG, and health albeit a positive effect of a varied group composition regarding coping styles has been suggested in several animal species (Koolhaas et al., 2007; Bergmüller and Taborsky, 2010).

The moment of measuring performance (BW or ADG) might be essential when assessing the relationship with behavior, as shown in this study. The life stage, and with that the (social) context and stability of the environment, may exert different effects on growth (Naguib et al., 2011; English et al., 2013). A stable environment might be best for proactive copers, whereas an unpredictable environment would be easier to deal with by the more flexible reactive copers (Geverink et al., 2004; Reimert et al., 2013a).

Thus, the response in the backtest was weakly associated with the ADG of piglets, in line with previous studies. We hypothesized that the response in the backtest might be related to other early life conditions as well, such as health, but this hypothesis could not be confirmed. The general health of the piglets was good, resulting in very little variation in the health measurements, which might explain why no relationship was found. Coping styles are characterized by different immunological responses, and therefore differences in vulnerability to disease (Goodkin et al., 1992; Koolhaas, 2008). It might be that more vulnerable smaller piglets with a proactive response are more likely to survive, or perhaps even adopted this response to survive, whereas other small piglets did not and died. Unfortunately there were no backtest responses available of piglets that did not survive.

Weight relative to the litter average was not related to the backtest response, which may elucidate that being small compared to litter mates is different from being small in general. This would point out that the behavioral response in the backtest would be rather affected by malnutrition or competition for nutrition, than by being low in rank (D'Eath and Lawrence, 2004).

The sow explained a notable part of the response, which is in line with the heritability of the backtest response ( $h^2 = 0.53$ , Velie et al., 2009). Also the intra-uterine environment of the sow (Baxter et al., 2008), the milk production, and the (nursing) behavior (Valros et al., 2002) may have contributed to the behavioral and physiological development of the offspring. Only six percent of the piglets were cross-fostered, and this did not result in significant differences in the backtest response, although pigs may have changed their response after cross-fostering (Van Erp-van der Kooij et al., 2003).

Harmful early life experiences, or a lack of a stable and nourishing early environment, may cause amongst others cognitive impairment and disease, and the adverse effects may be permanent (e.g. Lupien et al., 2009; De Kloet et al.,

2005; Murgatroyd et al., 2009). It has been suggested that animals with a more active coping strategy may be more vulnerable to develop aberrant behaviors, such as tail biting (Korte et al., 2009), which may be triggered by challenges to the allostasis (De Kloet et al., 2005; Maccari and Morley-Fletcher, 2007). Minimizing harmful early life challenges is therefore not only important for the welfare of the animal, but also has an important role in providing a sound base for adaptation to conditions in later life (e.g. Anisman et al., 1998; Veenema, 2009).

### **5.5 Conclusions**

Piglets with a lower ADG from birth till d 14, and a lower BW at d 14, slightly struggled more in the backtest. The response in the backtest was unrelated to birth weight, weaning weight, BW relative to the rest of the litter, ADG till weaning, teat order, and measures on health. Therefore, confirmation of a relationship between the backtest response and other early life challenges than ADG and BW, failed. Although associations between the response to the backtest and ADG and BW around the test day were weak, our results confirm results found in previous studies. Irrespective of the strength and duration of the adaptation, it remains important to minimize challenges that might negatively affect animal health, welfare, and behavior.

### **5.6 Acknowledgements**

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# **Part II**

**Indirect genetic effects on growth rate in pigs**



# 6

## **Growth performance and carcass traits in pigs selected for indirect genetic effects on growth rate in two environments**

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### Abstract

Production traits such as growth rate may depend on the social interactions between group members. These social interactions might be partly heritable and are referred to as indirect genetic effects (IGE), social-, associative-, or competitive genetic effects. IGE may contribute to heritable variation in traits, and can thus be used to increase the response to selection. This, however, has hardly been tested by selection experiments. Our objective was to determine the effects of one generation of selection on IGE for growth (IGEg) in pigs on ADG, BW, ADFI, feed efficiency, and post-mortem measurements. Sires ( $n = 24$ ) and dams ( $n = 64$ ) were selected to create a high vs. low contrast for IGEg in the offspring ( $n = 480$ ). The IGE difference was 2.8 g ADG per pen mate, corresponding to 14 g higher ADG in high IGEg offspring compared to low IGEg offspring when housed in groups of 6 (i.e.  $(6-1) \times 2.8 = 14$ ). Male (barrows) and female (gilts) offspring were housed in groups of 6 of the same IGEg classification, in either barren concrete pens or pen enriched with straw and wood shavings ( $n = 80$  pens). Pigs were followed from birth to slaughter. Data were analyzed in a mixed model with pen as random factor. There was no difference in ADG between high and low IGEg pigs during the finishing period (wk 10 to 23). Opposite to expectations, high IGEg tended to have a 17 g lower ADG from weaning to slaughter ( $P = 0.08$ ), which was caused by a higher BW of low IGEg pigs in wk 5 ( $P = 0.008$ ). This led to a 2.3 kg lower carcass weight ( $P=0.02$ ) and 2.2 mm less muscle depth for high IGEg pigs ( $P = 0.03$ ). High IGEg pigs had a higher stomach wall damage score ( $P = 0.01$ ). Pigs on straw had a 25 g lower ADG during finishing ( $P = 0.03$ ), and less stomach wall damage ( $P < 0.001$ ). Fewer interventions against harmful behavior were required in high IGEg pigs. The unexpected results regarding IGEg may be due to several reasons. Despite initial power calculations showing good power, the IGEg contrast between groups may have been too small. Moreover, measures that were taken to limit harmful behavior may have had a substantial role. Harmful behavior such as tail biting may affect ADG and might underlie the effects of selection on IGEg in pigs. Research under commercial circumstances, where harmful behavior is likely to be more profound, may give more accurate insight into the benefits of selecting for IGEg.

Key words: genotype by environment, growth, housing, indirect genetic effect, pig, production

## 6.1 Introduction

Group housed animals may affect each other's production by their social interactions (a.o. Rodenburg et al., 2010). The effect that an animal has on its group members is partly heritable, and is known as indirect genetic effect (IGE), also referred to as social-, associative, or competitive genetic effect, or social breeding value. By including IGE in the selection criteria, both the genetic merit of the individual for its own performance and its effect on social partners are taken into account (Griffing, 1967). IGE may contribute to heritable variation in traits, and can thus increase response to selection (Muir, 2005; Bijma et al., 2007b). Genetic estimates showed that this is true for poultry (Muir, 2005; Ellen et al., 2008; Muir et al., 2013), mink (Alemu et al., 2014b) and pigs (Bergsma et al., 2013), but selection experiments are rare in livestock (Rodenburg et al., 2010).

In pigs (*Sus scrofa*), IGE have been estimated to contribute to the heritable variation in ADG, feed intake, and androstenone (Chen et al., 2010; Bergsma et al., 2013; Duijvesteijn et al., 2012), but these estimates require confirmation by selection experiments. Genotype by environment (G×E) interactions may exist for production traits in pigs (Schinckel et al., 1999; Wallenbeck et al., 2009), and therefore the effect of selection on IGE for growth might be different in different environments (Dominik and Kinghorn, 2008).

Our objectives were to conduct a selection experiment to determine the effects of selection based on IGE for growth (IGEg) for production traits in pigs, and to examine possible G×E interactions for pigs housed in conventional barren pens and enriched pens. In a one generation selection experiment, 480 pigs with either high or low IGEg were studied from birth to slaughter and assessed for ADG, BW, feed efficiency, back fat thickness, muscle depth and stomach lesions.

## 6.2 Material and methods

This study was carried out in strict accordance with the recommendations in the European Guidelines for accommodation and care of animals. The protocol was approved by the Institutional Animal Care and Use Committee of Wageningen University (Protocol Number: 2010055f).

### Estimation of IGE for growth

The estimation of IGE for growth has been described previously (Camerlink et al. 2013), and is therefore described only briefly here. Estimated breeding values for IGE for growth are expressed in g ADG during the finishing phase (from 25 – 110 kg), and are hereafter abbreviated as IGEg. Twenty-four boars and 64 sows were divergently selected on IGEg to create a genetic contrast, i.e. difference between

groups, in the offspring for IGEg whereas average direct breeding value (DBV) was kept equal for both offspring groups. Boars were selected from available TOPIGS AI Tempo boars (commercial synthetic boar line with Great Yorkshire genetic background), and sows originated from a herd of 120 'TOPIGS-20' sows (sow line of Great Yorkshire × Dutch Landrace). The contrast for estimated IGEg in the offspring prior to the trial was on average 3.6 g ADG. After the trial, IGEg of the parents were re-estimated in same manner as prior to the trial but including more data. Breeding values of parents were re-estimated on the extended data, including more offspring information, but excluding records of the offspring that participated in the trial. After re-estimation, the average estimated IGEg was 1.5 for high IGE pigs and -1.3 for low IGE pigs, resulting in a contrast of 2.8 g ADG. The average DBV for ADG was 12.5 for high and 12.4 for low IGE pigs. The resulting contrast in expected ADG depends on the number of group members of individuals. Offspring were housed in groups of six from weaning until slaughter and, therefore, the IGE contrast corresponds to an expected growth difference of  $(6-1) \times 2.8 = 14$  g ADG during the finishing phase (Bijma et al., 2007b), with a corresponding SE of 6.3 g/day (Appendix 1). The contrast of 14 g ADG corresponds to an expected difference in body weight of 2.2 kg between the high and low group at the end of the 160-d trial (on ~110 kg).

### **Animals and housing**

A total of 480 offspring were studied over five batches of 96 piglets each, between September 2010 and January 2012. Piglets were born in conventional farrowing crates (TOPIGS experimental farm, The Netherlands). Piglets were only cross-fostered if litter size exceeded 14 piglets, and only within IGE group. Tails and teeth were kept intact. Male piglets were castrated at 3 d of age. At ~27 d of age, piglets were weaned and a maximum of eight healthy piglets per sow were selected (selection criteria described below) and transported to experimental farm De Haar (Wageningen, The Netherlands).

From weaning on, a 2 × 2 experimental arrangement was applied with IGE (low vs. high) and housing conditions (barren vs. enriched) as factors at the pen level. Pigs were housed with six pigs per pen (3 castrated males and 3 females), giving a total of 80 pens. Pigs within a pen originated from different sows and had never been housed together. Half of the pigs from each IGEg group, and half of the selected piglets from each sow, were allocated to barren pens, and the other half to enriched pens. Pigs of high IGEg were never mixed with pigs with low IGEg.

Barren pens had a concrete floor, which was half solid and half slatted. Enriched pens had a solid floor with a deep litter bedding of straw and wood shavings. At the

start of the trial each enriched pen was provided with ~1.5 kg straw and ~11.6 kg wood shavings. Daily, ~1.8 kg of straw and ~2.9 kg of wood shavings were added to each enriched pen. Both barren and enriched pens had a space allowance of 1.0 – 1.2 m<sup>2</sup> / pig, depending on the barn. The treatment groups were equally divided over the two barns. Each pen contained a metal chain with ball. To limit excessive tail biting behavior, all pens (including barren pens) received a handful of wood shavings per day from wk 6 onwards. For the same reason, a jute sack was attached to the wall from wk 8 onwards. The jute sack was chewed on and ‘consumed’ by the pigs and was replaced by a new sack when it was consumed till approximately two third of the length. Pigs were housed in these pens from weaning until slaughter at 23 wk of age. Dry pelleted commercial feed was offered *ad libitum*. From 4 to 7 wk of age pigs had a feeder offering space to three pigs, and from wk 7 to 23 pigs had a single space feeder. Diet composition changed according to commercial practice (see Table 1) whereby during the first day the previous feed and the new feed were mixed to create a gradual transition. Water was continuously available from a single nipple drinker per pen. Temperature was set at a minimum of 25°C until 10 d after weaning, hereafter at 22°C for 3 wk, followed by 20°C until slaughter. Lights and a radio were on from 7:00 till 19:00 h.

Pigs were twice daily checked for their health. Skin lesions and wounds were treated with an antimicrobial spray (Chlortetracycline spray). Measures to limit tail biting were taken to guarantee a certain level of animal welfare. When a tail wound due to tail biting occurred, a repulsive substance (PHB spray or Stockholm tar, alternated) was smeared on the bitten tails. As soon as a pig’s tail was shortened due to being tail bitten (i.e. a severe tail wound) the affected pig, or the biting pig (determined by behavioral observation) was removed from the pen. This led to the exclusion of six bitten high IGE pigs and three low IGE bitten pigs and one tail biter (low IGE). Other health problems (as diagnosed by visual observations) were similar between both IGE groups and were, with the total number of affected pigs between brackets: lameness (5), umbilical hernia (4), meningitis (2), anal prolapse (2), pneumonia (2), or other reasons (3). In total, 17 high IGE pigs and 11 low IGE pigs were lost to follow-up.

## 6 IGEg and productivity

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**Table 1.** Diet composition from birth to slaughter.

Wk of age	% CP	% Ileal digestible Lys
0 to 4	21	1.5
4 to 6	17.8	1.25
6 to 8	16.0	1.07
8 to 12	16.8	1.05
12 to 23*	14.5	0.83

\* Plus additional Ca, P, Vit D3.

### **Production parameters and post-mortem measurements**

Pigs were weighed individually at d 1 of age (birth), d 27 (weaning), and at wk 5, 10, 17, and 23 (before slaughter). The amount of feed consumed from weaning till slaughter was recorded per pen during the following 5 periods: wk 4, wk 5 to 10, 10 to 17, and 17 to 23. Average daily feed intake (ADFI) per pig was approximated by dividing the ADFI per pen by the number of animals present in the pen (corrected for animals lost to follow-up). Feed efficiency was calculated as average ADG per pig divided by the approximated ADFI per pig.

At 23 wk of age, all high and low IGE pigs of the same batch were jointly transported over a distance of 80 km to a commercial abattoir. At slaughter, records were collected on net carcass weight, back fat thickness, and muscle depth were obtained from the standard measurements from the abattoir. From the net carcass weight, the carcass yield was calculated as the dressing percentage (net carcass weight / live weight × 100). The stomach of each pig was collected and assessed for stomach wall damage with a score of 0 – 5, according to the protocol of Hessing et al. (1994). A score of 0 indicated a normal pars-esophagus, leading up to score 5 for hyperkeratosis with many and severe erosions, or ulcers, or occlusion of the esophagus into the stomach. Due to inaccurate machine settings at the abattoir, the ear tags of pigs in batch 5 got could not be recognized, resulting in n = 375 for post-mortem measurements.

### **Data analysis**

Statistical analyses were performed using SAS (SAS Inst. Inc., Cary, version 9.2). Residuals of the response variables all approached normality.

Before weaning (lactation period) all pigs where housed under the same housing conditions. High IGE sows farrowed on average one day earlier than low IGE sows ( $P < 0.01$ ), and had less piglets at weaning (High  $12.2 \pm 0.08$ ; Low  $12.8 \pm 0.08$ ;  $P=0.02$ ). Including age at weaning and litter size at weaning as covariates in the



model improved the model fit. The effect of selection for IGEg on the response variables ADG and BW from birth till weaning of the selected pigs ( $n = 480$ ) was analyzed with the following mixed model (Mixed Procedure),

$$y = \mu + \text{IGE group} + \text{sex} + \text{litter size} + \text{weaning age} + \text{batch} + \underline{\text{pen}} + e, (1)$$

where pen was a random effect nested within IGE group and batch.

After weaning, housing condition (barren vs. enriched) and its interaction with IGE group and batch were added to the model. Age and litter size at weaning were also significant predictors for most production traits after weaning and therefore remained in the model as covariates. The number of animals (per  $\text{m}^2$ ) may influence the amount and type of social interactions, such as tail biting (e.g. Schröder-Petersen and Simonsen, 2001), and may affect growth (e.g. Hyun et al., 1998). We corrected for reduced group size due to animals being lost to follow-up by assigning for each pig the variable 'pigdays', which is the sum of the number of days that each pen mate (so excluding the pig itself) was present in the pen. 'Pigdays' did indeed affect several parameters and was therefore retained in the model. All response variables except for ADFI were analyzed with the following mixed model (Mixed Procedure),

$$y = \mu + \text{IGE group} + \text{housing} + \text{IGE group} * \text{housing} + \text{sex} + \text{'pigdays'} + \text{weaning age} + \text{litter size} + \text{batch} + \text{batch} * \text{housing} + \underline{\text{pen}} + e, (2)$$

where pen was a random effect nested within IGE group, housing condition and batch. ADFI was recorded by pen, and therefore analyzed with model 2 excluding the random pen effect (so on pen level) in a general linear model (GLM Procedure). To facilitate interpretation of the data, ADFI was presented per pig by assigning the average ADFI per pen to all pigs present in the pen (see section 'Production parameters'). Data are presented as LSmeans  $\pm$  SEM.

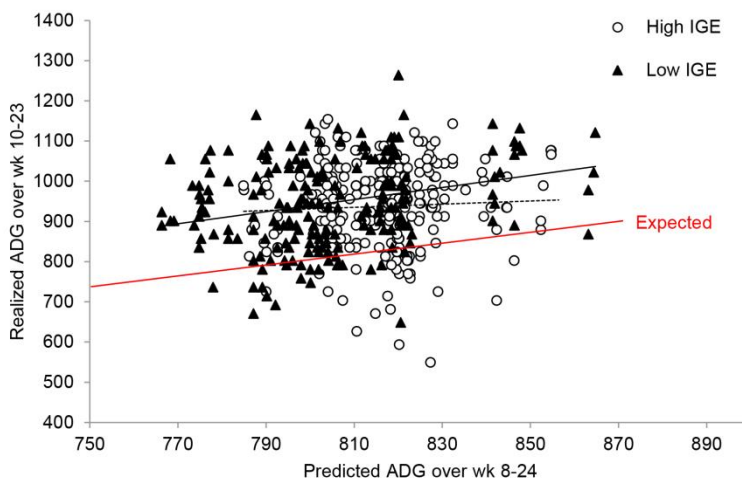
## 6.3 Results

### Effects of selection on IGEg

ADG during the finishing period was considered the most important parameter in this study, because IGE were estimated based on this trait. ADG during the finishing period, from 10 to 23 wk of age, showed no significant difference between the IGE groups (High  $934 \pm 8$  g; Low  $951 \pm 8$  g;  $P = 0.16$ ) but high IGE pigs tended to have a lower ADG from weaning to slaughter (High  $867 \pm 6$  g; Low  $884 \pm 7$ ;  $P = 0.08$ ). IGE

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groups did not differ in ADG during the lactation period, i.e. from birth till weaning (High  $248 \pm 8$  g ; Low  $249 \pm 8$  ;  $P = 0.74$ ). Both IGE groups had on average a high ADG (Fig. 1). The group of 18 low IGE pigs with expected AGD above 840 g (Fig. 1) is due to three sires with high DBVs. From the group of 16 high IGE pigs with a realized ADG below 750 g (Fig. 1), 14 out of the 16 pigs could be attributed to three sires which were in total mated to ten different dams. Surprisingly, two of these boars had the highest estimated IGEg, whereas estimated IGEg of the third boar dropped in the re-estimation from 4.3 to 0.5.



**Figure 1.** Realized ADG for high and low IGEg pigs as a function of predicted ADG, calculated as  $800 + \text{estimated DBV} + \text{sum of estimated IGEg of each pen mate}$  ( $n = 452$ ), including a regression line for each IGEg group.

BW did not significantly differ between the high and low IGE group during the lactation period, giving both groups an equal BW at weaning (Table 2). In the first week after weaning (wk 5), high IGE pigs gained less BW than low IGE pigs (Table 2), and had a lower ADFI and poorer feed efficiency (Table 3). After wk 5 ADFI and feed efficiency did not differ anymore between the groups, but high IGE pigs tended to be lighter till slaughter (Table 2).

High IGE pigs had a lower carcass weight and less muscle depth than low IGE pigs, but had similar carcass yield, back fat thickness and meat percentage (Table 4). Carcass weight and muscle depth were strongly related ( $P < 0.001$ ), but when muscle depth was corrected for carcass weight the effect of IGE group remained ( $P=0.03$ ). High IGE pigs had a higher stomach wall damage score (Table 4).

**Table 2.** LSmeans with SEM for body weight (BW) for high and low IGEg pigs, by day (d) or week (wk) of age ( $n = 480$ ).

D/Wk of age	High IGEg	Low IGEg	SEM	<i>P</i> -value
d 1	1.5	1.6	0.06	0.30
d 27	8.1	8.3	0.2	0.17
wk 5	8.9	9.2	0.1	0.008
wk 10	33	34	0.3	0.053
wk 17	84	86	0.6	0.056
wk 23	118	120	0.9	0.052

**Table 3.** LSmeans with SEM for high IGEg pigs (High) and low IGEg pigs (Low) regarding average daily feed intake (ADFI, kg/pig/d) (calculated on pen level,  $n = 80$ ), and feed efficiency for wk 4-5, 5-10, 10-17, and 17-23 ( $n = 480$ ).

Age (wk)	ADFI				Feed efficiency			
	High	Low	SEM	<i>P</i> -value	High	Low	SEM	<i>P</i> -value
4	0.23	0.27	0.01	0.0003	0.79	0.70	0.03	0.03
5 to 10	1.1	1.1	0.03	0.75	0.46	0.45	0.00	0.30
10 to 17	2.2	2.2	0.06	0.80	0.47	0.46	0.01	0.34
17 to 23	2.7	2.7	0.06	0.99	0.33	0.33	0.00	0.89

**Table 4.** LSmeans with SE for post-mortem measurements for high and low IGEg pigs ( $n = 375$ ).

Measurement	High IGEg	Low IGEg	SEM	<i>P</i> -value
Carcass weight (kg)	92.0	94.3	0.7	0.02
Carcass yield (dressing %)	78.4	78.8	0.2	0.17
Back fat thickness (mm)	18.2	18.4	0.3	0.64
Meat (%)	55.1	55.2	0.2	0.66
Muscle depth (mm)	58.4	60.6	0.5	0.003
Stomach wall score (0–5)	2.8	2.4	0.1	0.01

### Effects of housing condition

Housing conditions did not significantly influence ADG from weaning to slaughter ( $P=0.36$ ), but from wk 10 to 23 pigs from barren pens had a higher ADG (Table 5). Pigs in barren pens had a lower BW only in wk 10 (Table 5). From wk 10 onwards ADFI was higher in barren pens (Table 5). The feed efficiency did not significantly differ between housing conditions. Housing conditions did not influence carcass weight ( $P = 0.32$ ), back fat thickness ( $P = 0.59$ ), meat percentage ( $P = 0.69$ ), or

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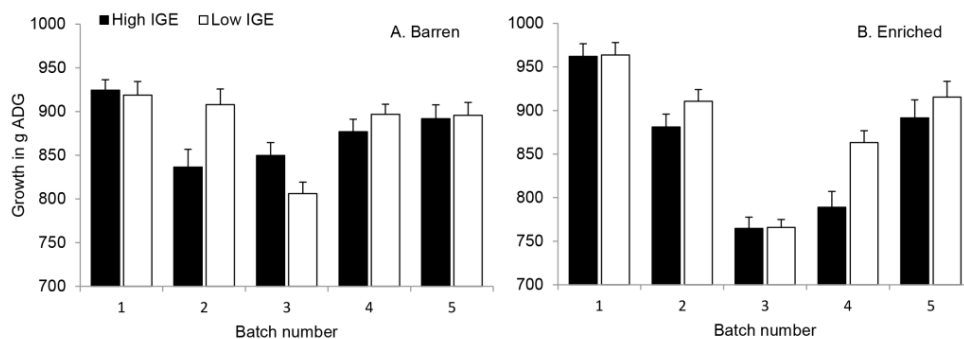
muscle depth ( $P = 0.57$ ), but pigs in enriched housing had a lower stomach wall damage score (Table 5).

The results on housing conditions were strongly influenced by batch effects, as seen in Fig. 2 (interaction batch\*housing all  $P < 0.01$ ). Pigs in enriched pens had during batch 1, 2, and 5 a higher ADG (wk 5-23 and wk 10-23) and BW (wk 17 and 23) than pigs in barren pens, but had a lower ADG than barren pens in batch 3 and 4. Similarly, pigs in pens enriched with straw and wood shavings had a lower, more favorable, stomach wall damage score during batch 1, 2 and 4, but had higher scores in batch 3 (interaction batch  $\times$  housing  $P = 0.06$ ).

**Table 5.** Significant<sup>1</sup> effects of housing conditions on the production performance of pigs, for conventional barren pens and pens enriched with straw and wood shavings.

Measurement	Wk of age	Barren	Enriched	SEM	<i>P</i> -value
BW	10	33.0	34.2	0.3	0.005
ADG	10-23	955	930	8	0.03
ADFI	10-17	2.3	2.2	0.06	0.05
ADFI	17-23	2.7	2.6	0.06	0.04
Stomach wall score (0–5)	23	2.9	2.4	0.1	0.0007

<sup>1</sup> Non-significant effects are omitted from the table.



**Figure 2.** Average daily gain (ADG; g/d) from wk 5-23 for high and low IGEg pigs in barren pens (A) and enriched pens (B), presented by batch ( $n = 480$ ). Only batch 3 and 4 took place during summer (batch 3: April – August 2014, batch 4: May – September 2014).

### G×E interaction

There were no significant G×E interactions between IGE group and housing condition for any of the measurements (all  $P > 0.10$ ).

## 6.4 Discussion

### Selection on IGEg

The offspring groups resulting from one generation of divergent selection for IGE on growth (IGEg), did not significantly differ in ADG. After re-estimation of the breeding values of the parents, the contrast in ADG between the high and low IGE groups decreased from 3.6 to 2.8 g ADG. This contrast corresponds to a 2.2 kg predicted difference in BW between the high and low IGE group at the end of the trial. Though this difference seems small, power calculations prior to the trial indicated that sample size would be sufficient to detect a difference of this size between the groups. Estimation of IGEg in pigs from field data, however, is difficult due to complex data structure, e.g. no fixed groups during life.

The breeding values were estimated from data from commercial farms. The environmental conditions on the experimental farm, however, differed from commercial circumstances. The larger space allowance, the small number of pigs per pen, *ad libitum* feeding, more frequent positive exposure to humans, and timely veterinary intervention (e.g. the treatment of tail wounds) made the circumstances in some aspects more favorable for growth as compared to commercial practice (Hemsworth, 2003; Ramaekers et al., 1996; Hyun et al., 1998; Taylor et al., 2010). These circumstances may have affected the effect of selection on IGEg, especially regarding tail biting. Tail biting is a main cause of reduced ADG as a result of behavior between group housed pigs, whereby ADG can reduce 1 to 11% in the recipient (Wallgren and Lindalh, 1996; Camerlink et al., 2012a; Sinisalo et al., 2012). Behavioral studies of the pigs from this trial showed that high IGEg pigs caused less tail damage to their pen mates (Camerlink et al., 2012b; Camerlink et al., submitted). Measures against tail biting were taken to guarantee a certain level of animal welfare and to prevent excessive losses of animals. The control measures that we took (daily treatment of damaged tails, removal of bitten animals, and provision of jute sacks and wood shavings) are reported to reduce tail biting and consequently may have reduced the impact of tail biting on ADG (Moinard et al., 2003).

Moreover, *ad libitum* feeding might have reduced aggression and competition for feed (Petherick and Blackshaw, 1987; Brouns and Edwards, 1994). Behavioral observations showed that the IGEg groups did not differ in amount of aggression at the feeder (Camerlink et al., 2013). Competition for feed might affect the expression of IGEg in pigs (Arango et al., 2005). This suggestion was strengthened by data from the offspring that were genetically selected for high or low IGEg but did not enter the current trial. These pigs were raised at the original farm and

were fed restricted or *ad libitum*. Evaluation of their growth rate indicated significant IGEg in the restricted fed pigs, but not in *ad libitum* fed pigs (personal communication TOPIGS Research Center IPG B.V.).

High IGEg pigs had a higher stomach wall damage score. Severe stomach lesions may reduce ADG with 35 to 75 g (Hessing et al., 1994; Elbers et al., 1995; but see Guise et al., 1997 and Dirkzwager et al., 1998 who found no effect). The difference between the IGEg groups might be attributed to the consumption of jute sacks, which was 30% lower in high IGEg pigs (Camerlink et al., 2014a; submitted). Jute sacks are fibrous and the ingestion of fibers may prevent the formation of stomach lesions (Nielsen and Ingvarsten, 2000; Friendship, 2003).

The higher net carcass weight of low IGEg pigs was not in line with our expectation. Low IGEg pigs also had a higher muscle depth. Weight and muscle depth are related (Ellis et al., 1996), but the effect of IGEg on muscle depth remained even significant after correcting for weight. Genetic estimates showed no contribution of IGE to the heritable variation in muscle depth (Hsu et al., 2010), suggesting that muscle depth is unaffected by IGE. It would therefore require more in-depth study to detect the cause of our findings for muscle depth.

Selection experiments in laying hens did yield positive response to selection on IGE for survival (Rodenburg et al., 2010). The current trial is, besides a small study on pigs mentioned in Rodenburg et al. (2010), and a multiple-generation selection experiment based on groups of half sibs (Gunsett, 2005), the first large scale selection experiment that has been carried out for IGEg in pigs. This makes it us cautious with drawing conclusions about the effect of selection for IGEg on production parameters and, more research would be necessary, preferably under commercial settings and with a larger number of pens.

### **Housing condition**

ADG showed large fluctuations between batches, and these fluctuations were most pronounced in the pens enriched with a deep litter layer of straw and wood shavings (Fig. 2). The fluctuations in ADG may be largely due to season. Average maximum temperature of batch 1, 2, and 5 was 23°C, whereas this was 25.8°C for batch 3 and 26.8°C for batch 4. Temperatures above ~25°C have been reported earlier to lead to reduced ADFI and ADG in pigs (Verstegen et al., 1978; NRC, 1981; Lopez et al., 1991; Hyun et al., 1998). In batch 3 and 4, the maximum temperature was above 25°C during 87 and 98 days, respectively. The profound reduction in ADG in enriched pens in batch 3 and 4, as well as the lower ADFI compared to barren pens, can be partly explained by the higher floor temperature in enriched

pens due to the insulating properties of straw and the absence of a slatted floor (Verstegen et al., 1978; Fraser, 1985).

Pigs in pens enriched with straw and wood shavings had less stomach wall damage than pigs in barren pens (Barren  $2.8 \pm 0.1$ ; Enriched  $2.4 \pm 0.1$ ;  $P = 0.004$ ), which is in accordance with literature (Ramis et al., 2005; Amory et al., 2006; Scott et al., 2006; Bolhuis et al., 2007), and may be due to straw consumption or reduced stress (Nielsen and Ingvarsten, 2000; Guy et al., 2002b; Amory et al., 2006; Van de Weerd and Day, 2009).

### **G×E interaction**

No interaction was detected between IGEg groups and housing conditions for any of the measured parameters. Selection for IGEg, however, did not yield the expected differences in ADG. Further, contrasting effects of straw provision on growth have been reported (reviewed by Van de Weerd and Day, 2009). This makes it at this stage difficult to be conclusive about the absence of G×E interactions. G×E interactions have mainly been shown for performance of different genotypes in a “test environment” vs. a commercial environment (Merks, 1989; Schinckel et al., 1999; Wallenbeck et al., 2009). The “test environment” of the current trial as a whole differed from the commercial environment as outlined at the start of the discussion section (Falconer, 1952; Schinckel et al., 1999). It remains important for both single housing effects like straw enrichment, as well as for the whole environmental circumstances from which performance data is obtained, to consider the possibility of G×E interactions in future trials (Dominik and Kinghorn, 2008).

### **6.5 Conclusion**

A single generation of genetic selection for IGEg did not influence the major production parameters in pigs. The effects of housing pigs on straw on ADG varied with batch, with lower performance in warmer conditions, and overall a slightly lower ADG during finishing, but straw housing had a positive effect on stomach health. No genotype by environment (G×E) interaction was detected for the effect of selection on IGEg and the effect of an enriched environment regarding production parameters in finishing pigs. Control measures to limit harmful behavior might have reduced the expression of IGEg on ADG in our experiment. We conclude that selection on IGEg in pigs did not yield the expected results in the current trial, but that research under commercial circumstances is required to determine the consequence of selection on IGEg.

## 6.6 Acknowledgements

This work was financially supported by the Dutch science council (NWO) and the Dutch Ministry of Economic Affairs. We would like to acknowledge TOPIGS for providing the animals and pedigree information. Many thanks to the animal care takers of experimental farm 'De Haar' and the colleagues and students from the Adaptation Physiology Group of Wageningen University who helped during the experiment, especially Fleur Bartels.

### Appendix 1: Power Calculation

The standard error on the estimated contrast depends on the numbers of selected sires and dams for the high and low direction, and on the prediction error variance (PEV) on their estimated breeding values. Average PEVs reported by ASReml were  $PEV_{D,sires} = 392$ ,  $PEV_{D,dams} = 660$ ,  $PEV_{I,sires} = 7.8$ ,  $PEV_{I,dams} = 13.0$ , both for the high and low direction of selection. With 5 group mates, total breeding values are given by  $A_T = A_D + 5A_I$ . Hence, assuming independence of direct and indirect estimated breeding values,  $PEV_T = PEV_D + 25PEV_I$ , so that  $PEV_{T,sires} = 587$  and  $PEV_{T,dams} = 985$ . For each direction of selection, 12 boars were selected and 33 sows. Thus the PEV on the average estimated total breeding value as  $PEV_{\bar{T},sires} = 587/12 = 48.9$  and  $PEV_{\bar{T},dams} = 985/33 = 29.8$ . The estimated high-low contrast equals

$\frac{1}{2}(PEV_{\bar{T},sires} + PEV_{\bar{T},dams})_{high} - \frac{1}{2}(PEV_{\bar{T},sires} + PEV_{\bar{T},dams})_{low}$ . Hence, the variance of the contrast equals  $2 \times \frac{1}{4}(PEV_{\bar{T},sires} + PEV_{\bar{T},dams}) = 39.4$ . Finally, the SE of the applied contrast was  $\sqrt{39.4} = 6.3$ .



# 7

## **Indirect genetic effects for growth in pigs affect aggressive and manipulative biting behaviour**

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Submitted

### **Abstract**

Indirect genetic effects (IGEs) are heritable effects of an individual on trait values of another, and are a result of social interactions. The objective was to determine the consequences of selection for IGEs for growth (IGEG) on the behavioural repertoire of pigs in a G×E set-up. One generation of selection was applied to create a high vs. low IGEG contrast in 480 pigs (4-23 weeks of age) housed in barren and straw-enriched pens ( $n = 80$ ). Results showed that high IGEG pigs showed 44% less aggressive biting ( $P = 0.03$ ), 24% less ear biting ( $P = 0.004$ ), and 34% less biting on enrichment material ( $P = 0.03$ ). High IGEG pigs had a lower tail damage score (high 2.0; low 2.2;  $P = 0.004$ ), and consumed 30% less jute sacks ( $P = 0.002$ ). Straw-bedding reduced biting behaviours additive to the effects of IGEG ( $P < 0.01$ ), resulting in no G×E interactions. In conclusion, selection on high IGEG reduced potentially harmful biting behaviours in pigs.

Key words: behaviour, indirect genetic effects, genotype-environment interaction, pig, tail biting, response to selection

## 7.1 Introduction

Social interactions among individuals may affect a variety of phenotypic traits (e.g. Frank, 2007). If these social effects on others are heritable they may affect response to selection, and thereby alter the outcome of both evolutionary processes in natural populations, and artificial selection programs in agriculture (e.g. Griffing 1967; Bijma and Wade 2008; McGlothlin et al., 2010). The impact of social interactions on response to selection can be studied within the framework of indirect genetic effects (IGEs). An indirect genetic effect (IGE), also known as an associative, social-, or competitive genetic effect, or a social breeding value, is a heritable effect of an individual on the trait values of its social partners (Griffing, 1967; Moore et al., 1997). For example, an individual may reduce the growth of its social partners because it carries genes making it highly competitive. IGEs are relevant both for the evolution of natural populations, and for response to artificial selection in domestic and agricultural populations, ranging from trees to laboratory animals and livestock (Wolf et al., 1998; Bijma, 2011a). Theory predicts that IGEs affect the response to selection (Griffing 1967; Moore et al., 1997; Bijma et al., 2007b), and there is a growing body of evidence for the existence of IGEs (e.g. Peeters et al., 2012; Alemu et al., 2014b). Studies indicate that competitive, aggressive, or injurious behaviours, but also cooperation, may underlie the observed IGEs (Agrawal et al., 2001; Mutic and Wolf, 2007; Wilson et al., 2009; Rodenburg et al., 2010; Alemu et al., 2014a). The link between IGEs and behaviour is especially relevant to livestock populations, where behaviour is an important component of animal welfare. First selection experiments in poultry yielded promising results on production and behaviour (e.g. Muir, 1996; Rodenburg et al., 2010; Muir et al., 2013). Yet, we are only at the start of discovering mechanisms underlying IGEs, and there is an urge for more empirical research (Wilson, 2013).

In domestic pigs (*Sus scrofa*), IGEs affect growth rate (here denoted as IGEg), meaning that pigs differ in the heritable effect they express on the growth rate of their pen mates (e.g. Bergsma et al., 2013). Commercially kept pigs have been selected primarily for growth rate and are kept in barren environments, which both may have increased competitive and aberrant behaviour (Rodenburg and Turner, 2012). Aberrant behaviour, such as repeatedly chewing on tails or ears of group mates, may affect growth and health of the bitten animal and is considered a severe welfare problem in pig husbandry (e.g. Schrøder-Petersen and Simonsen, 2001). Selection on IGEg might contribute to a solution to simultaneously improve both productivity and welfare (Rodenburg et al., 2010).

Consequences of selection for IGEg on the behavioural repertoire of pigs are largely unknown, as well as the potential dependency of IGEg on the environment. The

genetic disposition for certain behaviours, for example aggression, may be expressed differently depending on the environment (e.g. Barr et al., 2003). It is therefore important to consider genotype-environment interactions (G×E) to assess whether changes due to selection for IGEs are consistent across environments (Danielson-François et al., 2009).

Here we studied whether selection for IGEs for growth (IGEG) alters the behaviour of pigs. Using a one generation selection experiment, we investigated which behaviours are targeted by selection for IGEG. In addition, we studied whether interactions exist between IGEG and the environment (G×E) in which the behaviour is expressed. Hereto, pigs were divergently selected for IGEG, and housed in contrasting conditions (barren versus straw-enriched) that were expected to yield differences in behaviour. This one of the first selection experiments on IGEs in a large mammal. The results will provide insight in the mechanisms underlying IGEs for growth, and in the potential of selection on IGEs to improve social interactions between group living animals.

### 7.2 Materials and methods

#### **Genetic selection on IGE for growth (IGEG)**

Background information on IGEs, and the estimation of IGEs for growth during the finishing phase (from 25 – 110 kg) for the current trial, here denoted as IGEG, has been given in detail in Camerlink et al. (2013). Briefly, sows (64 Topigs-20 sows: sow line of Great Yorkshire × Dutch Landrace) and boars (24 Tempo boars: commercial synthetic boar line with Great Yorkshire genetic background) were selected based on their estimated breeding value for IGEG. Sires and dams with the most extreme high and low IGEG of the available population were mated within their IGEG group (high vs. low), while the direct breeding value was kept equal between groups. This resulted in a contrast of 14 g ADG (Average Daily Gain) between high and low IGEG offspring (40 high IGEG litters and 40 low IGEG litters). Hence, high IGEG offspring would increase the growth of their pen mates, whereas low IGEG offspring would decrease the growth of their pen mates. Offspring were studied over five batches of 96 pigs each ( $n = 480$ ), between September 2010 and February 2012. The Animal Care and Use Committee of Wageningen University approved the experiment (Protocol Number: 2010055f).

#### **Animals and housing**

Piglets were born in conventional farrowing pens with farrowing crates (TOPIGS experimental farm, Beilen, The Netherlands). Tails and teeth were kept intact. Male

piglets were castrated (at 3 d of age), because IGEg have currently been estimated on gilts and castrated males. Cross fostering was applied only if litter sizes exceeded 14 piglets, and always within the same IGEg group. At ~14 days of age, piglets were subjected to the backtest to assess their coping style (Hessing et al., 1993). Classification of piglets based on their response in the backtest, for which no relationship with IGEg was found (Reimert et al., 2013a), was used to standardize group composition with regard to coping style. Piglets were weaned at 26 days of age, whereby maximum eight piglets per sow were selected. Selection was based on good health, sex, and backtest response. Selected piglets ( $n = 480$  in total) were transported to experimental farm De Haar (Wageningen, The Netherlands).

From weaning to slaughter (4 – 23 wk of age), a 2×2 experimental arrangement was applied with IGEg (low vs. high) and housing conditions (barren vs. enriched) as factors at the pen level. Pigs were housed with six per pen, leading to 80 pens in total. Group composition was balanced for sex (1:1) and backtest classification (at least two of each classification). Half of the pigs from each IGEg group, and half of the selected piglets from each sow, were allocated to a barren pen, and the other half to an enriched pen.

Barren pens had a floor which was half solid concrete and half slatted. Enriched pens had a solid floor with a bedding of 12 kg of wood shavings and 1.5 kg of straw. Fresh wood shavings (3 kg / pen) and straw (0.25 – 1.5 kg / pen depending on age) were added to enriched pens daily. Pen dimensions were either 1.90 m × 3.20 m or 2.25 × 3.25 m (1 – 1.2 m<sup>2</sup> / pig), depending on batch, and were within batch equal between barren and enriched pens. All pens had a metal chain with ball attached to the pen wall as toy. Dry pelleted commercial feed was offered *ad libitum* from a single space feeder. Feed was provided according to commercial practice, with a total of four feed changes whereby on the first day the old and new feed types were mixed to create a gradual transition between feed types. Water was continuously available from a single nipple drinker per pen. Temperature was until 10 days after weaning set at a minimum of 25°C, and was hereafter set at 22°C for 3 weeks, followed by 20°C until slaughter. Lights and a radio were on from 7:00 till 19:00 h. To reduce damaging tail biting behaviour, i.e. chewing on the tail of a conspecific which can lead to injury and in extreme cases even to mortality of the bitten animal, all pens received a handful of wood shavings per day from week six onwards and a jute sack was attached to the wall from week eight onwards. Pigs were housed in these pens from weaning until slaughter. Due to diverse health reasons including tail biting, 18 high IGEg and 11 low IGEg pigs were removed from the experiment.

### **Behavioural observations**

Behaviours of individual pigs were recorded at 4, 5, 8, 12, 16, and 21 wk of age. Each pig was identified by a spray marked number on the back, which was refreshed before behavioural observations. Behaviour, as described in Table A1 (Appendix), was scored during live observations using 2-min instantaneous scan sampling for 6 h during the active period of the day, consisting of six 1 h blocks from 8:00 – 11.30 h and from 14.00 – 17:30 h with after each hour a 15 minute break. This procedure resulted in 180 observations per pig per observation day, with one observation day in each of the weeks mentioned. The Observer 5.0 software package (Noldus Information Technology B.V., Wageningen, The Netherlands) installed on a hand-held computer was used for behaviour recordings. Observations were carried out by observers who were unaware of the IGEg of the pigs.

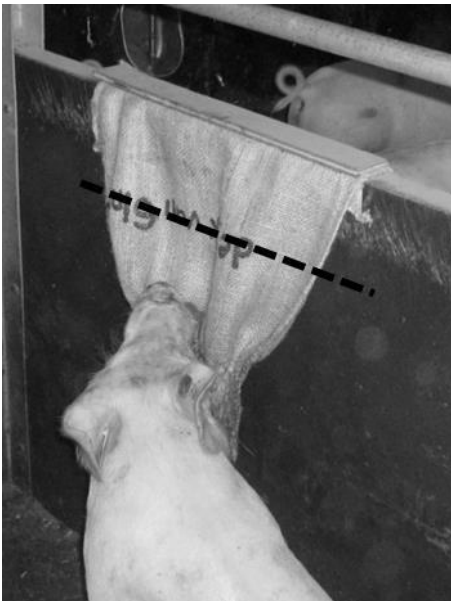
### **Tail damage scores**

Tail damage scores can serve as an indicator for the amount of tail biting behaviour in a pen. Scores were obtained using an adapted procedure from Zonderland et al. (2008). Scores ranged from 1 – 4, with score 1 being no visible tail damage; score 2 for hair removed from the tail; score 3 for bite marks; and score 4 for a clearly visible wound. Tail damage was scored each week on each individual pig, leading up to 20 observations per pig. When a pig had to be removed from the trial due to being bitten severely its score was set to 4 for the remaining period till slaughter. When a tail biter had to be removed from the pen it kept its last score before being removed from the pen. Scores were obtained by multiple observers who were trained to score in the same way, and who were unaware of the IGEg of the pigs.

### **Interventions to limited damage due to tail biting**

Oral manipulation amongst pigs is the repeatedly biting on the tail, ear or paw of a group member, and may result in injury, impaired health or mortality of the bitten animal. Oral manipulation such as tail biting may start harmlessly, but when no measures are taken many animals may be severely damaged (Statham et al., 2009). During the trial, measures were taken to reduce tail biting to an acceptable level to prevent the loss of animals and to guarantee a certain level of animal welfare. Tail biting wounds became significant from six weeks of age. To reduce the amount of damaging tail biting behaviour, a handful of wood shavings was provided to each pen from week six onward and from week eight a jute sack was attached to the pen wall as material to chew on. The jute sack was a commercially available sack of approximately 60 × 105 cm, which was over the width attached to the pen wall and

was replaced when there was less than 1/3 of the sack left (Figure 1). When the sack was replaced, the remainders were approximated in cm<sup>2</sup>. The amount of jute sack that was 'consumed' was noted by pen. To reduce tail biting, the tails of bitten pigs were alternating between days covered with the aversive P.B.H. spray (Kommer Biopharm B.V.) or Stockholm tar (Rapide®). Pigs were removed from the pen when they had a reduction in tail length, irrespective of the amount of reduction. Six high IGEg pigs and three low IGEg pigs, from 8 different pens in total, were removed from the trial due to reduced tail length. One tail biter (low IGEg) was removed to limit further tail damage of its five pen mates.



**Figure 1.** Jute sack attached to pen wall as distraction material to limit tail biting. The sack was replaced when the sack was 'consumed' till the dashed line or further.

### **Data analyses**

Statistical analyses were performed using SAS (SAS 9.2, Institute Inc.). Data were analysed and presented by production phase as applied in commercial pig farming to facilitate comparison between animal behaviour studies. The nursery phase is from 4 to 8 wk of age, whereas the finishing phase is generally from 8 wk of age till slaughter (here at 23 wk of age).

Behavioural scans were analysed on pen level ( $n = 80$ ) and averaged over production phase (nursery phase: observations wk 4, 5, and 8; finishing phase: observations wk 11, 12, 16 and 21). Hereto the behaviours of pigs were averaged

by pen (6 pigs / pen). Residuals of the response variables were checked for normality, and if needed, behaviours were arcsine square root transformed. Behaviours by pen and production phase were analysed in a General Linear Model (GLM Procedure), and included IGEg group, housing condition, the interaction between IGEg group and housing condition, and batch as fixed class effects.

The weekly tail damage scores were averaged into two scores per pig, one for the nursery phase (wk 4 – 7) and one for the finishing phase (wk 8 – 23). Scores were analysed at individual animal level ( $n = 480$ ) in a Generalized Linear Mixed Model (MIXED Procedure) with IGEg group, housing condition, the interaction between IGEg group and housing condition, sex, and batch as fixed class effects, and as random factor pen nested within IGEg group, housing condition and batch.

The total  $\text{cm}^2$  of 'consumed' jute sacks per pen (from wk 8 – 23) was analysed at pen level ( $n = 80$ ) in a General Linear Model (GLM Procedure) with IGE group, housing condition, the interaction between IGE group and housing condition, and batch as fixed class effects. To facilitate the interpretation of consumed bags in  $\text{cm}^2$ , results are presented in number of jute sacks consumed (total  $\text{cm}^2 / (60 \times 105)$ ). The amount of jute sacks per pen was correlated to the average tail damage scores per pen by Pearson correlation.

In the Results, average trait values for the treatments will be reported as (untransformed) LSmeans  $\pm$  SEM.

### 7.3 Results

#### Nursery phase

Over the observation moments between wk 4 and 8 of age, differences in behaviour between the IGE groups were small, and did not show a systematic pattern. Pigs with high IGEg showed 20% nosing contact with pen mates (nose-nose and nose-body contact), and tended to show 25% less aggressive biting (Table 1). In addition, high IGEg pigs tended to spent less time lying inactive and defecate less than low IGEg pigs (Table 1). There was no difference in overall activity (all activity minus lying inactive and sleeping) ( $P = 0.54$ ), the sum of all explorative behaviours (see Appendix for behaviours) ( $P = 0.55$ ), or the sum of all aggressive behaviours ( $P=0.85$ ). IGEg group interacted with housing condition for drinking and belly nosing, and tended to interact for rooting, nose contact, and head knocks (Table 2). Other behaviours were not significantly affected by IGEg group, or its interaction with housing.



### Finishing phase

During the finishing phase, when pigs were observed at 12, 16 and 21 wk of age, high IGEg pigs showed systematically less biting behaviour than low IGEg pigs. Although the frequencies of the observed behaviours are low, of the observed time high IGEg pigs spent 40% less on aggressive biting of pen mates, and 27% less on oral manipulation in the form of biting the ears of pen mates than low IGEg pigs did (Table 1). High IGEg pigs were not only biting their pen mates less, but also their environment. They were chewing 40% less on the distraction materials provided, which were the chain with ball and jute sack (Table 1). High IGEg pigs were 40% more often observed to perform comfort behaviour, such as scratching the skin (Table 1). Similar to the nursery phase, high IGEg pigs tended to urinate and defecate less than low IGEg pigs (Table 1). There was no difference between the IGE groups in overall activity ( $P = 0.31$ ), explorative behaviour ( $P = 0.46$ ), or aggressive behaviour ( $P = 0.29$ ). There was a significant interaction between IGEg group and housing condition for lying inactive and locomotion, and there tended to be G×E interactions for comfort behaviour, drinking, pen exploration, and nosing objects (Table 3).

**Table 1.** Behaviours during the nursery and finishing phase in percentage of behavioural scans for the difference between high and low IGEg pigs<sup>1</sup>. Values are LSmeans of untransformed data with standard error (SEM).

Behaviour	High IGEg	Low IGEg	<i>P</i> -value
Nursery (4 – 7 wk)			
Aggressive biting	0.09 ± 0.01	0.12 ± 0.01	0.06
Lying inactive	11.2 ± 0.3	11.9 ± 0.3	0.08
Nose contact	0.24 ± 0.02	0.30 ± 0.02	0.03
Urinate/defecate	0.37 ± 0.2	0.43 ± 0.2	0.09
Finishing (8 – 23 wk)			
Aggressive biting	0.03 ± 0.005	0.05 ± 0.005	0.006
Comfort behaviour	0.10 ± 0.01	0.06 ± 0.01	0.005
Chewing toy	0.90 ± 0.13	1.50 ± 0.13	0.005
Ear biting	0.11 ± 0.01	0.15 ± 0.01	0.03
Urinate/defecate	0.30 ± 0.02	0.34 ± 0.02	0.10

<sup>1</sup> Only significant results are included in the table ( $P < 0.10$ ).

## 7 IGEg and behaviour

**Table 2.** Behaviours during the nursery phase (wk 4 – 7) in percentage of behavioural scans for each treatment group: high and low IGEg pigs both in barren (B) and enriched (E) pens ( $n=80$  in total), with  $P$ -values for the difference between IGEg groups ( $P$ -IGE), the difference between housing conditions ( $P$ -HC), and their interaction (IGE $\times$ HC). Values are LSmeans of untransformed data with standard error (SEM).

Behav. nursery	High	High	Low	Low	SEM	$P$ -IGE	$P$ -HC	IGE $\times$ HC
	E	B	E	B				
Sleeping	38	47	39	46	1.1	0.94	<0.001	0.30
Lying inactive	9.6	12.8	10.6	13.2	0.39	0.08	<0.001	0.44
Standing	2.2	2.9	2.0	2.7	0.2	0.31	<0.001	0.91
Locomotion	2.5	2.5	2.6	2.7	0.13	0.24	0.89	0.72
Sitting	0.82	0.90	0.78	1.0	0.06	0.60	0.01	0.25
Comfort behav.	0.31	0.24	0.30	0.24	0.03	0.92	0.02	0.87
Eating	7.9	8.2	8.7	8.3	0.2	0.89	0.09	0.56
Drinking	1.5	1.8	1.6	1.5	0.09	0.26	0.22	0.02
Urinate/defecate	0.29	0.45	0.36	0.5	0.03	0.09	<0.001	0.75
Playing	1.1	0.63	0.96	0.66	0.1	0.66	<0.001	0.46
Exploration floor	16	11	14	11	0.5	0.14	<0.001	0.43
Nosing object	1.8	2.5	1.9	2.9	0.14	0.13	<0.001	0.37
Rooting	5.8	1.6	5.4	2.2	0.4	0.49	<0.001	0.10
Rooting object	0.07	0.26	0.09	0.31	0.03	0.23	<0.001	0.59
Chewing	10	3	10	3	0.5	0.73	<0.001	0.69
Chewing toy	0.28	0.33	0.15	0.37	0.04	0.26	0.0002	0.13
Nosing body	0.60	1.0	0.63	0.96	0.05	0.87	<0.001	0.55
Nose contact	0.26	0.23	0.27	0.34	0.03	0.03	0.47	0.06
Belly nosing	0.05	0.53	0.11	0.25	0.09	0.20	<0.001	0.02
Mounting	0.26	0.23	0.19	0.26	0.03	0.53	0.53	0.12
Fighting	0.19	0.18	0.15	0.25	0.03	0.18	0.15	0.15
Head knock	0.16	0.11	0.09	0.13	0.02	0.17	0.07	0.07
Biting	0.08	0.10	0.09	0.14	0.01	0.06	0.005	0.23
Fighting at feeder	0.09	0.11	0.08	0.10	0.01	0.54	0.23	0.99
Tail biting	0.02	0.15	0.02	0.17	0.02	0.80	<0.001	0.46
Ear biting	0.10	0.40	0.09	0.37	0.03	0.63	<0.001	0.92
Manip. other	0.11	0.50	0.15	0.50	0.04	0.40	<0.001	0.30

**Table 3.** Behaviours during the finishing phase (wk 8 – 23) in percentage of behavioural scans for each treatment group: high and low IGEg pigs both in barren (B) and enriched (E) pens, with *P*-values for the difference between IGEg groups (*P*-IGE), the difference between housing conditions (*P*-HC), and their interaction (IGE×HC). Values are LSmeans of untransformed data with standard error (SEM).

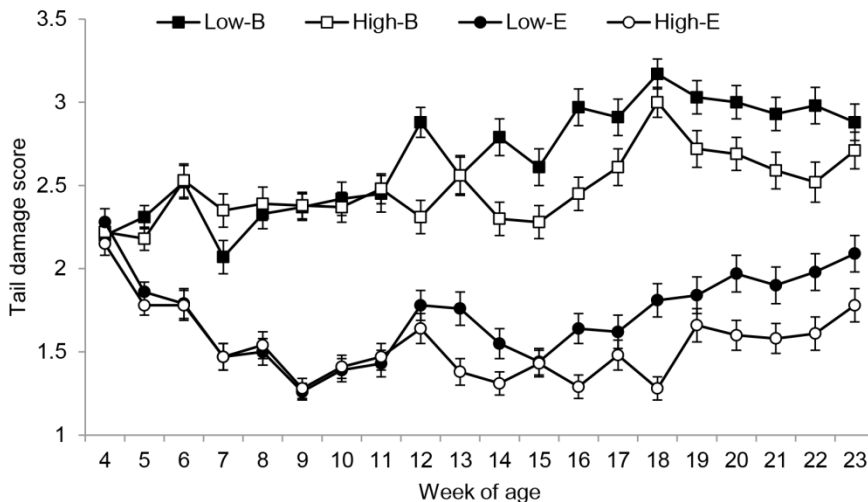
Behav. finishing	High	High	Low	Low	SEM	<i>P</i> -IGE	<i>P</i> -HC	IGE× HC
	E	B	E	B				
Sleeping	51	55	50	53	1	0.14	0.004	0.54
Lying inactive	14	17	16	17	0.4	0.12	0.002	0.03
Standing	1.1	0.88	0.96	0.95	0.1	0.65	0.12	0.15
Locomotion	0.97	0.79	0.76	0.82	0.1	0.11	0.33	0.04
Sitting	1.9	1.3	2.0	1.4	0.1	0.50	<0.001	0.80
Comfort behav.	0.13	0.07	0.08	0.05	0.01	0.005	<0.001	0.06
Eating	7.2	8.0	7.2	8.1	0.2	0.72	<0.001	0.91
Drinking	2.8	1.9	2.8	2.3	0.1	0.13	<0.001	0.08
Urinate/defecate	0.26	0.34	0.32	0.36	0.03	0.09	0.02	0.41
Playing	0.08	0.05	0.13	0.11	0.03	0.14	0.28	0.69
Exploration floor	8.0	6.0	7.5	6.8	0.4	0.73	0.004	0.09
Nosing object	1.9	1.4	1.8	1.7	0.1	0.37	0.004	0.08
Rooting	1.8	0.4	1.6	0.45	0.1	0.82	<0.001	0.40
Rooting object	0.08	0.06	0.08	0.07	0.01	0.99	0.74	0.85
Chewing	5.8	3.5	5.6	3.4	0.2	0.41	<0.001	0.86
Chewing toy	0.82	1.1	1.1	1.8	0.2	0.005	0.03	0.22
Nosing body	0.75	0.87	0.79	1.0	0.1	0.21	0.02	0.52
Nose contact	0.17	0.17	0.15	0.15	0.02	0.34	0.76	0.95
Belly nosing	0.03	0.13	0.02	0.09	0.03	0.37	0.002	0.40
Mounting	0.03	0.00	0.01	0.01	0.01	0.45	0.18	0.23
Fighting	0.05	0.03	0.03	0.02	0.01	0.25	0.07	0.39
Head knock	0.03	0.04	0.04	0.03	0.01	0.82	0.80	0.92
Biting	0.01	0.04	0.04	0.05	0.01	0.006	0.03	0.30
Fighting at feeder	0.03	0.05	0.05	0.06	0.01	0.30	0.19	0.97
Tail biting	0.05	0.18	0.07	0.17	0.02	0.70	<0.001	0.51
Ear biting	0.08	0.14	0.11	0.18	0.02	0.03	0.004	0.86
Manip. other	0.17	0.40	0.20	0.40	0.04	0.70	<0.001	0.73

### Effect of housing condition on behaviour

Enrichment with straw significantly influenced almost all behaviours during the nursery and finishing phase (Table 2, Table 3). Pigs in enriched pens were more active compared to pigs in barren pens, which was seen from less time spent on sleeping, lying inactive and standing. Pigs in enriched pens especially showed less tail biting, ear biting, and belly nosing, and instead spent more time on play, comfort behaviour, and nosing and rooting the pen than pigs in barren pens.

### Tail damage scores

Pigs already showed tail damage from the moment of weaning, with an average tail damage score of 2.2 (Figure 2). During the nursery phase (wk 4 – 7) there was no difference between the IGEg groups for tail damage ( $P = 0.93$ ), but a clear difference was present between barren and enriched pens (tail damage score nursery: barren  $2.3 \pm 0.04$ ; enriched  $1.8 \pm 0.04$ ;  $P < 0.001$ ). During the finishing phase (wk 8 – 23) high IGEg pigs had a lower tail damage score (high  $2.0 \pm 0.05$ ; low  $2.2 \pm 0.05$ ;  $P = 0.004$ ), and the positive effect of enrichment remained (mean tail damage score finishing: barren  $2.6 \pm 0.05$ ; enriched  $1.6 \pm 0.05$ ;  $P < 0.001$ ). This resulted in an additive effect of IGEg group and straw enrichment on tail damage, without interactions between these two factors ( $P = 0.79$ ).



**Figure 2.** Tail damage score for high IGEg pigs in barren pens, high IGEg pigs in enriched pens, low IGEg pigs in barren pens, and low IGEg pigs in enriched pens. Note that the y-axis ranges from 1 – 3.5 while tail damage scores from individual pigs may range from 1 – 4.

### **Consumption of jute sacks**

From week eight onward a jute sack was attached to the wall of each pen to limit tail biting behaviour (Figure 1). Chewing on a jute sack was indeed related to chewing on a tail, with a positive correlation between the consumption of jute sacks per pen and average tail damage on pen level ( $r_p = 0.34$ ;  $P = 0.003$ ). In pens with high IGEg pigs these sacks had to be replaced 30% less often than in pens with low IGEg pigs. Over a period of 15 weeks, high IGEg pigs consumed  $2.9 \pm 0.3$  jute sacks per pen, whereas low IGEg pigs consumed  $4.2 \pm 0.3$  sacks per pen ( $P = 0.002$ ). Pigs in barren pens consumed  $4.3 \pm 0.3$  jute sacks whereas in enriched pens on average  $2.8 \pm 0.3$  jute sacks were consumed ( $P < 0.001$ ). There was no interaction between IGEg group and housing condition for the consumption of jute sacks ( $P=0.84$ ).

## **7.4 Discussion**

We have investigated the behavioural consequences of a single generation of divergent selection for IGEg in pigs in two housing systems. The diverging IGEg groups showed structural differences in biting behaviours directed towards pen mates and to the physical environment during the finishing phase. This indicates that selection on IGEg may alter a range of behaviours, and even behaviours not related to group members, such as biting on objects in the environment. This suggests that selection on IGEg does not merely alter social interactions, but rather results in changes in an internal state of the animal from which differences in behaviour may arise.

### **Potential underlying mechanisms**

The origin of biting behaviour may be found in amongst others aggression, frustration, stress, or maintenance of dominance relationships (Scott, 1948; Marler, 1976; Schrøder-Petersen and Simonsen, 2001). Pigs of high IGEg were suggested to be better in establishing dominance relationships (Canario et al., 2012), and pigs selected for high IGEg showed subtle differences in aggressive behaviour (Camerlink et al., 2013). Although the expression of aggressive and competitive behaviours might have been tempered by *ad libitum* feeding (Camerlink et al., 2014a), these behaviours did not seem the major factor underlying the effects of IGEg in the currently studied pigs. Aggression and competition in general, however, are associated with IGE in a wide range of taxa (reviewed by Wilson, 2013). Another hypothesis is that IGEg might alter activity (Rodenburg et al., 2010), whereby the positive effect on the growth rate of others would occur due to

apathy of the animal, resulting in a reduced number of social interactions, and thus also a reduced negative impact on the growth rate of others. The activity level of high and low IGEg pigs did not differ in the current study, which suggests no such response to selection.

The varying biting behaviours seem more to originate from frustration or stress. Pigs have a strong intrinsic need to root and forage, and when this need cannot find an outlet in the physical environment it may be redirected to group members (e.g. Schrøder-Petersen and Simonsen, 2001). Tail biting, ear biting, and chewing on distraction material may therefore have a similar motivational background. These behaviours have also been related to frustration, stress, and fearfulness (Taylor et al., 2010; Zupan et al., 2012). Additional behavioural and physiological data suggest that high IGEg pigs may be better capable of handling stressful situations and are less fearful (Camerlink et al., 2013, Reimert et al., 2013a, 2014). Similarly, laying hens selected on IGEs for survival, which is directly related to cannibalistic pecking, were less sensitive to stress and were less fearful (reviewed in Rodenburg et al., 2010). Tail biting and cannibalistic pecking have similar underlying needs (e.g. urge to forage, feed or explore) and causes (e.g. stress or nutritional deficiencies). Though this concerns different species, and selection for IGE on different traits, the behavioural responses to selection have remarkable similarities which may suggest a similar mechanism in pigs and laying hens. Together, the various behaviours that are altered through selection on IGEg seem to reflect an internal state rather than solely social interactions.

### **The effect of selection**

In this study, many behaviours have been tested for statistical significance, which increases the risk of false positives due to chance. However, we found a systematic pattern of less biting behaviour in high IGEg pigs, which was supported by extreme *P*-values that are unlikely to be chance results. We believe that the four significant results all relating to biting behaviour, with an average *P*-value of  $\sim 0.005$  (biting, chewing toy, jute sacks consumed, and tail damage score) indicate a true effect. We did not observe differences between IGEg groups in tail biting behaviour itself, which might be due to the scan sampling method, whereby short lasting behaviours are easily missed. The higher tail damage in low IGEg pigs indicates that low IGEg pigs did spend more time on tail biting or were biting more fiercely. Biting behaviour, and especially tail biting, is considered an important animal welfare issue and our results suggest that selection on IGEg may contribute to a solution. The potential effect of IGEg on harmful biting behaviour might have been underestimated in the current trial. The circumstances of the trial were more

favourable compared to common (Dutch) intensive farming conditions (more space per animal), and control measures were taken to limit tail biting (daily treatment of wounded tails, provision of wood shavings and jute sacks, and the removal of animals with shortened tails). In particular, part of the disposition to bite may have been redirected to chewing on the jute sack (Fraser, 1991; Van de Weerd and Day, 2009). This together may have reduced tail biting and may have prevented a severe outbreak (Zonderland et al., 2008; Statham et al., 2009). Interference in possible underlying mechanisms of IGEGs, for example changing resource availability, might alter the effect of selection (Arango et al., 2005; Wilson, 2013). With no interference in the cannibalistic pecking of laying hens, clear differences between high and low IGEG selection lines were found (reviewed in Rodenburg et al., 2010). From a scientific perspective, measures to limit tail biting would ideally have been omitted, but this would go against ethical regulations of animal experiments. If biting behaviour would be one of the mechanisms underlying IGEG in pigs, then control measures may have reduced the expression and effect of selection.

### **Considerations for implementation**

Previously, behavioural changes were suggested in a small experiment applying selection on IGEG in pigs (Rodenburg et al., 2010), and in a multiple-generation selected experiment based on the performance of groups of half sibs (Gunsett, 2005). The current study is, however, the first large scale experiment evaluating the behavioural consequences of selection on IGEG in a large mammal. Knowledge on the mechanisms behind IGEG in pigs may contribute to the optimization of pig breeding and farming. For example, insight in which inherited behaviours affect growth rate of group mates may outline the potential possibilities, and potential profitability, of reducing or enhancing specific social interactions. Follow-up research under commercial conditions, and selection over multiple generations, would be essential to gain further insight in the magnitude and potential variability of the behavioural changes on the long term. If selection on high IGEG causes pigs to show less harmful biting behaviour, then over generations, other behaviours might emerge in relation to IGEG.

### **Benefits from both genetics and environment**

G×E interactions may be present for pig production traits (Schinckel et al., 1999), but are to date not shown for pig behaviour (e.g. Guy et al., 2002b). Little G×E interactions for pig behaviour were found in the current study, and it is therefore not expected that genetic selection on IGEG would alter behaviour differently in different housing conditions. Provision of straw resulted in more behaviour

directed towards the environment, which is in accordance with literature (e.g. Fraser et al., 1991). The reduction in damaging behaviour and the lower tail damage scores of pigs on straw clearly point out the potential of substrate to improve pig health and welfare. Tail damage was further reduced in pigs selected for high IGEg, which suggests that differences in the genetic disposition to perform tail biting remain present also when suitable substrate is provided. This shows that biting behaviour can be reduced from two approaches, namely by redirecting the biting behaviour towards the environment instead of conspecifics through the provision of suitable substrate, and by reducing the motivation to bite through selection on IGEg. Straw is often regarded the most suitable substrate to reduce tail biting (Zonderland et al., 2008; Van de Weerd and Day, 2009), but selection on IGEg may give an additional reduction that is cumulative over generations, leading to a further increase in animal welfare.

### **7.5 Conclusion**

Selection on high IGE for growth in pigs reduced biting behaviour, which was expressed in lower occurrences of aggressive biting, ear biting, biting on materials provided for chewing (including jute sacks), and less tail damage due to tail biting. The availability of straw in the pen reduced the expression of pen-mate directed behaviours. Hereby straw may redirect the biting behaviour to the environment, whereas selection for IGEg may reduce the disposition to bite. Both may therefore lead to improvements in animal welfare. We outlined some aspects for further research and would like to emphasize that the impact of selection for IGEs for production traits may reach further than solely social interactions.

### **7.6 Acknowledgements**

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## Appendix

**Table A1.** Ethogram.

Behaviour	Description
<b>General individual</b>	
Sleeping	Lying without performing any other described behaviour, eyes closed
Lying inactive	Lying without performing any other described behaviour, eyes opened
Standing	Standing without performing any other described behaviour
Locomotion	Walking or running without performing any other described behaviour
Sitting	Sitting or kneeling without performing any other described behaviour
Comfort behaviour	Rubbing body against objects or pen mate, scratching body with hind leg or stretching (part of) body
Eating feeder	Eating at feeder
Drinking	Drinking from drinking nipple
Urinate/defecate	Urinating or defecating
<b>Exploration</b>	
Exploration floor	Sniffing, touching or scraping floor
Nosing object	Nosing above floor level
Rooting	Rooting pen floor or in wood shavings or straw
Rooting object	Rooting above floor level or object
Chewing	Non-feed chewing or chewing straw
Chewing toy	Chewing toy: chain with ball or jute sack
<b>Social</b>	
Nosing head or body	Touching/sniffing any part of a pen mate except nose
Nose contact	Mutual nose contact
Playing	Individual or group wise gamboling, pivoting: running around the pen, sometimes with gently nudging of pen mates
Belly nosing	Rubbing belly of a pen mate with up and down snout movements
Mounting	Standing on hind legs while having front legs on other pig's body
<b>Aggression</b>	
Fighting	Ramming or pushing a pen mate with or without biting the pen mate. Can be either mutual or individual
Head knocking	Head knock given at place other than feeder
Biting	Bite given at other place than feeder
Fighting at feeder	Push, head knock or bite given at feeder
<b>Oral manipulation of group mates</b>	
Tail biting	Nibbling, sucking or chewing the tail of a pen mate
Ear biting	Nibbling, sucking or chewing the ear of a pen mate
Manipulating other	Nibbling, sucking or chewing part of the body of a pen mate



# 8

## **Indirect genetic effects and housing conditions in relation to aggressive behaviour in pigs**

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### **Abstract**

Indirect Genetic Effects (IGEs), also known as associative effects, are the heritable effects that an individual has on the phenotype of its social partners. Selection for IGEs has been proposed as a method to reduce harmful behaviours, in particular aggression, in livestock and aquaculture. The mechanisms behind IGEs, however, have rarely been studied. The objective was therefore to assess aggression in pigs which were divergently selected for IGEs on growth (IGEG). In a one generation selection experiment, we studied 480 offspring of pigs (*Sus scrofa*) that were selected for relatively high or low IGEG and housed in homogeneous IGEG groups in either barren or enriched environments. Skin lesion scores, a proxy measure of aggression, and aggressive behaviours were recorded. The two distinct IGEG groups did not differ in number of skin lesions, or in amount of reciprocal fighting, both under stable social conditions and in confrontation with unfamiliar pigs in a 24 h regrouping test. Pigs selected for a positive effect on the growth of their group members, however, performed less non-reciprocal biting and showed considerably less aggression at reunion with familiar group members after they had been separated during a 24 h regrouping test. The enriched environment was associated with more skin lesions but less non-reciprocal biting under stable social conditions. Changes in aggression between pigs selected for IGEG were not influenced by G×E interactions with regard to the level of environmental enrichment. It is likely that selection on IGEG targets a behavioural strategy, rather than a single behavioural trait such as aggressiveness.

**Keywords.** social genetic effect, aggressive behaviour, environmental enrichment, swine, skin lesion scores

## 8.1 Introduction

The social behaviour of group housed animals is of great importance for their health, welfare, and productivity which may decline due to receipt of harmful social behaviours. Harmful social behaviours, such as aggression, are considered an important problem in commercial livestock farming (Gonyou, 1994; Turner, 2011). Here, we assess the potential of a new breeding method using information on indirect genetic effects, to reduce aggression in pigs.

An Indirect Genetic Effect (IGE), also known as social genetic effect, associative effect or competitive effect, is a heritable effect of an individual on the trait values of its social partners or group mates (Griffing, 1967; Moore et al., 1997; Wolf et al., 1998; Muir, 2005). The classical example of an IGE is the maternal genetic effect of a mother on trait values of her offspring in mammalian species (Dickerson, 1947; Willham, 1972; Kirkpatrick and Lande, 1989; Wolf et al., 1998). Note that the term 'maternal genetic effect' does not refer to the effects of genes transmitted by the mother to her offspring, but to the heritable component of the environment that the mother provides to her offspring, e.g., via maternal care behaviour. In other words, with IGEs, the social environment that an individual experiences contains a heritable component (Wolf et al., 1998). Another well-known case of IGEs in livestock populations occurs in cannibalistic laying hens, where the survival probability of an individual depends on the genotype of its cage mates (Muir, 2005; Peeters et al., 2012). IGEs have been studied in several animal species, such as cattle, mice and deer (Van Vleck and Cassady, 2005; Wilson et al., 2009; Bijma, 2011a; Wilson et al., 2011), as well as in plants and trees (Cappa and Cantet, 2008; Brotherstone et al., 2011; Wolf et al., 2011; Costa e Silva et al., 2013).

IGEs can have a profound effect on heritable variation in traits and on response to selection (Griffing, 1967; Moore et al., 1997). For example, they can fully remove heritable variation in a trait despite a positive classical heritability (Wilson et al., 2011; Costa e Silva et al., 2013), and may cause a negative response to positive selection (Griffing, 1967; Muir, 2005). Hence, when present, IGEs are highly relevant for livestock genetic improvement. By including IGEs in the breeding criteria, both the additive genetic merit of an individual for own performance, the so-called direct genetic effect, and its indirect genetic effect on the performance of its social partners are taken into account. For example, an animal may be a less attractive candidate for selection if it has a high level of individual performance in an economically important trait but shows much aggression towards others, thereby reducing their performance. Due to the potential of IGEs to increase both production and animal welfare, IGEs have become an increasingly important research topic in animal breeding (Bijma, 2011a).

IGEs are hypothesized to be related to behaviour, and in particular to aggression and competition (Moore et al., 1997; Muir, 2005; Wilson et al., 2009; Chen et al., 2007; Rodenburg et al., 2010; Canario et al., 2012). However, the actual behaviour of animals with diverging estimated IGEs has rarely been studied. In mice, IGEs have been shown to affect agonistic behaviours (Wilson et al., 2009) whilst in laying hens, selection for IGEs on survival time reduced harmful feather pecking behavior (Ellen et al., 2008; Rodenburg et al., 2008). In pigs, where IGEs are estimated based on the growth of group members (Chen et al., 2007; Bergsma et al., 2007; Bergsma, 2011), there are indications that pigs with diverging IGEs for growth, though not genetically selected for IGE, differ in the amount of skin lesions (Rodenburg et al., 2010; Canario et al., 2012), which is a commonly used proxy measure of aggression (Marchant-Forde and Marchant-Forde, 2005; Turner et al., 2006).

Aggression is a natural behaviour that contributes to the establishment of dominance relationships, and is most common and intense when unfamiliar conspecifics first meet (Marchant-Forde and Marchant-Forde, 2005; Marler, 1976). Once dominance relationships have been established, aggression is usually limited. In commercial farming, aggression is more likely to escalate, due to management practices such as regrouping unfamiliar animals, and the confined enclosures which may impede retreat after a threat (Petherick and Blackshaw, 1987). Aggression is considered a problem for animal welfare and production (Turner, 2011; Marchant-Forde and Marchant-Forde, 2005; Cutts et al., 1998). Aggressiveness is moderately heritable and can be genetically selected against (Turner, 2011; Benus et al., 1991), but phenotyping behavioural traits or their proxy measures is time consuming. Genetic selection for IGEs on growth does not require additional phenotyping and, moreover, targets social interactions as a whole rather than a single behaviour. Genetic selection for IGEs has therefore been proposed as a potential method to improve group production and to reduce harmful behaviours in livestock (Turner, 2011; Bijma, 2011a).

In commercial pig farming, pigs are regrouped with unfamiliar pigs as standard management practice, with intense aggression as a result. For several weeks after regrouping, pigs may have an impaired immune response and reduced growth (Marchant-Forde and Marchant-Forde, 2005; Stookey and Gonyou, 1994; Hyun et al., 1998; De Groot et al., 2001). The level of aggression may vary among environments, as has been shown in amongst others, humans (Miles and Carey, 1997), mice (Haemisch et al., 1994), fish (Kadry and Barreto, 2010), and pigs (Van de Weerd and Day, 2009). In pigs for example, the availability of bedding substrate suitable for rooting and chewing, such as long-stemmed straw, has been shown to crucially affect behaviour (reviewed by Tuytens, 2005) and mood (Mendl et al.,

2009; Brydges et al., 2011). Moreover, the expression of a genetic disposition for aggressiveness may largely depend on the environment (reviewed by Nelson and Trainor, 2007). To assess whether the outcome of selection for IGEs differs within different environments, the effect of environmental conditions and the extent of genotype by environment interactions should be estimated.

This study therefore investigated whether pigs selected for either high or low IGE on growth, and housed in either a conventional barren pen or a straw-enriched pen, show differences in aggression under regrouping situations and stable social conditions. The hypothesis that pigs selected for high IGE for growth would show less aggression towards group members was assessed by observations on skin lesion scores and aggressive behaviours in pigs divergently selected for IGE on growth.

## 8.2 Materials and Methods

### Ethics

This study was carried out in strict accordance with the recommendations in the European Guidelines for accommodation and care of animals. The protocol was approved by the Institutional Animal Care and Use Committee of Wageningen University (Protocol Number: 2010055f).

### Indirect Genetic Effects

This section briefly summarizes the theory on IGEs. In quantitative genetics, phenotypic trait values ( $P$ ) in the absence of IGEs are usually modelled as the sum of a heritable component, the breeding value ( $A$ ), and a residual component, the environment ( $E$ );  $P = A + E$  (Falconer and Mackay, 1996). When individuals affect each other's trait values, this model has to be extended with IGEs (Griffing, 1967),

$$P_i = A_{D,i} + E_{D,i} + \sum_{j=1}^{n-1} A_{S,j} + \sum_{j=1}^{n-1} E_{S,j}$$

where  $i$  denotes the focal individual,  $j$  one of its  $n-1$  group mates,  $A$  denotes heritable effects (also known as breeding values), subscript  $D$  denotes direct effects and subscript  $S$  denotes indirect effects. Hence, with IGEs the trait value of an individual is the sum of its own direct genetic effect,  $A_{D,i}$ , the sum of the IGEs of all its group mates,  $\sum_{j=1}^{n-1} A_{S,j}$ , and a non-heritable component,  $E_{D,i} + \sum_{j=1}^{n-1} E_{S,j}$ .

With this model, response to selection is determined by the change in the so-called

total breeding value ( $A_T$ ) (Moore et al., 1997; Bijma, 2011b),

$A_{T,i} = A_{D,i} + (n - 1)A_{S,i}$ , where  $n - 1$  is the number of group mates excluding the individual itself. Thus,  $A_{T,i}$  represents for each individual the effect of its genes on its own phenotype, plus the effects of its genes on the phenotypes of its group mates.

### Indirect Genetic Effect (IGE) estimation

Estimated breeding values (EBV) for IGEs were based on growth rate during the finishing phase (from app. 25 – 110 kg), here abbreviated as IGEg. EBVs were estimated using Best Linear Unbiased Prediction and a so-called animal model (Henderson, 1975). Following (Muir, 2005; Arango et al., 2005; Bijma et al., 2007b), the animal model included both the direct effect of the individual, the IGEg of each of its group mates, and a random group effect. Full details of the model are given in (Bergsma, 2011).

Subsequently, the dams and sires with the most extreme high and low IGEg of the available population were selected to create a F1 population, see Table 1.

**Table 1.** Selection of animals based on estimated IGEg contrast.

	High IGEg		Low IGEg		Contrast (g/day)
	N	Est. IGEg*	N	Est. IGEg	
Selected sires	13	4.36 ± 0.1	11	-1.65 ± 0.1	6.01
Selected dams	34	-0.35 ± 0.05	31	-1.66 ± 0.05	1.31
Offspring	240	2.00 ± 0.6	240	-1.62 ± 0.5	3.62

\* Estimated Indirect Genetic Effect for growth rate in grams per day

Dams (Topigs-20 sows: sow line of Great Yorkshire × Dutch Landrace) were selected out of in total 120 sows from the TOPIGS experimental farm. Sires (Tempo boars: commercial synthetic boar line with Great Yorkshire genetic background) were selected from in total 532 TOPIGS AI boars. The contrast for estimated IGEg between the high and low selected offspring was on average 3.6 g/day (Table 1). Average accuracy of the estimated IGEg of the sires was 0.63. Sires and dams were selected so that the average estimated direct genetic effect was similar for both offspring groups (High: 11 ± 2 g ADG; Low: 8 ± 2 g ADG;  $P = 0.36$ ). After weaning, offspring were housed in groups of six (see section Animals and housing). The IGE contrast, therefore, corresponds to an expected growth difference of  $(6-1) \times 3.6 = 18$  g/day (Bijma et al., 2007b). Theoretically, this would mean an expected difference of 2.9 kg in body weight between the pigs from the high and low group at the end of the 160-days trial (at ~110 kg). Power calculations, taking into account



both the uncertainty in the genetic selection differential and the additional noise in the observed response to selection due to non-genetic effects (the  $E$ -terms in the above expression for  $P_i$ ), indicated that this response was expected to be significant ( $P < 0.05$ ).

### **Animals and housing**

A total of 480 offspring were studied over five batches of 96 piglets each. Piglets were born in conventional farrowing crates (TOPIGS experimental farm, Beilen, The Netherlands). Tails and teeth were kept intact, but male piglets were castrated at three days of age. Cross fostering was applied only if litter sizes exceeded 14 piglets, and always within the same IGE group. At approximately 14 days of age, piglets were subjected to the backtest to assess their coping style (Hessing et al., 1993; Bolhuis et al., 2003). Hereby a piglet is placed in a supine position for 60 s whereby its response is indicative of its behavioural strategy. At 26 days of age, piglets were weaned and a maximum of eight (non-cross fostered) piglets per sow were selected. Selection was based on general health, sex, and backtest classification. At weaning, the average weight did not significantly differ between the high and low IGE group. Selected piglets were transported to experimental farm De Haar (Wageningen, The Netherlands). During transportation, all litters were kept separately to avoid aggression. Transportation did not lead to notable skin lesions.

From weaning on, a 2x2 experimental arrangement was applied with IGE (low vs. high) and housing conditions (barren vs. enriched) as factors at the pen level. Within each batch, pigs were housed in 16 pens of six individuals each, giving a total of 80 pens.

On arrival at the farm, each pig was placed immediately in a pen with five unfamiliar pigs. Each pig was identified by a spray marked number on the back, which was refreshed before tests and observations. Group composition was within pen balanced for sex (1:1) and backtest classification (1:3 pro-active to re-active coping style, according to the distribution of the whole tested population). The distinct IGE groups were never mixed. Half of the pigs from each IGE group, and half of the selected piglets from each sow, were allocated to a barren pen, and the other half to an enriched pen.

Barren pens had a floor which was half solid concrete and half slatted whilst enriched pens had a solid floor with a deep litter bedding of sawdust and straw. All pens had a space allowance of  $\sim 1.0 \text{ m}^2/\text{pig}$ , and contained a metal chain with galvanized ball (75 mm diameter). Dry pelleted commercial feed was offered *ad libitum* from a single space feeder. Water was continuously available from a single

## 8 IGEg and aggression

nipple drinker per pen. Lights were on from 7:00 till 19:00 h. From week eight onwards, all pens received a handful of sawdust per day and a jute sack attached to the wall to reduce damaging tail biting behaviour. Pigs were housed in these pens from weaning until slaughter at 23 weeks of age. Due to diverse health reasons, 18 high IGE pigs and 11 low IGE pigs were removed from the experiment.

### Tests and observations

The timeframe in which the tests and observations were carried out are presented in Table 2. Data on tests and skin lesions were recorded by a single observer, who was unaware of the IGE group of the pigs. Live behavioural observations were performed by several observers who were unaware of the IGE group of the pigs. These observers were trained beforehand to score in the same way and were balanced across treatment groups.

**Table 2.** Tests and observations by week of age (w). Pigs ( $n = 480$ ) were slaughtered at 23 w of age.

Age	Test	Behavioural observations	Skin lesions
2 w	Backtest		
4 w	Weaning (d 26)	Scan sampling* (d 27 and d 29)	4 h before weaning 24 h after weaning
5 w		Scan sampling	
8 w		Scan sampling	
9 w	Regrouping test (24 h)	Scan sampling Continuous observation (video)	1 h before regrouping 24 h after regrouping
10 w	Response to weighing	Scan sampling	
16 w		Scan sampling	
18 w			9 w after regrouping
21 w		Scan sampling	

\*2-min Instantaneous scan sampling, generally for 6 h per day of observation per pig.

### Regrouping test

In commercial farms, pigs are usually relocated and regrouped at around nine weeks of age. To simulate this situation, pigs of nine weeks of age were regrouped for 24 h within IGE group and housing condition. The (temporary) new group consisted of three unfamiliar pairs of pigs and within each pair was balanced for sex (1:1) and within group was balanced for backtest classification (1:3 pro-active to reactive coping style). None of the pigs in the newly composed groups were full-sibs.

Pigs were relocated, within 15 min, into a pen that was unfamiliar to all pigs. Pigs were kept in the new group composition for 24 h, after which they were relocated to their initial pens and reunited with their original pen mates. Behaviour was video recorded from 2 h before the regrouping test until 48 h after the start of the test.

### **Skin lesion scores**

Skin lesions were counted as the number of lesions by body region, following the procedure of Turner et al. (2006). Body regions were front (head, neck, shoulders and front legs), middle (flanks and back), and rear (rump, hind legs and tail). For each body region, a differentiation was made between superficial and deep skin lesions. Deep skin lesions were lesions where skin was broken, showing signs of haemorrhage. Skin lesions were counted before and after encounters with unfamiliar pigs, see Table 2. For the skin lesion score 24 h after regrouping, a cell counter was used to facilitate the counting of lesions.

### **Live behavioural observations**

Behaviours of individual pigs were recorded on eight days in total, see Table 2. The ethogram included reciprocal fighting, aggressive non-reciprocal biting, head knocks and aggression at the feeder. Aggression at the feeder included all reciprocal fights, aggressive non-reciprocal bites, and head knocks given within <1m distance from the feeder. All other active behaviours were summed to approximate a general activity level. Behaviour was scored during live observations using 2-min instantaneous scan sampling, for 6 h per day between 8:00 and 17:00 h. The Observer 5.0 software package (Noldus Information Technology B.V., Wageningen, The Netherlands) installed on a hand-held computer, was used for behavioural recordings.

### **Video observations after the regrouping test**

Videos from immediately after the regrouping test, when pigs were reunited with their original pen mates, were analysed for number of aggressive interactions per pen. From the moment that all six pigs had returned to their home pen until 30 min thereafter, the number of reciprocal fights, non-reciprocal (series of) bites, head knocks and fights at the feeder were counted per pen. Reciprocal fights and non-reciprocal series of bites were counted from the start of a series of aggressive interactions until either the end of the fight or series of non-reciprocal bites, or a pause of at least 3 s.

### **Response to handling at weighing**

Response to handling at weighing previously showed a positive genetic correlation with aggression ( $r_g$  0.41 – 0.60) (D'Eath et al., 2009), and was therefore included in this study. At 10 weeks of age pigs were weighed and the response of the pigs to handling at weighing was scored. This was the first time that the pigs experienced a weigh crate. Behaviour during weighing was scored as previously described (D'Eath et al., 2009). Briefly, each pig received three scores: a 1 – 5 score for the ease of entering the crate, a 1 – 3 score for movements in the crate and, a 1 – 3 score for ease of leaving the crate. The lower the score, the more resistance the pig showed to handling or being in the crate. The number of vocalizations was recorded from entering the crate until the moment the pig left the crate.

### **Data analysis**

Statistical analyses were performed using SAS (SAS 9.2, Institute Inc.). Residuals of the response variables were checked for normality.

To test whether the skin lesion score differed between IGE groups and housing conditions, pre-mixing skin lesion scores were subtracted from the number of skin lesions after regrouping. Negative values were set to zero. The number of skin lesions on the body as a whole (sum front, middle and rear) was square root transformed to achieve a normal distribution, and analysed in a mixed model (Mixed Procedure), with IGE group, housing condition, the interaction between IGE group and housing condition, sex and batch as fixed effects and pen nested within IGE group, housing condition and batch as random effect. Scores on the separate body parts were not normally distributed after transformation and were analysed as described above, but with the raw data in a generalized linear model with Poisson distribution (Glimmix Procedure).

Scan samples from the live behavioural observations were expressed as the proportion of total observation time spent on a behaviour and were analysed separately for each observation day. To obtain a normal distribution, behaviours were arcsine square root transformed. Effects of IGE group and housing condition on aggressive behaviour were analysed in a mixed model as described above (Mixed Procedure). Including general activity in the model did not lead to considerable changes in the reported P values and was therefore omitted from the model. The number of aggressive interactions as observed from video footage was recorded on a pen level and therefore analysed with a general linear model (GLM Procedure) including the effects of IGE group, housing condition and batch.

Response to handling at weighing was tested for differences between IGE groups and housing conditions. Data on batch 3 had to be omitted due to technical

problems with the weigh crate. Scores on entering the crate were analysed with a mixed model as described above for skin lesions (Mixed Procedure). For movements in the crate and leaving the crate, score 1 was combined with score 2, since only 3 pigs had score 1 for movements in the crate, and 15 pigs had score 1 for leaving the crate. Scores for movement in the crate and on leaving the crate were therefore analysed using a generalized mixed model with a binary distribution and a logit link function (Glimmix Procedure).

Data are presented as (untransformed) means  $\pm$  SEM.

### 8.3 Results

#### **Skin lesions**

The number of skin lesions did not significantly differ between high IGE and low IGE pigs at any scoring time or on any body region (Table 3). Intensity of the lesions (superficial or deep) did not significantly differ between high and low IGE pigs ( $P=0.54$ ). Pigs housed in enriched pens had higher skin lesion scores at all sampling points under stable social conditions and at 24 h after the regrouping test on the middle and rear of the body, and had also more deep lesions on the total body (Barren:  $6.8 \pm 0.4$ ; Enriched:  $8.1 \pm 0.4$  lesions;  $P = 0.004$ ). The interaction between IGE group and housing condition had no significant effect on the lesion scores ( $P=0.87$ ). Female pigs had more skin lesions on all scoring days (mean total lesion score over all scoring days: females  $139 \pm 5$  vs. male  $124 \pm 5$ ;  $P = 0.05$ ), but this effect differed by body region on each recording day.

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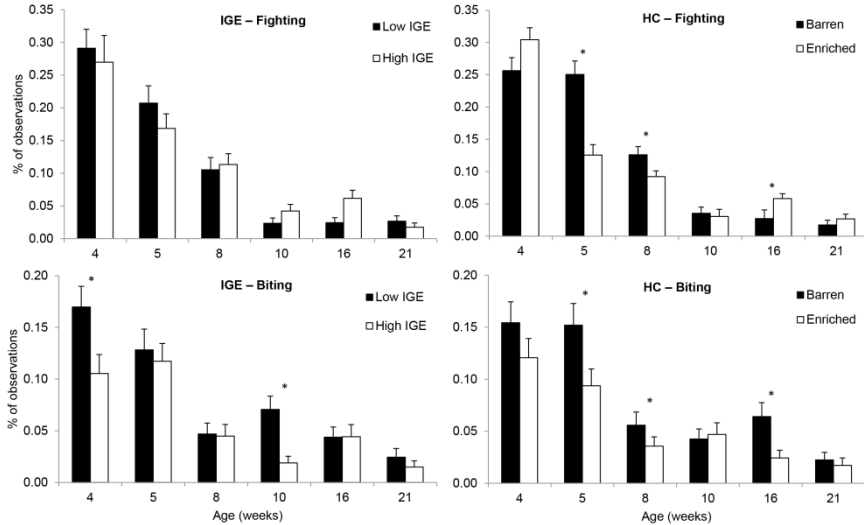
**Table 3.** Number of skin lesions for high and low IGE pigs in barren and enriched housing, for each body region (F=front; M=middle; R=rear), by week of age (w) with weaning at 4 w of age and the regrouping test (RT) at 9 w. P-values are given for the difference between IGE groups (IGE) and housing conditions (HC).

Age		High IGE		Low IGE		P-value	
		Barren	Enriched	Barren	Enriched	IGE	HC
4w	F	17.8 ± 2.4	22.2 ± 2.4	20.4 ± 2.4	23.0 ± 2.4	0.16	0.18
	M	6.9 ± 1.1	9.9 ± 1.1	8.5 ± 1.1	10.1 ± 1.1	0.41	0.14
	R	4.5 ± 0.8	5.1 ± 0.8	4.3 ± 0.8	6.1 ± 0.8	0.61	0.16
9w	F	2.8 ± 0.4	4.2 ± 0.4	3.0 ± 0.4	4.9 ± 0.4	0.18	<0.001
	M	1.9 ± 0.4	4.7 ± 0.4	1.9 ± 0.4	3.6 ± 0.4	0.66	<0.001
	R	0.7 ± 0.2	1.7 ± 0.2	0.6 ± 0.2	1.5 ± 0.2	0.64	<0.001
9w RT	F	34.6 ± 3.0	41.9 ± 3.0	33.4 ± 3.0	35.4 ± 3.0	0.96	0.64
	M	25.3 ± 3.1	35.4 ± 3.1	27.6 ± 3.0	31.4 ± 3.0	0.75	0.23
	R	11.1 ± 1.8	15.5 ± 1.8	14.5 ± 1.8	17.5 ± 1.8	0.07	0.17
16w	F	3.3 ± 0.4	5.1 ± 0.4	3.3 ± 0.4	5.4 ± 0.4	0.79	<0.001
	M	1.9 ± 0.4	3.7 ± 0.4	2.1 ± 0.4	3.9 ± 0.4	0.87	<0.001
	R	1.5 ± 0.3	2.7 ± 0.3	1.5 ± 0.3	2.9 ± 0.3	0.86	<0.001

### Behavioural observations

High IGE pigs showed less non-reciprocal biting behaviour than low IGE pigs in week 4 (High:  $0.10 \pm 0.02$ ; Low:  $0.17 \pm 0.02$  % of observations;  $P = 0.006$ ), three days after weaning, and week 10 (High:  $0.02 \pm 0.01$ ; Low:  $0.07 \pm 0.01$ ;  $P < 0.001$ ), seven days after the regrouping test (Figure 1). There was no significant difference between high and low IGE pigs in the number of reciprocal fights, except for week 16, when high IGE pigs in enriched pens fought more (High:  $0.06 \pm 0.01$ ; Low:  $0.02 \pm 0.01$ ;  $P = 0.02$ ). The IGE groups did not differ in the amount of head knocks ( $P = 0.32$ ) or fights at the feeder ( $P = 0.62$ ). Housing conditions influenced the amount of aggression during the weeks after the regrouping situations, whereby pigs in barren pens showed more biting in week 5 (Barren:  $0.15 \pm 0.02$ ; Enriched:  $0.09 \pm 0.02$  % of observations;  $P = 0.03$ ) and week 16 (Barren:  $0.06 \pm 0.01$ ; Enriched:  $0.02 \pm 0.01$ ;  $P = 0.03$ ; Figure 1). Pigs in barren pens also showed more reciprocal fighting in week 5 (Barren:  $0.2 \pm 0.03$ ; Enriched:  $0.1 \pm 0.03$ ;  $P = 0.008$ ) and week 8 (Barren:  $0.14 \pm 0.02$ ; Enriched:  $0.08 \pm 0.02$ ;  $P = 0.04$ ; Figure 1). There tended to be an interaction between IGE group and housing condition for non-reciprocal biting in week 4 ( $P = 0.06$ ), due to a higher in amount of biting in low IGE pigs in barren pens as compared to high IGE pigs in enriched pens (High-E:  $0.11 \pm 0.02$ ; Low-B:  $0.21 \pm 0.02$  % of observations;  $P = 0.004$ ). An opposite interaction tended to exist for

fighting in week 16, where high IGE pigs in enriched pens fought more than low IGE pigs in barren pens (High-E:  $0.09 \pm 0.01$ ; Low-B:  $0.02 \pm 0.01$ ;  $P = 0.004$ ).



**Figure 1.** Aggressive behaviour from life observations. Percentage of observation spent on reciprocal fighting and non-reciprocal biting for IGE group (low and high IGE) and housing condition (HC, barren and enriched) over weeks of age outside regrouping situations (4 w and 9 w). Significant differences are indicated by \* $P < 0.05$ .

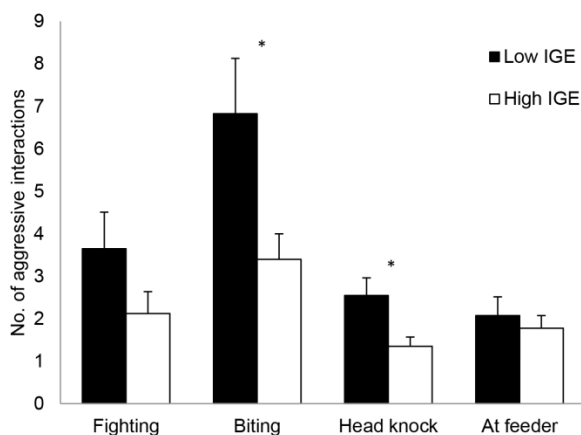
On the day after weaning, the amount of non-reciprocal biting and reciprocal fighting did not differ between IGE groups (Biting:  $P = 0.97$ ; Fighting:  $P = 0.63$ ) or between housing conditions (Biting:  $P = 0.78$ ; Fighting:  $P = 0.12$ ). During the regrouping test at 9 weeks of age, the amount of non-reciprocal biting and reciprocal fighting did not differ between IGE groups (Biting:  $P = 0.98$ ; Fighting:  $P = 0.14$ ). Pigs in enriched pens showed more biting during the regrouping test (Barren:  $0.32 \pm 0.04$ ; Enriched:  $0.46 \pm 0.05$  % of observations;  $P = 0.02$ ), but not more reciprocal fighting ( $P = 0.35$ ). Female pigs showed more aggressive behaviour during all observation days (Females:  $0.42 \pm 0.02$ ; Males:  $0.35 \pm 0.02$ ;  $P = 0.02$ ), except for weaning and the first week after weaning (weeks 4 and 5). In week 5, males showed more aggression (Females:  $0.53 \pm 0.04$ ; Males:  $0.64 \pm 0.04$ ;  $P = 0.03$ ).

### Aggression at reunion

The distinct IGE groups showed considerable behavioural differences upon reunion with familiar group members after having been separated for 24 h during the

## 8 IGEg and aggression

regrouping test. In the first 30 min after reunion, pigs from high IGE pens had on average  $8.0 \pm 1.8$  aggressive interactions, whereas pigs from low IGE pens had  $15.7 \pm 1.8$  aggressive interactions ( $P = 0.004$ ). In high IGE pens, there was less non-reciprocal biting (High:  $3.4 \pm 0.6$ ; Low:  $6.8 \pm 1.3$  occurrences in 30 minutes;  $P=0.008$ ) and there were fewer head knocks (High:  $1.4 \pm 0.2$ ; Low:  $2.6 \pm 0.4$  occurrences in 30 minutes;  $P = 0.02$ ; Figure 2). In 9 out of 60 cases low IGE pens had more than 20 aggressive interactions (range 0 – 49), while none of the high IGE pens reached this number of encounters (range 0 – 18). There was no effect of housing condition on the amount of aggression shown ( $P = 0.85$ ), nor an interaction between IGE group and housing condition ( $P = 0.44$ ).



**Figure 2.** Aggression at reunion. Frequency of aggressive interactions within low and high IGE pens during the 30 min after reunion by type of aggressive behaviour. Aggression at feeder includes fighting, biting and head knocks given within <1 m of the feeder. Significant differences are indicated by \* $P < 0.05$ .

### Response to handling at weighing

In general, pigs entered the weigh crate after little encouragement by an animal handler. High IGE pigs entered the weigh crate more easily than low IGE pigs (High: score  $3.8 \pm 0.1$ ; Low: score  $3.6 \pm 0.1$ ;  $P = 0.03$ ). Pigs housed in enriched pens also entered the crate more easily (Enriched: score  $3.8 \pm 0.1$ ; Barren: score  $3.6 \pm 0.1$ ;  $P=0.04$ ). Pigs mostly stood still in the crate (score  $2.8 \pm 0.02$ ) and left the crate after some encouragement of the animal handler (score  $2.4 \pm 0.04$ ). There was no significant effect of IGE group on movements in the crate ( $P = 0.75$ ) or resistance to leaving the crate ( $P = 0.79$ ), nor for housing conditions ( $P = 0.97$  for movements on



the crate;  $P = 0.50$  for leaving the crate). There was no interaction between IGE group and housing condition on any of the measurements for response to weighing (overall  $P = 0.30$ ).

### **8.4 Discussion**

We hypothesized, as aggression may reduce growth (Stookey and Gonyou, 1994; Hyun et al., 1998) that animals selected for high IGE for growth (IGEg) would be less aggressive than animals selected for low IGE. In this study, high IGE and low IGE pigs did not differ in number of skin lesions or in time spent fighting. High IGE pigs, however, performed less biting and showed considerably less aggression at reunion with familiar group members after they had been separated during a 24 h regrouping test at 8 w of age. Pigs in enriched housing conditions had more skin lesions but showed less aggressive behaviour. There was no significant interaction between IGE group and housing condition. It therefore seems unlikely that possible changes in aggressive behaviour of pigs selected for IGEg would differ between barren and enriched pens.

#### **IGEg and skin lesions**

Previous studies on pigs with estimated breeding values for IGE on growth showed that high IGE pigs had more skin lesions on the front of the body after regrouping, but had fewer lesions under stable social conditions in the weeks after regrouping (Rodenburg et al., 2010; Canario et al., 2012). Skin lesions on the front of the body are typically received during reciprocal fighting and those on the rear of the body indicate that the pig has been bullied (Turner et al., 2009). It was therefore suggested that high IGE pigs are more competent at establishing dominance relationships. In the current study, skin lesion scores did not significantly differ between the IGE groups. This discrepancy with the previous study might be due to differences in the experimental design. This was the first study where a large number of pigs were selected on extremes of estimated IGEg and housed in distinct IGE groups, whereas in previous studies pigs were randomly grouped together without prior knowledge of their IGEg (Canario et al., 2012). Based on skin lesion scores alone, we could not confirm that high IGE pigs would show less aggression, or would be better able to establish dominance relationships, than low IGE pigs.

#### **IGEg and aggressive behaviour**

Behavioural observations did reveal differences in aggression between high and low IGE pigs. The main result was that high IGE pigs showed considerably less aggression in the first 30 min after reunion with familiar pen mates after 24 h

exposure to unfamiliar pigs in a regrouping test. We expected to see a difference within the 24 h of regrouping because this period is often studied for the intense aggression that occurs in this timeframe. In commercial farming, animals are not reunited after regrouping, but this unexpected finding may provide important information on behavioural strategies that may change in animals selected for IGEg. We here outline three potential mechanisms.

One hypothesis for why high IGE pigs fought less when they were reunited with familiar pen mates could be that dominance relationships were more stable in high IGE groups beforehand, or that high IGE pigs apply a different dominance style (Ruis et al., 2002) and, that therefore, high IGE pigs could re-establish their dominance relationships with less aggression at reunion. High IGE pigs showed less non-reciprocal biting in both weeks after a regrouping situation, which would be in line with this hypothesis (Rodenburg et al., 2010; Canario et al., 2012). Also when aggression is limited, as non-reciprocal biting in the weeks after regrouping occurred on an average of only 0.4% of the behavioural scans, dominance relationships may still have an effect on health and stress levels (Sapolsky, 2005; Creel, 2001). Although instantaneous scan sampling may underestimate the amount of short lived behaviours such as non-reciprocal biting (Altmann, 1974), and in reality the amount of aggressive interactions would be higher as observed from scan samples, we are cautious about drawing conclusions based upon this difference in IGE groups.

Another hypothesis could be that low IGE pigs experience more stress after social interruptions such as regrouping, or that they were more inclined to direct their stress or frustration towards pen mates than high IGE pigs given the same level of stress (Hyun et al., 1998; Scott, 1984). Differences between the IGE groups became apparent after weaning and regrouping, expressed in non-reciprocal biting. Non-reciprocal biting is also referred to as bullying behaviour (D'Eath et al., 2009), but may also have an important function in stress-induced aggression as biting may suppress the release of stress-induced noradrenaline and ulcer formation (Tanaka et al., 1998; Dudink et al., 2006). Potentially, low IGEg pigs evaluate a social interruption differently or are more likely to direct their response towards group members.

A third hypothesis could be that high IGE animals are better able to recognize or remember their original group members. During stressful situations, social recognition or social memory may be impaired (Takahashi et al., 2004; Souza and Zanella, 2008), which may increase aggression (Zayan, 1990; Ferguson et al., 2002; Bielsky et al., 2004). It is possible that high IGE animals have better social recognition, or are better able to cope with stressful situations as the differences in

aggressive behaviour between IGE groups were in all cases present in the week after a stressful regrouping event.

From both this study and the studies of Rodenburg et al. (2010) and Canario et al. (2012) it seems that selection for IGEg does affect aggression related behaviour in pigs. Previous studies showed that selection for IGEs influenced aggression in mice (Wilson et al., 2009), and influenced feather pecking behaviour in laying hens (Rodenburg et al., 2008). It is possible that selection for IGEg affects a range of behavioural traits of which aggression is one. This range of traits may for example affect the way in which dominance relationships are established (Rodenburg et al., 2010; Canario et al., 2012) or social cohesion is maintained (De Waal, 1986). The fact that high IGE pigs entered the weigh crate more easily shows that selection for IGEg changes more than the expression of aggression alone. Difficulty with entering the crate might reflect an aggressive temperament (D'Eath et al., 2009; Crump, 2004), but may also reflect, for example, stress susceptibility, fear of humans or novel situations, or sociability by moving towards or away from group members.

### **Housing conditions and aggression**

The environment can contribute to the expression of aggression, irrespective of the genetic merit of an individual for aggressiveness (Van Loo et al., 2002; Nelson and Trainor, 2007). The direction in which the environment affects aggression, however, appears to differ both between and within species (Haemisch et al., 1994; Loo et al., 2002; Van de Weerd and Day, 2009). The same holds for pigs, where enriched pens may lead to less aggression (Lyons et al., 1995), no difference in aggression (Arey and Franklink, 1995; Bolhuis et al., 2005a; Scott et al., 2006), or more aggression (Morgan et al., 1998; Spoolder et al., 2000) as compared to barren pens of equal size. In the current study, pigs in straw-enriched pens had more skin lesions under stable social conditions, but showed less non-reciprocal biting than pigs in barren pens. Though the number of skin lesions may be underestimated due to skin dirtiness (Whittaker et al., 1999; Spoolder et al., 2000; Guy et al., 2002c), as pigs in the barren pens had a more dirty skin (unpublished results), lesions were clearly visible and were scored when the observer was in close proximity to the animal.

Animals in an enriched environment may have more injuries, like skin lesions (Arey and Franklink, 1995; Van de Weerd and Day, 2009), due to higher activity levels or due to competition over resources (Elwood et al., 1998), such as fresh substrate or a dry lying area (Andersen et al., 2000). Skin lesions under stable social conditions may have also been caused by play behaviour or comfort behaviour, like scratching, which occurred more in enriched environments (Dudink et al., 2006; Camerlink et

al., submitted). When skin lesions, which are considered as a heritable trait (Turner et al., 2006; Turner, 2011), are used to reduce aggression through direct breeding, the likelihood of increased skin lesions due to an enriched environment should be taken into account. During regrouping situations, housing conditions may have less effect on the number of skin lesions as animals will fight regardless of their environment when they first meet an unfamiliar conspecific (Marler, 1976), and lesion scores may better reflect the amount of aggressive interactions.

### **Selection for IGEg**

At present, very little is known of the mechanisms underlying IGEs for growth rate in pigs. When behaviours underlie IGEg, differences in behaviour may be a precursor to differences in growth. If that is true, one generation of selection might not be sufficient to detect differences in growth between groups despite the a priori power calculations which suggested a sufficient contrast. For the trait under selection, i.e. growth rate, indeed no phenotypic differences were found between both IGE groups (Camerlink et al., 2014a). Differences in behaviour, however, may already be present after one generation of selection. Differences in aggressive behaviour between the IGE groups in this study were small and point to a difference in behavioural strategy rather than aggressiveness per se. Similar indications come from a selection experiment in laying hens selected based on total breeding value for survival time, which showed distinct patterns in harmful pecking behaviour (Rodenburg et al., 2008) while the differences in pecking-related mortality were less clear (personal communication ED Ellen). It would be worthwhile to investigate these behavioural differences after multiple generations of selection for IGEg.

### **8.5 Conclusion**

This is the first study where a large number of pigs was selected and grouped based on IGE for growth (IGEG). Selection for high IGEg did not affect the major aggression parameters in pigs, namely skin lesion scores and fighting during regrouping. The results show, however, that this first stage of selection considerably reduced aggression at reunion with familiar group members and gave a small reduction in non-reciprocal biting in the weeks after regrouping. Changes in aggressive behaviour as a consequence of selection for IGEg do not seem to be influenced by a G×E interaction with regard to the level of environmental enrichment. Aggression may be one facet of the possible ways in which group housed animals may influence each other's growth. If IGEg are included in the breeding criteria it would be important to consider the possible changes in behaviour over generations.

## **8.6 Acknowledgements**

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# 9

## **Aggression and affiliation during social conflict in pigs**

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Submitted

### Abstract

Social conflict is mostly studied in relation to aggression. A more integral approach, including aggressive and affiliative behaviour as well as physiology, may however give a better understanding of the animals' experience during social conflict. The experience of social conflict may also be reflected in the spatial distribution between conspecifics. The objective was to assess the relationship between behaviour, physiology, and spatial integration in pigs (*Sus scrofa*) during social conflict. Hereto, 64 groups of pigs (9 wk of age) were studied in a 24 h regrouping test whereby pairs of familiar pigs were grouped with 2 unfamiliar pairs, in either barren or straw-enriched housing. We recorded inter-individual distances, lying in body contact, aggressive and affiliative behaviour, skin injuries, body weight, and haptoglobin. These variables could be summarized into three principal component analysis factors. The three factors were analysed in relation to spatial integration. Results show that pigs stayed up to 24 h after encounter in closer proximity to the familiar pig than to unfamiliar pigs. Pigs with a high factor 1 score were more inactive, gave little social nosing, had many skin lesions and a high body weight. They spaced further away from the familiar pig ( $b = 3.7$  cm;  $P = 0.02$ ) and unfamiliar ones ( $b = 1.5$  cm;  $P < 0.01$ ). Pigs with were much involved in aggression (factor 2), and had a strong increase in haptoglobin (factor 3 describing stress), tended to be relatively further from unfamiliar pigs than from familiar ones ( $b = 0.07$  times further;  $P = 0.06$ ). Results on lying in body contact were coherent with results on distances. Pigs in enriched housing spaced further apart than pigs in barren housing ( $P < 0.001$ ). The combined analysis of measures revealed animals may either promote or slow down group cohesion, which would not have been revealed from single parameters. This emphasizes the importance of an integral approach to social conflict.

Keywords: pig, spatial integration, cohesion, aggressive behaviour, distance, social interaction, haptoglobin



## 9.1 Introduction

When unfamiliar animals first meet this may result in social conflict. Social conflict may involve excessive aggression, and efforts have been made to reduce aggression within this context (Marchant-Forde & Marchant-Forde, 2005; Turner, 2011). Aggression, however, only samples part of the behavioural repertoire that animals may express to solve social conflicts. Alongside aggression there may be subtle affiliative behaviours, such as social grooming and body contact, that may promote reconciliation and group cohesion (De Waal, 2000; Kaburu & Newton-Fisher, 2013). These behaviours are well studied in primates (Arnold & Aureli, 2007), but largely ignored in most other species (Spruijt et al., 1992; Lim & Young, 2006; Kutsukake & Clutton-Brock, 2008). Assessing animals, or their welfare, should not only require assessment of aggression, but might also require taking into account cognitive processes and social skills that may promote social cohesion (Turner, 2011; Duboscq et al., 2014).

In gregarious animals, social cohesion may be measured by the distance between group members (i.e. their spatial integration) and their affiliative interactions (Warburton & Lazarus, 1991; Blumstein et al., 2009; Turner et al., 2013). These measures may reflect social acceptance, and have been suggested to reflect the animals' experience of a stressful situation (Arnold & Aureli, 2007; Turner et al., 2013). Animals may show clear preferences for whom they allow in close proximity and will move away or show aggression when disliked animals approach too closely (McBride, 1971; Durrell et al., 2004). This is especially relevant in livestock farming, where animals may be introduced to unfamiliar conspecifics several times during the production cycle and are commonly kept under minimal space requirements, allowing little room to move away from each other (Andersen et al., 2004; Febrer et al., 2006).

In commercially kept pigs, regrouping aggression is considered to be a major welfare issue (Arey & Edwards, 1998). Regrouping, whereby unfamiliar animals encounter each other, is a common management strategy in commercial farming. Regrouping results in aggressive interactions, which amongst others causes (skin) injuries (e.g. Turner et al., 2006; Stukenborg et al., 2011), and alters stress physiology (e.g. Fernandez et al., 1994). Aggression in pigs has been studied for decades (reviewed by Petherick & Blackshaw, 1987), but up to now remains a persistent problem, which may emphasize the need for a different approach. Insight into pigs' experience of social conflict might contribute to a solution, but this has hardly been studied (Mendl et al., 1992; Turner et al., 2013).

To solve complex behavioural issues, and to achieve sustainable welfare improvement, an integral approach might be required (Blumstein et al., 2010). We

aimed to take such an approach in pigs. Our objective was to assess behavioural and physiological characteristics that may be related to the spatial integration between pigs during social conflict. We hypothesized that the spatial integration of regrouped pigs would depend on aggressive interactions as well as on positive social contact. The objective was to investigate which characteristics in behaviour and physiology would contribute most to small inter-individual distances, indicative of social cohesion.

### 9.2 Material and methods

This study was part of a larger trial in which animals were selected for diverging indirect genetic effects for growth (IGeG) and either housed in barren and enriched pens (described in Animals and housing). Because these factors may influence the social interactions between animals, they were taken into account in the current study. All protocols were approved by the Animal Care and Use Committee of Wageningen University (Protocol Number: 2010055f).

#### Animals and housing

A total of 384 pigs of 9 weeks of age, housed in 64 pens, were studied over four batches. These animals were offspring from 64 Topigs-20 sows (sow line of Great Yorkshire × Dutch Landrace) and 24 Tempo boars (commercial synthetic boar line with Great Yorkshire genetic background), which were selected on either 'high' or 'low' indirect genetic effects for growth (IGeG). IGeG is a breeding value that accounts for the genetic effect that a pig may have on the growth rate of its group members (Griffing, 1967; Muir, 2005 and Bijma et al., 2007). Details of the selection on IGeG are described in Camerlink et al. (2013). Piglets were housed in conventional farrowing crates until weaning (at 26 days of age).

From weaning until slaughter, pigs were housed in groups of six (three females and three castrated male pigs) of the same IGeG classification. Each group contained at least one pig from both sexes that had an active response in the backtest, with a maximum of three (Camerlink et al., 2014b). The response of piglets in a backtest may be indicative of a piglet's coping style or behavioural strategy (Benus et al., 1991), and may relate to its aggressive behaviour as well as other traits (Bolhuis et al., 2005).

In the 2 × 2 experimental arrangement that was applied from weaning, half of each IGeG group (high vs. low) was housed in barren pens and the other half was housed in enriched pens. The barren conventional pens had a 60% solid concrete and 40% slatted floor. Enriched pens had a solid floor with a deep litter bedding of straw and wood shavings. Space allowance in both housing conditions was between 1.0 – 1.2

m<sup>2</sup> per pig, depending on the barn. Pen dimensions were 1.90 m × 3.20 m in two batches, whereas in the other two batches pens measured 2.25 × 3.25 m. Each pen contained a single space feeder, a nipple drinker, and a metal chain with a ball. Lights were on between 07:00 and 19:00 h. The thermostat was set at 20°C and pigs were fed *ad libitum* with dry pelleted feed.

### **Regrouping test and skin lesion score**

At nine weeks of age, pigs were regrouped for 24 h (~12:00 h to ~12:00 h the following day) within their IGEg group and housing condition. From each pen, one male and one female pig were relocated into an unfamiliar pen where they were joined with two unfamiliar other pig pairs from different pens. None of the pigs in the new pen were full-sibs, and pen composition was balanced for backtest response. Pigs received a number sprayed on their back for recognition, and a coloured dot on their neck (stock marker spray) to identify the pig pair. Video cameras were mounted above the pens to enable video recordings. After 24 h, pigs were returned to their initial pen, and the number of fresh skin lesions was counted for the anterior, middle, and rear regions of the body immediately upon return (Turner et al., 2006). In addition to the number of skin lesions per body region, the body region where the greatest percentage of skin lesions was observed was noted as the predominant location. For each pig, body weight at 9 weeks of age was known.

### **Spatial distribution**

Data on spatial distribution of pigs were obtained from the video footage that was available from the regrouping test. For each pen there were video recordings from 11:00 – 19:00 h at the day of regrouping, and from 07:00 – 12:00 h the following day. Every hour, from the moment that all six pigs had entered the new pen, a screenshot was made from the video footage. The screenshot was made when at least 4 of the 6 pigs were lying. In case more than 2 pigs were standing, the video was forwarded until the moment that at least 4 pigs were lying. In this way, 13 to 14 images were obtained per pen. For each pen, a grid with corresponding x and y coordinates was made at an appropriate scale to be overlaid on the video playback. For each pig, the x and y coordinate at the height of the neck was noted. When the neck of a pig could not be located due to objects in front of the lens (e.g. feeder), the middle of the pig was taken as a reference point. When the distances were calculated, a distinction was made between the familiar pig of the pair and the 4 unfamiliar pigs. It was also noted whether a pig was lying with at least 50% of its body in direct contact with a familiar or unfamiliar pig.

### **Blood collection and haptoglobin determination**

Haptoglobin is an acute phase protein that may reflect amongst others immune activation and distress (human: Langois & Delanghe, 1996; cattle: Lomborg et al., 2008; pigs: Pineiro et al., 2007; Salamano et al., 2008). Pigs were blood sampled in the week before the regrouping test (wk 8) and at the third day after the test (wk 9) by puncture of the jugular vein. The order of sampling was randomized over IGEg group and housing condition. Blood was collected in a serum tube and stored at room temperature. The samples were incubated for one hour at 37°C, and thereafter centrifuged at 20°C at a speed of 5251 g for 12 min. The serum obtained was stored at -80°C. The haptoglobin concentration was determined from the serum using a commercial kit based on the hemoglobin-binding capacities of haptoglobin (Phase<sup>TM</sup> Haptoglobin, Tridelata Development Limited, Maynooth, Ireland), which has been validated for pigs (GD Animal Health Service, Deventer, the Netherlands). Hemoglobin (100 µl) was added to sera (7.5 µl) and gently mixed. Thereafter, chromogen (140 µl) was added and the solution was incubated for 5 min at RT and the absorbance read immediately at 600 nm in a microplate reader. The concentration of haptoglobin (mg/ml) was calculated with a standard linear curve for known concentrations of haptoglobin. The difference between the basal level and the level following regrouping (wk 8 subtracted from the levels at wk 9) was used for analyses, and is here referred to as  $\Delta$ haptoglobin.

### **Live behavioural observations**

Behaviour of the pigs was observed live during the regrouping test by 2-min instantaneous scan sampling for six hours. The Observer 5.0 software package (Noldus Information Technology B.V., Wageningen, The Netherlands) installed on a hand-held computer was used for behaviour recordings. Observations were divided into 1 h blocks (with 15 min breaks between each block) from 14:00 – 17:30 h on the day of regrouping and from 08:00 – 11:30 h the following day. This procedure resulted in 180 observations per pig. Behaviours that were analysed were inactivity (lying with the eyes closed or eyes open), aggression (reciprocal fighting, head knocks, and unilateral biting), and social nosing (nosing the body of a pen mate and nose-nose contact with a pen mate). For aggressive behaviour and social nosing both the giver and receiver of the behaviour were recorded as either a familiar pig or an unfamiliar one.

**Data preparation**

The distance between two spatial coordinates was calculated using  $a^2 + b^2 = c^2$ , in which  $a = x_{\text{pig1}} - x_{\text{pig2}}$ , where  $x_{\text{pig1}}$  is the x-coordinate of the chosen pig and  $x_{\text{pig2}}$  is the x-coordinate of another pig. The same procedure was used for  $b$ , which is the difference between the y-coordinates of two pigs. The square root of the resulting  $c^2$  was the distance between two pigs.

The distances to the four unfamiliar pigs were averaged, resulting in one value for the distance to the familiar pig and one value for the average distance to the unfamiliar pigs. Due to the lying positions of the pigs, the individual markings on the back of the pigs could not always be identified, but the pig pairs could always be identified due to different colour markings (each pen was composed of 3 familiar pig pairs). Therefore, the average distance to unfamiliar pigs was only available per pig pair. Pig pairs where one of the pigs was removed from the experiment were excluded from analysis ( $n = 5$ ). A relative distance between familiar and unfamiliar pigs was calculated by dividing the average distance of the two familiar pigs to the unfamiliar pigs by the distance to the familiar pig.

Residuals of the variables were obtained from a general linear model (Proc GLM) with housing condition, IGEg group, and batch as fixed effects. For  $\Delta$ haptoglobin one outlier was removed (3.2 mg/ml) which was 4.4 SD higher than the mean (0.14 mg/ml) and 1.3 SD higher than the second highest value. The skin lesion scores were square root transformed, and the behavioural observations were transformed by arcsine square root. After transformation, all residuals followed a normal distribution.

**Principal component analysis (PCA)**

The behavioural and physiological data were correlated with Pearson correlations on the residuals of the GLM. Most variables were moderately correlated (data not shown) and were therefore analysed in a principal component analysis (PCA). The skin lesions on the anterior, middle, and rear of the body were strongly correlated ( $r_p$  0.45 – 0.73; all  $P < 0.001$ ), and therefore only the total number of skin lesions was entered into the PCA with orthogonal rotation. The PCA resulted in three factor with an Eigenvalue above 1 (Table 1).

## 9 Social conflict

**Table 1.** Loadings on the factors extracted by the principal component analysis, after orthogonal rotation, of variables recorded on individual pigs ( $n = 480$ ).

Measure	Factor 1	Factor 2	Factor 3
Skin lesions	<b>0.55</b>	<i>0.45</i>	0.04
Body weight	<b>0.60</b>	-0.02	0.10
$\Delta$ Haptoglobin	0.09	-0.02	<b>0.92</b>
Aggression given	-0.09	<b>0.80</b>	0.16
Aggression received	0.13	<b>0.75</b>	-0.22
Social nosing given	<b>-0.65</b>	-0.08	0.11
Social nosing received	<i>0.37</i>	<i>-0.36</i>	-0.30
Inactivity	<b>0.78</b>	-0.11	0.03
Eigenvalue	1.85	1.56	1.03
Variance explained (%)	23.5	19.4	12.8

Values between 0.30 – 0.50 are in italics, values above 0.50 are in bold.

### Data analysis

The relationship between spatial integration and the behaviour and physiology of pigs was analysed using a mixed model (Proc MIXED) with IGEg group, housing condition, and batch as fixed effects, and the pen during regrouping as a random effect (nested within IGEg group, housing condition, and batch). The response variables were the distance to the familiar pig, the average distance of a pig pair to unfamiliar pigs, the relative distance between the two, and the proportion of observations that pigs spent in body contact with a familiar or an unfamiliar pig. The three PCA factors were included as explanatory variables, and interactions between these variables were explored.

The effect of familiarity was analysed by pig pair in a repeated model whereby for each pair the distance toward the familiar pig was known and the average distance toward the unfamiliar pigs, and similar for lying in body contact. In a mixed model the spatial integration measures were included as response variables whereas the variable 'familiarity' (familiar or unfamiliar) and batch were the explanatory variables. Pig pair was included as a random effect to account for the repeated observation ( $n=2$ ) per pair, and was nested within pen, IGEg group, housing condition, and batch. The model on observations over time (~14 observations within 24 h) included the observation as fixed effect (1 – 14), while the pair (nested with pen, IGEg group, housing condition, and batch) was included as random effect. Data preparation, the PCA analysis, and data analysis were carried out with SAS 9.2. Values presented are (untransformed) LSmeans  $\pm$  SEM.

### 9.3 Results

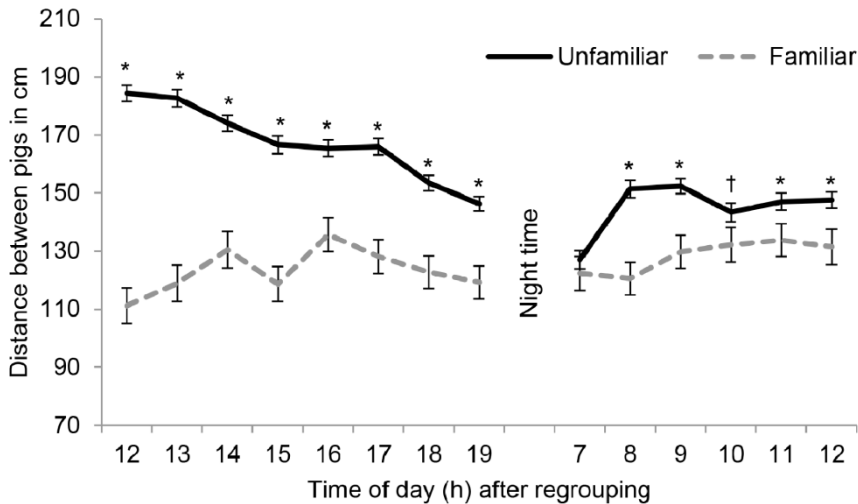
#### Familiarity

Pigs stayed in close proximity to the pig they were familiar to, whereas they spaced away from unfamiliar pigs (Figure 1). On average, familiar pigs lay  $125 \pm 2$  cm apart, whereas their average distance to unfamiliar pigs was  $158 \pm 2$  cm ( $F_{1,187} = 205$ ;  $P < 0.001$ ). Pigs stayed in closer proximity to the familiar pig than to the unfamiliar pigs until night time (Figure 2; all  $P < 0.001$ ). On the following morning, the distance between unfamiliar pigs was smaller, but remained significantly larger than the distance between familiar pigs (all  $P < 0.05$ ), except at 07:00 h ( $P = 0.39$ ), which was the first hour after the dark period, and at 10:00 h ( $P = 0.07$ ).

The closer proximity between familiar pigs was also reflected in the amount of body contact. Familiar pigs lay with at least half of their body in direct contact with each other on an average of  $14 \pm 0.7\%$  of the observations (range 0 – 71%), but in contact with one or more of the unfamiliar pigs on  $21 \pm 0.7\%$  (range 0 – 54%) of observations. If pigs did not differentiate between familiar and unfamiliar pigs when resting, the chance that a pig would lie next to the familiar pig would be four times smaller ( $1/5$ ) than to one of the unfamiliar pigs ( $4/5$ ). When corrected for chance, the frequency of lying in body contact with an unfamiliar pig would equate  $5 \pm 0.7\%$ . Therefore, pigs lay in contact with the familiar pig more often than with unfamiliar pigs as would be expected by chance ( $F_{1,187} = 22$ ;  $P < 0.001$ ).



**Figure 1.** Pigs resting closely together with their familiar pig while resting far apart from unfamiliar pig pairs.



**Figure 2.** Distance between familiar pigs and their average distance to the four unfamiliar pigs over the course of 24 hour after regrouping,  $n = 192$  pig pairs.

### Principal component analysis

The principal component analysis revealed three factors, which together explained 55.6% of the variation (Table 1). A high score of factor 1 related to inactivity, a low amount of giving social nosing towards others, a high number of skin lesions, and a high body weight. Pigs with a high factor 1 score are hereafter mentioned as ‘antisocial’ pigs. A high score of factor 2 was mainly explained by a high amount of aggressive behaviour given and received, as well as a high number of skin lesions. Pigs with a high factor 2 score are hereafter mentioned as ‘fighting’ pigs (not termed as ‘aggressive’, because it also includes pigs that received much aggression and are therefore not necessarily aggressive themselves). A high score of factor 3 explained the increase in the level of haptoglobin, i.e.  $\Delta$ haptoglobin. As haptoglobin was here included as a physiological measure of stress, pigs with a high factor 3 score were termed ‘stressed’ pigs. The receipt of social nosing was the only variable that did not clearly associate with one of the factors (Table 1). Separate analysis of this variable in the mixed models indeed did not reveal a relationship with measures on the distances or body contact.



### Inter-individual distances

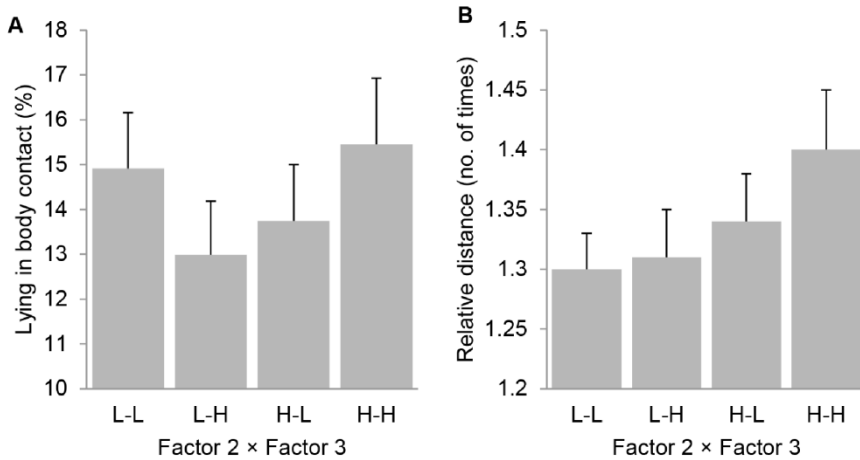
The 'antisocial' pigs (high factor 1 score) spaced far away from the familiar pig ( $b = 2.8 \pm 1.2$  cm;  $F_{1,303} = 5.37$ ;  $P = 0.02$ ), as well as from unfamiliar pigs ( $b = 1.0 \pm 0.4$  cm;  $F_{1,301} = 5.71$ ;  $P = 0.02$ ). Opposite, animals that were active, involved little in aggression, and gave much social nosing were closely situated to other pigs. Pigs spent  $1.8 \pm 1.3\%$  of the behavioural scans giving social nosing, of which on average 20% was directed towards the familiar conspecific.

The 'fighting' pigs (high factor 2 score) gave and received high amounts of aggressive behaviour. Aggressive behaviour, which occurred on average on  $1.1 \pm 1.4\%$  of the behavioural scans, was directed towards unfamiliar pigs on 90% of occasions. 'Fighting pigs' did not significantly differ in their distances toward the familiar pig or toward unfamiliar pigs ( $P = 0.53$ ;  $P = 0.96$ , respectively).

'Stressed' pigs did not differ in their distance toward the familiar pig ( $P = 0.23$ ) or unfamiliar pigs ( $P = 0.45$ ). The haptoglobin concentration after regrouping was on average  $0.70 \pm 0.03$  mg/ml (range 0.04 – 3.5), whereas the difference between the concentration after and before regrouping ( $\Delta$ ) was on average  $0.14 \pm 0.03$  mg/ml (range -2.0 – 2.3). These values are within a normal range for healthy animals.

### Relative distance

Pigs were on average  $1.3 \pm 0.02$  times further away (range 0.8 – 3.3) from unfamiliar pigs than from the pig they were familiar to, which is here referred to as the relative distance. Although 'antisocial' pigs spaced further away from the unfamiliar pigs as well as from the familiar pig, this was only in absolute distance, and not relative to each other ( $F_{1,303} = 0.92$ ;  $P = 0.43$ ). Since both absolute distances were increased, the relative distance to unfamiliar pigs as compared to the distance to the familiar pig remained the same. The distance of a pig toward its familiar pair mate as compared to its distance toward unfamiliar pigs, i.e. the relative distance, tended to increase by the interaction between factor 2 'fighting' and factor 3 'stressed' ( $b = 0.03 \pm 0.02$ ;  $F_{1,303} = 3.04$ ;  $P = 0.08$ ). Hereby 'fighting' pigs which were 'stressed' were on average 0.3 times further away from unfamiliar pigs than other pigs were (Figure 3A). The relative distance to unfamiliar pigs was not affected by the separate contribution of factor 2 ( $F_{1,303} = 0.35$ ;  $P = 0.55$ ) or factor 3 ( $F_{1,303} = 0.86$ ;  $P = 0.36$ ).



**Figure 3.** The effect of the interaction between factor 2 (fighting) and factor 3 (stress) on the relative distance (number of times that a pig is further apart from the unfamiliar pig than from the familiar pig) (A); and the percentage of lying in body contact with the familiar pig (B). The interaction is analysed linearly, but for clarity here presented in categories. The bars represent the average value of pigs with a factor 2 score below (L) or above (H) zero, and a factor 3 score below (L) or above (H) zero (zero was the mean factor score).

### Lying in body contact

Lying in body contact with the familiar pig tended to be affected by the interaction between factor 2 and factor 3, whereby ‘fighting’ pigs which were ‘stressed’ tended to lie most in body contact (Figure 3B;  $b = 1.0 \pm 0.5$ ;  $F_{1,303} = 3.67$ ;  $P = 0.06$ ). Lying in body contact with the familiar pig was not affected by factor 1 (antisocial) ( $F_{1,303} = 0.18$ ;  $P = 0.67$ ), or the separate contribution of factor 2 ( $F_{1,303} = 0.0$ ;  $P = 0.98$ ) or factor 3 ( $F_{1,303} = 0.30$ ;  $P = 0.58$ ). Lying in body contact with unfamiliar pigs was not affected by the interaction between factor 2 and factor 3 ( $F_{1,303} = 2.14$ ;  $P = 0.14$ ), nor by the single contribution of factor 1 ( $F_{1,303} = 0.29$ ;  $P = 0.59$ ), factor 2 ( $F_{1,303} = 0.04$ ;  $P = 0.84$ ), or factor 3 ( $F_{1,303} = 0.10$ ;  $P = 0.75$ ).

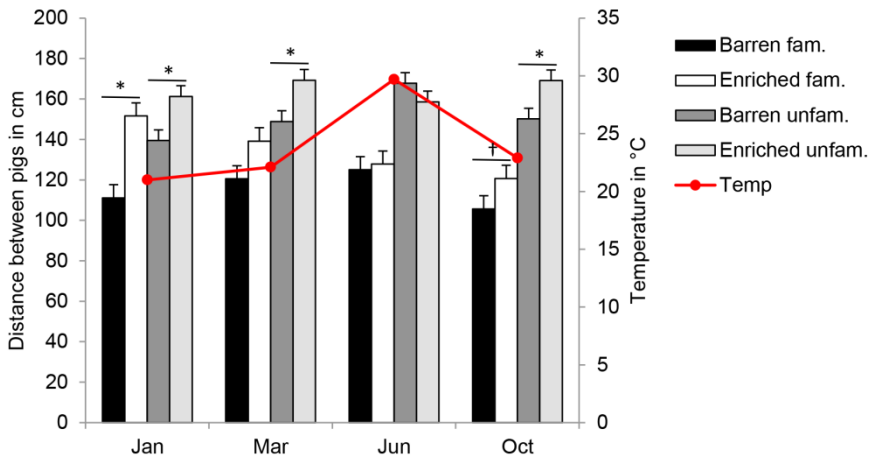
### Enriched housing conditions

Pigs in pens that were enriched with a deep litter layer of straw and wood shavings kept a larger distance to familiar and unfamiliar pigs than those in barren pens (Table 2). However, the relative distance to unfamiliar pigs was smaller, which means that pigs in enriched pens were relatively closer to unfamiliar pigs than to the familiar pig as compared to pigs in barren pens (Table 2). Pigs in barren pens lay

twice as much in body contact with familiar or unfamiliar pigs than pigs in enriched pens (Table 2). Straw bedding conserves heat and temperature may affect proximity between pigs. At observation days that ambient temperature was highest, there was no significant difference between housing conditions (Figure 4), whereas the difference between housing conditions was apparent in the batches where ambient temperature was lower (Figure 4).

**Table 2.** Effect of barren and enriched housing on the distances between pigs,  $n = 369$ . Absolute distances are in cm, whereas the relative distance equals the number of times that a pig is further away from the unfamiliar pig compared to the familiar pig. Body contact is expressed in percentage of observations. Values are LSmeans  $\pm$  SEM.

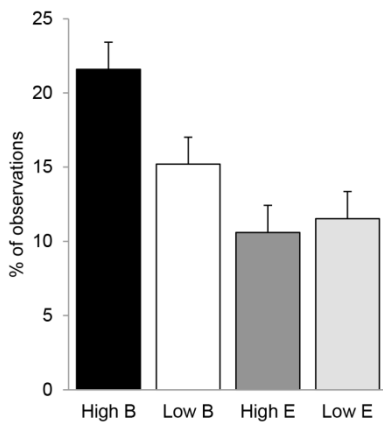
	Barren	Enriched	<i>P</i> -value
Distance to familiar pig	115 $\pm$ 3	136 $\pm$ 3	< 0.001
Distance to unfamiliar pigs	151 $\pm$ 3	165 $\pm$ 3	< 0.001
Relative distance	1.4 $\pm$ 0.04	1.3 $\pm$ 0.04	0.04
Body contact with familiar pig	18 $\pm$ 1.3	11 $\pm$ 1.3	< 0.001
Body contact with unfamiliar pigs	28 $\pm$ 1.4	14 $\pm$ 1.4	< 0.001



**Figure 4.** Distances between familiar and unfamiliar pigs in barren and enriched pens, presented by the month in which the regrouping took place (batch). The secondary axis shows the maximum temperature in the barn at the day of regrouping.

### Indirect genetic effects

There were no significant effects of selection on ‘indirect genetic effect for growth’ (IGEG) as a main effect (all  $P > 0.10$ ). The genotype by environment set-up, however, revealed an interaction for lying in body contact with the familiar pig ( $F_{1,57} = 4.1$ ;  $P = 0.048$ ). Pigs which are genetically selected to have a positive effect on the growth rate of their group members (high IGEG pigs) were lying most frequently in body contact with their familiar pig when they were housed in barren pens. In contrast, of the four treatment group (IGEG  $\times$  housing condition), high IGEG pigs were lying least frequently in body contact with the familiar pig when they were housed in enriched pens (Figure 5).



**Figure 5.** Percentage of observations that a pig was lying in body contact with the familiar pig, given for pigs which were genetically selected for either high or low IGEG, and housed in barren (B) and enriched (E) pens.

## 9.4 Discussion

We aimed to assess the relationship between behavioural and physiological characteristics of pigs and their spatial integration during social conflict. Pigs clearly distinguished between familiar and unfamiliar pigs over the 24 h period after mixing, whereby they remained closer to the familiar pig. Behavioural and physiological measures were largely interrelated. The results highlight that reduced aggression does not necessarily equate to reduced social tension, which may be reflected by large spatial distances. It is therefore important to consider a spectrum of parameters before conclusions are drawn upon the contribution of an animal to the functioning of a group.

### **Characteristics of pigs with a large inter-individual distance**

Pigs with a high factor 1 score in the principal component analysis, i.e. 'antisocial' pigs, were inactive pigs with a high number of skin lesions, high body weight, and little social nosing behaviour. These pigs spaced further away from all other pigs irrespective of familiarity. It seems plausible that these pigs were exhausted of fighting and were therefore less active. As a result of fighting and higher body weight, they may have had an increased body temperature (De Jong et al., 1999), which might make them space further away from all others. This withdrawn position may have led to less social interactions in the form of social nosing. These pigs might also have been unsuccessful in their fights and consequently might not have been allowed in close proximity (Ewbank & Meese, 1971). It could also be that these pigs were dominant. Dominant pigs may keep a larger portable (personal) space than subordinates (McCort & Graves, 1982) which may reflect their own choices or the unwillingness of other animals to closely approach them (McBride, 1971). This high dominance status would be in line with the high body weight (Rushen, 1987), and high amount of aggression as reflected in the skin lesions (Turner et al., 2006). Irrespective of the underlying cause, the response of the 'antisocial' pigs hampered the social cohesion.

### **The role of aggression**

A high factor 2 score, i.e. 'fighting' pigs, described much involvement in aggressive behaviour, which was apparent through a high amount of aggressive behaviour given and received. 'Fighting' pigs did not have any significant effect on the measures of spatial integration, which indicates that studying aggression alone may miss important aspects of social conflict. A potential reason why factor 2 did not relate to any of the measures of spatial integration might be the simultaneous inclusion of given and received aggression in the PCA. The amount of aggressive

behaviours that are given and received are correlated (e.g. Turner et al., 2006). Giving aggression may provoke a different behavioural repertoire than receiving aggression, and this may be reflected in the inter-individual distances. That these different types of involvement in aggression loaded equally on factor 2 may have caused that factor 2 did not reveal any significant effects on the spatial integration.

### **The role of social nosing**

Factor 1 comprised social nosing behaviour, in counter direction to measures on inactivity, aggression, and body weight. Social nosing in pigs may amongst others contribute to recognition and affiliation, and may result in acceptance of a conspecific within the group (Ewbank & Meese, 1971; Camerlink & Turner, 2013). From the current observations, it was not possible to determine whether pigs were nosing a conspecific to recognize the individual, or to express affiliative behaviour. Both may be true, as pigs can easily recognize and remember familiar conspecifics (Ewbank & Meese, 1971), yet twenty percent of the social nosing was directed towards the familiar group mate. Studies from other species indicate that both recognition and affiliative behaviour may have a positive effect on social cohesion (McComb et al., 2000; Arnold & Aureli, 2007). Most studies are based on stable social groups, whereby affiliative behaviour may for example function as a tool to reconsolidate (Kutsukake & Clutton-Brock, 2008). The current study, however, concerned newly formed groups, and the social nosing towards unfamiliar conspecifics might therefore be more likely related to recognition and getting acquainted to each other, which may include sorting out dominance relationships (Kutsukake, 2009; Bonnani et al., 2010). The establishment of dominance relationships may depend on amongst others aggressiveness and physiological differences such as body weight (Rushen, 1987; Andersen et al., 2000; Li and Johnston, 2009; but see a.o. Jensen and Yngvesson, 1998). Pigs with a low factor 1 score were lighter, had less skin lesions, and were more active. These small pigs might have actively avoided fights, or may have gained their rank without the necessity to fight as a result of their low weight compared to others (Andersen et al., 2000). The pigs with a low factor 1 score gave more social nosing and were more likely to approach other pigs, including unfamiliar ones. This suggests that these pigs could better cope with social conflict than pigs with other predominant factor scores.

### **The role of stress**

Factor 3 score described the increase in haptoglobin concentration in the blood. Haptoglobin concentrations may be heightened with physical stress such as

infection, but also with psychological stress (humans: Langois & Delanghe, 1996; cattle: Lomborg et al., 2008; pigs: Pineiro et al., 2007; Salamano et al., 2008). Factor 3 had no influence on the spatial integration between pigs. The interaction with factor 2, however, did affect the integration. The largest relative distances, thus stronger distinction between familiar and unfamiliar pigs, was seen in 'fighting' pigs that were 'stressed'. As a response to psychological stress, these animals may have remained closer to the familiar conspecific, as was reflected in the high frequency of lying in body contact with the familiar pig. The presence of a familiar conspecific may have a stress-buffering effect due to social support in pigs (Ruis et al., 2001; Rault, 2012; Reimert et al., 2013). Pigs have been reported to prefer lying beside a familiar pig for up to six days after mixing, especially in more aggressive groups (Erhard et al., 1997; D'Eath, 2002). The increased  $\Delta$ haptoglobin concentration, as well as the tendency to remain in close proximity to the familiar conspecific, suggests that these animals indeed experienced more stress, either by unsuccessful fights or by a heightened vulnerability to stress (Mendl et al., 1992).

### **Enriched housing conditions**

Apart from the individual pig characteristics that may influence the distance between pigs, the enriched housing caused a considerable increase in the distances between animals, regardless of familiarity. The relative distance towards unfamiliar pigs, however, became smaller in enriched pens, which may have been due to the constraints of the pen dimensions imposing a maximum distance that could be reached within the limited space requirements. Activity in general will increase body temperature, and the insulating properties of straw may preserve body heat more than concrete (Fraser, 1985; Camerlink et al., in press), which might cause animals to space further apart. The increased ambient temperature in the month of June, however, hardly affected the distances (Figure 4), which suggests a role for other factors.

The increased distance might, however, also indicate increased social tension or aggression in enriched pens. Straw-enrichment may increase aggressive behaviour (van de Weerd & Day, 2009) due to the availability of defensible resources such as fresh straw or a dry lying area (Elwood et al., 1998; Camerlink et al., 2013). A reduction, or lack of impact on aggression from straw enrichment has however also been reported (Munsterhjelm et al., 2009; van de Weerd & Day, 2009). In an earlier study we reported that the pigs on straw did not show more aggressive behaviour, but did have more skin lesions as a result of enriched housing (Camerlink et al., 2013), which might be related to increased activity (Munsterhjelm et al., 2009; Camerlink et al., 2013). Environmental enrichment may direct the attention

towards the physical environment rather than to the social environment (Fraser, 1991), which might have influenced the distances between pigs in enriched pens.

### **Indirect genetic effects**

Pigs that were selected on high IGEg, this a positive genetic effect on the growth of pen mates, and housed in barren pens, spent almost twice as many observations in body contact with the familiar pig than pigs from other treatment groups. The inter-individual distance between animals may decrease with genetic selection for social traits, as has been observed in quail selected for social reinstatement behaviour, and this may decrease further in novel and potentially stressful environments (François et al., 1999). Stress is likely to be greater in barren housed animals as compared to enriched housed animals (Hughes & Duncan, 1988; pigs: De Jonge et al., 1996). As argued above, being in close contact with a familiar conspecific may reduce stress. Previous studies suggested that high IGEg pigs are better capable of handling stress (Camerlink et al., 2013; Reimert et al., 2013; Reimert et al., 2014). It might be that this capacity to cope with stress relates to a higher tendency to give or seek social support.

### **An integral approach to social conflict**

The combination of behavioural and physiological data revealed that spatial integration depends mostly on aggression, sociability, and stress vulnerability. If we would like to improve spatial integration between unfamiliar animals upon encounter, this would not necessarily require animals with little aggression, but would rather require animals that cope well with social stress, either through social behaviour or by effective fighting strategies. Absence of fighting is not the same as being free of social tension, and therefore an integral approach may be necessary when assessing animal welfare.

## **9.5 Acknowledgements**

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# 10

## General discussion

### Outline

- 10.1 Introduction
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- 10.3 Effects on behaviour
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  - Positive effects on others
  - Personality
- 10.4 Effects on animal welfare
- 10.5 Genotype by environment interactions
- 10.6 Estimation of IGEg in pigs
- 10.7 Potential underlying mechanisms
- 10.8 Improving welfare of pigs
  - Solutions from genetics
  - Solutions from housing
  - Implementation of strategies to improve welfare
- 10.9 Conclusions

## 10.1 Introduction

Social interactions occur in any given situation where animals encounter each other and may influence health and welfare. When these social interactions are harmful, the recipient may show a reduced performance. In these cases, interactions between animals may put constraints on the response to genetic selection, both in natural populations and agriculture (e.g. Griffing, 1967; Goodnight, 1985; Agrawal et al., 2001). Social interactions are therefore relevant for genetic and behavioural studies. The interplay between these scientific disciplines may give insight in novel methods to improve animal welfare related to social interactions. Social interactions partly depend on genetics and this can be addressed through selection on indirect genetic effects, which account for the heritable component of social effects. An indirect genetic effect (IGE), also referred to as associative-, competitive-, or social genetic effect or social breeding value, is the heritable effect of an individual on trait values of its social partners (Griffing, 1967; Muir, 2005, Bijma et al., 2007b). For example, highly aggressive individuals may harm group members, and their aggressiveness may have a genetic background. IGE-models may be used to account for this genetic effect on group members, which is not accounted for in traditional breeding value estimation.

Including IGE in the estimation of breeding values is suggested as a new method that might improve production performance as well as animal welfare related to social interactions (Muir and Craig, 1998; Muir, 2005; Rodenburg et al., 2010). This is especially relevant to livestock in intensive farming systems. Here, high stocking densities and the occurrence of harmful behaviours often affect health, productivity, and welfare of the animals. Harmful behaviours, such as excessive aggression and cannibalism, are mostly derived from natural behaviours which are, due to housing conditions and management, redirected or overexpressed into aberrant or maladaptive behaviours. The consequences are often harmful for the group mates as well as for the animal itself. Research has offered much insight in harmful behaviours, but up to now their occurrence forms a persistent problem to livestock farming. Currently, the problems arising from harmful behaviours are mostly controlled through measures against the consequences rather than against the cause, e.g. pigs are tail docked and hens are beak trimmed to reduce the severity of the injuries on victims. For the welfare of animals and the sustainability of farming systems, it is of great importance that harmful behaviours between group housed animals are minimized. If a new breeding strategy could improve welfare of those animals within several generations of selection, than it is worth to investigate the merit of this method compared to other efforts to improve animal welfare. As only a handful of animal breeding companies dominate the vast

majority of the genetic improvement of all intensively kept pigs and poultry, the consequences of an improved selection method has the potential to reach livestock production worldwide.

IGE, thus the heritable effects on others, are usually demonstrated by statistical data analysis, but selection experiments to identify the biological background of the effects are rare. The potential underlying mechanisms behind IGE are largely unknown, and unravelling these is complicated by the fact that social interactions, and thus IGE, are presented differently within and across species. Independent of fundamental questions on the mechanisms, there are questions surrounding the application of IGE into breeding that need to be investigated. Especially the suggested contribution of IGE to production performance, behaviour, and animal welfare (e.g. Rodenburg et al., 2010) requires confirmation.

In this chapter, these main issues on IGE are addressed with regard to pigs. Through several studies, among which a large scale one-generation selected experiment, I discuss the contribution of 'IGE on growth rate' (**IGEG**) to pig production performance, behaviour, and welfare, the potential underlying mechanisms, and issues surrounding genetic estimation of IGEG in pigs. Thereafter I discuss the potential of genetic selection and enriched housing conditions to improve the welfare of pigs.

**Conclusion 1.** IGE on production traits are suggested to improve pig production, behaviour, and welfare but this requires confirmation. Also, potential underlying mechanisms are largely unknown and the estimates of genetic parameters need validation. In this chapter, these main questions are addressed focussing on IGE for growth rate (**IGEG**) in pigs.

### 10.2 Effects on productivity

The demand for animal products worldwide is estimated to increase roughly around 60-100% in the coming 30 years (FAO, 2011; Valin et al., 2014). Thereof, the demand for pork may increase ~60% in middle income countries and ~170% in low income countries (estimates for 2030; FAO, 2011). As a response, farmers may aim to increase productivity and production efficiency. Animal breeding has been very effective in increasing productivity and production efficiency, but in a number of cases selection may also have contributed to trade-offs (Rauw et al., 1998), such as an increase in undesired behaviour (Cassady, 2007; D'Eath et al., 2010; Turner, 2011). For example, a high growth rate may coincide with high aggressiveness, as aggressiveness may contribute to access to feed resources (Andersen et al., 2004).

Group members of animals that show harmful behaviour may be negatively affected in their productivity, and thus a negative response to selection may occur due to social interactions (e.g. Griffing, 1967; Goodnight, 1985; Agrawal et al., 2001). By including IGE into the selection criterion, the heritable social effects of individuals on their group mates may be accounted for in the genetic parameter estimations for productivity, resulting in more accurate estimated breeding values (Griffing 1967; Bijma et al., 2007b). More accurate estimated breeding values would enable to increase response to selection, i.e. meaning that group productivity would increase (Lynch and Walsh, 1998).

Prior to the application of the IGE model, several extensive group selection trials have been carried out. Multiple generations of group selection in laying hens (Muir, 1996) and pigs (Gunsett, 2005) resulted in profound increases in productivity and favourable changes in behaviour, e.g. reduced cannibalism (Muir, 1996). Group selection also accounts for social interactions, and the trials applying group selection have built a base for the later IGE models (Muir, 2005). The few selection experiments where animals were selected based on the application of IGE-models indicated a positive response in poultry, which was related to changes in behaviour (Muir, 2005; Ellen et al., 2008; Muir et al., 2013). In pigs, genetic parameters have been estimated which show an important role for IGE on growth rate during the finishing phase (IGEG) (Bergsma et al., 2013). The effects of IGEG on productivity, however, could not be confirmed through (pilot) trials based on IGEG (Chapter 6; Camerlink et al., 2010; Rodenburg et al., 2010). Our large scale selection experiment, where parents were selected for either high or low IGEG, did not result in the expected response in growth rate of offspring, which was the trait under selection (Chapter 6). More remarkable, results on body weight and growth rate even tended to be in the opposite direction (Chapter 6). These observations conflict with the significant variance due to IGEG found by Bergsma et al. (2013) in a statistical analysis of a similar population. Possible reasons for this may relate to the difficulties in estimation, and the expression of IGEG, and are discussed in section 6 'Estimation of IGEG in pigs'.

The selection experiment did reveal changes in pig behaviour, whereby potentially harmful behaviour such as biting pen mates and the resulting tail damage were reduced in high IGEG pigs (Chapter 7; discussed in following paragraph). Selection on IGEG is suggested to improve productivity through a change in behaviour that may affect productivity. The responses in behaviour suggest that selection was effective, but that the extent to which harmful behaviour was expressed was not profound enough to affect growth rate. This may be due to measures that were taken to limit harmful behaviour in order to guarantee a certain level of animal

welfare. Preliminary results showed that these measures may have halved the expression of tail biting behaviour (Ursinus, 2014 personal communication). Moreover, pigs in the current study had intact tails and this may have reduced the consequences of tail biting on growth. Tail biting leads to wounds on the tail of the recipient. In tail docked pigs, these wounds are close to the spinal cord, which is a quick route for infections to spread through the body (Schrøder-Petersen and Simonsen, 2001). Internal organs may be infected and a growth reduction is then a likely consequence (Schrøder-Petersen and Simonsen, 2001). With intact tails, which are ~10 cm longer than docked tails, the tail base may be affected less rapidly.

In the trials up to now, selection on IGEg did not significantly influence productivity. This may partly to be a result of the lower intensity of tail biting behaviour as compared to commercial practice, in combinations with a reduced chance that tail wounds would result in a growth reduction. A selection experiment under commercial circumstances would therefore be recommended.

**Conclusion 2.** Quantitative genetic data analysis suggests the presence of IGE on growth rate in pigs. However, this could not be confirmed in a one-generation selection experiment.

### 10.3 Effects on behaviour

IGE result from social interactions that may be of different origin, e.g. individuals may influence each other through not only behaviour but also through disease transmission (Lipschutz-Powell et al., 2012; trees: Costa e Silva et al., 2013). In the majority of studies, IGE are suggested to be associated with behaviour (Rodenburg et al., 2010; Bijma, 2011a). Depending on the sign of the genetic correlation between direct and indirect genetic effects, IGE may contribute positively or negatively to response to selection, and these cases have been termed as cooperation and competition.

#### **Harmful effects on others**

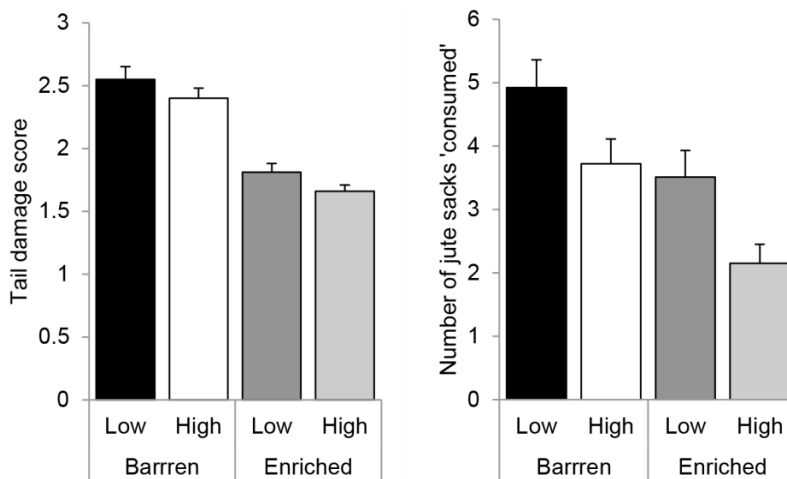
The harmful effects between group members can well be observed in intensively reared farm animals, such as poultry and pigs. Due to barren and confined housing conditions and management procedures, a considerable part of the herd or flock develops aberrant harmful behaviour. In pigs, this is expressed in excessive aggression and oral manipulation of pen mates, whereby tail biting is most evident. Aggressive encounters may result in stress, and the physiological responses to

stress may result in a (temporary) growth reduction (Tan et al., 1991; Ekkel et al., 1995; Marchant-Forde and Marchant-Forde, 2005). Oral manipulation, which is the repeated biting, sucking, rooting, or nibbling on body parts of a conspecific, may vary in intensity (e.g. Schrøder-Petersen et al., 2004). For tail biting, which is the specific biting on the tail of another pig, the reported effects vary from a reduction in growth rate up to 11%, to the death of the victim (Chapter 2; Smith and Penny, 1998; Schrøder-Petersen and Simonsen, 2001). The effect that behaviour may exert on growth may thus vary in severity.

In our experiment, pigs selected for a high IGEg, e.g. a positive effect on the growth of their group mates, showed less biting behaviour (Chapter 7). This reduced biting behaviour was reflected in less unilateral aggressive bites, less ear biting, and less chewing on pen objects such as a toy and jute sack (Figure 1). High IGEg pigs also inflicted less tail damage due to tail biting (Figure 1). The biting on pen objects such as the jute sack (i.e. burlap, hessian or gunny bag / sack) might have reduced the biting on group mates (Chapter 7).

Previous studies on IGEg in pigs suggested a relationship with aggression, whereby pigs with a high IGEg would show more aggressive behaviour when pigs are regrouped with unfamiliar pigs, but less aggression later on when dominance relationships are assumed to be settled (Rodenburg et al., 2010; Canario et al., 2012). Regrouping of unfamiliar animals may result in excessive aggression (Marler, 1976; Marchant-Forde and Marchant-Forde, 2005). Our detailed study of pigs selected on IGEg showed only minor changes in parameters related to aggression (Chapter 8). During a 24 h regrouping test no differences were found between the IGEg groups (Chapter 8 and 9), but when the pigs were reunited with the former pen mates, directly after the 24 h regrouping test, high IGEg pigs showed considerably less aggression than low IGEg pigs (Chapter 8). We hypothesized that this might be related to a better establishment of dominance relationships in the initial groups (Chapter 8), which would be in line with the suggestions of Rodenburg et al. (2010) and Canario et al. (2012). The difference in biting behavior after the regrouping test may, however, also relate to stress sensitivity. Analysis of the behaviour and physiology, including stress physiology, around regrouping indicated that animals which were involved in much aggressive interactions were not necessarily the ones that experienced most stress or fear (Chapter 9). Rather, the interaction between a PCA factor describing involvement in aggression and a PCA factor describing stress through the increase in haptoglobin levels ( $\Delta$ ), showed that pigs which were much involved in aggression and had a higher  $\Delta$ haptoglobin spaced considerably further away from unfamiliar pigs, whether this was not apparent for aggressive pigs having low  $\Delta$ haptoglobin. Commonly, the animals that

show the most extreme social interactions are studied, and conclusions upon welfare may be drawn based on the animals that show clear signs of (received) aggression, such as skin lesions. The severity of skin lesions may also be used to reduce aggression through direct breeding (Turner et al., 2006; 2009; Turner, 2011). Our work, however, suggests that clear signs of aggression such as skin lesions, gives limited information about how the animal perceives the situation. Breeding against outer signs of behaviour might reduce the expression of that behaviour, e.g. create resilient or stoic animals (D'Eath et al., 2010), but might result in negative emotional states, such as fear, and may thereby be detrimental for animal welfare.



**Figure 1.** Tail damage score and number of jute sacks consumed for low IGEg (Low) and high IGEg (High) pigs in barren and enriched pens.

### **Positive effect on others**

Most work on IGE in livestock focusses on harmful social interactions. Positive interactions, however, should not be neglected as these may as well influence productivity, behaviour, and welfare. Although the effects may seem less explicit, positive interactions are essential to physical and mental health in social species (e.g. House et al., 1988; humans: Diener and Chan, 2011). For example, the presence of a mother to interact with may drastically improve health and cognitive development of the offspring (e.g. primates: Harlow, 1958; Ruppenthal et al., 1967; pigs: Oostindjer et al., 2011b). Maternal effects, amongst which mother-offspring interactions and the uterine environment, are a well-known type of cross-generation IGE of the mother on her offspring (reviewed by Wolf et al., 1998; Hunt



and Simmons, 2001; but see Bouwman et al., 2010 for parameter estimates in pigs).

IGE have been associated with cooperation in terms of the positive sign of the genetic correlation between direct-indirect genetic effects (pigs: Chen et al., 2010), but has to my knowledge not been related to biologically positive, i.e. beneficial, social interactions in animals. In farm animals, positive interactions are far less studied than harmful interactions (reviewed by Boissy et al., 2007; Yeates and Main, 2008), which is partly due to priorities to reduce harmful behaviours in the light of welfare regulations. Recent work on amongst others social support, indicate that animals, including farm animals, may influence each other's emotional state in a positive and negative way (e.g. Rault et al., 2012; pigs: Reimert et al., 2013b).

Positive social interactions are associated with hormones such as oxytocin (reviewed by e.g. Insel, 2010; IsHak et al., 2011). Oxytocin has many positive aspects for health and welfare (e.g. IsHak et al., 2011; pigs: Rault et al., 2013a; Reimert et al., submitted), and may have a beneficial effect on growth (Uvnäs-Moberg et al., 1998). In pigs, gentle tactile contact in the form of social nosing, whereby an individual gently touches another with its snout, was found to be positively associated with growth rate (Chapter 2). This effect on growth, however, was not confirmed in a later study (Chapter 3), and a suggested link between social nosing and oxytocin (administered intranasally) could not be confirmed (Chapter 4). In line with the theory on IGE, however, pigs with an estimated IGEg above group average (those pigs were not selected for IGEg and kept in mixed IGEg groups) showed more social nosing than pigs with an estimated IGEg below group average (Camerlink et al., 2011). The association between IGEg and social nosing, however, was not apparent in our selection experiment (Chapter 7). Although the effect of social nosing on growth rate is still uncertain and needs confirmation, these studies do give indications that pigs can have a beneficial effect on the growth rate of pen mates, and that this might be reflected in IGEg. Although selection on IGEg did not result in differences in behaviour that might be classified as positive, another selection experiment in pigs, which was based on selection of half sib groups over multiple generations, reported that pigs had become more docile (Gunsett, 2005)<sup>2</sup>. An improvement in welfare related to behaviour may be reached through the reduction of harmful behaviour as well as the enhancement of behaviours that may be beneficial to group members. For future research, it would

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<sup>2</sup>Gunsett (2005) reported the results of the group selection experiment on a conference. The conference paper unfortunately did not include data on the behaviour, except the statement that pigs had become more docile.

be recommended to continue to consider both harmful and beneficial social interactions to gain insight in the full scope of IGE.

### **Personality**

Personality is highly related to the expression of behaviour and, moreover, is also associated with growth (Stamps, 2007; Biro and Stamps, 2007). It was hypothesized that personality, which may be reflected in coping styles (e.g. Koolhaas, 2007), might be related to IGE, potentially as a confounding factor between behaviour and growth. Pigs with a more proactive coping style were previously found to be more rigid in their aggression (Bolhuis et al., 2005a; Melotti et al., 2011), and differ in their growth rate (but the direction of results on growth are inconsistent; Van Erp-Van der Kooij et al., 2003; Cassady, 2007; Spake et al., 2012). If selection on IGEg would result in less proactive coping styles, potentially through the link with aggressive interactions, this might affect productivity. All animals in our selection experiment were subjected to multiple personality tests (Reimert et al., 2013a; 2014). In an explorative study of the behaviour of the piglets before they were selected for the trial, we found that piglets with a lower growth rate and lower weight around test day responded more proactively in a backtest, which is a test that may reflect the coping strategy of pigs (Chapter 5). The response in the backtest, however, did not relate to the IGEg classification (Reimert et al., 2013a). The behavioural tests later in life indicated a reduced fearfulness in high IGEg pigs (Reimert et al., 2014), but from the results it is not expected that a shift will take place in the distribution of coping styles.

**Conclusion 3.** Selection for IGEg revealed that after one generation, pigs already showed structural changes in behaviour. High IGEg pigs, i.e. the offspring of parents selected for a positive effect on the growth rate of their pen mates, showed less potentially harmful biting behaviour.

### **10.4 Effects on welfare**

Animal welfare is of growing concern to society worldwide. Animal welfare has been formulated as one of the pillars of sustainable livestock farming, and is thereby an integral part in global aims for sustainable food production (e.g. Keeling, 2005; Tucker et al., 2013). Animal welfare has been defined based on animals' physiological state, emotional state, or their expression of natural behaviour (reviewed in Duncan, 2005). Most definitions relate to the five freedoms, which

state that an animal should be free of hunger, discomfort, pain, stress & disease, and should be able to express normal behaviour (FAWC, 1979). This broad concept, which is moreover largely influenced by humans' perception on animal welfare, makes it difficult to make clear statements on when 'overall' welfare is improved, rather than single parameters (e.g. McGlone, 2001; Ohl and Van der Staay, 2012). Improving animal welfare is an important issue in Europe (e.g. Veissier et al., 2008; Johnston, 2013), but international trade and the rapidly emerging economy of the BRIC countries<sup>3</sup> are likely to cause that animal welfare issues will increasingly be addressed globally (e.g. Maciel and Bock, 2013).

It has often been hypothesized that selection on positive IGE may improve animal welfare (Muir, 2005; Rodenburg et al., 2010), but the overall welfare of animals selected for IGE has never been quantified by a welfare assessment method, although the extreme mortality rates in poultry selection experiments leave little to doubt (reviewed by Muir and Craig, 1998). Here, I assess the welfare of pigs that were selected for IGEg and kept in diverging housing conditions, by means of the Welfare Quality® (WQ) protocol. The WQ protocol is a standardised protocol that has been developed to assess on-farm animal welfare in the main livestock species (Blokhuis et al., 2010), and the first validations of the protocol for pigs have been made (Temple et al., 2011a; 2011b). The measures that are included in the WQ protocol for pigs are briefly described in Table 1. As input to the assessment I used the part of the data that was described in the previous chapters, supplemented with weekly obtained data on the vitality of the animals (Camerlink et al., in prep.). The details of the animals and housing are described Chapter 6 to 9. Results are divided into regular observations days (wk 6-23 of age), and observation days around regrouping, which were the first 14 days after weaning (14 observations) and once in the first week after a 24 h regrouping test (wk 9 of age; details of the regrouping test can be found in Chapter 8). Regrouping is commonly applied for production purposes and causes many behavioural and physiological disturbances, whereby adverse effects may be noticeable up to several days to weeks (e.g. Arey, 1999; De Groot et al., 2001). Data obtained around regrouping may not be comparable to the common 'steady' situation and were therefore presented separately. Separate analysis of these periods after regrouping may also give insight in these situations where welfare is most at stake.

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<sup>3</sup>BRIC countries refer to Brazil, Russia, India, and China. For pig production, mainly Brazil is an emerging producer which can, partly due to low cost prices, relatively easily integrate animal welfare standards to comply with European demands for pork products.

## 10 General discussion

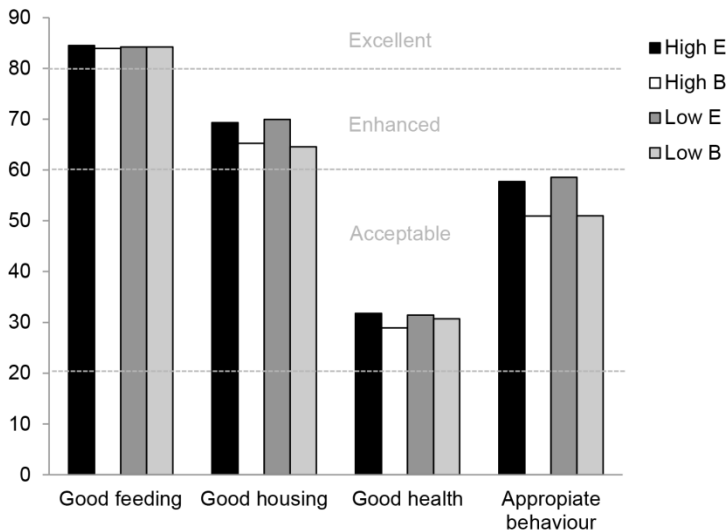
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**Table 1.** Measures included in the welfare assessment of the Welfare Quality® protocol. Principles indicate the welfare categories that are specified in the protocol.

Principles	Measures
Good feeding	Body condition score, water supply
Good housing	Bursitis, absence of manure on the body, shivering, panting, huddling, space allowance
Good health	Lameness, wounds on the body, tail damage, mortality, coughing, sneezing, pumping, rectal prolapse, scouring, skin condition, ruptures and hernias, castration, tail docking
Appropriate behaviour	Social behaviour, exploratory behaviour, fear of humans <sup>1</sup> , Qualitative Behavioural Assessment <sup>1</sup>

<sup>1</sup>Not included in current calculation.

Assessment of the welfare by means for the WQ protocol revealed no differences in overall welfare of the four different treatment groups: low IGEg pigs in barren pens, high IGEg pigs in barren pens, low IGEg pigs in pens enriched with straw bedding, and high IGEg pigs in enriched pens. Selection for IGEg did neither alter any of the welfare categories during regular observation moments (Figure 3), nor during regrouping moments. In the period around regrouping all welfare scores were slightly lower, which was mainly due to more wounds on the body (skin lesions), reduced thermo comfort (huddling and shivering), more diarrhoea (weaning diarrhoea), and more negative behaviour (aggression). Enriched housing resulted in higher scores in the category ‘appropriate behaviour’ during regular observation moments. During regrouping the contrast between the housing conditions became slightly more apparent. In the category ‘good housing’ barren pens had a score of 65 during regrouping, whereas enriched pens scored 70 (both classified as ‘enhanced’ by WQ), which was approximately 5 to 10 points lower than in the regular situation (Figure 3). In the category ‘appropriate behaviour’ barren pens scored 50, whereas enriched pens scored 58 (both classified as ‘appropriate’ by WQ), approximately 5 points lower than in the regular situation (Figure 3). The differences in housing conditions around regrouping were mainly due to more huddling in barren pens (barren: score 40 out of 100; enriched: score 3 out of 100), and more diarrhoea in barren pens (barren: score 80 out of 100; enriched: score 70.5 out of 100). Overall, regrouping reduced the welfare as compared to the regular situation.



**Figure 3.** Overall assessment of welfare of pigs selected for high or low IGEg and housed in barren (B) or enriched (E) pens. Scores are averages of multiple observations over wk 6 – 23 of age (excluding regrouping moments).

Differences in welfare due to genetic selection did not become evident from the assessment with the WQ protocol, and were only marginally shown for enriched housing. This can mean that there were no differences in welfare, or that the WQ protocol was unable to detect the differences. The previous chapters and paragraphs clearly outline that high IGEg pigs showed less potentially harmful behaviour and had less tail damage, and that enriched housing greatly reduced the occurrence of harmful oral manipulation. The WQ assessment combines tail wounds with other wounds and lameness, and in the final score, the percentage of pigs with tail damage is hardly visible. Although frequencies of biting behaviour were low (Chapter 7), these differences were significant and should have been reflected in the category of appropriate behaviour and the subcategory for absence of injuries (category good health). The weighing on tail biting and tail damage in the WQ protocol seems hardly to account for the possible consequences of tail wounds, and may thereby underestimate the importance of tail biting at its onset. As tail biting is highly related to the welfare of pigs (e.g. Anonymous, 2001<sup>4</sup>), a

<sup>4</sup>Anonymous 2001 refers to a paper by 22 scientists who assess which factors were important for animal welfare. For the welfare of growing and finishing pigs, they indicated abnormal behaviour (tail biting) and aggression as most detrimental for welfare considering Dutch pig husbandry. Health problems were ranked second.

recommendation would be to put more weight on the scores for tail biting behaviour and tail damage.

The effect of enriching the environment with a deep litter layer of straw and wood shavings resulted in a slightly higher welfare score only on appropriate behaviour, and on the days around regrouping. In practice, the differences between the two housing conditions were substantial at each given moment in time (Chapter 7). Straw applied as bedding may amongst others increase thermal and physical comfort (Day et al., 2002; Tuytens, 2005), which was in the WQ assessment reflected in the lower scores on huddling after weaning. The minor difference in the scores on housing as compared to the major differences in practice, suggest that the WQ protocol is unable to detect the enormous welfare improvement of straw housing as compared to barren housing (but see Temple et al., 2011b). Providing straw to pigs has proven its beneficial effect on pig welfare (reviewed by Arey, 1993; Tuytens, 2005). Moreover, the result that barren pens scored 'enhanced' in the category housing, disregards the many welfare problems that arise from this type of housing.

Another point that merits discussion is that the WQ assessment categories may not reflect what is truly going on. Namely, tail wounds (category health) exist because of the receipt of maladaptive behaviour (category behaviour), whereas this behaviour develops as a consequence of the barren housing conditions in which natural behaviour cannot be expressed in an appropriate manner (category housing). In the current assessment the category housing is 'enhanced' and behaviour scores high within the classification of 'acceptable', whereas health scores are relatively low within the range of 'acceptable'. The actual situation was reverse; pigs were of good health, whereas the barren housing conditions and the occurrence of maladaptive behaviour, expressed by oral manipulation, may be considered as unacceptable to animal welfare.

The WQ assessment did not reveal the full welfare benefits that were clearly visible from the original data, and the results should therefore be interpreted with care. The Welfare Quality® protocol is one way to assess animal welfare (e.g. Broom, 1991; Smulders et al., 2006; Smulders, 2009; Brscic et al., 2009). The first scientific validations from the WQ protocol for pigs report that it can be a useful method to assess welfare (Temple et al., 2011a), but also concerns were raised for little variation in the scores for health (Temple et al., 2011a), and that with comparing diverging housing conditions the results on behaviour might not clearly reflect the actual situation (Temple et al., 2011b). In line with the studies by Temple et al., the current results also suggest that the protocol might need some

amendments, especially regarding harmful behaviours and its subsequent effects on health.

As outlined at the beginning of this paragraph, animal welfare is hard to define due to the many perspectives on welfare. Consequently, animal welfare is hard to measure, and might never fulfil everyone's perception of 'good welfare'. The aim to improve animal welfare would require specification in objective terms to enable quantification of the improvements. Both selection on IGEg and enriched housing did reduce aggressive and manipulative biting behaviour. These behaviours have been widely acknowledged as harmful to the welfare of pigs (e.g. reviewed by Spooler et al., 2011). Based on that, I would conclude that selection on IGEg in pigs may result in improved welfare.

**Conclusion 4.** Assessment of welfare by the Welfare Quality® protocol did not show effects of selection on IGEg and only a minor improvement due to enriched housing. The Welfare Quality® protocol for pigs may require amendments, and results should therefore be interpreted with care. It is widely acknowledged that biting behaviour such as tail biting harms the welfare of pigs. Biting behaviour was reduced through selection on IGEg, and selection on IGEg may therefore contribute to improving aspects of animal welfare.

### 10.5 Genotype by environment interaction

Genotypes may be expressed differently depending on the environment, which is known as genotype by environment (G×E) interaction. Although intensive pig farming is quite similar worldwide, G×E interactions are present for growth rate in pigs (Schinckel et al., 1999), and may depend on differences in climate (Bloemhof et al., 2008) or housing conditions (Guy et al., 2002a). G×E interactions for pig behaviour have been reported for maternal behaviour of sows (Baxter et al., 2011) but have, to my knowledge, not been reported for behaviour in finishing pigs (Hill et al., 1998; Guy et al., 2002b). Present farming requires that animals have the ability to cope well with a range of environments, and therefore it is important to know whether effects of selection on IGEg would give consistent results across environments. Moreover, a G×E set-up would enable to compare the welfare improvements due to genetic selection and housing conditions. In our selection experiment, half of each IGEg group was housed in conventional barren pens and the other half was housed in pens enriched with a deep litter layer of straw and wood shavings. Provision of enrichment material to current pen designs may be

increasingly applied as current EU regulations state that pigs should have provision of substrate (EC Directive 2001/93/EC, 200). Straw is thereby one of the most effective enrichment materials to reduce tail biting in pigs (Bracke et al., 2006). Theoretically, the least harmful behaviour would occur when pigs selected for high IGEg would be housed in straw-enriched pens, whereas most would occur in low IGEg pigs housed in barren pens. The welfare impacts of the two intermediate treatment groups, i.e. high-barren and low-enriched, were uncertain at the start of the trial, but should especially reveal the separate impact of genetics and housing. The results of the selection experiment revealed hardly any G×E interactions for production and behaviour. Few interactions of minor significance are described in Chapter 6 to 9. Several parameters, such as tail damage and biting, which were profoundly lower in the enriched pens, were for both IGEg groups almost equally altered in both housing conditions (Chapter 7). This resulted in an additive rather than interactive effect of genetics and environment. Thus as hypothesized, high IGEg pigs in enriched pens indeed showed least harmful behaviour, whereas low IGEg pigs in barren pens showed most (Figure 1). From the two intermediate treatment groups, low IGEg pigs in enriched pens showed less harmful behaviour than high IGEg pigs in barren pens. This revealed that the improvements of enriched housing are more profound than the current one-generation selection for IGEg. However, that one generation of divergent selection already resulted in a significant reduction of biting behaviour implies that these effects might further increase over multiple generations of selection. The additive effect of selection suggests a certain robustness of the selection method across housing conditions, and moreover shows that both strategies, i.e. genetic selection and enriched housing, may contribute to improved animal welfare.

**Conclusion 5.** A genotype by environment experiment, with selection on IGEg (high vs. low) and housing conditions (barren vs. enriched) as treatments at pen level, revealed no profound G×E interactions for productivity or behaviour, which suggest a certain robustness of the selection method. Selection on high IGEg reduced biting behaviour additive to the reduction due to enriched housing.



### 10.6 Estimation of IGEg in pigs

Prior to the selection experiment, direct and indirect breeding values were estimated for growth rate during the finishing phase. In the selection, the average direct breeding value was kept around zero for both IGEg groups. Power calculations indicated that the size of the trial would be sufficient to detect differences in growth rate. Nevertheless, growth rate was not affected in the expected direction. Estimation of IGEg for pigs faces several difficulties. Studies that aimed to estimate IGEg in pigs reported either that effects could not be estimated on the current data (Arango et al., 2005), that effects were marginal (Chen et al., 2008; 2009), or that effects were very substantial (Bergsma et al., 2008). Improved analysis of these studies, partly with additional data, indicated that IGEg were present but that the initial calculations included errors (Muir et al., 2010). New estimates indicated smaller but significant effects of IGEg (Bergsma et al., 2013). The small effects, however, can to a certain extent increase with the number of group mates (Bijma et al., 2007b; Bijma, 2010). With the correct model, estimation remains difficult due to the data structure in which the group composition of pigs changes several times during the production cycle. Another potential relevant issue that complicates accurate estimation of IGEg effects might be the exclusion of pigs that do not have records on growth rate. If the lack of a growth record was due to death or replacement as a result of social interactions, for example due to tail biting which may indeed result in death (reviewed by Schrøder-Petersen and Simonsen, 2001), a detrimental social effect is not captured in the estimates.

Estimates of IGEg are based on data from commercial farms. This means that pigs were mostly gilts (females) and barrows (castrated males) which were housed in conventional barren pens and were tail docked. The selection experiment was in line with these characteristics of commercial farming, apart from that all pigs had intact tails and that half of the animals were housed in enriched pens. Some characteristics of the selection experiment, however, fundamentally differed from the commercial situation. Mainly, pigs were kept under more favourable circumstances, whereby especially more measures were taken to limit tail biting behaviour (for extensive discussion see Chapter 6 and 7). Tail biting can reduce ADG up to 11% (e.g. Wallgren and Lindalh, 1996; Camerlink et al., 2012a; Sinisalo et al., 2012), and limiting this behaviour may have mitigated the effects on growth, and thus the expected effect of selection on IGEg.

It has been suggested before that the effect of selection on IGE, both in pigs as in poultry, may depend on the severity of the social interaction (laying hens: Craig, 1982; Craig 1994 cited in Muir and Craig, 1998; pigs: Arango et al., 2005). In laying

hens, cannibalistic behaviour may result in increased mortality and consequently in reduced production. In pigs, changes in social behaviour due to selection on IGEg may be less noticeable as social behaviours in pigs have more subtle effects on growth (Chapter 2). Although moderate tail biting may already result in reduced growth (Chapter 2), growth is mostly reduced in the extreme cases (Wallgren and Lindalh, 1996; Sinisalo et al., 2012). These extreme cases may eventuate in mortality when the pig has been injured for longer time and management failed to respond timely. In commercial pig farming these extremes in behaviour are, sadly, not an exception (as amongst others tail lesion data from abattoirs reveal) (EFSA, 2007; reviewed by Taylor et al., 2010). The estimation of IGEg on commercial data may indicate true effects under these conditions, and might then relate to biting behaviour. This would require conformation through selection under commercial circumstances.

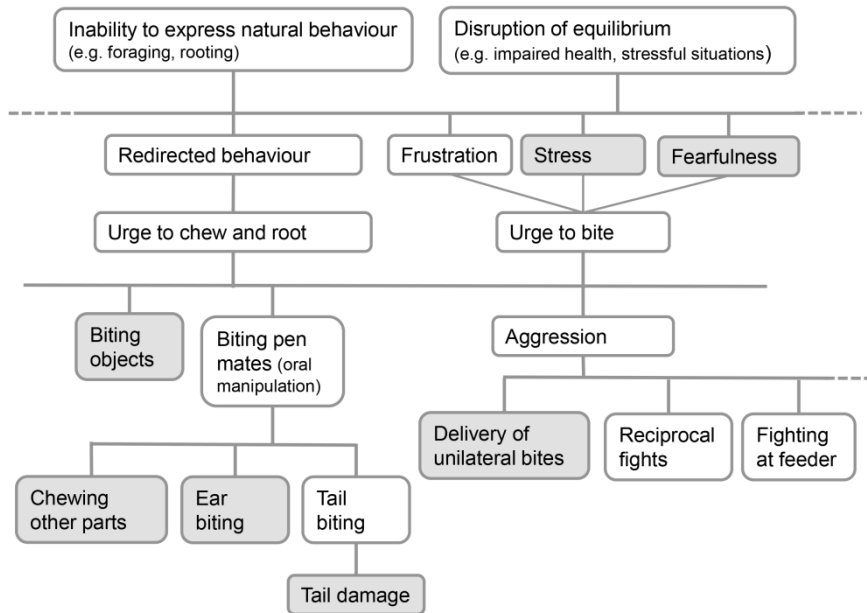
**Conclusion 6.** Estimating IGEg for pigs faces various difficulties and the relatively favourable circumstances in our experiment may have obscured the effects of IGEg. Evaluation under circumstances where social interactions do result in reduced growth, are required to give clarity on the effects of IGEg in practice.

### 10.7 Potential underlying mechanisms

IGE are estimated for various traits, as social interactions are expressed differently within and across species. Therefore, multiple underlying mechanisms may exist. In animal studies, competition, aggression, and cannibalism have been suggested (Moore et al., 1997; Muir, 2005; Wilson et al., 2009; Chen et al., 2007; Rodenburg et al., 2010; Canario et al., 2012). Selection on IGE hypothetically might also originate from apathy or a reduced activity, which may reduce the frequency of interactions, and thereby causes the animal to not affect group members (D'Eath et al., 2010; Rodenburg et al., 2010; Turner, 2011). Apart from behaviour, individuals may also affect each other's performance through disease transmission (Lipschutz-Powell et al., 2012; trees: Costa e Silva et al., 2013).

Our behavioural studies of pigs selected for IGEg indicated that high IGEg pigs differed in aggressive biting, and showed less manipulative biting behaviour. The aggressive bites may reflect, apart from aggression itself, frustration and stress (e.g. Scott, 1948; Hori et al., 2004) (Figure 2). Manipulative behaviour mainly originates from the inability to express natural behaviour such as foraging and

rooting (e.g. Van Putten, 1979; Studnitz et al., 2007), and may in addition be triggered by stress (reviewed by Schröder-Petersen and Simonsen, 2001) (Figure 2). Our selection experiment revealed a range of differences in behaviour and stress physiology (as reflected in haptoglobin levels), suggesting that high IGEg pigs were less sensitive to stress or were less fearful than low IGEg pigs (Chapter 8; Reimert et al., 2013a; 2014). Stress is a broad concept, e.g. physiological stress or mental stress, and the exact context under which high IGEg pigs would be better capable of handling stress, for example specific stressful events such as novel situations, would require more study. The fact that a behavioural category within a species, i.e. biting in pigs, may already have different underlying causes emphasizes the complexity of unravelling potential underlying mechanisms of IGE.



**Figure 2.** Schematic representation of the occurrence of biting behaviour in pigs. Boxes with shade indicate that selection for IGEg significantly altered these aspects (this thesis; Reimert et al. 2013; 2014).

**Conclusion 7.** The various biting behaviours that were altered through selection on IGEg, together with differences in stress physiology, seem to indicate a reduced stress sensitivity of high IGEg pigs. This would however require more study.

### 10.8 Improving welfare of pigs

Animal welfare concerns are mostly raised with regard to intensive livestock production due to its massiveness, painful interventions on animals, and behavioural problems. Regarding solutions there has been the question whether we should adapt the environment to the animal, or whether we should adapt the animal to the environment (D'Eath et al., 2010). Given the current situation, where both genetics and housing conditions have contributed to the development of aberrant behaviours in farm animals, solutions have to come from both sides (De Goede et al., 2013).

#### **Solutions from genetics**

One reason why animal breeding may be required to solve welfare issues, is that even in outdoor production systems animals may still perform aberrant, potentially harmful behaviour (laying hens: Bestman and Wagenaar, 2003; pigs: Walker and Bilkei, 2006, Olsen, 2001). Housing conditions may thus not eliminate all welfare problems. It has been raised that genetic selection could harm the integrity of the animal (e.g. Olssen et al., 2006; D'Eath et al., 2010; Thompson, 2010). Genetic selection has, however, taken place ever since domestication and behaviour has therefore been subject to deliberate genetic selection for centuries. Hence, the current livestock populations are already a result of human intervention. The ethical concerns about integrity mainly regard the extremes of selection, e.g. selection for blind hens, and such extremes conflict with aims formulated for sustainable breeding (e.g. Gamborg and Sandøe, 2005; Ellen et al., 2009). Direct genetic selection against harmful behavioural is possible (e.g. D'Eath et al., 2010; Turner, 2011), but requires specific trait records which are time consuming to obtain (D'Eath et al., 2010), and possible trade-offs may arise (Rauw et al., 1998; D'Eath et al., 2010; Thompson, 2010). Moreover, targeting a single behaviour may only contribute to solving part of the welfare problem, and often ignores the actual cause of the behavioural problems, namely the housing conditions or management procedures. Animal welfare is a broad concept, and selection on IGE, which rather targets an overall positive effect on others, may therefore be a better approach to improve welfare than direct selection against specific behaviours. Moreover, research on cannibalism in laying hens reveals both an IGE originating from the actor (the pecker) and a direct genetic effect originating from the victim, and both effects contribute significantly to the total heritable variation in mortality due to cannibalism (Ellen et al., 2008). This indicates that behaviours may not only depend on the individual performing the behaviour, but also on the recipient being more predisposed to receive or to provoke certain behaviour. This may also be the case

in recipients, i.e. victims, of tail biting (Zonderland et al., 2011; Brunberg et al., 2013). The predisposition to be recipient or to provoke the receipt of behaviour may easily be overlooked in direct behavioural observation, whereas selection for the combination of direct and indirect genetic effects utilizes the full heritable variation underlying the trait.

### **Solutions from housing**

Solutions to improve animal welfare through adapted housing conditions have received much attention, but implementation into practice often requires large investments in labour and housing, and is hampered by differences in perceptions or lack of knowledge-transfer between parties, e.g. initiatives of farmers to start innovative large scale farm concepts may be obstructed by society (De Bakker et al., 2012). Mainly in Europe, improvements have been made in space allocation and the possibility to roam freely and to interact with conspecifics (Veissier et al., 2008). Some crucial elements, however, still lack in the majority of housing systems. This refers mainly to material or substrate that enables the expression of internal needs such as foraging, exploring, and body care, which have proven to decrease behavioural problems in all kinds of species to a great extent (e.g. pigs: Tuytens, 2005; Bracke and Hopster, 2006; Studnitz et al., 2007; captive wild animals: Mason et al., 2007; rats: Simpson and Kelly, 2011). Providing substrate to pigs, such as straw or peat, seems the most effective method to improve welfare within the current barren housing systems (Beattie et al., 1998; Tuytens, 2005; Pedersen et al., 2005; Bracke et al., 2006; Vanheukelom et al., 2011; Chapter 7).

### **Implementation of strategies to improve welfare**

The implementation of a new genetic selection method mainly depends on breeding companies. As conflicting results have been found in quantitative genetic data analysis and a one-generation selection experiment, and economic values attached to animal welfare related traits are yet unclear, pig breeding companies may be hesitant to include IGEg in their breeding programs for productivity, even though the results seem promising for the reduction of biting behaviour.

The effect of straw has been studied extensively in research, but is in most pork producing countries only little implemented in practice. Implementation into practice, and investigation of possible constraints with the implementation into current farm designs, deserves priority.

Improving animal welfare relates to better health and productivity, and thereby may increase profit (e.g. Kingwell, 2002). The profit, however, may be overshadowed by many costs (e.g. Bornett et al., 2002). Changes in the farming

system or management often encompass a trial and error phase which most farms cannot afford to risk (Bock and Van Huik, 2007). For example, keeping pigs with long instead of docked tails may result in tail biting outbreaks when management is not yet adapted to the situation<sup>5</sup>. As a consequence, the farmer may face substantial losses before the farming system and management are fully adapted, and not in the least, animal welfare may (temporary) be worse than before. To implement a welfare-enhancing strategy it is therefore crucial that the possible consequences of a transition, e.g. from tail docking to keeping pigs with long tails, are well known and accounted for in terms of risk management. Currently, it seems that animal welfare solutions are not primarily a matter of gaining more scientific knowledge, but of gaining more practical knowledge on problems that farmers experience when taking initiative to make such a transition. Providing advice and support to farmers is thereby essential. As part of the 'Seeking sociable swine' project, two stakeholder workshops were organized. At these workshops relevant stakeholders from the sector participated, including amongst others farmers, feed companies, veterinarians, and scientists working on pig welfare. The workshops showed that much of the scientific knowledge on, for instance, the causes of harmful behaviour has not reached farmers and farm advisers, and that information transfer would require the right format of communication, e.g. dialogues (Benard, submitted).

Animal welfare is only one part of a sustainable agriculture, and has to be in balance with other aspects, such as productivity and environmental footprint (Tucker et al., 2013). Before implementation, it is important to evaluate all aspects of a strategy, and not only animal welfare aspects. For example, organic farming may be favourable for animal welfare, but may be less favourable in terms of environmental impact as compared to conventional farming (De Boer, 2003)<sup>6</sup>. Thus, an apparent improvement on one aspect can have a negative impact on other aspects of sustainability of the system (Tucker et al., 2013). To assess the sustainability of selection on IGEg in pigs, it might be important to gain more insight in the impact on productivity, as growth rate and feed efficiency may influence the overall sustainability of a system (e.g. pigs: Eriksson et al., 2005).

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<sup>5</sup>In Europe there is a ban on tail docking, which originates from animal welfare concerns about surgical interventions inflicted to the animal. In practice, an estimated 90% of the pigs are tail docked because farms can receive an exception on this regulation if it seems not feasible to keep pigs with long tails (EFSA, 2007). This exception on the regulation is likely to be withdrawn in the near future. First initiatives are taken to keep pigs with intact tails.

<sup>6</sup>Such an assessment may be made through for example Life Cycle Analysis.

Thus, the welfare of pigs may be improved both by genetic selection for IGEg and by enrichment of the housing conditions with substrate such as straw. For the implementation of genetic selection on IGEg more knowledge is required from application in practice. For the integration of enrichment materials to current housing conditions, and for the success of transitions towards improved welfare, e.g. intact tails, it is important that constructive dialogues, e.g. two-way knowledge transfer, are formed between science and sector to come to solutions. Multidisciplinary (research) programmes may be an effective method to construct such dialogues, and bring together the specific knowledge from each stakeholder group (e.g. Neef and Neubert, 2011; current program: Benard and de Cock-Buning, 2014).

**Conclusion 8.** Genetic selection and housing conditions may both contribute to improved animal welfare. Given the current body of scientific research on farm animal welfare, it is now most essential that knowledge reaches the sector, and that a bridge between science and sector results in constructive welfare improvements.

### 10.9 Conclusions

A single generation of selection for IGEg did not improve production performance of pigs, but did lead to structural behavioural changes whereby high IGEg pigs showed less aggressive and manipulative biting behaviour and inflicted less tail damage. The estimation of IGEg in pigs is complex, and a selection trial in commercial practice might give insight in the true effects. The differences in biting behaviour, together with the reduced fearfulness of high IGEg pigs in behavioural tests and stress physiology, suggest that high IGEg pigs may be less sensitive to stress, and that potential underlying mechanisms of IGE may thus reach further than the expression of single behaviours that can be harmful to others. No profound genotype by environment interactions were found, which suggests that effects of selection on IGEg may apply to diverse housing conditions. Assessment with the Welfare Quality® protocol did not demonstrate a welfare improvement due to genetic selection, but the separate physiological and behavioural differences indicate otherwise, whereby selection would positively influence the welfare of pigs. As to improve pig welfare, it would be recommended to establish constructive two-way knowledge transfer between science and sector.





## Summary

Social interactions occur in any given situation where animals encounter and, depending on the nature and strength of interaction may influence health, performance, and welfare. When social interactions originate from heritable traits, for example inherited behaviour, the effect of these interactions can be approximated through indirect genetic effects. An indirect genetic effect (IGE) is a heritable effect of an individual on the production performance of others. Social behaviours, either positive or negative, have been most often suggested as underlying mechanism for IGE. IGE are relevant to genetic studies as they account for heritable social interactions, and thereby may increase the accuracy of genetic estimates. IGE would enable selection of animals that have a good own performance as well as a positive effect on the performance of their group mates. IGE may also be relevant for animal behaviour and welfare studies, as selection on IGE may have the potential to improve social behaviour, and thus welfare.

In intensively reared pigs, harmful behaviours may affect the health and growth of others, and may result in serious welfare problems that require a solution. IGE have been proposed as a method to improve productivity and welfare simultaneously. In this thesis, this was studied through a selection experiment whereby pigs were selected based on IGE on growth rate (IGEG), meaning that the IGE is the inherited effect that a pig has on the on the growth rate of its group mates.

The objectives of this thesis were a) to investigate the effect of selection for IGEG in pigs on their production performance, behaviour, and welfare in different housing conditions; and b) to gain insight in potential mechanisms underlying these effects in pigs. It was hypothesized that selection for higher IGEG would improve growth rate, behaviour, and welfare when pigs of the high IGEG category would be housed together. It was also hypothesized that harmful behaviours would underlie IGEG. Hereto, the possible relationships between pig behaviours and growth were explored through several studies which are outlined in the first part of the thesis (Chapter 2 to 5). The second part of the thesis (Chapter 6 to 10) reports the results of a one-generation selection experiment where 480 pigs were divergently selected for either high or low IGEG, and housed in either conventional barren pens or pens enriched with a deep litter layer of straw and wood shavings.

Chapter 2 shows that pigs may reduce each other's growth rate through oral manipulation. In contrary, growth rate may increase in pigs that receive much social nosing. Social nosing was further investigated in chapter 3, were the relationship between growth rate and social nosing could not be confirmed, and neither depended on dominance relationships. Social nosing was suggested as form of affiliative behaviour, but in chapter 4 social nosing was unaffected by intranasal

administration of oxytocin. The link between behaviour and growth may be intertwined with personality. Chapter 5 explored this through the backtest, a test which may indicate coping strategies or personality in piglets. Piglets that responded more active in the backtest had a lower growth rate.

One generation of divergent selection for IGEg in pigs did not result in the expected response in growth rate (Chapter 6). In contrary, results on body weight even tended to be in opposite direction. Selection did lead to structural behavioural changes which could, under commercial conditions, explain a reduced growth (Chapter 7). Pigs selected for a positive effect on each other's growth rate, i.e. high IGEg pigs, showed less biting behaviour, which was apparent from less unilateral aggressive bites, less ear biting, less chewing on enrichment material, and less tail damage due to tail biting. Tail biting itself did not differ between the IGEg groups in the behavioural observations, but the less severe tail damage did indicate that high IGEg pigs were tail biting less or less severe. In chapter 8, aggressive behaviour was further explored, as aggression had been suggested to underlie IGEg in pigs. High IGEg pigs showed only minor changes in the major aggression parameters, but did show considerably less aggression when they were reunited with familiar pen mates after being separated for 24 h during a regrouping test. Chapter 9 approached the same regrouping test from a more integral perspective, combining behavioural and physiological data with the distances between pigs, whereby the distances may reflect social tension. This revealed that pigs that are involved in much aggression are not necessarily the ones that experience most stress, but that the animals that don't stand out might be most affected.

Enrichment with straw and wood shavings resulted in more pen-directed behaviour, e.g. rooting and nosing, and less pig-directed behaviour, e.g. oral manipulation (Chapter 7). The effects of selection were similar in both housing conditions, with no profound genotype by environment interactions for production performance or behaviour. Genetic selection and enrichment had additive effects on the observed behaviours, and in particular chewing and biting.

The biting behaviour of the selected pigs related to aggression and oral manipulation. Aggression may have a background in stress, frustration, and fear, whereas oral manipulation may have a background in redirected foraging behaviour as well as stress. Other tests and observations on the same pigs suggested a reduced fearfulness and reduced stress sensitivity in high IGEg pigs. If selection would continue, biting behaviours might reduce, however, over time other behaviours may arise in relation to IGEg in pigs.

In chapter 10 all data on the selection experiment were combined to assess the welfare by means of a Welfare Quality® protocol. This did not reveal improved

welfare due to selection for IGEG, and only showed minor welfare improvements due to enriched housing conditions. The separate physiological and behavioural differences, however, did reveal welfare improvements in favour of selection for IGEG and enriched housing.

The selection experiment suggested that the severity of the social interactions may play an important role in the expression of IGEG (Chapter 7 and 8). If IGE for growth rate in pigs function through behaviour, and the behaviours that might affect growth rate are limited by the experimental set-up to comply with animal welfare standards, then the expected effect of IGEG, as estimated from field data, may not surface in the experimental setup. The observed systematic behavioural differences, which might have led to reduced growth had they not been limited, suggested that selection was effective. This, however, requires further validation. That no profound G×E interactions were found suggests that selection for IGEG would be effective in a range of housing conditions, and indicates a certain robustness of IGEG.

This thesis was part of the project 'Seeking sociable swine', which addressed strategies to improve animal welfare. The pig experiments confirmed the expectations that selection on high IGEG, and enriched housing, are beneficial to the welfare of pigs, and that the two strategies complement each other. To improve animal welfare, it is however of utmost importance that there is constructive two-way information transfer between science and sector.

To conclude, several studies among which a one-generation selection experiment, suggested that including IGE on growth rate in the breeding criterion reduced biting behaviour which may have its origin in aggression and oral manipulation. Implementation of selection on IGEG would require further study in commercial practice, where social interactions may be more profound than under experimental conditions. The results showed that both selection on IGEG and enriched housing are effective in reducing harmful behaviour and may thereby improve the welfare of pigs. Thus, most 'sociable swine' are found when pigs are selected for positive IGEG and housed in enriched pens.



## Samenvatting

Sociale interacties komen voor in elke situatie waar individuen elkaar treffen, en afhankelijk van het type en de intensiteit van de interacties kan gezondheid, productiviteit, en welzijn worden aangetast. Wanneer sociale interacties voortkomen uit erfelijke eigenschappen, bijvoorbeeld erfelijk gedrag, kunnen de sociale effecten geschat worden door middel van indirect genetische effecten. Indirect genetische effecten (IGE) zijn de erfelijke effecten van een individu op de (productie) prestatie van anderen. De hypothese is dat sociale gedragingen, positief danwel negatief, ten grondslag liggen aan IGE. IGE zijn relevant voor genetische studies omdat ze de genetische component van sociale effecten weergeven waardoor het mogelijk is om de nauwkeurigheid van genetische (fokwaarde) schatting te verbeteren. IGE geven de mogelijkheid om dieren te selecteren die een goede prestatie van zichzelf hebben, alsmede een positief effect op de prestatie van hun groepsgenoten. IGE zijn eveneens relevant voor studies naar diergedrag en welzijn, gezien de aanname dat selectie op IGE sociaal gedrag positief zou beïnvloeden, en dus een positief effect zal hebben op dierenwelzijn.

In de intensieve varkenshouderij kunnen schadelijke gedragingen, zoals orale manipulatie (op elkaar kauwen) en extreme agressie, de gezondheid en groei van groepsgenoten aantasten. Dit leidt regelmatig tot serieuze welzijnsproblemen en een oplossing is noodzakelijk. Genetische selectie op IGE is voorgesteld als een methode om productiviteit en welzijn gelijktijdig te bevorderen. In dit proefschrift is dat bestudeerd door middel van een selectie experiment waarbij varkens waren geselecteerd gebaseerd op IGE voor groei (IGEG). Dit betekent dat de IGE de erfelijke effecten zijn die een varken heeft op de groeiprestatie van zijn groepsgenoten.

De doelstellingen van dit promotieonderzoek waren a) het onderzoeken van het effect van selectie op IGEG op de productie, het gedrag en het welzijn van varkens in verschillende huisvestingscondities; en b) inzicht verwerven in mogelijke onderliggende mechanismen van deze effecten. De hypothese was dat selectie voor een hoge IGEG de productie, het gedrag en het welzijn ten goede zou komen wanneer varkens van uitsluitend de hoge IGEG categorie gezamenlijk zouden worden gehuisvest. Een andere hypothese was dat schadelijk gedrag een onderliggende factor zou zijn van IGEG. Het mogelijk verband tussen gedrag en groei in varkens werd onderzocht in verscheidene studies welke zijn samengevoegd in het eerste deel van dit proefschrift (hoofdstuk 2 t/m 5). Het tweede deel van dit proefschrift (hoofdstuk 6 t/m 10) beschrijft de resultaten van een één-generatie selectie experiment waarbij 480 varkens uit de extremen van de populatie werden geselecteerd voor hoog danwel laag IGEG. De helft van de varkens werd gehuisvest

in gangbare kale hokken en de andere helft in hokken verrijkt met een dikke laag stro en zaagsel.

Hoofdstuk 2 toont dat varkens die oraal manipulatief gedrag vertonen richting groepsgenoten, zoals staart- en oorbijten, de groei aantasten van het slachtoffer. Tegenovergesteld, varkens die veel sociaal gesnuffel ontvangen groeien beter. Dit sociaal snuffelen was benoemd als 'social nosing'. Social nosing was verder onderzocht in hoofdstuk 3, waar het verband tussen groei en social nosing niet kon worden herbevestigd en evenmin beruste op dominantie hiërarchie. Social nosing was geopperd als een vorm van affiliatief gedrag maar social nosing werd niet beïnvloed door intranasale toediening van oxytocine (hoofdstuk 4). De relatie tussen gedrag en groei kan beïnvloed worden door persoonlijkheid. Hoofdstuk 5 ging hier op in middels de 'backtest'. Dit is een test die een indicatie kan geven van het type persoonlijkheid van biggen. Biggen die actiever reageerden in de backtest hadden een lagere groei.

Eén generatie van selectie op IGEg in varkens leidde niet tot de verwachte toename in groei (hoofdstuk 6). Gewicht neigde zelfs lager te zijn in hoog IGEg varkens dan in laag IGEg varkens. Selectie had wel structurele gevolgen voor gedrag. Dit gedrag zou onder commerciële omstandigheden een groei reductie kunnen verklaren (hoofdstuk 7). Varkens die waren geselecteerd op een positief effect op de groei van anderen, dus varkens met een hoog IGEg, vertoonden minder bijtgedrag. Dit was te zien in een reductie van zowel agressief bijtgedrag, oorbijten, kauwen op verrijkmateriaal en staartschade ten gevolge van staartbijten. Staartbijten zelf verschilde niet tussen de IGEg groepen in de gedragsobservaties, maar de minder ernstige staartschade duidt erop dat hoog IGEg varkens minder of minder hard beten. In hoofdstuk 8 was agressie nader onderzocht vanwege een eerder gesuggereerde rol met betrekking tot IGEg. Hoog IGEg varkens verschilden minimaal in de hoofdparameters die op agressie duiden, maar vertoonden aanzienlijk minder agressie tijdens hereniging met hokgenoten van wie zij 24 uur gescheiden waren geweest tijdens een hergroeperingstest. Hoofdstuk 9 benaderde diezelfde hergroeperingstest met een meer integrale aanpak, waarbij gedrag en fysiologie werden gecombineerd met de afstanden tussen varkens. Afstanden tussen varkens werden gemeten als reflectie van sociale spanningen. De combinatie van parameters toonde aan dat varkens die vaak betrokken waren in agressie niet per se degenen zijn die het meeste stress ervaren, maar dat juist de dieren die niet opvallen in gedragsanalyses mogelijk het meeste lijden onder de situatie.

Verrijking met stro en zaagsel resulteerde in meer omgevingsgericht gedrag, zoals wroeten en snuffelen, en minder gedrag gericht op hokgenoten, zoals orale

manipulatie (hoofdstuk 7). De effecten van selectie waren evenredig in beide huisvestingscondities, met geen nadrukkelijke genotype × omgeving interacties met betrekking tot productie of gedrag. Genetische selectie en omgeving waren additief aan elkaar voor de geobserveerde gedragingen, met name voor kauwen en bijten. Het bijtgedrag van de geselecteerde varkens relateerde aan orale manipulatie en agressie. Agressie kan worden veroorzaakt door stress, frustratie en angst terwijl orale manipulatie een achtergrond heeft in omgericht fourageer gedrag en ook stress. Andere testen en observaties aan dezelfde dieren lijken erop te wijzen dat hoog IGEg varkens minder angstig en minder stressgevoelig zijn. Als selectie zou worden doorgezet zouden bijtgedragingen mogelijk afnemen. Echter, in de loop der tijd kunnen andere gedragingen zich ontwikkelen in relatie tot IGEg in varkens. In hoofdstuk 10 zijn alle gegevens van het selectie experiment gecombineerd om het welzijn te beoordelen. Dit werd gedaan middels het Welfare Quality® protocol. De waardering volgens het Welfare Quality® protocol toonde geen verbetering van het welzijn door selectie op IGEg en slechts kleine verbeteringen in het welzijn vanwege de verrijkte huisvestingscondities. De afzonderlijke fysiologische en gedragsverschillen duiden echter wel op een welzijnsverbetering ten gunste van IGEg en verrijkte huisvestingscondities.

Het selectie experiment suggereert dat de ernst van de sociale interacties een belangrijke rol speelt in de expressie van IGEg (hoofdstuk 7 en 8). Indien IGE voor groei in varkens zouden worden veroorzaakt door gedrag, en de gedragingen die groei kunnen aantasten zijn gereduceerd om het welzijn in de experimentele opzet te waarborgen, dan kan het verwachte effect van IGEg, zoals geschat van praktijkgegevens, mogelijk niet tot uitdrukking komen. De waargenomen systematische gedragsverschillen, welke tot een groeireductie hadden kunnen leiden mits de gedragingen niet ingeperkt waren, suggereert dat selectie wel effectief was. De schatting van IGEg behoeft echter verdere validatie. De afwezigheid van genotype × omgeving interacties suggereert dat selectie op IGEg effectief zou zijn in diverse huisvestingscondities en duidt op een zekere robuustheid van IGEg.

Dit promotieonderzoek was onderdeel van het project 'Seeking sociable swine', welke betrekking heeft op strategieën om dierenwelzijn te verbeteren. De experimenten bevestigden de verwachtingen dat zowel selectie op hoog IGEg als verrijkte huisvestingscondities gunstig zijn voor het welzijn van varkens en dat de twee strategieën elkaar aanvullen. Om dierenwelzijn daadwerkelijk te verbeteren is het echter uiterst belangrijk dat er functionele wederzijdse informatieuitwisseling is tussen wetenschap en de sector.

In conclusie, meerdere studies, waaronder een één-generatie selectie experiment, wijzen erop dat het opnemen van IGE voor groei in de fokstrategie de mogelijkheid heeft om bijgedrag te verminderen, wat relateert aan agressie en orale manipulatie. Implementatie van selectie op IGEg behoeft nader onderzoek in commerciële praktijksituaties waar sociale interacties mogelijk intenser zijn dan in experimentele studies. De resultaten tonen aan dat zowel selectie op IGEg en verrijkte huisvestingscondities effectief kunnen zijn in het reduceren van schadelijk gedrag en daarmee een verbetering kunnen geven in het welzijn van varkens. Dus, genetische selectie op een hoog IGEg in combinatie met een verrijkte huisvesting zal resulteren in meest 'sociale zwijnen'.



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### Glossary

This glossary includes the most essential terms to understand the content of this thesis.

**Finishing period:** Phase of the production cycle in pig husbandry which commonly indicates the period from  $\pm 8$  weeks of age till slaughter at  $\pm 24$  weeks of age. Also referred to as fattening phase of period.

**Indirect genetic effect (IGE):** Heritable effect of an individual on the trait values of social partners. Also referred to as associative-, competitive-, or social genetic effects or social breeding value. See illustration 1 and 2.

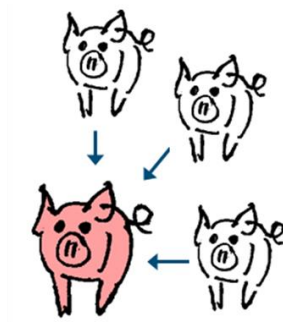
**IGeG:** Indirect genetic effect for growth rate during the finishing period in pigs. The high IGeG and low IGeG refer to an either positive (high) or negative (low) estimated IGeG as based to the population average, and indicates a relatively positive or negative effect on the growth rate of pen mates during the finishing period.

**Jute sack:** A sack of approximately 60×100 cm made of jute, which is a strong coarse fiber. Jute sack is also referred to as burlap, hessian or gunny bag or sack. The description of the use of the jute sack in the selection experiment, including a picture of the application in practice, is given in chapter 6, page 103.

**Oral manipulation:** Repeated biting, sucking, rooting, or nibbling on body parts of another pig such as the ears or tail. See illustration 5.

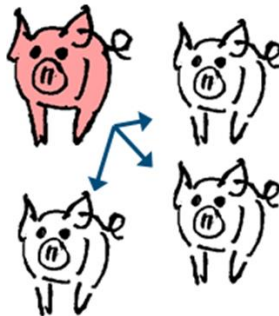
**Tail biting:** Repeated biting or nibbling on the tail of another pig. See illustration 5.





$$P_i = \underbrace{A_{D_i} + E_{D_i}}_{\text{Own genetics}} + \sum_{i \neq j} \underbrace{(A_{S_j} + E_{S_j})}_{\text{Genetics of others}}$$

**Illustration 1.** Schematic representation of estimating the phenotype while including indirect genetic effects ('genetics of others').



$$TBV_i = \underbrace{A_{D_i}}_{\text{DBV}} + \underbrace{(n - 1)A_{S_i}}_{\text{SBV: effect on others}}$$

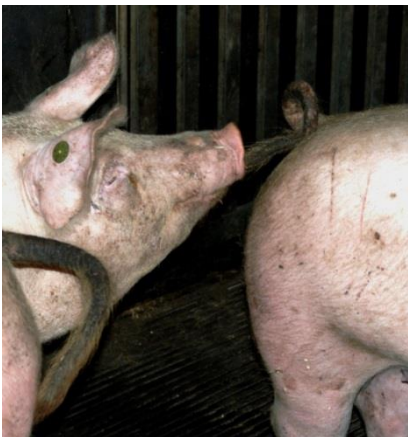
**Illustration 2.** Schematic representation of estimating the total breeding value (TBV) while including indirect genetic effects. DBV refers to the direct breeding value whereas SBV (social breeding value) refers to the indirect genetic effects.



**Illustration 3.** Skin lesions due to aggression.



**Illustration 4.** Social nosing: snout contact.



**Illustration 5.** Tail biting



**Illustration 6.** Lying in body contact

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## Register

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## Acknowledgements

In group living species, social interactions such as competition and cooperation may influence health, well-being, and productivity. In some populations, competition is limited, and evolved forms of cooperation can be observed. Individuals that have a beneficial effect on their group members, i.e. a high Indirect Genetic Effect or Social Breeding Value, may be highly valued by the others. This is especially seen in humans (*Homo sapiens*). Humans are a gregarious species which in nature would life in small social groups. In commercial settings, they are often randomly grouped into enclosures. The group wise housing of particular high intellectual individuals may result in high production performances and an increased well-being. Four years of observation of a university population in Wageningen resulted in the determination of typical characteristics of these highly social individuals. Most prominent characteristics were soft eyes and a smiley face. Examples hereof are given in Figure 1. These individuals showed to be highly skilled in complementing short-comings of other group members, thereby bringing balance in the overall work. This resulted in high quality output which could not have been reached by the single individual. With this I would like to acknowledge all people depicted in Figure 1 for their great contribution to the project.



Figure 1.

A special mention is in place or the people from outside Wageningen University who contributed to the project. Data, pigs, and ideas were kindly provided by Rob Bergsma, Egbert Knol, and René Heijting from TOPIGS Research Center IPG B.V. I would like to acknowledge Antonio Arts from VION for his excellent help and hospitality during the collection of data.

## Acknowledgements

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The carry out of the experiment would not have been feasible without the great help of the technicians Fleur Bartels, Monique Ooms, and Merel Verhoeven and students: Iris Vork, Justine Jeanpierre, Sophie van Nieuwamerongen, Leonie Jacobs, Sofie de Graaf, Jordy Groffen, Laura ten Berge, Lieske van Eck, David Jansen, Suzanne Hendrikx, and Rosalie van Emous.

The social environment has greatly contributed to the work pleasure, inspiration, and achievements. Thank you Sociable Swine team: Naomi, Inonge, and Marianne, for working together to accomplish all ideas. Nanda and Inonge: with the three of us like pigs in a straw pen, oinking and rooting around in data, diving into the straw to hide away when it became too much, and nosing into scientific questions. We complemented each other well and I can easily attribute most work involving numbers or details to you both. You were the best ‘pen mates’ a knorrie could have ☺. Elske, thank you for creating an atmosphere where colleagues easily become friends. Ewa and Naomi, thank you for sharing your constant positive Social Breeding Value with such an enthusiasm that even someone with a negative SBV like me eventually admits to mini social gatherings. And of course for all your advices!

The theses of Marije Oostindjer and Marcin Pszcola have been a great inspiration and example to this thesis, especially in finalizing it. Thank you both for sharing your scientific skills and contributions to which people can take an example.

The joy of thesis work was largely increased by the colleagues from SRUC, former SAC, and especially Suzanne Desire and Simon Turner. Simon, you inspired and encouraged me in many ways and because of that most of this thesis has been written while (hill) running. With the help of your ideas and guidance this thesis has got several additional chapters. Luckily there are three more years to come!

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***“If by knowing six people you are connected to everyone in the world (Six degrees of separation, Karinthy, 1929), than by helping six people you can help everyone.”***

## Curriculum Vitae



Irene Camerlink was born on the 19<sup>th</sup> of June 1986 in Apeldoorn, The Netherlands. In 2003 she started a bachelor in Animal Sciences at Van Hall Larenstein in Leeuwarden, where she did four internships related to pigs. From 2007 to 2009 she studied Animal Sciences at Wageningen University, with a specialization in Animal Production Systems. During her MSc, she worked on the application of homeopathy to treat piglet diarrhoea. She published the work and received the Vithoukas

award for best international peer-reviewed publication of 2011 in the field of homeopathy.

After her graduation, she started as a PhD student at the 'Animal Breeding and Genomics Centre' and the 'Adaptation Physiology Group' of Wageningen University, under the supervision of Dr Liesbeth Bolhuis and Dr Piter Bijma. In her PhD, she focussed on indirect genetic effects on growth rate in pigs, and the consequences of selection hereon for the behaviour and production of pigs in different environments. In 2012, she spent three months at SRUC (former SAC) in Edinburg, Scotland to collaborate with Dr Turner on aggression in pigs. This resulted in additional in-depth studies of social behaviour in pigs.

Alongside her PhD Irene wrote and published a book on life philosophy, and accomplished two part-time post-HBO studies. This gave her the qualification of meditation teacher and coach, and EMDR (Eye Movement Desentization & Reprocessing) therapist. In 2012 she started her own practice in EMDR therapy for the treatment of mental trauma in humans.

From 2014 she started as a researcher at SRUC, Edinburgh Scotland, in a project on aggression in pigs.

*"Never withhold what comes naturally"*

## List of publications

### Refereed journal articles (first author)

- Camerlink, I., Ellinger, L., Bakker, E.J., Lantinga, E.A. (2010) Homeopathy as replacement to antibiotics in the case of *Escherichia coli* diarrhoea in neonatal piglets. *Homeopathy* 99(1), 57–62.
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- Camerlink, I., Ursinus, W.W., Bijma, P., Kemp, B., Bolhuis, J.E. Indirect genetic effects for growth in pigs alter behaviour beyond competition and cooperation. Submitted
- Camerlink, I., Turner, S.P., Ursinus, W.W., Reimert, I., Bolhuis, J.E. Aggression and affiliation during social conflict in pigs. Submitted
- Camerlink, I., Ursinus, W.W., Bijma, P., Bolhuis, J.E. Improving animal welfare through genetics and environment: quantifying solutions for pig welfare. In prep.
- Camerlink, I., Reimert, I., Bolhuis, J.E. Oxytocin in relationship to social nosing behaviour in pigs (*Sus scrofa*). In prep.

### Refereed journal articles (co-author)

- Reimert, I., Rodenburg, T.B., Ursinus, W.W., Duijvesteijn, N., Camerlink, I., Kemp, B., Bolhuis, J.E. (2013) Backtest and novelty behavior of female and castrated male piglets, with diverging social breeding values for growth. *J Anim Sci* 91, 4589-4597.
- Duijvesteijn, N., Benard, M., Reimert, I., Camerlink, I. Differences and similarities between farmers, citizens and animal scientists in assessing pig behaviour by Qualitative Behavioural Assessment. Submitted.



**Conference contributions**

- Camerlink, I., Bergsma, R., Duijvesteijn, N., Bolhuis, J.E., Bijma, P. (2010) Consequences of selection for social genetic effects on ADG in Finishing Pigs - A pilot study. In: Book of Abstracts of the 9th World Congress on Genetic Applied to Livestock Production (WCGALP), 1-6 August 2010, Leipzig, Germany.
- Camerlink, I., Bijma, P., Bolhuis, J.E. (2011) Improving pig welfare and production simultaneously by breeding for social genetic effects. In: Book of abstracts of the 62nd Annual Meeting of the European Federation of Animal Science 2011. Book of abstracts No. 17 (2011), 29 August – 2 September 2011, p. 20.
- Camerlink, I., Bolhuis, J.E., Bijma, P. (2012) Social interactions among finishing pigs divergently selected for social genetic effects on growth in barren and straw housing. In: Book of abstracts of the 4th International Conference on Quantitative Genetics, 17 – 22 June 2012, p. 161.
- Camerlink, I., Bijma, P., Ursinus, W.W., Bolhuis, J.E. (2012) Behaviour of finishing pigs divergently selected for social genetic effects in barren and straw-enriched pens. In: Proceedings of the 46th congress of the International Society for Applied Ethology, 31 July – 4 August 2012, p. 35.
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- Benard, M., Camerlink, I., Duijvesteijn, N., Reimert, I., Bijma, P., Bolhuis, J. E. (2011) Seeking a sociable swine: an interdisciplinary approach. In: Book of abstracts of the 62nd Annual Meeting of the European Federation of Animal Science 2011. Book of abstracts No. 17 (2011), 29 August – 2 September 2011, p. 21.

### Miscellaneous

- Ter Beek, V., Camerlink, I. (2013). A revolution in thinking about pig tails. *Pig Progress* 29.6 2013
- Lamers, J., Ursinus, W.W., Camerlink, I. (2012). Damage due to unnoted biting (Dutch). *Varkens* 76, p. 34.
- Lamers, J., Camerlink, I., Duijvesteijn, N. (2012). Sharing results and listening to experiences (Dutch). *Varkens* 76, p. 7.
- Lamers, J., Duijvesteijn, N., Camerlink, I. (2012). Asocial pig influences others (Dutch). *Varkens* 76, p. 34.
- Lamers, J., Camerlink, I. (2012). Boar behaviour remains persistent (Dutch). *Varkens* 76, p. 35.
- Rotgers, G., Benard, M., Camerlink, I., Duijvesteijn, N., Reimert, I. (2012). Pig farmer and researcher distrust each other (Dutch). *V-focus* 9.

## Training and supervision plan



<b>The basic package (3 ECST)</b>	<b>Year</b>
WIAS Introduction Course	2009
NWO: Ethics and Animal Welfare, Lunteren, Netherlands	2011
<b>Scientific Exposure (27 ECTS)</b>	
<i>International conferences (7.2 ECTS)</i>	
9th World Congress on Genetics Applied to Livestock Production (WCGALP), Leipzig, Germany	2010
62nd EAAP Annual Meeting, Stavanger, Norway	2011
Annual meeting NVG, Soesterberg, Netherlands	2011
46th International Society for Applied Ethology (ISAE), Vienna, Austria	2012
4th International Conference on Quantitative Genetics (ICQG), Edinburgh, UK	2012
Annual meeting NVG, Soesterberg, Netherlands	2012
47th International Society for Applied Ethology (ISAE), Florianopolis, Brazil	2013
64th EAAP Annual Meeting, Nantes, France	2013
International conference on Individual differences, Groningen, Netherlands	2013
<i>Seminars and workshops (2.6 ECTS)</i>	
Developments in genome-wide evaluation and genomic selection, Wageningen	2009
WIAS Science Day, Wageningen	2010
Symposium 'Food production', Ede, Netherlands	2010
Workshops NWO Talent day, Utrecht, Netherlands	2010
WIAS Science Day, Wageningen	2011
Workshops NWO Talent day, Utrecht, Netherlands	2011
Seminar 'Scientific Research in Animal Welfare', Wageningen	2011
Seminar 'Genomics and Animal Breeding', Wageningen	2011
Symposium 'How to eat like a pig', Wageningen	2011
Symposium NWO 'The Value of Animal Welfare', Utrecht, Netherlands	2011
WIAS Science Day, Wageningen	2012
Symposium 'Animals in 3D', Utrecht, Netherlands	2012
Symposium NWO 'The Value of Animal Welfare', The Hague, Netherlands	2013
<i>Presentations (10 ECTS)</i>	
WCGALP, Leipzig, Germany (oral)	2010
EAAP, Stavanger, Norway (oral)	2011
SCwD Symposium Antibiotics in livestock farming, Driebergen, Netherlands (invited speaker)	2011
WIAS Science Day 2011, Wageningen (poster)	2011

## Training and supervision plan

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NVG, Soesterberg, Netherlands (oral)	2011
WIAS Science Day, Wageningen (oral)	2013
ISAE, Vienna, Austria (oral)	2012
ICQG, Edinburgh, UK (poster)	2012
NVG, Soesterberg, Netherlands (poster)	2012
EAAP, Nantes, France (oral)	2013

### **In-depth studies (17 ECTS)**

#### *Disciplinary and interdisciplinary courses (11.1 ECTS)*

Quantitative Genetics: Selection Theory, Wageningen	2010
NWO: Sustainability, Lunteren, Netherlands	2010
Genetics of competition, Edinburgh, UK	2012
Interpretation of animal stress responses, Denmark	2013
NWO: Policy, The Hague, Netherlands	2013
ONWAR: Cognitive neuroscience, Amsterdam, Netherlands	2013

#### *Advanced statistics courses (1 ECTS)*

Design of Experiments, Wageningen	2010
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#### *PhD students' discussion groups (0.2 ECTS)*

Welfare discussion group	2010
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#### *MSc level courses (5 ECTS)*

Genetic Improvement of Livestock ABG-31306	2009
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### **Professional skills support sources (3 ECTS)**

Supervising MSc thesis work, Wageningen	2011
Techniques for writing and presenting a scientific paper, Wageningen	2012
Communication with the media and the general public, Wageningen	2013
Voice and presentation training, Wageningen	2013
Last stretch of the PhD programme, Wageningen	2013

#### Research skills training (3 ECTS)

External training period, SAC, Edinburgh, UK (3 months)	2012
External training period, SRUC (former SAC), Edinburgh, UK (1 month)	2013
Getting started in Asreml, Wageningen	2013

### **Didactic skills training (11 ECTS)**

#### *Lecturing (0.6 ECTS)*

Lecture in MSc course Health Welfare and Management	2012
Lecturing in BSc course Adaptation physiology	12-13

### *Supervising theses (10.5 ECTS)*

Supervising 5 BSc students	10-13
Supervising 3 MSc students	10-13

### **Management skills training (2 ECTS)**

#### *Organisation of seminars and courses*

Organisation symposium 'Vreedzame Varkens', Sterksel, Netherlands	2012
Organisation symposium 'Varkens in zicht', Sterksel, Netherlands	2013

### **Education and Training Total (60 ECTS)**



## Colophon

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Ministry of Economic Affairs



Netherlands Organisation for Scientific Research



